Wildlife response to management regime and habitat loss in the Terai Arc Landscape of Nepal

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Authors' contributions

DJI, KEJ, SR, LT, EKM, and GBF conceived the ideas and designed methodology; LT, DJI, and DRT collected the data; LT and PAB processed the data; GBF analysed the data; GBF and LT led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Abstract

The establishment of protected areas and buffer zones has been widely adopted in many countries to mitigate biodiversity loss. However, in contrast to the growing evidence about the beneficial impacts of protected areas, ecological outcomes of buffer zones have rarely been measured. Here, we use data from a large camera trap survey and multispecies occupancy modelling to assess the effectiveness of different management regimes (Bardia National Park, its buffer zone, and areas outside the buffer zone) at safeguarding wildlife in the Terai Arc Landscape of Nepal. Using areas outside the buffer zone as the counterfactual to compare occurrence probability of 25 mammal species >1 kg, we revealed a positive effect of the national park and the buffer zone on seven and six species, respectively. Three species had greater occurrence probability outside the buffer zone than in the national park, but no species had greater occurrence probability outside the buffer zone than inside the buffer zone. Analysis of species richness indicated that management regime differentially affects species groups. For non-threatened and herbivorous species, the buffer zone performed better than areas outside the buffer zone and similar to, or better than, the national park. However, for threatened species and large animalivores (carnivores and insectivores) the national park outperformed the other management regimes. Our results also suggest that the buffer zone partially mitigated the impacts of habitat loss outside the national park, indicating that management regime may play a role in modulating the effect of agriculture on wildlife in human-dominated landscapes in Nepal.

Keywords: anthropogenic pressure; area-based conservation; buffer zone; camera trap; mammals; occupancy modelling; protected area effectiveness.

1. Introduction

Area-based conservation measures, such as the establishment of protected areas, have been widely adopted to mitigate biodiversity loss (Maxwell et al., 2020). Protected areas usually support higher biodiversity levels than similar unprotected lands (Cazalis et al., 2020; Gray et al., 2016) and are effective at reducing habitat conversion (Joppa and Pfaff, 2011; Ribas et al., 2020), therefore, they are an important tool in maintaining the health of ecosystems and the suite of species characteristic of a regional biome (Ingram et al., 2021). However, parks and reserves do not exist in isolation with the regional context influencing the amount of human disturbance around these areas and the status of ecosystem processes and species populations inside their borders (Hansen and DeFries, 2007). In response, several countries have designated buffer zones that regulate the types and intensity of human activities around parks and reserves (Martin and Piatti, 2009; Weisse and Naughton-Treves, 2016). Buffer zones objectives vary widely, but they often have the dual goal of improving conservation effectiveness as well as providing goods and services to the local community (Budhathoki, 2004; Lamichhane et al., 2019; Sayer, 1991). From a biodiversity conservation perspective, buffer zones may limit the propagation of anthropogenic effects to core areas of parks and reserves (Hansen and DeFries, 2007; Mehring and Stoll-Kleemann, 2011) and can provide additional habitat for species (Jotikapukkana et al., 2010), however, their ecological outcomes have rarely been directly measured.

Assessments of buffer zone effectiveness at avoiding habitat loss have been conducted only on a few occasions and revealed mixed results (de Almeida-Rocha and Peres, 2021; Mehring and Stoll-Kleemann, 2011; Nagendra et al., 2005; Weisse and Naughton-Treves, 2016). Furthermore, despite a handful of studies showing that some wildlife species do use buffer zones (Bamford et al., 2014; Jotikapukkana et al., 2010; Salafsky, 1993), few have attempted a more systematic assessment of buffer zone effectiveness on biodiversity. Some of these assessments found greater wildlife populations in protected areas than in the corresponding buffer zones, but the differences were not statistically different for most species (Paolino et al., 2016; Rosenblatt et al., 2019). Another study reported that in general threatened species benefited from the core protected area while more common species usually benefited from the buffer zone (Shen et al. 2020). However, buffer zones are not intended to function as strict protected areas, therefore more complete assessments should also include comparisons with areas that are not managed for biodiversity conservation. The lack of studies investigating wildlife responses across the full gradient of management regimes encompassing the protected area, buffer zone, and unmanaged areas outside precludes the formal evaluation of buffer zones, and drastically limits the understanding about the effectiveness of distinct area-based conservation measures.

Not all species in a community are likely to benefit equally from area-based conservation measures, as traits (e.g., body size, diet) and threat status influence wildlife responses to human pressure (Magioli et al., 2021; Rovero et al., 2020). For example, species in higher trophic levels are usually more sensitive to anthropogenic impacts (Estes et al., 2011; Suraci et al., 2021), and larger and threatened mammals benefit more from stricter levels of habitat protection (Drouilly et al., 2018; Ferreira et al., 2020; Rich et al., 2016; Velho et al., 2016). Therefore, more well-informed and effective conservation measures that deliver the desired outcomes can be implemented by understanding how different species respond to different management regimes and whether species of conservation concern are benefitting from these interventions (Ingram et al., 2021).

Nepal is a case in point where area-based conservation measures under distinct management regimes are a core component of the country’s conservation strategy, such as national parks and their buffer zones (Heinen and Shrestha, 2006). In the Terai Arc Landscape, a stretch of lowlands in the foothills of the Himalayas, effective habitat management is essential to regulate conversion of natural vegetation and to safeguard globally threatened species (MoFSC, 2015). National parks in Nepal are managed for biodiversity conservation where hunting, land clearing, and livestock grazing are not permitted (Heinen & Shrestha, 2006). Conversely, buffer zones are mixed-use areas established around national parks and managed by local user groups with the objective of promoting activities to meet the local communities’ needs for natural resources and to mitigate human-wildlife conflicts (Budhathoki, 2004; DNPWC, 2016). In the Terai, areas outside these two designations are mostly used for agriculture and the remaining forest patches are locally managed under more permissive regulations (MoFSC, 2015).

We conducted a large, standardised camera trap survey encompassing areas of Bardia National Park in the Terai Arc Landscape of Nepal, its buffer zone, and lands outside the buffer zone to assess the effectiveness of different management regimes at safeguarding wildlife using a multi-species occupancy model. We then used estimates of species richness to investigate whether management regime differentially affects species groups according to ecological function and threat status. We expected a gradual decrease in the number of threatened and large species from the national park to areas outside the buffer zone, and we anticipated the positive effect of management on large species to be stronger on animalivores than on herbivores. Additionally, we investigated whether the conditions in the buffer zone can mitigate the negative effects of natural habitat conversion to agriculture outside Bardia National Park. Although we anticipated a negative effect of agriculture on the occurrence probability of most species, we expected this effect to be weaker in the buffer zone when compared to areas outside the buffer zone.

2. Material and methods

2.1 Data Collection

2.1.1 Camera trap survey

Our camera trap survey covers three management regimes (national park, buffer zone, outside buffer zone) that represent a gradient of interventions and restrictions on the use of natural resources (Supporting information 1). Bardia National Park in particular is a well-implemented protected area with more than 200 staff members, 23 range posts and regular patrolling by the army to enforce the park’s rules and regulations (DNPWC, 2016). Camera trap deployment locations were selected from a 2x2 km grid equally covering the three management regimes assessed (Fig. 1) and encompassing areas which are representative of these management regimes in Nepal, whilst keeping elevation within a narrow range across the study area. Proportion of natural vegetation in the areas surveyed varies across management regimes (Table 1), reflecting what is usually found in the Terai Arc Landscape (MoFSC, 2015) and the effect of management on habitat conversion (Nagendra et al., 2005).

Camera traps (model Browning Dark Ops HD Pro, black flash) were deployed singly as close as possible to survey grid centroids (Fig. 1) and placements were not biased towards roads or trails. Cameras were attached to trees or wooden posts at a height of *ca*. 50 cm and were operational 24h/day with a 1s delay between sequential triggers. No bait or lure was used to attract animals. For this study we used data collected in the Nepali spring season between 15th March and 15thApril 2019 in 148 survey sites totalling 4,576 survey days (Table 1).

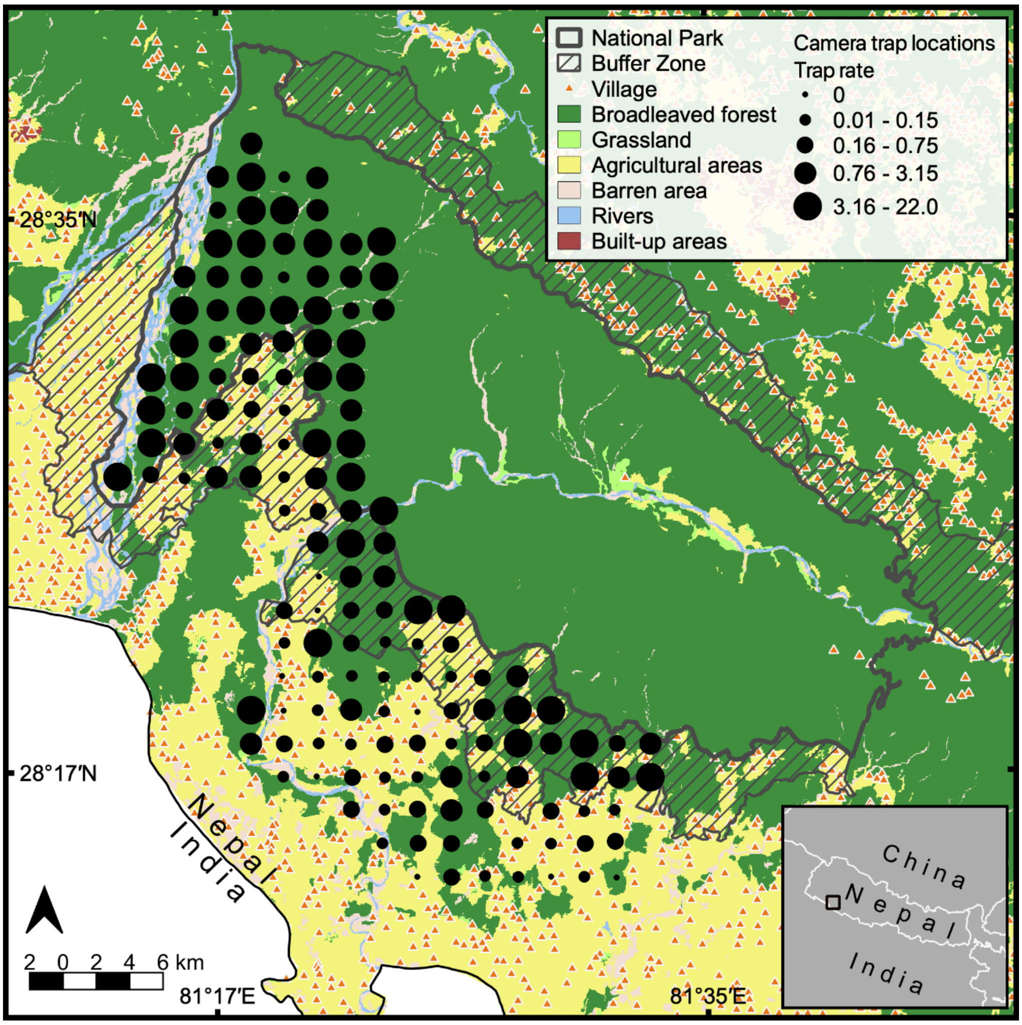

Figure 1: Camera trap locations in the Terai Arc Landscape of Nepal within Bardia National Park, its buffer zone, and outside the buffer zone. Size of the black circles represents trap rate (number of wildlife photos per survey day; see Statistical analysis for details) between March-April 2019.

Table 1: Survey effort, number of wildlife photos, and land cover of the management regimes surveyed in and around Bardia National Park in the Terai Arc Landscape of Nepal.

	Camera trap sites	Survey effort (days)	Wildlife photos	Agricultural land (%)[a]	Natural vegetation (%)[a]
Bardia National Park	50	1,520	6,448	3.02	90.62
Buffer Zone	50	1,544	2,656	40.18	55.18
Outside Buffer Zone	48	1,512	729	64.47	29.89
Total	148	4,576	9,833		

[a] Proportion of agricultural land and natural vegetation were measured in a 500-m buffer around each camera trap site using the classification from Uddin et al. (2015); values are the means across camera trap sites.

2.1.2 Environmental variables

We obtained data on land cover from the 2010 national land cover database for Nepal (Uddin et al., 2015). Using this layer, we calculated proportion of agricultural land and natural vegetation (aggregating forests, shrublands, and grasslands) in a 500-m buffer around each camera trap site to represent the landscape more directly influencing the survey site (Table 1). We also calculated proportion of forest in a 50-m buffer around each camera trap as a proxy for canopy cover in the close vicinity of the survey site. Proportion of forest in the 500- and 50-m buffers are highly correlated (cor = 0.91), but we opted for the smaller scale assuming it represented canopy conditions more accurately near the camera. Finally, because riverine habitat can influence distribution of some wildlife species in the study area (Dinerstein, 1979; Wegge et al., 2009), we calculated the Euclidian distance between camera traps and a permanent river.

2.1.3 Species' threat status and functional groups

We classified all mammal species with average weight >1 kg according to threat status and broad functional group (Table S1) to assess the effect of management on different groups of species. The threshold in species weight was necessary because smaller mammal species could not be confidently identified in most photos. Threat status was obtained from Nepal's Redlist (Jnawali et al., 2011) and species were classified as either threatened (Vulnerable, Endangered, and Critically Endangered) or non-threatened (all other categories, including the two Data Deficient species recorded to avoid overestimating threatened species richness). Species were assigned to broad functional groups using information about diet and body mass from the literature (Jones et al., 2009; Wilman et al., 2014). First, we classified species as either small or large based on a 20 kg cut-off, following a natural break in body mass of the species recorded and because the median body mass of the studied community is 17.6 kg. We then adapted the approach by Rovero et al. (2020) and classified species as herbivores if 70% or more of the diet was comprised of plant material and as animalivores if 70% or more of the diet was comprised of animals, either vertebrates or invertebrates. None of the species had less than 70% plant material or animals in the diet, thus we did not create an omnivorous group. Using these classifications, we assigned species to four broad functional groups: small herbivore, small animalivore, large herbivore, and large animalivore.

2.2 Statistical analysis

2.2.1 Species identification and detection histories

From the 430,613 camera trap photos obtained during the 30-day survey period, we selected 57,668 for processing based on a minimum interval of 1 minute between sequential photos in the same camera trap site. This subsetting process is highly unlikely to impact detection histories produced for each species as photos taken within a minute were virtually always from the same species. Species in the selected photos were identified following Baral & Shah (2008) and we adopted a systematic process to check the accuracy of identifications (Supporting Information 2; Tables S2, S3). We built detection/non-detection histories for all native mammal species >1 kg recorded, aggregating five consecutive survey days at a sampling site as a single survey occasion to increase model efficiency (e.g., Deere et al., 2018; Drouilly et al., 2018). We also created 15 all-zero detection histories as part of the data augmentation procedure to estimate species richness in a multispecies occupancy model (Dorazio et al., 2006). These all-zero detection histories represent mammal species >1 kg that potentially occur in the region (DNPWC, 2016) and were never recorded in our survey, but they do not influence results for the species recorded (Kery & Royle, 2016).

2.2.2 Estimating the effect of management regime

We adopted a Bayesian multi-species occupancy framework to analyse the camera trap data (Dorazio et al., 2006; Kery & Royle, 2016) and we first implemented a model to estimate occurrence probability and species richness in each management regime surveyed while including distance to rivers as a potential confounding variable (Supporting Information 3). Given the influence of management regime on habitat conversion, we did not include a variable related to vegetation cover in the occurrence component of this model to avoid decomposing the effect of management into other variables. In the detection component of the model, we included the type of mount for the camera trap (tree or wooden post) and the proportion of forest in a 50-m buffer around the camera as covariates. This was to account for variation in deployment and because shade provided by trees in more forested areas may affect the probability that the sensor will detect a passing animal (Welbourne et al., 2016). Using this model, we calculated the effect of management as the difference in occurrence probability for each species between pairs of management regimes while holding distance from rivers constant at the mean value. Only estimates for species with at least five records overall are presented to avoid making inferences based on very few data points. We use the term ‘occurrence probability’ rather than ‘occupancy probability’ as our target species do not occupy the small detection area in front of camera traps during the whole study period (MacKenzie et al., 2006).

2.2.3 Assessing the effect of management regime on species groups

We estimated site species richness in each management regime for subsets of the mammal community according to threat status and broad functional group to investigate whether management differentially affected species groups. The model described above was used to obtain the sum of species belonging to each group at a camera trap site for each iteration of the Bayesian sampling process (Dorazio et al., 2006). In total, we estimated site species richness for six groups (threatened, non-threatened, small herbivore, large herbivore, small animalivore, large animalivore). We also estimated overall site species richness to compare species group responses to that of the whole community. We then calculated the difference in mean site species richness between pairs of management regimes to formally assess the effect of management on this metric.

2.2.4 Estimating the effect of habitat loss

To investigate the effect of natural habitat conversion to agriculture on occurrence probability, we implemented a second multi-species occupancy model including management regime and proportion of agricultural land (Supporting Information 3). Furthermore, to test whether management regime modulates the effect of habitat loss on wildlife, we estimated a distinct slope for the effect of agriculture in each management regime (i.e., interaction between the two variables). Because the first model did not indicate an important effect of rivers (Supporting Information 3; Table S4) and to avoid a model with many parameters in relation to the number of species detections, distance to rivers was not included in this model. We present results for the effect of agriculture on the buffer zone and outside the buffer zone only, as agriculture inside the national park is negligible. Additionally, we only present results for species with at least five records in a management regime.

All models were implemented in JAGS (Plummer, 2013) through R (R Development Core Team, 2018) using the package JagsUI (Kellner, 2017). We ran three chains of 100,000 iterations with a burn-in of 50,000 and a thinning rate of 10. Average R-hat values for estimated parameters were 1.0 in both models and no model parameter had R-hat greater than 1.1, indicating convergence (Gelman and Hill, 2006). We used vague priors for all parameters estimated and conducted a prior sensitivity analysis, as well as an assessment of model fit (Supporting Information 3; Table S4). Throughout the study we use the mean of the posterior distribution (posterior mean) of each parameter for inference.

3. Results

3.1 Effect of management regime on species' occurrence

Differences in occurrence probability between the national park and areas outside the buffer zone indicated a clear positive effect of strict habitat protection on seven species (chital *Axis axis*, grey langur *Semnopithecus hector*, sambar *Rusa unicolor*, barking deer *Muntiacus vaginalis*, tiger *Panthera tigris*, porcupine *Hystrix indica*, and one-horned rhino *Rhinoceros unicornis* – Fig. 2). In addition, there is some evidence (majority of posteriors were positive) that sloth bear *Melursus ursinus* and hog deer *Axis porcinus* also benefit from the national park. On the other hand, nilgai *Boselaphus tragocamelus*, jackal *Canis aureus*, and jungle cat *Felis chaus* had greater occurrence outside the buffer zone than in the national park (Fig. 2), indicating these species and probably the Indian grey mongoose *Herpestes edwardsii* (herein grey mongoose) do not benefit from stricter levels of habitat protection in the region.

Buffer zone had a positive effect on six species when compared to areas outside the buffer zone. Four of those species also responded positively to the national park (chital, grey langur, sambar, barking deer) but two only responded to the buffer zone (four-horned antelope *Tetracerus quadricornis* and wild boar *Sus scrofa* – Fig.2). Of the four species that benefitted both from the buffer zone and the national park, the positive effect was greater in the national park for half of them (grey langur and sambar) and similar for the other half (chital and barking deer). None of the species assessed had greater occurrence probability outside the buffer zone than in the buffer zone, although some evidence suggests that this is the case for grey mongoose (majority of posteriors were negative).

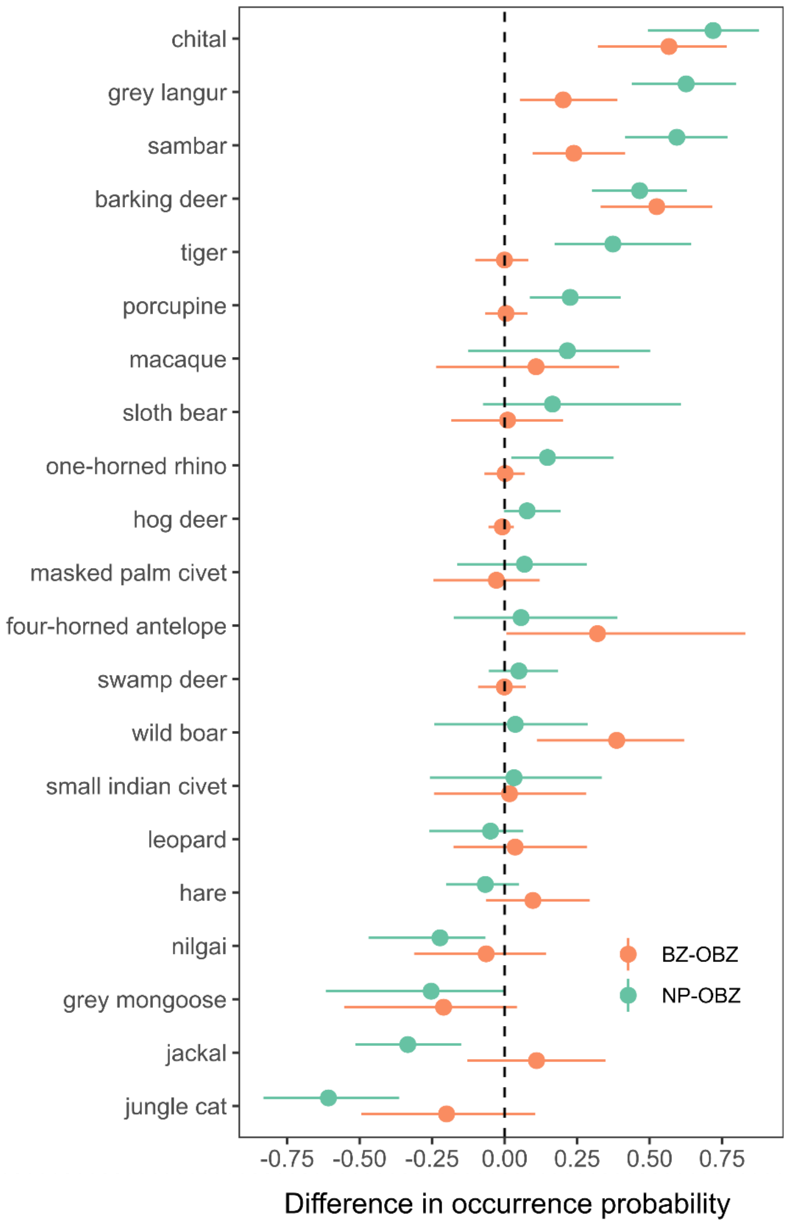

Figure 2: Effect of management regime on wildlife occurrence in the Terai Arc Landscape of Nepal. Estimates in areas outside the buffer zone (OBZ) were treated as the counterfactual and subtracted from estimates in the buffer zone (BZ-OBZ) and in Bardia National Park (NP-OBZ). Circles represent the posterior mean of the difference in occurrence probability and lines represent the 95% credible interval. Only species with at least five records overall are shown.

3.2 Effect of management regime on species groups

Estimates of site species richness clearly indicate that management regime differentially affects species groups, with strong variation in response according to threat status and broad functional group (Fig. 3). The pattern observed for the whole community (Fig. 3A) reflects the pattern for herbivores (either small or large – Fig. 3D,E), but it is strikingly different from other species group (Fig. 3B,C,F,G). As predicted, for threatened species and particularly for large animalivores, the national park clearly outperformed the buffer zone and areas outside the buffer zone, with much higher estimates of species richness (Fig. 3C,G). On the other hand, for non-threatened species and herbivores the buffer zone performed better than areas outside the buffer zone and similar to, or better than, the national park (Fig. 3B,D,E).

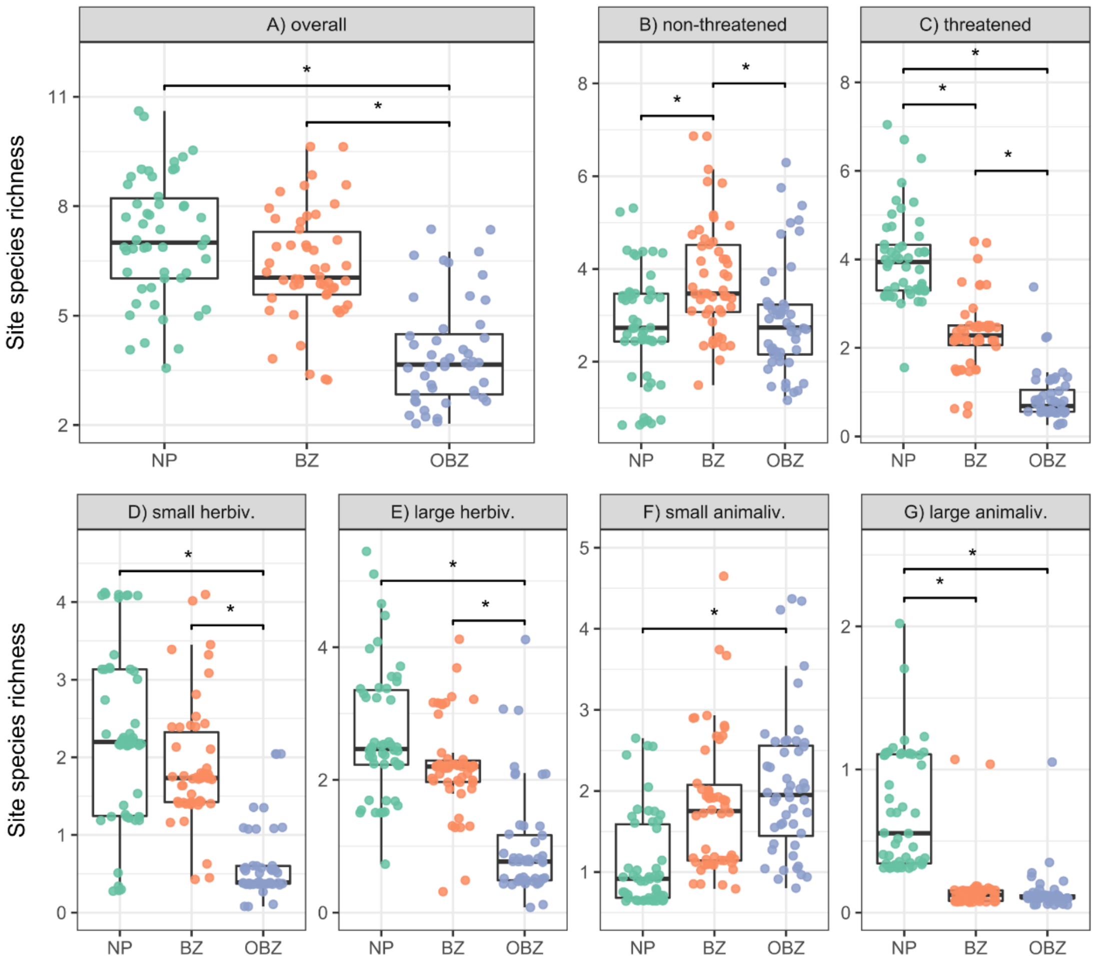

Figure 3: Effect of management regime on mammal species groups in the Terai Arc Landscape of Nepal. Estimates of site species richness are shown for the whole community (overall) and for six groups according to threat status and broad functional group. Asterisks (*) indicate pairs of management regimes for which the 95% credible interval of the difference in mean species richness do not include zero. herbiv. = herbivores; animaliv. = animalivores.

3.3 Effect of habitat loss on species' occurrence

Habitat loss to agriculture had a clear negative effect on the large mammal community in general and on most species, with posteriors being largely negative in at least one management regime for 11 of 14 species but frequently in both (Fig. 4A,B). Only jungle cat and, to a lesser extent, jackal responded positively to agriculture (Fig. 4A,B). As anticipated, conditions in the buffer zone seem to partially mitigate the negative impacts of agriculture: in seven of the ten cases where comparisons between the buffer zone and outside it are possible, model coefficients were smaller outside the buffer zone, indicating a stronger negative effect (Fig. 4A). Only for grey mongoose was there some evidence of a stronger negative impact of agriculture in the buffer zone than outside it, whereas for the other three species (chital, small Indian civet *Viverricula indica*, and jungle cat) the effect was similar in both areas (Fig. 4A). These results indicate that the decline in occurrence probability for the same increase in agricultural land is greater outside the buffer zone for the community overall, as well as for nilgai, wild boar, macaque *Macaca mulatta*, and hare *Lepus nigricollis* (Fig. 4B) – and that jackal's occurrence increases with the amount of agriculture in the buffer zone but stays constant outside the buffer zone (Fig. 4B).

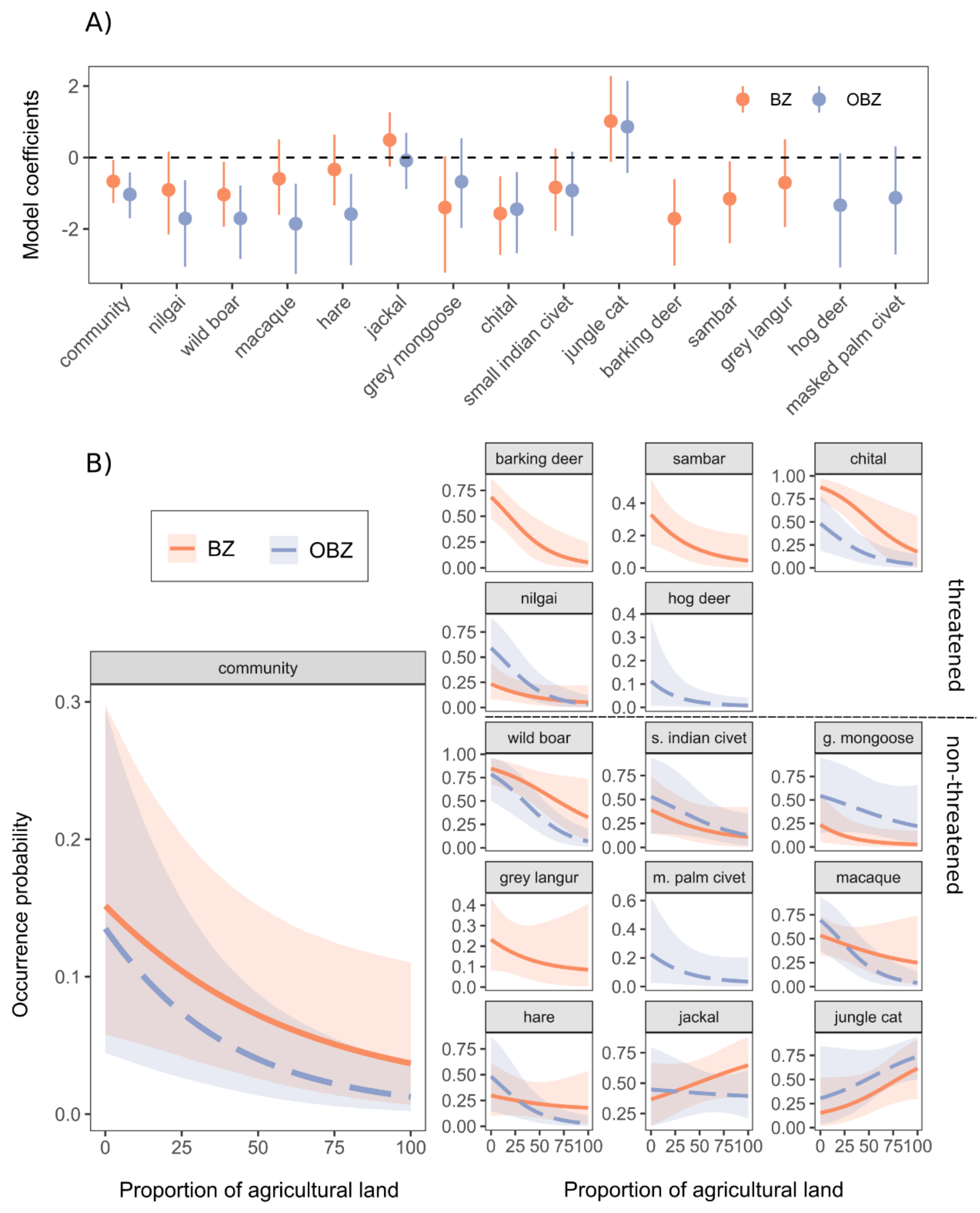

Figure 4: Effect of habitat loss caused by agriculture on wildlife occurrence in the Terai Arc Landscape of Nepal. A) Model coefficients for the effect of agricultural lands in the buffer zone (BZ) and outside the buffer zone (OBZ) of Bardia National Park. Circles are the posterior means and lines the 95% credible interval. B) Predicted community (larger panel) and species (smaller panels) responses to the proportion of agricultural land near the survey site in the buffer zone (BZ) and outside the buffer zone (OBZ). Lines are the posterior means and shaded areas are

the 95% credible intervals. Community response is based on the model hyperparameter and represents the average response of all species assessed. Species-level results are shown only for species with at least five records in a management regime.

4. Discussion

4.1 Wildlife response to distinct management regimes

Our results demonstrated that area-based conservation in the Terai Arc Landscape has an overall positive impact on wildlife with survey sites in the national park and in the buffer zone supporting substantially greater species richness than sites outside the buffer zone (3.1 and 2.4 more species per site, respectively). To our knowledge this is the first study to formally investigate wildlife responses across the management gradient provided by a protected area, its buffer zone, and areas outside both designations, producing new evidence on the conservation potential of different types of management regimes. Additionally, our findings complement an assessment showing the effectiveness of buffer zone in reducing deforestation in eastern Terai (Nagendra et al., 2005) and for the first time reveal positive effects of this management regime on wildlife in Nepal.

Despite the potential conservation benefits of buffer zones, our assessment also revealed some of their limitations. We found no difference between the buffer zone and areas outside the buffer zone for four globally threatened species (tiger, one-horned rhino, sloth bear, and hog deer), whereas they seem to benefit from the national park. Furthermore, a direct comparison between buffer zone and national park revealed that only one threatened species had greater occurrence probability in the buffer zone, whereas five threatened species had greater occurrence probability in the stricter management regime (Table S5). These results highlight the need for greater levels of protection to safeguard some of the most threatened species in the Terai and are in line with assessments conducted elsewhere showing the importance of stricter management regimes for some mammal species (Rich et al., 2016; Velho et al., 2016), including species of conservation concern (Ferreira et al., 2020). Our findings also echo those from other parts of the Terai and similar habitats in adjoining landscapes showing that many ungulates respond negatively to anthropogenic pressure (Lakhar et al., 2020) and suggesting that strict habitat protection is associated with greater diversity of forest-specialist birds (Dahal et al., 2014) and better-quality forests (Gurung et al., 2015; Timilsina and Heinen, 2008).

4.2 Differential effect of management regime on species group

The gradual decrease in threatened species richness from the national park to outside the buffer zone and the greater non-threatened species richness in the buffer zone clearly show that management regime differentially affects groups of species. These findings highlight that species of conservation concern benefit the most from stricter levels of protection in the region, but also that the buffer zone provides important habitat for less sensitive species in the landscape. On the other hand, the extremely low species richness outside the buffer zone for herbivores and large animalivores indicates a large degree of defaunation. Given that body size and trophic guild are intrinsically linked to species' ecological roles (Hevia et al., 2017), presumably many of the functions performed by wildlife are absent outside the buffer zone with unknown consequences for ecosystem functioning – although livestock will perform some level of browsing and grazing in these areas. Another striking pattern that emerged was the strong difference in large animalivores richness between the national park and the buffer zone. Top predators are known to be disproportionately affected by anthropogenic pressure (Estes et al., 2011; Suraci et al., 2021) and this pattern of threatened and larger mammal species benefiting from stricter management regimes has been reported in South America

(Ferreira et al., 2020), Africa (Drouilly et al., 2018; Rich et al., 2016), and Asia (Velho et al., 2016), pointing to a consistent response to habitat protection across biogeographic regions.

4.3 Synergistic effect of management regime and habitat loss

We revealed that management regime may modulate the impact of agriculture on wildlife, although this mitigation effect seems to benefit only a subset of the community that is less sensitive to anthropogenic pressure. A possible mechanism driving this effect is the total amount of natural habitat in the landscape, which is known to have a strong influence on biodiversity (Watling et al., 2020). At the landscape level (i.e., larger scale than the survey site), the greater natural vegetation cover in the buffer zone when compared to areas outside it could provide more and potentially better-quality habitats to wildlife, which may in turn minimise the negative impacts of agriculture on species occurrence. A similar effect has been observed for birds in eastern Terai, where greater proportion of natural habitat in the landscape mitigated to some extent the negative impacts of local-scale disturbances (Dahal et al., 2015).

Although proximity to the national park (i.e., source-sink dynamics) could also be proposed as a potential mechanism for the buffer zone's mitigation effect, we do not believe it has a strong influence on the results observed here. Most species for which there is evidence of an interaction between management and agriculture had greater occurrence probability in the buffer zone than in the national park and none of them are among the species that benefitted from stricter levels of protection. Finally, we acknowledge that other sources of pressure unaccounted for in our model (e.g., livestock density) may vary between the two management zones compared and this could have some influence on the results presented here.

4.4. Influence of local context and short survey duration

We acknowledge that the positive effects of the national park and the buffer zone revealed here are not only driven by management regime *per se* but also likely to be influenced by local context. For example, the large abundance of wildlife in the Karnali river valley (Dinerstein, 1979; Wegge et al., 2009) was one of the drivers for the establishment of Bardia National Park (DNPWC, 2016). We accounted for this – at least partially – by estimating the effect of management while controlling for distance to rivers and by implementing an exploratory model with the Karnali river (rather than any river) that returned very similar occurrence estimates (Table S6). Likewise, the reintroduction of one-horned rhinos to Bardia National Park (DNPWC, 2016) has a direct link to the population currently found there. However, given that the global population of the species is almost exclusively found in or around protected areas and that anti-poaching actions are needed to safeguard them (Ellis and Talukdar, 2019), it is clear that one-horned rhinos do benefit from strict habitat protection. Finally, part of the national park and buffer zone effectiveness is very likely due to the larger area of natural vegetation in these management regimes than outside the buffer zone. Nevertheless, we contend that this is still an effect of management regime due to their stricter regulations (Budhathoki, 2004) and effectiveness in avoiding habitat loss (Nagendra et al., 2005).

Our data was gathered over 30-day period and cannot capture eventual seasonal variation in occurrence that has been observed in other Terai-like ecosystems in the region (Goswani et al., 2021). It is possible therefore that our results do not represent year-long patterns of occurrence in the management regimes assessed. However, even if the results reported here are not representative of the effect of management through longer periods of time, they still have implications for conservation as the strong response to management during at least a portion of the year indicates this is a key factor influencing local wildlife populations. We also believe that a stark change in occurrence probability between seasons would be necessary to invalidate our general conclusions given the large effect sizes we found in many cases. Nevertheless, for a more complete understanding of the impact of management on wildlife in the region, future research should investigate whether the effects observed in our study are also found in other times of the year, in other years, and elsewhere in the Terai.

4.5. Implications for wildlife conservation in the Terai Arc Landscape and beyond

Our work provides evidence that wildlife responds differently to distinct management strategies indicating that a diverse approach to habitat protection and management is needed if the goal is to represent most species in a community. However, our study and similar findings from other biogeographic regions also show that management regimes providing stricter levels of habitat protection are likely to be more beneficial for mammal species that are most in need of conservation interventions. More specifically in the Terai Arc Landscape, the broader patterns reported here could be used to inform area-based conservation measures. For instance, the positive effect of Bardia's buffer zone on herbivores and non-threatened mammals is likely to be observed in other parts of the Terai where natural cover in the buffer zone is similar to or greater than the surrounding landscape. Additionally, the fact that buffer zones may mitigate negative impacts of agriculture has important implications for wildlife conservation in human-dominated landscapes of Nepal and thoroughly understanding its mechanisms should be a priority. However, rural communities in the region rely heavily on agriculture (DNPWC, 2016) and any strategies adopted to reduce its impact on biodiversity must not be detrimental to these communities. Finally, our analyses indicate that at least part of the effectiveness of Bardia National Park is due to the management regime itself, which suggests that the 14% of the Terai Arc Landscape in Nepal under strict habitat protection regimes (MoFSC, 2015) are crucial to safeguard threatened and large mammals in the country.

References

Bamford, A.J., Ferrol-Schulte, D., Wathan, J., 2014. Human and wildlife usage of a protected area buffer zone in an area of high immigration. Oryx 48, 504–513. https://doi.org/10.1017/S0030605313000215

Baral, H.S., Shah, K.B., 2008. Wild Mammals of Nepal, 1st ed. Himalayan Nature, Kathmandu, Nepal.

Budhathoki, P., 2004. Linking communities with conservation in developing countries: buffer zone management initiatives in Nepal. Oryx 38, 334–341. https://doi.org/10.1017/S0030605304000584

Cazalis, V., Princé, K., Mihoub, J.B., Kelly, J., Butchart, S.H.M., Rodrigues, A.S.L., 2020. Effectiveness of protected areas in conserving tropical forest birds. Nat Commun 11, 1–8. https://doi.org/10.1038/s41467-020-18230-0

Dahal, B.R., McAlpine, C.A., Maron, M., 2015. Impacts of extractive forest uses on bird assemblages vary with landscape context in lowland Nepal. Biol Conserv 186, 167–175. https://doi.org/10.1016/j.biocon.2015.03.014

Dahal, B.R., McAlpine, C.A., Maron, M., 2014. Bird conservation values of off-reserve forests in lowland Nepal. For Ecol Manage 323, 28–38. https://doi.org/10.1016/j.foreco.2014.03.033

de Almeida-Rocha, J.M., Peres, C.A., 2021. Nominally protected buffer zones around tropical protected areas are as highly degraded as the wider unprotected countryside. Biol Conserv 256, 109068. https://doi.org/10.1016/j.biocon.2021.109068

Deere, N.J., Guillera-Arroita, G., Baking, E.L., Bernard, H., Pfeifer, M., Reynolds, G., Wearn, O.R., Davies, Z.G., Struebig, M.J., 2018. High Carbon Stock forests provide co-benefits for tropical biodiversity. Journal of Applied Ecology 55, 997–1008. https://doi.org/10.1111/1365-2664.13023

Dinerstein, E., 1979. An ecological survey of the Royal Karnali Bardia Wildlife Preserve, Nepal. Part II: habitat/animal interactions. Biol Conserv 16, 265–300.

DNPWC, 2016. Bardia National Park and its Buffer Zone Management Plan (2016-2020). Ministry of Forest and Soil Conservation, Kathmandu, Nepal.

Drouilly, M., Clark, A., O'Riain, M.J., 2018. Multi-species occupancy modelling of mammal and ground bird communities in rangeland in the Karoo: A case for dryland systems globally. Biol Conserv 224, 16–25. https://doi.org/10.1016/J.BIOCON.2018.05.013

Ellis, S., Talukdar, B., 2019. Rhinoceros unicornis [WWW Document]. The IUCN Red List of Threatened Species 2019. URL https://dx.doi.org/10.2305/IUCN.UK.2019-3.RLTS.T19496A18494149.en. (accessed 12.20.21).

Estes, J. a, Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S. a, Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R., Wardle, D. a, 2011. Trophic downgrading of planet Earth. Science 333, 301–6. https://doi.org/10.1126/science.1205106

Ferreira, G.B., Collen, B., Newbold, T., Oliveira, M.J.R., Pinheiro, M.S., de Pinho, F.F., Rowcliffe, M., Carbone, C., 2020. Strict protected areas are essential for the conservation of larger and threatened mammals in a priority region of the Brazilian Cerrado. Biol Conserv 251, 108762. https://doi.org/10.1016/j.biocon.2020.108762

Gelman, A., Hill, J., 2006. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge, UK, UK. https://doi.org/https://doi.org/10.1017/CBO9780511790942

Goswami, V.R., Vasudev, D., Joshi, B., Hait, P. and Sharma, P., 2021. Coupled effects of climatic forcing and the human footprint on wildlife movement and space use in a dynamic floodplain landscape. Sci Total Environ *758*, 144000.

Gray, C.L., Hill, S.L.L., Newbold, T., Hudson, L.N., Börger, L., Contu, S., Hoskins, A.J., Ferrier, S., Purvis, A., Scharlemann, J.P.W., 2016. Local biodiversity is higher inside than outside terrestrial protected areas worldwide. Nat Commun 7, 12306. https://doi.org/10.1038/ncomms12306

Gurung, M.B., Bigsby, H., Cullen, R., Manandhar, U., 2015. Estimation of carbon stock under different management regimes of tropical forest in the Terai Arc Landscape, Nepal. For Ecol Manage 356, 144–152. https://doi.org/10.1016/j.foreco.2015.07.024

Hansen, A.J., DeFries, R., 2007. Ecological mechanisms linking protected areas to surrounding lands. Ecological Applications 17, 974–988. https://doi.org/10.1890/05-1098

Heinen, J.T., Shrestha, S.K., 2006. Evolving policies for conservation: An Historical Profile of the Protected Area System of Nepal. Journal of Environmental Planning and Management 49, 41–58. https://doi.org/10.1080/09640560500373048

Hevia, V., Martín-López, B., Palomo, S., García-Llorente, M., de Bello, F., González, J.A., 2017. Trait-based approaches to analyze links between the drivers of change and ecosystem services: Synthesizing existing evidence and future challenges. Ecol Evol 7, 831–844. https://doi.org/10.1002/ece3.2692

Ingram, D.J., Ferreira, G.B., Jones, K.E., Mace, G.M., 2021. Targeting Conservation Actions at Species Threat Response Thresholds. Trends Ecol Evol. https://doi.org/10.1016/j.tree.2020.11.004

Jnawali, S.R., Baral, H.S., Lee, S., Acharya, K.P., Upadhyay, G.P., Pandey, M., Shrestha, R., Joshi, D., Lamichhane, B.R., Griffiths, J., Khatiwada, A.P., 2011. The Status of Nepal's Mammals: The National Red List Series. Department of National Parks and Wildlife Conservation.

Jones, K.E., Bielby, J., Cardillo, M., Fritz, S.A., O'Dell, J., Orme, C.D.L., Safi, K., Sechrest, W., Boakes, E.H., Carbone, C., Connolly, C., Cutts, M.J., Foster, J.K., Grenyer, R., Habib, M., Plaster, C.A., Price, S.A., Rigby, E.A., Rist, J., Teacher, A., Bininda-Emonds, O.R.P., Gittleman, J.L., Mace, G.M., Purvis, A., 2009. PanTHERIA: a species-level database of life history, ecology, and geography of extant and recently extinct mammals. Ecology 90, 2648–2648. https://doi.org/10.1890/08-1494.1

Joppa, L.N., Pfaff, A., 2011. Global protected area impacts. Proceedings of the Royal Society B: Biological Sciences 278, 1633–1638. https://doi.org/10.1098/rspb.2010.1713

Jotikapukkana, S., Berg, Å., Pattanavibool, A., 2010. Wildlife and human use of buffer-zone areas in a wildlife sanctuary. Wildlife Research 37, 466. https://doi.org/10.1071/WR09132

Kellner, K., 2017. Package jagsUI - A Wrapper Around "rjags" to Streamline "JAGS" Analyses.

Lahkar, D., Ahmed, M.F., Begum, R.H., Das, S.K. and Harihar, A., 2020. Responses of a wild ungulate assemblage to anthropogenic influences in Manas National Park, India. Biol Conserv 243, 108425. https://doi.org/10.1016/j.biocon.2020.108425

Lamichhane, B.R., Persoon, G.A., Leirs, H., Poudel, S., Subedi, N., Pokheral, C.P., Bhattarai, S., Gotame, P., Mishra, R., de Iongh, H.H., 2019. Contribution of Buffer Zone Programs to Reduce Human-Wildlife Impacts: the Case of the Chitwan National Park, Nepal. Hum Ecol 47, 95–110. https://doi.org/10.1007/s10745-019-0054-y

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. Occupancy estimating and modeling – inferring patterns and dynamics of species occurrence. Elsevier Academic Press, London, UK.

Magioli, M., Ferraz, K.M.P.M. de B., Chiarello, A.G., Galetti, M., Setz, E.Z.F., Paglia, A.P., Abrego, N., Ribeiro, M.C., Ovaskainen, O., 2021. Land-use changes lead to functional loss of terrestrial mammals in a Neotropical rainforest. Perspect Ecol Conserv. https://doi.org/10.1016/j.pecon.2021.02.006

Martin, O., Piatti, G., 2009. World Heritage and Buffer Zones. UNESCO, Paris.

Maxwell, S.L., Cazalis, V., Dudley, N., Hoffmann, M., Rodrigues, A.S.L., Stolton, S., Visconti, P., Woodley, S., Kingston, N., Lewis, E., Maron, M., Strassburg, B.B.N., Wenger, A., Jonas, H.D., Venter, O., Watson, J.E.M., 2020. Area-based conservation in the twenty-first century. Nature 586, 217–227. https://doi.org/10.1038/s41586-020-2773-z

Mehring, M., Stoll-Kleemann, S., 2011. How Effective is the Buffer Zone? Linking Institutional Processes with Satellite Images from a Case Study in the Lore Lindu Forest Biosphere Reserve, Indonesia. Ecology and Society 16, art3. https://doi.org/10.5751/ES-04349-160403

MoFSC, 2015. Strategy and Action Plan 2015-2025, Terai Arc Lanscape, Nepal. Ministry of Forest and Soil Conservation, Kathmandu, Nepal.

Nagendra, H., Karmacharya, M., Karna, B., 2005. Evaluating forest management in Nepal: Views across space and time. Ecology and Society 10, e24. https://doi.org/10.5751/ES-01230-100124

Paolino, R.M., Versiani, N.F., Pasqualotto, N., Rodrigues, T.F., Krepschi, V.G., Chiarello, A.G., 2016. Buffer zone use by mammals in a Cerrado protected area. Biota Neotrop 16. https://doi.org/10.1590/1676-0611-BN-2014-0117

Plummer, M., 2013. JAGS Version 3.4.0 user manual.

R Development Core Team, 2018. R: a language and environment for statistical computing. R Foundation for Statistical Computing.

Ribas, L.G. dos S., Pressey, R.L., Loyola, R., Bini, L.M., 2020. A global comparative analysis of impact evaluation methods in estimating the effectiveness of protected areas. Biol Conserv 246. https://doi.org/10.1016/j.biocon.2020.108595

Rich, L.N., Miller, D.A.W., Robinson, H.S., McNutt, J.W., Kelly, M.J., 2016. Using camera trapping and hierarchical occupancy modelling to evaluate the spatial ecology of an African mammal community. Journal of Applied Ecology 53, 1225–1235. https://doi.org/10.1111/1365-2664.12650

Rosenblatt, E., Creel, S., Schuette, P., Becker, M.S., Christianson, D., Dröge, E., Mweetwa, T., Mwape, H., Merkle, J., M'soka, J., Masonde, J., Simpamba, T., 2019. Do protection gradients explain patterns in herbivore densities? An example with ungulates in Zambia's Luangwa Valley. PLoS One 14, e0224438. https://doi.org/10.1371/journal.pone.0224438

Rovero, F., Ahumada, J., Jansen, P.A., Sheil, D., Alvarez, P., Boekee, K., Espinosa, S., Lima, M.G.M., Martin, E.H., O'Brien, T.G., Salvador, J., Santos, F., Rosa, M., Zvoleff, A., Sutherland, C., Tenan, S., 2020. A standardized assessment of forest mammal communities reveals consistent functional composition and vulnerability across the tropics. Ecography 43, 75–84. https://doi.org/10.1111/ecog.04773

Salafsky, N., 1993. Mammalian Use of a Buffer Zone Agroforestry System Bordering Gunung Palung National Park, West Kalimantan, Indonesia. Conservation Biology 7, 928–933. https://doi.org/10.1046/j.1523-1739.1993.740928.x

Sayer, J., 1991. Rainforest buffer zones: Guidelines for protected area managers. IUCN.

Shen, X., Li, S., McShea, W.J., Wang, D., Yu, J., Shi, X., Dong, W., Mi, X. and Ma, K., 2020. Effectiveness of management zoning designed for flagship species in protecting sympatric species. Conservation Biology 34, 158-167. https://doi.org/10.1111/cobi.13345

Suraci, J.P., Gaynor, K.M., Allen, M.L., Alexander, P., Brashares, J.S., Cendejas-Zarelli, S., Crooks, K., Elbroch, L.M., Forester, T., Green, A.M., Haight, J., Harris, N.C., Hebblewhite, M., Isbell, F., Johnston, B., Kays, R., Lendrum, P.E., Lewis, J.S., McInturff, A., McShea, W., Murphy, T.W., Palmer, M.S., Parsons, A., Parsons, M.A., Pendergast, M.E., Pekins, C., Prugh, L., Sager-Fradkin, K.A., Schuttler, S., Şekercioğlu, Ç.H., Shepherd, B., Whipple, L., Whittington, J., Wittemyer, G., Wilmers, C.C., 2021. Disturbance type and species life history predict mammal responses to humans. Glob Chang Biol gcb.15650. https://doi.org/10.1111/gcb.15650

Timilsina, N., Heinen, J.T., 2008. Forest structure under different management regimes in the Western Lowlands of Nepal. Journal of Sustainable Forestry 26, 112–131. https://doi.org/10.1080/10549810701879628

Uddin, K., Shrestha, H.L., Murthy, M.S.R., Bajracharya, B., Shrestha, B., Gilani, H., Pradhan, S., Dangol, B., 2015. Development of 2010 national land cover database for the Nepal. J Environ Manage 148, 82–90. https://doi.org/10.1016/j.jenvman.2014.07.047

Velho, N., Sreekar, R., Laurance, W., 2016. Terrestrial Species in Protected Areas and Community-Managed Lands in Arunachal Pradesh, Northeast India. Land (Basel) 5, 35. https://doi.org/10.3390/land5040035

Watling, J.I., Arroyo-Rodríguez, V., Pfeifer, M., Baeten, L., Banks-Leite, C., Cisneros, L.M., Fang, R., Hamel-Leigue, A.C., Lachat, T., Leal, I.R., Lens, L., Possingham, H.P., Raheem, D.C., Ribeiro, D.B., Slade, E.M., Urbina-Cardona, J.N., Wood, E.M., Fahrig, L., 2020. Support for the habitat amount hypothesis from a global synthesis of species density studies. Ecol Lett 23, 674–681. https://doi.org/10.1111/ele.13471

Wegge, P., Odden, M., Pokharel, C.Pd., Storaas, T., 2009. Predator–prey relationships and responses of ungulates and their predators to the establishment of protected areas: A case study of tigers, leopards and their prey in Bardia National Park, Nepal. Biol Conserv 142, 189–202. https://doi.org/10.1016/J.BIOCON.2008.10.020

Weisse, M.J., Naughton-Treves, L.C., 2016. Conservation Beyond Park Boundaries: The Impact of Buffer Zones on Deforestation and Mining Concessions in the Peruvian Amazon. Environ Manage 58, 297–311. https://doi.org/10.1007/s00267-016-0709-z

Wilman, H., Belmaker, J., Simpson, J., de la Rosa, C., Rivadeneira, M.M., Jetz, W., 2014. EltonTraits 1.0: Species-level foraging attributes of the world’s birds and mammals. Ecology 95, 2027–2027. https://doi.org/10.1890/13-1917.1