

Why we went to the woods?: effects of human disturbance on species presence in a disturbed Myanmar forest ecosystem

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Abstract

Human activities are affecting habitats and wildlife populations worldwide. Tropical forests are one of the most affected environments, mainly due to deforestation and poaching. Since high levels of anthropogenic pressure on forest ecosystems, including illegal logging and hunting, occur in southwest Myanmar (Rakhine State), we analyzed the effects of human disturbance on medium to large mammals in this region. We used camera-trapping data collected over three consecutive years to investigate occurrence probabilities of 10 species: five common species exploited for bushmeat consumption, and five threatened species targeted by the illegal wildlife trade. We used a hierarchical single-species multi-season occupancy model implemented in a Bayesian framework to evaluate the effects of human disturbances and persistent habitat characteristics, such as the proportion of remaining pristine evergreen forest and the elevation, on occurrence probabilities. We found that occupancy probabilities of three out of five target species for the illegal wildlife trade were positively linked to forest habitats, whereas among common species hunted for bushmeat consumption the Northern red muntjak and the Malayan porcupine were negatively affected by human presence. The effects of human and habitat covariates were varied for other species of both groups. We confirmed results from previous studies that human disturbance is a driver of occurrence probabilities for some species in tropical areas. Our findings suggest that as protection of rainforest habitat is fundamental to the conservation of tropical ecosystems, law enforcement, patrolling, and local engagement activities are also recommended to mitigate forest and species exploitation. Finally, camera trapping could be a first step to identify areas where human presence affects species occupancy and help local authorities to develop more fine-tuned conservation plans.

Introduction

Tropical forests host an extraordinary diversity of habitats and wildlife and provide fundamental ecosystem services (Laurance, 1999; Myers *et al.*, 2000). About 15% of extant tropical forests are in Southeast Asia (Stibig *et al.*, 2014), where rates of deforestation and forest degradation are among the highest in the tropics (Achard *et al.*, 2002). In these areas, the two main anthropogenic threats are deforestation for land conversion or illegal logging and hunting for bushmeat consumption and wildlife trade. These actions can negatively affect wildlife communities with consequences on entire ecosystems (Derhè *et al.*, 2018). Although it is well established that deforestation and conversion of natural

habitats is one of the major causes of biodiversity loss (Sala *et al.*, 2000), the effects of illegal hunting on wildlife at different scales have received less attention in Southeast Asia compared with Africa and the Neotropics (Corlett, 2007). Local hunting for bushmeat consumption is a widespread practice in tropical areas and affects mainly mammal populations (Fa, Peres & Meeuwig, 2002; Milner-Gulland & Bennett, 2003; Laurance *et al.*, 2012; Ripple *et al.*, 2016; Tilman *et al.*, 2017). Most frequently, medium to large-sized mammals are hunted with non-specific techniques like snares, causing shifts in species composition as well as in community structure (Jerozolinski & Pees, 2003; Hegerl *et al.*, 2017; Tilker *et al.*, 2019, 2020; Oberosler *et al.*, 2020a). Moreover, Southeast Asia is one of the centers of

the international illegal wildlife trade (IWT), a thriving industry that leads to poaching for pets, medicinal and animal products, and ultimately causes species decline or even extinction (McEvoy *et al.*, 2019). The IWT also fosters cross-species spillovers and the spread of diseases (Rao *et al.*, 2010; Evans *et al.*, 2019).

Myanmar is considered a biodiversity hotspot (Myers *et al.*, 2000) with a large portion of the country occupied by natural forests, representing a priority for the conservation of many threatened species (McEvoy *et al.*, 2019). On the other hand, Myanmar forests are subject to severe anthropogenic pressures with high rates of deforestation (Mon *et al.*, 2010; Bhagwat, Humphreys & Jones, 2017) and poaching for local meat consumption and international trade (Evans *et al.*, 2019).

In this study, we focused on an area in southwest Myanmar (Rakhine State) characterized by high levels of human disturbance due to the presence of densely settled areas on the coast, where people exploit forest resources (Cremonesi *et al.*, 2021a). The area is close to a protected area and the main threats are deforestation from illegal logging and hunting for personal consumption and the IWT both at local and national levels (Gaffi *et al.*, 2020). It has already been documented by previous camera trap studies that human activities in this area impact species' activity patterns (Cremonesi *et al.*, 2021a). We used camera trap data from a 3-year monitoring campaign to investigate occurrences of target species and how environmental and human-related covariates could influence occupancy probabilities. Percentage of evergreen forest, elevation, and distance from settlements were used as environmental and human-related covariates to identify an effect on wildlife. We also used video records of human activity/presence as a measure of human impact. Our target species were the most commonly hunted animals sold locally for bushmeat and the most threatened species involved in the IWT. We used hierarchical multi-seasons occupancy models to evaluate covariate effects on occurrence probabilities while accounting for imperfect detections (Rich *et al.*, 2016). We hypothesized that anthropogenic disturbance (such as human presence or distance from settlements) negatively affects target species occurrence and distribution. We also expected that for some species, occupancy probabilities could be related to environmental covariates such as pristine evergreen forest or elevation.

Materials and methods

Study area

The study area was in Rakhine State (southwest Myanmar) close to the border of the Rakhine Yoma Elephant Range Wildlife Reserve (RYER) in Gwa and Thandwe townships (17° 22' 0" N, 94° 36' 0" E, Fig. 1). The area is characterized by patches of continuous evergreen forest alternated with degraded forest, bamboo brakes, and croplands. In Myanmar, about 70% of the people live in rural areas (Myanmar Ministry of Health 2011), resulting in major

exploitation pressure on forests resources, including agricultural activities, illegal logging for such highly sought-after trees as Burmese iron woods (*Xylia xylocarpa*) and teak woods (*Tectonia grandis*), and illegal hunting for meat consumption. In 2000–2010, Rakhine was ranked second in deforestation rate of all Myanmar (Wang & Myint, 2016). In addition, Rakhine experienced the third largest deforestation rate in the world in 2010–2015 with an estimated 1.7% forest cover annual loss, with drastic consequences for native species (Reddy *et al.*, 2019). Illegal logging is still now one of the main income sources for local communities (Gaffi *et al.*, 2020). In our study area, during 3 years of monitoring (dry season), we found constant and intense logging activity in all the sites. Over-harvesting occurred mainly due to the absence of an appropriate selective logging cycle as found in other parts of Myanmar (Saung *et al.*, 2021). The mammal communities exhibit species composition and ecosystem functions (e.g., trophic niches and body mass groups) comparable with other tropical region studies (Rovero *et al.*, 2019; Oberosler *et al.*, 2020a), but with a lower diversity compared with other regions of Myanmar (Cremonesi *et al.*, 2021b).

Monitoring scheme

We surveyed four sites (Fig. 1), deploying a mean of 29.92 (± 1.18) camera traps per site each year according to a 30.2×1 km cells grid, for a total surveyed area of 240 km². We used Acorn Ltl-5210 camera traps and surveyed two out of four sites simultaneously. Each monitoring session lasted for a minimum of 45 days, and then camera traps were removed and placed in the other two sites. This monitoring scheme was kept active from 2016 to 2019, during the dry season from November to April. The time period was chosen for logistics reasons since only 60 cameras were available and we preferred to cover more sites and a larger area (240 km²), even if it meant keeping the cameras active for less time to remain within the dry season. As affirmed by MacKenzie & Royle (2005), it is sometimes better to survey more areas less intensively when dealing with rare species. We surveyed four environmentally homogenous sites to achieve better coverage of the overall study area while simplifying the logistics of accessing forest patches. We used GPS waypoints (Garmin GPSMAP 64s, average positioning error ± 10 m) to check distances between cameras during their placement to maintain a minimum distance of 1 km between them. We placed each camera at 60 cm above the ground without using bait. We placed cameras close to forest trails to increase the probability of detecting medium to large mammals and to avoid the disturbances of major roads related to humans. We set passive infrared sensor sensitivity level at medium values and a picture resolution of 640×480 pixels. We set up the cameras to record 20 s videos, with a 2-min interval between consecutive videos to exclude repeated triggering. We left cameras working 24 h per day and did not revisit cameras until the end of the monitoring period.

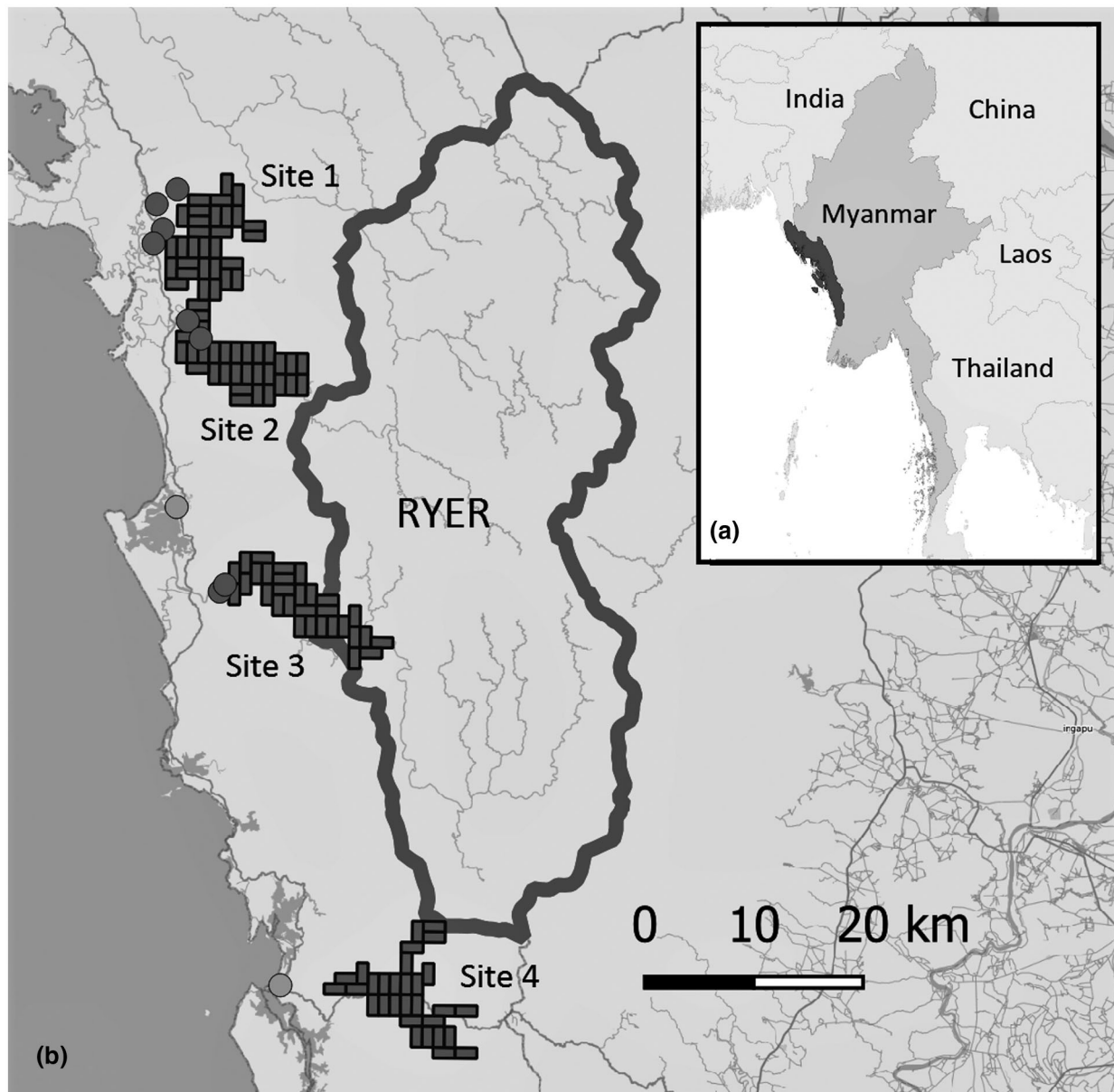


Figure 1 Study area location in Myanmar. (a) Myanmar borders, Rakhine state in dark gray. (b) Detailed map of the four camera trap sites in Rakhine State. Continuous black line represents the protected area of the Rakhine Yoma Elephant Range (RYER). Dots represent the main settlements. Dark gray boxes are the grids used for the camera trap placement.

Target species

Out of a total pool of 78 837 videos, we removed “empty” ones (i.e., false triggers) and used only videos that allowed species-level identification, also excluding non-target species such as small mammals (<1 kg), birds, and reptiles. Among all the 25 recorded species, we selected a sample of 10 species (Table 1), having at least 10 detections per year, based on two different criteria: 1. commonly hunted species for bushmeat consumption, local markets, and restaurants; 2. threatened species hunted for the IWT as pets, animal

products (e.g., bones, skulls, paws), and traditional medicine (e.g., scales, skins, bile). The species selected for the first criterion were the Northern red muntjak *Muntiacus vaginalis*, the Malayan porcupine *Hystrix brachyura*, the wild pig *Sus scrofa*, the large Indian civet *Viverra zibetha*, and the common palm civet *Paradoxurus hermaphroditus*. These species are considered by the IUCN Red List as Least Concern (LC), but on which exist a strong pressure by human activities, making them potentially threatened over time (Evans *et al.*, 2019; McEvoy *et al.*, 2019; Nijman & Shepherd, 2017). Under the second criterion, we selected the Asiatic

Table 1 Checklist of medium to large mammals detected by camera traps at Rakhine Yoma Elephant Range (RYER) in Myanmar

Latin name	Common name	IUCN	2016	2017	2018	Criterion
<i>Arctictis binturong</i>	Binturong	VU	2	0	6	/
<i>Atherurus macrourus</i>	Asiatic brush-tailed porcupine	LC	2	0	0	/
<i>Bos gaurus</i>	Gaur	VU	3	2	32	/
<i>Canis aureus</i>	Golden jackal	LC	1	0	1	/
<i>Capricornis rubridus</i>	Red serow	NT	7	7	0	/
<i>Catopuma temminckii</i>	Asiatic golden cat	NT	12	31	23	I
<i>Cuon alpinus</i>	Dhole	EN	6	8	7	/
<i>Elephas maximus</i>	Asian elephant	EN	38	44	76	I
<i>Helarctos malayanus</i>	Sun bear	VU	43	89	66	I
<i>Herpestes urva</i>	Crab-eating mongoose	LC	4	7	0	/
<i>Hystrix brachyura</i>	Malayan porcupine	LC	92	154	156	B
<i>Macaca leonina</i>	Northern pig-tailed macaque	VU	27	70	56	I
<i>Manis javanica</i>	Sunda pangolin	CR	0	1	3	/
<i>Muntiacus vaginalis</i>	Northern red muntjak	LC	160	276	202	B
<i>Neofelis nebulosa</i>	Clouded leopard	VU	23	11	4	/
<i>Paradoxurus hermaphroditus</i>	Asian palm civet	LC	44	45	41	B
<i>Pardofelis marmorata</i>	Marbled cat	NT	0	1	14	/
<i>Prionailurus bengalensis</i>	Leopard cat	LC	29	49	43	I
<i>Prionodon pardicolor</i>	Spotted linsang	LC	0	0	1	/
<i>Rusa unicolor</i>	Sambar	VU	8	12	0	/
<i>Sus scrofa</i>	Wild pig	LC	50	80	71	B
<i>Trachypithecus phayrei</i>	Phayre's leaf monkey	EN	0	1	0	/
<i>Ursus thibetanus</i>	Asian black bear	VU	3	2	1	/
<i>Viverra zibetha</i>	Large Indian civet	LC	85	63	82	B
<i>Viverricula indica</i>	Small Indian civet	LC	0	1	0	/

IUCN column shows the threat category of each species (LC = least concern; NT = near threatened; VU = vulnerable; EN = endangered; CR = critically endangered). Events columns (2016, 2017, 2018) indicate the number of detections for each year. In bold are shown the selected species for the analysis with at least 10 detections for each year. The criterion column shows if the species were selected because they are hunted for bushmeat consumption (B) or for the illegal wildlife trade (I).

golden cat *Catopuma temminckii*, the sun bear *Helarctos malayanus*, the leopard cat *Prionailurus bengalensis*, the Asian elephant *Elephas maximus*, and the Northern pig-tailed macaque *Macaca leonina* (McCarthy et al., 2015; Ross et al., 2015; Nijman & Shepherd, 2017; Scotson et al., 2017; Evans et al., 2019; McEvoy et al., 2019; Boonratana et al., 2020). Except for the leopard cat, all of these species are considered threatened by the IUCN (i.e., not Least Concern) due to habitat loss, poaching, and human-wildlife conflicts (Supporting Information Data S1). We decided to include the Northern pig-tailed macaque, even though it is not traditionally a target species for camera traps due to its arboreal habit. However, as described in literature (Boonratana et al., 2020) and confirmed in our videos, the species spends a large amount of time on the ground for movement or feeding activities. We recognize that for some large mammals, such as elephants and wild pigs, our camera trap monitoring scheme does not guarantee independence between all cameras, undermining the site closure assumption of occupancy modeling and potentially affecting estimates of covariate effects or leading to underestimation in occupancy. As suggested by Gray (2012), when sites are smaller than the potential home range of some species (e.g., elephants) it is more appropriate, when analyzing data within an occupancy framework, to consider results (ψ) as the intensity of use

around sites rather than a measure of occupancy (see also MacKenzie et al., 2006).

Covariates

We initially classified human detections (defined as the number of human events per sampling occasion divided by the camera traps days of operation) according to the three following categories: (1) "hunting," that is videos showing people walking with guns, crossbows or clearly identifiable weapons, or carrying dead animals; (2) "logging," that is recordings showing people with chainsaws, carrying petrol, transporting logs, and using domestic animals (water buffalo, *Bubalus bubalis*) for this purpose; and (3) "presence," that is simply presence of humans for which we could not identify as carrying on a specific activity and therefore could be associated with a mere passage of people within the camera range or with some illegal activity not identifiable by our method. We are aware that with our approach we are probably underestimating hunting activities, since the most common tools in SE Asia are snares (Belecky & Gray, 2020), and they are quite difficult to detect with cameras. We are also aware that some impact by logging activities can be evaluated only in a long-term situation longer than 3-year campaigns and, therefore, we did not consider "logging"

effects as those caused by fragmentation/degradation. Rather, we considered logging as the disturbance to wildlife from constant and intense human presence in the forest with people and domestic animals cutting and transporting logs, the noises of working people and chainsaw activities and the forest camps that are also often associated with hunting both for trade and food for loggers (Meijaard *et al.*, 2005). Due to these reasons, we considered for the following analysis to group all the human activities into one single covariate (PRES), used as a proxy of human disturbance on wildlife, as human presence is not uniform but can be present with different activities.

In addition, we also analyzed the effect of two environmental covariates, the percentage of pristine evergreen forest in the area and the elevation (meters at sea level) recorded at each camera site. The proportion of evergreen forest (EVER) around each camera was estimated in QGIS v3.1 (QGIS Development Team, 2019) using a land cover map produced by Landsat-8 OLI reflectance data (Fava & Colombo, 2017), and calculating the proportion of pixels classified as evergreen forest in a circular buffer with a radius of 500 m around each camera trap (as an average value for a medium to large mammal home range). We used this measure as an indicator of the proportion of nondegraded habitat in the area, ranging from 0 to 1, where 1 represents 100% evergreen forest around the camera. Terrain elevation is considered a major driver in mammal occurrence patterns, as shown in several previous studies in Southeast Asia (Gray *et al.*, 2014; Huang *et al.*, 2020; Oberosler *et al.*, 2020b). Elevation (ELEV) at our study sites ranged from 11 to 387 m and was recorded at each camera site using a GPS unit. The last covariate considered was the distance of each camera from main settlements, evaluated using available data in the Myanmar Information Management Unit and the previously cited geo-dataset (Fava & Colombo, 2017). To calculate the Euclidean distance between each camera GPS location and the nearest village (VILL, that is, pixels classified as settled areas), we used the NNJoin plugin in the Geoprocessing Tools package of Quantum GIS version 3.10 (QGIS Development Team, 2019). The minimum village distance was 0.8 km, whereas the maximum distance was 18.6 km. We used the “distance from villages” covariate as a proxy of a long-term indirect human pressure. We expect that occurrence probabilities of commonly hunted and threatened species would be negatively affected by the human pressure (presence and villages) and positively affected by the environmental covariate of evergreen forest, whereas we expect varying effects of elevation depending on the species’ elevation preferences.

Data analysis

We decided to pool the data of the four sites together treating them as a single area (RYER). This decision was made considering that the four sites are ecologically similar and cover comparable covariate gradients. In addition, the monitoring was performed during the same dry season and without environmental changes along the 3 years. Before pooling

data, we verified a possible site effect on occupancy for each species using the same model implementation explained below with “SITE” (as a factor of 4 levels) as the only covariate in the models. We found no site effect on occupancy probabilities for any of our target species (Supporting Information Data S3).

We first standardized all the continuous covariates to have mean zero and standard deviation one (Schielezeth, 2010). We then calculated variance inflation factors (VIF) for all the covariates and found no collinearity problems ($VIF < 10$ for all variables, Naimi *et al.*, 2014; see Supporting Information Data S4).

To estimate the covariate effects on occurrence and detection probabilities, we used a multi-season, single species occupancy analysis with a hierarchical modeling approach (MacKenzie *et al.*, 2002) implemented in a Bayesian framework (Supporting Information Data S2). We considered a sampling occasion time span of 5 days (Oberosler *et al.*, 2020b) which led to a median of 13 sampling occasions for all the camera traps each year. We first set up for each species all the detection data (i.e. binary, detected (1) or not (0), for each occasion and camera trap in each year) as a $Y_{i,j,k}$ array (where i indicates the camera station, j the sampling occasion, and k the year). True occurrence was modeled as a Bernoulli random variable $z_{i,k} \sim \text{Bern}(\psi_{i,k})$ with occupancy probability $\psi_{i,k}$, where $z_{i,k} = 1$ when the species was present at site i during year k or $z_{i,k} = 0$ otherwise. We modeled occurrence probabilities as a function of the four environmental and human-related variables described before (PRES, EVER, ELEV, VILL). Following Oberosler *et al.* (2020b), we built the model using an autologistic formulation where occupancy in year k is dependent on occupancy in the previous year, $k - 1$ (Zipkin, Grant & Fagan, 2012). This autologistic model is more efficiently implemented in a Bayesian framework. Occurrence probabilities $\psi_{i,k}$ for years >1 were modeled as:

$$\text{logit}(\psi_{i,k}) = \alpha_0 + \alpha_1 z_{i,k-1} + \alpha_P \text{PRES} + \alpha_{\text{El}} \text{ELEV} + \alpha_V \text{VILL} + \alpha_{\text{Ev}} \text{EVER}.$$

In the formula α_0 is the intercept, $\alpha_1 z_{i,k-1}$ is the effect of a site having been occupied the previous year while α_P , α_{El} , α_V , α_{Ev} represent the magnitude of covariate effects on occurrence probabilities. The occurrence probabilities for the first year were modeled as:

$$\text{logit}(\psi_{i,k}) = \alpha_2 + \alpha_P \text{PRES} + \alpha_{\text{El}} \text{ELEV} + \alpha_V \text{VILL} + \alpha_{\text{Ev}} \text{EVER}.$$

In the formula α_2 is the intercept of occupancy in the first year. Binary detections were modeled as a Bernoulli random variable dependent on occurrence: $y_{i,j,k} \sim \text{Bern}(p_i * z_{i,k})$ where p is the detection probability at site i when the species is present. We modeled detectability as a function of the distance from villages assuming that animals would be more elusive close to settlements, and because many papers found that areas with lowered canopy height, as we found in areas surrounding villages, lead to denser forest floor vegetation

and high light penetration, limiting camera traps (Laurance *et al.*, 2002; Rovero *et al.*, 2014; Oberosler *et al.*, 2020b):

$$\text{logit}(p_{i,t}) = \beta_0 + \beta_v \text{VILL}.$$

Due to the small number of detections for the species *Catopuma temminckii*, we adopted “simplified” models, running them with one covariate at time to obtain reliable parameter estimates for further considerations. We fit the model in a Bayesian framework using Markov Chain Monte Carlo (MCMC) methods, implemented in the software JAGS 4.3.0 (Plummer, 2003), and ran our model through R 4.1.0 (R Core Team, 2018) with the packages *rjags* 4-10 (Plummer, 2018) and *dclone* 2.3-0 (Solymos, 2010). For each model we used three chains, run 150 000 times after 10 000 burn-in iterations, and thinned the remaining cycles every 20 draws. We used vague priors (see Supporting Information Data S2) and we visually inspected the chains to verify the model’s convergence and checked the Gelman-Rubin diagnostic (Brooks & Gelman, 1998). If the 95% Bayesian Credible Interval (BCI) for a covariate’s coefficient did not include zero, we considered the effect as significant (Hespanhol *et al.*, 2019) and we only report on those significant effects.

Results

Each year we had an overall effort of 107 camera traps working for an average of 56.47 ± 6.75 days. We analyzed 5152 videos of medium to large mammals, identified at species level, with 2478 belonging to wildlife and 2674 to humans. Of these human detections, we identified 737 cases of illegal human activities, of which 249 classified as hunting and 488 as logging. We found 1937 videos of generic human presence in the forest, without any recognizable illegal activity recorded by the camera trap.

The effects of the environmental and human covariates varied among species (Fig. 2 and Supporting Information Data S5). Among the species hunted for meat consumption, the Northern red muntjak and the Malayan porcupine were negatively related to human presence (α_P : mean -0.52 , 95% BCI -0.94 to -0.14 and α_P : mean -0.57 , 95% BCI -1.03 to -0.15 , respectively). The Northern red muntjak was also positively associated with the distance from villages (α_V : mean 0.33 , 95% BCI 0.007 to 0.66), while the Malayan porcupine was negatively associated with this covariate (α_V : mean -0.31 , 95% BCI -0.06 to -0.01). For the wild pig, we found no significant effects of the covariates on its occurrence probability. For the other two commonly hunted species, the large Indian civet and the common palm civet, we found for the former a negative effect of elevation (α_{EI} : mean -0.58 , 95% BCI -1.02 to -0.15) and for the latter a positive effect of evergreen forest (α_{EV} : mean 1.21 , 95% BCI 0.02 to 2.80).

Among the target species for the IWT, three out of five species were positively associated with the presence of continuous intact evergreen forests (sun bear, α_E : mean 0.51 , 95% BCI 0.12 to 0.90 ; Northern pig-tail macaque, α_E : mean

0.62 , 95% BCI 0.04 to 1.19 and leopard cat, α_E : mean 1.33 , 95% BCI 0.22 to 2.60). Sun bear occupancy was also positively related to elevation (α_{EI} : mean 0.69 , 95% BCI 0.26 to 1.14), whereas both the Asiatic golden cat and the Northern pig-tail macaque increased in occurrence probability with the distance from villages (α_V : mean 0.69 , 95% BCI 0.15 to 1.97 ; α_V : mean 0.67 , 95% BCI 0.09 to 1.30 , respectively). The two species for which human activities showed any significant effect were the Northern pig-tail macaque and the leopard cat, the former with a negative and the latter with a positive relationship (α_P : mean -1.15 , 95% BCI -2.49 to -0.03 and α_P : mean 2.48 , 95% BCI 0.07 to 6.03 , respectively). The autocorrelation term estimates (α_t), representing the effect of a site having been occupied the previous year, were negative for two species (*Sus Scrofa* and *Helarctos malayanus*) and positive for the others (Supporting Information Data S5).

Plotting the mean occurrence probabilities across all sites for each year, we can see that patterns varied among species and years (Fig. 3). Some species showed consistent or increased mean values across years (even if not significant) whereas none of the species experienced a decrease along the 3 monitoring years.

Looking at the effects on detectability values, we found that four species were positively associated with the distance from villages (Northern red muntjak, β_V : mean 0.15 , 95% BCI 0.02 to 0.29 ; Asiatic golden cat, β_V : mean 0.54 , 95% BCI 0.23 to 0.70 , Malayan porcupine, β_V : mean 0.30 , 95% BCI 0.13 to 0.47 , and the wild pig, β_V : mean 0.60 , 95% BCI 0.24 to 0.94), however for the leopard cat, we found a negative effect (leopard cat, β_V : mean -0.52 , 95% BCI -0.82 to -0.24).

Discussion

Our study confirmed that the pressures exerted by human activities in tropical forests are an important driver for the occurrence of some of the target species. We found high levels of anthropogenic disturbance in our study area, as revealed by an extremely high human presence recorded in the area, with 2674 videos out of 5152 attributable to anthropogenic events (in comparison, 2478 videos are comprised of all other studied species). Camera trapping allowed us to identify different illegal human activities – mainly hunting and logging – but as stated above, our method probably underestimated some activity, like hunting, due to missing key data that are undetectable by camera traps, such as the presence of snares. This is supported by unpublished data that 27% of 22 interviewed villages in RYER practice active hunting using snares, and that 100% of the interviewed subjects consume bushmeat at home, proving that the practice is very common and widespread. We can therefore confidently state that our recordings of general human presence also contain undetected snaring activities. Moreover, we could say that camera traps, in addition to underestimating hunting data, also do not necessarily reflect the real spatial distribution of hunting pressure since they detect hunters but not the hunting events (they may instead reflect hunter distribution).

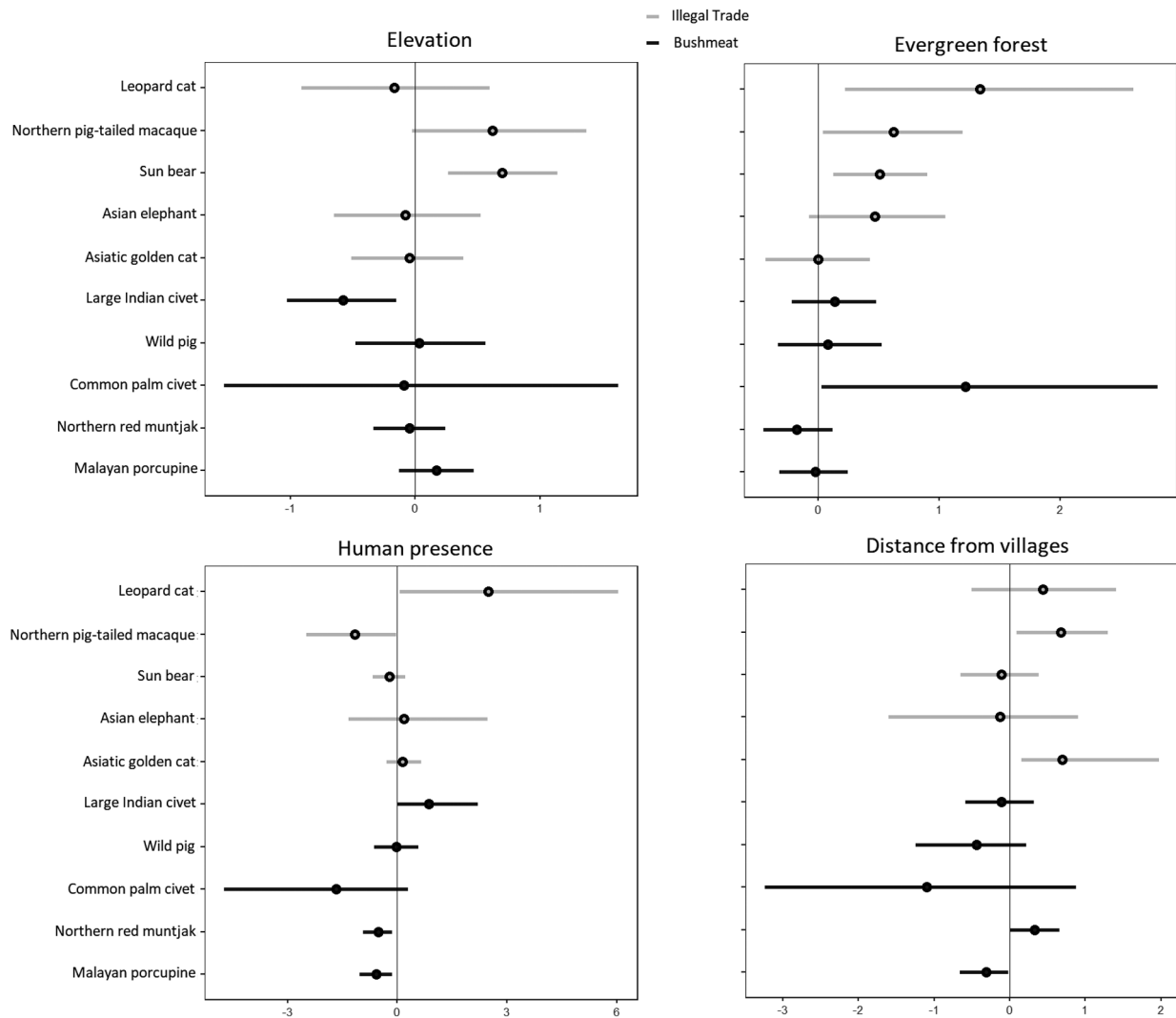


Figure 2 Estimates of covariate effects (elevation [m a.s.l.], evergreen forest [percent evergreen forest in a 500-m buffer around the camera trap], human presence [number of human events per sampling occasion divided by the camera trap days of operation] and distance from villages [Euclidean distance between each camera location and the nearest village]) on species occupancy in Rakhine (Myanmar), estimated using Bayesian multi-season single-species occupancy models with camera-trapping data collected between 2016 and 2019. Dots represent posterior means and lines 95% Bayesian credible intervals (BCI). We focused on 10 species: five common species exploited for bushmeat consumption (black lines), and five threatened species targeted by the illegal wildlife trade (grey lines). If 95% BCIs do not overlap zero, we considered the covariate effect significant.

We agree with Tilker *et al.* (2020), in that the study of spatial patterns of biodiversity in heavily defaunated landscapes “may require novel methodological and analytical approaches using multiple detection methods to increase detections for rare species, include anthropogenic covariates that capture different aspects of hunting pressure.” For example, recently Dobbins *et al.* (2020) developed an illegal activities map using acoustic records (in an area where hunting occurs with guns) that was much more detailed and realistic compared with camera trap data. Even though camera traps alone are likely insufficient to quantify hunting pressure, they were useful to detect the general human presence in the forest and to underline its effect on wildlife distribution.

The hierarchical Bayesian models indicated that four out of ten species were negatively affected by human-related covariates whereas two species showed positive responses. Among the species hunted for bushmeat consumption we found that even non-threatened species as the Northern red muntjak and the Malayan porcupine were negatively affected by human presence. These two species are the main target for bushmeat consumption (Steinmetz *et al.*, 2008; Duckworth *et al.*, 2016; Evans *et al.*, 2019) and are even considered the most heavily targeted of the common species for bushmeat in Myanmar (McEvoy *et al.*, 2019). Since earlier studies showed that mammal’s distribution and activity patterns could be influenced by humans’ activities in the forest (Carter *et al.*, 2015; Díaz-Ruiz

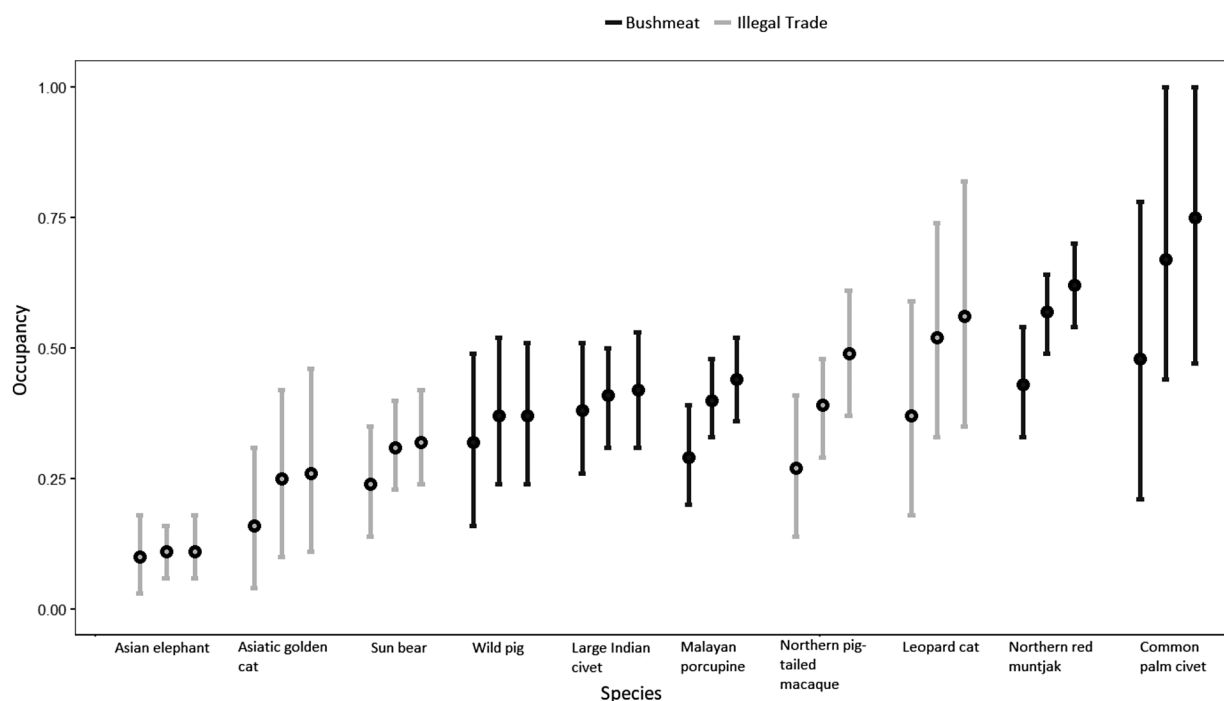


Figure 3 Mean occupancy across all sites in a given year from 2016 to 2019 for 10 mammal species camera-trapped in Rakhyne (Myanmar), estimated with Bayesian multi-season single-species occupancy models. Dots represent posterior means and lines the 95% Bayesian credible intervals. We focused on 10 species: five common species exploited for bushmeat consumption (black lines), and five threatened species targeted by the illegal wildlife trade (grey lines).

et al., 2016; Oberosler *et al.*, 2017; Gaynor *et al.*, 2018; Mas-sara *et al.*, 2018; Dias *et al.*, 2019), it is reasonable to assume that the Northern red muntjak and the Malayan porcupine tend to spatially avoid high levels of human presence, as in our case, given the high demand for wild meat in this area. However, these species presented opposite effects regarding the distance from villages: the Northern red muntjak increased in occurrence far from settlements whereas the occurrence of Malayan porcupine decreased with distance from human settlements, confirming that this species can be found in many habitats including agricultural areas close to villages (Lunde, Aplin & Molur, 2016).

Wild pig's occupancy was not affected by any of the covariates, suggesting that it is an adaptable species as also found in other works worldwide (Keuling & Leus, 2019). In addition, it has been previously demonstrated that in our study area, wild pigs avoid humans temporally by shifting their behavior into more nocturnal activity (Cremonesi *et al.*, 2021a). For the two civet species, occasionally hunted for meat consumption (Lynam *et al.*, 2005; Lau, Fellowes & Chan, 2010; McEvoy *et al.*, 2019), neither showed any significant relationship with human covariates (though the large Indian civet was marginally affected by human presence, see Supporting Information Data S5). We found that for the large Indian civet occurrence probability was affected negatively by elevation, whereas for the common palm civet we found a positive association with pristine evergreen forest habitat. Other works have shown that the two civet species occupy a

wide range of habitats and show a high flexibility in behavior even in disturbed environments (Duckworth *et al.*, 2016; Timmins *et al.*, 2016). It is our opinion that more attention is needed for species listed as “least concern” that are commonly hunted species but attract much less conservation attention than threatened species (Redford, Berger & Zack, 2013). Hunting rates are often not sustainable and such pressures could have detrimental effects in the long term, causing shifts in the community species composition, especially due to the use of unselective hunting methods like snares.

For the species related to the IWT, we mainly found positive relationships with evergreen forests. Northern pig-tailed macaque, sun bear, and leopard cat were positively affected by the percentage of continuous evergreen forest. The sun bear is recognized to be a forest-dependent species (Augeri, 2005; Scotson *et al.*, 2018) and many other works have underlined the importance of well preserved and extensive forests for the species (Wong *et al.*, 2013; Scotson *et al.*, 2017). The sun bear is known to be commonly poached for its gall bladders (i.e., bile) and paws (Scotson *et al.*, 2018) in Myanmar (Bisi *et al.*, 2019; Gaffi *et al.*, 2020) and the absence of any human effects from our models could be related to the elusiveness and very low density of the species in the area and to the positive relationship with elevation. However, in a different study, we confirmed that sun bears increase nocturnal activity in our study area and likely to avoid direct human disturbance (Cremonesi *et al.*, 2021a). It will be important to take specific conservation actions for

this species, such as preserving large areas of evergreen forest habitats, as suggested also by the recently developed ten-year Conservation Action Plan in RYER (Gaffi *et al.*, 2020). Both the Northern pig-tailed macaque and the leopard were positively associated with evergreen forests. Both species are poorly studied, and the degree of anthropogenic pressure they can tolerate is yet to be ascertained. Some studies confirmed that the two species are actively hunted and traded in Myanmar (Ross *et al.*, 2015; McEvoy *et al.*, 2019). However, it will be interesting to better investigate these patterns to understand the degree of threats since we found that both species were affected in two different ways by human covariates: the Northern pig-tailed macaque was negatively affected by human presence and increased in occurrence away from villages whereas the leopard cat was positively associated with human presence. Similarly, Ross *et al.* (2015) showed that leopard cats can be found in logged forest and close to rural settlements. The leopard cat, despite being a target of the IWT, is still considered as “Least Concern” by the IUCN. In contrast, the occurrence of the Asiatic golden cat increased with the distance from settlements, showing how this species avoids spatially anthropogenic contexts. Asiatic golden cats are still requested on the market for pelts, with trading records along the Myanmar–Thailand border (Nijman & Shepherd, 2015). Because the Asiatic golden cat is classified as a near threatened species, and few focused studies on golden cats have been undertaken (Petersen *et al.*, 2021), it is paramount to gain a clearer picture of the species’ status in RYER.

We initially expected but did not find a positive relationship between intact evergreen forest and the Asian elephant, which is considered a forest-dependent species (Choudhury *et al.*, 2008), and consequently susceptible to forest loss and degradation (Leimgruber *et al.*, 2003). A possible explanation could be that during our 3 years of monitoring, we have added to the evidence of elephant herd presence near villages and crops, suggesting that in areas densely populated by humans, as in our case, elephants occur not only in forests but they also occupy human-modified areas (Goswami, Vasudev & Oli, 2014; Kumar, Vijayakrishnan, Singh, 2018). A Conservation Action Plan has been developed for Asian elephants at a national level (Hedges *et al.*, 2018), but it is additionally necessary to develop a structured monitoring scheme in the RYER area, since the species is present but not quantified and it is still highly requested in the illegal trade for their use in Chinese traditional medicine (Menon & Tiwari, 2019).

Our findings agree with previous studies on the effect that human activities can have on tropical forest mammals in SE Asia and suggest that habitat protection alone will not be sufficient unless anthropogenic threats, such as hunting, are also addressed. Tilker *et al.* (2019) found that species in hunted sites showed lower occupancy than in degraded sites, and village density was one of the main predictors, suggesting that where present, hunting may be more threatening to tropical fauna than habitat degradation. Benítez-López *et al.* (2017) also found that mammal abundance declined by 83% in hunted compared with unhunted tropical areas, bringing to

light the urgent problem of bushmeat hunting as a global crisis (Ripple *et al.*, 2016). Defaunation has become a major problem especially in SE Asia, and the IWT exacerbates threats caused by growing human density and infrastructure development, increasing the vulnerability of protected areas (Harrison *et al.*, 2016; Tilker *et al.*, 2020). This is true for all Southeast Asian countries, but investigating how environmental and anthropogenic factors affect tropical biodiversity remains important, particularly in understudied countries such as Myanmar, to identify the most significant threats. Myanmar is considered the largest expanse of potential species range for many mammals in mainland Southeast Asia; however, the extent to which these species rely on much of Myanmar’s forests is unknown (Murray *et al.*, 2020).

Because strong pressure from human activities may inflict long-term consequences even for common species, law enforcement may be necessary to reduce human pressure. First, the importance of the persistence of evergreen forest for some threatened species, indicated by our analysis, suggests the need for stronger regulation of factors that have been causing habitat degradation in Rakhine for many years, both inside and outside protected areas. Logging regulations in the study area are often not fully enforced due to the lack of resources and staff. A first step would be to identify the mechanisms of illegal timber trade and how the trade network is structured in order to support the enforcement agencies patrolling the area and empower local communities to protect the forest. Then, conservation actions should also include areas outside protected areas, creating buffer zones to control and regulate human pressure (Cavada *et al.*, 2019; Gaffi *et al.*, 2020; Oberosler *et al.*, 2020b). To discourage hunting activities, the authors in collaboration with locals and NGOs, are working to promote community guardian groups involving members of the local communities trained to patrol and identify illegal activities across our study areas, especially for snares that we were not able to identify with camera traps. We are also planning to promote community forest groups for the management of areas over about 80 km² for sustainable use of forest resources and as an alternative income source to illegal activities. Finally, due to the high presence of humans and settlements close to the forests, we believe that it is fundamental to invest in education and local engagement efforts in villages close to the protected areas to increase people’s awareness on sustainable use of forest resources.

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Conflict of interest

The corresponding author confirms on behalf of all authors that there is no conflict of interest.

Data availability statement

The datasets analyzed during the current study are available from the corresponding author on reasonable request.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. List of the selected species and their main reasons to be hunted in Myanmar.

Data S2. R and JAGS code for the multi-seasons, single-species community model fitted to detection/non-detection data.

Data S3. Table with the effect of the site covariate (α_S) on the 10 selected species.

Data S4. Model output of the variance inflation factors.

Data S5. Table with the effect of the covariates of human presence (α_P), distance from settlement (α_V), illegal activities (α_I), and evergreen forest (α_E) on the 10 selected species.