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**Title**

‘The human shield effect’: human-wildlife co-occurrence patterns in the coffee forests of southwestern Ethiopia

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## **Abstract**

Understanding species (co)-occurrence patterns and how these are affected and mediated by humans is essential for the development of management plans to guide coexistence between humans and wildlife. Here, we evaluated two opposing hypotheses regarding the effects of humans on species occurrence: “humans as super-predators” and “humans as shield”, using an existing camera-trap dataset of mammal species occurrence collected in the coffee forests of southwestern of Ethiopia. We applied a multispecies occupancy modelling framework to explicitly examine co-occurrence patterns between humans, top-predators, prey, and crop-raiders, along a gradient of forest integrity (characterized by forest cover and fragmentation). We examined co-occurrence patterns during both coffee and non-coffee harvest seasons. Our results show partial support for the “humans as shield” hypothesis. We found (i) signs of co-occurrence between humans and prey in areas of low forest integrity during both survey seasons, and between humans and raiders during the coffee-season, (ii) signs of co-occurrence between prey and raiders during both seasons, (iii) no signs of negative or positive co-occurrence between humans and top-predators. Our findings indicate that a possible “shield effect” between humans and prey within a predator space, might be undergoing at the edges of coffee forests. Our findings suggest that incorporating humans as one more species in the ecological system can contribute to shed light into the effects of humans on species occurrence and ultimately contribute to inform management for coexistence.

## **Keywords**

Human-wildlife interactions, mammals, multispecies occupancy model, shield effect, tropical forests

## 1. Introduction

Human disturbance on natural ecosystems and wildlife habitat has become pervasive across the globe (IPBES 2019, Díaz et al. 2019). The direct impacts of human disturbance on biodiversity, such as the destruction of habitat and overexploitation, have been widely investigated (Pereira et al. 2012). In turn, studies addressing the indirect impacts of human disturbance are now increasingly gaining research attention. For instance, recent evidence suggests that across human-dominated landscapes, human disturbance is altering wildlife behavior (Wilson et al. 2020) including disrupting movements (Doherty et al. 2021), foraging behavior (Smith et al. 2015) and pressing many species to shift their activity periods towards nocturnality (Gaynor et al. 2018; Suraci et al. 2019). These changes in wildlife behavior are likely to entail changes not only in fitness and survival rates (Leblond et al. 2013), but also in patterns of species co-occurrence and on how species interact with each other. However, the influence of human disturbance on species co-occurrence and interactions remains poorly understood. This represents an important knowledge gap since co-occurrence and interactions among species contribute to maintain the stability and resilience of ecological communities in the face of environmental change (Wong and Candolin, 2015).

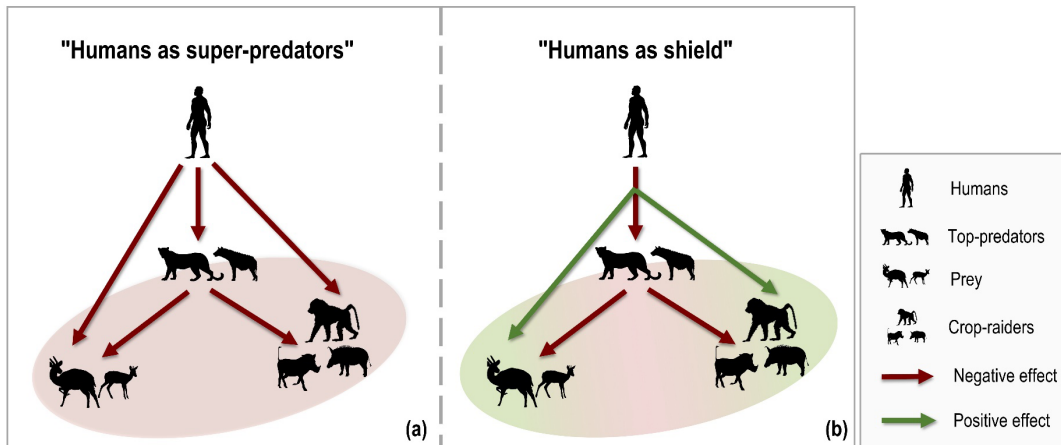
Natural predator-prey systems are an ideal system to study how patterns of species co-occurrence and species interactions might be affected by human disturbance. In predator-prey systems, species have clearly defined ecological roles and hierarchies on the trophic network, where top-predators represent a key ecological group with an important role in structuring the ecological network and the functioning of the ecosystem (Ripple et al. 2014). The presence or absence of top-predators in the system can trigger a series of effects on lower trophic groups, known as trophic cascades (Estes et al. 2011; Graves et al. 2021). This top-down influence on trophic cascades can be mediated through direct predation, by means of interspecific competition (Ripple et al. 2014) or by inducing behavioral changes through the creation of landscapes of fear (Gaynor et al. 2019). However, since humans are themselves “super-predators” (Darimont et al. 2015; Suraci et al. 2019), human disturbance on natural predator-prey systems may disrupt co-occurrence patterns, and predator-prey relationships (Mills and Harris, 2020), ultimately disturbing the role that top-predators have on ecosystems (Smith et al. 2015). On the other hand, there is also evidence that responses to human disturbance and human presence may vary, since some species are able to tolerate humans (Carter et al. 2012) or may even benefit, to some extent, from human proximity or presence (Warren et al. 2011). For instance, in the last couple of decades, several studies have demonstrated a “human shield effect” (Berger, 2007) in which some species use humans as a shield against direct competitors or against predators (Atickem et al. 2014; Muhly et al. 2011).

Understanding species co-occurrence patterns is one of the pre-conditions to understand how species interact with each other. Further, understanding how these patterns may be affected by human disturbance is particularly important in landscapes where the intersection of humans and wildlife is high. In such landscapes, where habitat and resources are shared, the co-occurrence of humans and wildlife can be frequent, and conflicts likely to occur. This is the case in many tropical forest landscapes of sub-Saharan Africa, where local livelihoods intersect closely with forest wildlife, leading to frequent conflicts (Naughton-Treves et al. 2017; Terada et al. 2021) and to challenges for both wildlife conservation and livelihood development. Further, many of these forest landscapes are undergoing deforestation and fragmentation, two processes conducive to alter species co-occurrence and to impact interacting species (Marjakangas et al. 2020; Morris, 2010). Therefore, generating knowledge on spatiotemporal patterns of species activity can contribute to inform on the capacity of species to coexist with humans and contribute to guide the development of plans that aim to co-manage humans and wildlife.

Here, using a multispecies occupancy model (Rota et al. 2016) we examine co-occurrence of top-predators, prey, crop-raiders and humans, at a fine spatial scale, in the smallholder landscapes of southwestern Ethiopia. In these landscapes, there is a strong overlap of humans and wildlife, making this region particularly interesting to examine interactions between wildlife and people. This region is within a hotspot of biodiversity, holding large complexes of moist evergreen Afromontane forest that support a diverse community of mammals, including top-predators (leopard and spotted hyena) (Rodrigues et al. 2021). Arabica coffee occurs naturally in these forests and is also traditionally grown and produced by local communities as a cash crop. Apart from coffee, forests support livestock grazing and provide farmers with a diverse array of products, including firewood and timber, medicinal plants, spices, and honey. Thus, forests and forest products represent an important dimension of local livelihoods (Shumi et al. 2019a) and human activity in the forest is ubiquitous (Beche et al. 2022). In addition, this is a region where conflicts with wildlife are common (Ango et al. 2017; Dorresteijn et al. 2017). Several mammal species that have the forest as primary habitat raid the food crops and cause losses to households' economy (Manlosa et al. 2019a). Further, considering the expected growth trajectories of rural population during the next decades (UN 2019) and the ongoing trends of deforestation and forest fragmentation (Ango et al. 2020) it is likely that conflicts with wildlife might be sustained or even increase in the future. However, the presence of top-predators in the landscape might potentially contribute to the control of crop-raiding species, either through direct predation or by creating a landscape of fear, thus, providing a service to farmers. On the other hand, the ubiquitous use and encroachment of the forest by local communities may disrupt interactions between top-

predators, prey, and crop-raiders and alter the organization of forest ecological communities. In light of these current and future challenges for the landscape, livelihoods and wildlife, it is important to gain a detailed understanding of how humans and wild mammals interact in these forests.

The aim of this study is therefore twofold: first, we aim to assess the effects of human presence in the forest (i.e., direct proxy of human disturbance) on species co-occurrence and second, we aim to understand if patterns of species co-occurrence vary along an environmental gradient of forest integrity (characterized by forest cover and fragmentation and representing an indirect proxy of human disturbance). To examine this, we formulate two major hypotheses (Fig. 1). In our first hypothesis, “*humans as super-predators*”, the presence of humans in the forest has a negative effect on the occurrence of all species groups (i.e., on crop-raiders, top-predators and their prey) and it will drive species occupancy along the gradient of forest integrity. Under this hypothesis, we expect that the occupancy of top-predators, prey and crop-raiders will be lower in the presence of humans than in its absence (Fig. 1a). This hypothesis is based on the general understanding that humans are perceived as a threat and as potential predators by wildlife and, hence, encounters with humans constitute an event to avoid (Smith et al. 2017; Suraci et al. 2019). Alternatively, we hypothesize that human disturbance in the forest will affect species differently and that these differences might be also manifested along the gradient of forest integrity. In particular, we expect that (i) top-predators will respond negatively to human presence, and that (ii) the occurrence of crop-raiders and prey species might benefit from human presence – in what is described in the literature as a “shield effect” (Berger, 2007) (Fig. 1b). We evaluate our hypothesis for two distinct seasons: non-coffee season and coffee harvest season (hereafter, coffee season). We make this distinction because we expect *a priori* a higher level of human disturbance in the forest during the coffee season, when most members of households are in the forest collecting coffee berries.



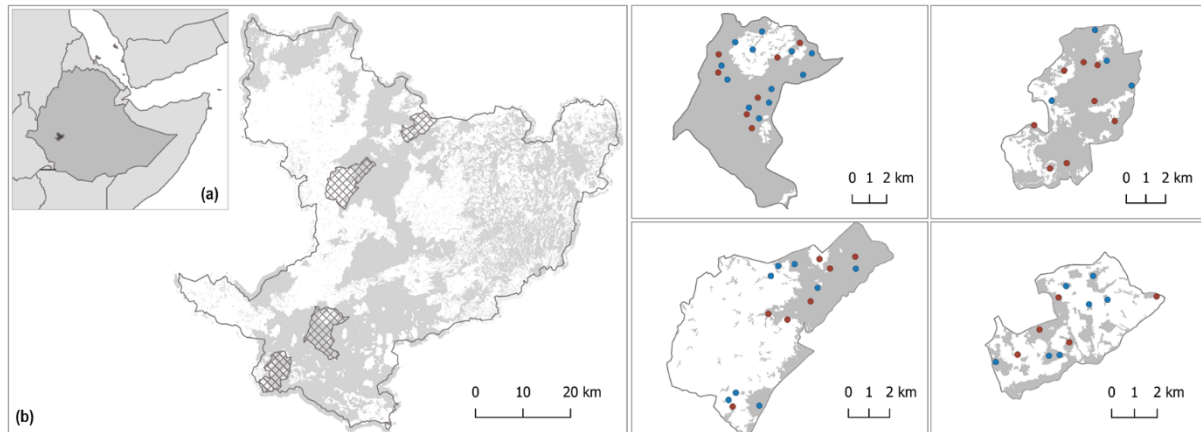
**Figure 1.** Conceptual illustration of the two research hypotheses: (a) “humans as super-predators” and (b) “humans as shield”. Under (a) “humans as super-predators” hypothesis, human presence in the forest displaces all species groups (top-predators, crop-raiders and prey), pushing prey and crop-raiders into the top-predator space. Under this hypothesis, occupancy of all species groups will be higher in areas where humans are absent than in areas where humans are present. In (b) “humans as shield” hypothesis, human presence displaces top-predators only, reducing predation risk for prey and crop-raiders. Under this hypothesis occupancy of prey and crop-raiders will be higher in the presence of humans than in their absence, and occupancy of top-predators will be higher in the absence of humans than in their presence.

## 2. Methods

### 2.1 Study area

The study area is located in the highlands of southwestern Ethiopia, in the Oromia region and Jimma zone (Fig. 2a). It comprises an area of about 3800 km<sup>2</sup> (Fig. 2b) and elevation ranges between 1300 – 3000m above sea level. This highland region holds remnants of moist evergreen Afromontane forest, rich in biodiversity (Buechley et al. 2015; Etana et al. 2021; Mertens et al. 2018; Rodrigues et al. 2018; Shumi et al. 2019b), with more than 30 mammal species recorded in the region (Rodrigues et al. 2021). The natural occurrence of Arabica coffee contributes to the high biodiversity value of these forests. Coffee is a shrub that occurs in the forest and that is grown and produced by local communities as a cash crop, being of major importance for the economy of many households (Manlosa et al. 2019b). Farmers grow coffee using traditional practices, under the shade of native forest trees. The coffee harvest season runs from early October to end of December, and during this period, household members spend the days in the forest picking coffee berries. The mammal community was

assessed in four *kebeles* (i.e., the smallest administrative unit; Fig. 2b) within the study area and located in two districts or *woredas*. The *kebele* area varied between 2345 and 5200 ha and population density between 66 and 137 people/km<sup>2</sup> (Rodrigues et al. 2021). Current forest cover in the study *kebeles* varies between 33 and 88%.



**Figure 2.** Study area location (a) in the southwest of Ethiopia, and (b) location of surveyed *kebeles* within the study area. The four panels on the right side represent the *kebeles* where mammal surveys were undertaken. Red and blue points illustrate sampling sites surveyed during the coffee and non-coffee seasons, respectively.

## 2.2 Data collection

Data on mammal species occurrence used in this study is a subset of data collected in 95 sites, randomly selected according to a stratified sampling design and gathered over a period of 15 months (between January 2016 and March 2017) (as in Rodrigues et al. 2021). Cameras were placed at knee height, without lure, and whenever possible distancing at least 500 m from other cameras - additional details on camera placement and camera rotation can be found in Rodrigues et al. 2021. The dataset included records on mammal species (Rodrigues et al. 2021) and humans. Records were classified within one-hour period (Rovero and Marshall, 2009), i.e., for each species, all pictures detected within a one-hour interval were classified as the same event. Since occupancy modelling requires the assumption of “closure” to changes between surveys (Rota et al. 2009) and given that 15 months is a rather long survey period that can violate the assumption of closure (for instance with births or deaths of individuals), we selected a subset of the data for analysis. The subset comprised approximately 6 months of the calendar year of 2016, encompassing two seasons of three months each: a non-coffee season (from



the end of June to the end of September) and a coffee-harvest season (from the beginning of October to the end of December). The full subset totalled 60 sampling sites (30 sites in each season), with 57 unique sites and 3 sampling sites common to the coffee and non-coffee seasons. Cameras within the subset were active between 13 and 145 days (average of  $101 \pm 31$  days).

We created four groups of species assemblages (hereafter species groups): “top-predators”, “prey”, “crop-raiders” and “humans”. “Top-predators” group included the leopard (*Panthera pardus*) and the spotted hyena (*Crocuta crocuta*) and “prey” the bushbuck (*Tragelaphus scriptus*) and the bushduiker (*Sylvicapra grimmia*). We restricted “prey” group to bushbuck and bushduiker since these are the preferable prey of leopards (Hayward et al. 2006), and approximately 2/3 of top-predator records in our subset correspond to leopards. In turn, hyenas are generalists with diet sources including wild and domestic prey and domestic waste (Owen-Smith and Mills, 2008; Yirga et al. 2015). However, among wild prey, hyenas seem to favour the consumption of medium to large-sized ungulates (Henschel and Tilson, 1988; Trinkel, 2010). “Crop-raiders” comprised the baboon (*Papio anubis*), warthog (*Phacochoerus africanus*) and bushpig (*Potamochoerus larvatus*), all species known to significantly impact livelihoods, mainly through damages to food crops (such as maize, teff and sorghum) (Ango et al. 2017). We excluded the grivet monkey (*Chlorocebus aethiops*) from this group because despite also causing damages to crops, this species uses both arboreal and terrestrial strata for foraging, whereas baboons, bushpigs and warthogs are predominantly terrestrial. All species included in “crop-raiders” are within the diet spectrum of the leopard and hyena, as alternative prey sources (Hayward et al. 2006). Although not among the chief prey, both leopards and hyenas are also potential predators of baboons (Bidner et al. 2018; Cowlshaw, 1994).

### **2.3 Environmental data**

We compiled several variables relevant to characterize camera trap sites in terms of forest cover and forest fragmentation. These included distance to the forest edge, total amount of edge, proportion of forest cover and mean forest patch area. Proportion of forest cover was selected because it provides information on the amount of forest habitat available in each sampling site, whereas distance to the forest edge, total amount of edge and mean forest patch area were selected as a simple indicator for how fragmented sampling sites are (with proximity to the edge, high amount of edge and small patch area indicating higher habitat fragmentation). Forest cover and fragmentation metrics were calculated in FRAGSTATS (version 4.2), using a map of forest cover derived from

RapidEye satellite imagery from 2015, with 5 m resolution (Rodrigues et al. 2018). We calculated the proportion of forest cover, total amount of edge, and mean patch area at the class level and within a moving window of 500 m. We chose this moving window size to approximate the distance between camera trap sites. Each site was also characterized in terms of elevation, derived from the ASTER Global Digital Elevation Model v2 (30 m resolution; <https://reverb.echo.nasa.gov/>). Elevation is a relevant variable for site characterization, because coffee growth is restricted to a specific elevation belt (between 1000 – 2000 m (Senbeta et al. 2014).

We performed a principal component analysis (PCA) on the selected environmental predictors, in order to summarize the environmental information and to reduce the autocorrelation among variables. The first axis of the PCA explained 72.8% of variance and was used to model species interactions. It described a combined gradient of increasing forest cover and decreasing fragmentation (i.e., from sites with high edge amount, low forest cover and closer to the forest edge to sites located in areas with low edge amount, high forest cover and towards the forest interior) (Table A1), which for simplicity, hereafter, we refer to as a gradient of forest integrity.

#### **2.4 Analytical framework: multispecies occupancy model**

To investigate the co-occurrence between “predators”, “prey”, “crop-raiders” and “humans” and how these may vary along a gradient of forest cover and fragmentation we implemented the multispecies occupancy modelling framework of Rota et al. (2016). Rota et al. (2016) occupancy model allows the evaluation of co-occurrence between two or more species in the presence or absence of each other, along an environmental gradient and while accounting for imperfect detection (Rota et al. 2016). Unlike other occupancy modelling approaches, this model does not require a priori specification of dominance or subordination of species over each other.

For each survey season (i.e., non-coffee and coffee seasons), we collapsed species’ groups occurrence data of 1-hour intervals into sampling occasions of one week (7 days). Non-coffee and coffee seasons encompassed 14 and 13 sampling occasions (or surveys), respectively. Sampling sites with less than two sampling occasions (i.e., two weeks) were excluded from the analysis. Within each season, and for each site and species group we derived detection histories, where “1” denoted a detection and “0” non-detection of the target species group at a certain sampling occasion. We fitted two models, one for each season (i.e., coffee and non-coffee seasons). The detection model on both seasons assumed unique but constant detection probabilities for each species group. Differences in detectability between the non-coffee season and the coffee season can be expected since these broadly coincide with the wet and dry seasons, respectively, but since we modelled the datasets separately, we

assumed constant detection probability within datasets and seasons. This constant detection probability reflects the within-season homogeneity in terms of both coffee production and climate conditions. In the southwest of Ethiopia, the period of coffee harvest (represented by the coffee season dataset) happens during *Bega*, the dry season spanning from October to January/February (Moat et al. 2017). The non-coffee dataset overlaps with *Kiremt*, the main wet season which starts in June and lasts until the end of September (Moat et al. 2017). Further, the decision to split the 6-month dataset into two seasonal datasets (i.e., coffee season and non-coffee season) was motivated by results of exploratory data analysis on the 6-month dataset which indicated model convergence issues due to the high number of estimated parameters when coffee was introduced in both detection and occupancy components of the models.

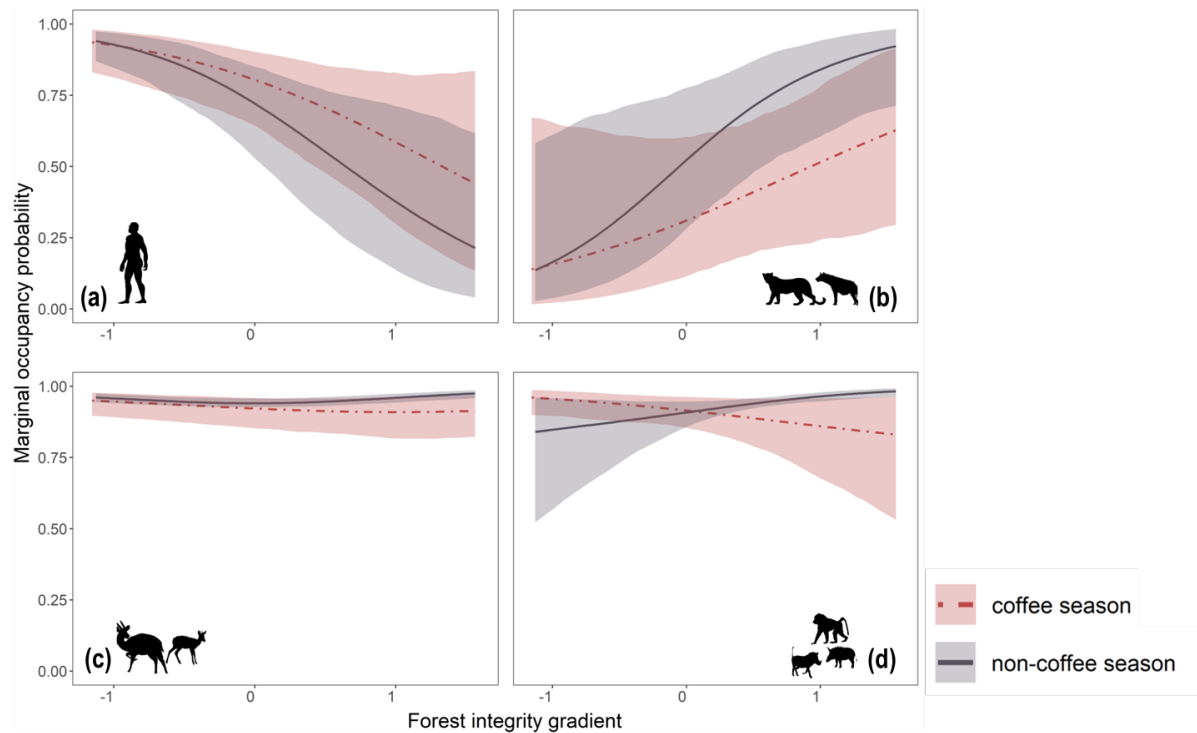
The occupancy model for both seasons was fitted with the first axis of the PCA only, scaled to improve model performance. We did not include the second axis of the PCA as a covariate due to the small size of our dataset. Likewise, we did not consider high-order interactions (i.e., interactions of three or more species groups at the same time), since these typically increase model complexity and can be difficult to interpret and to derive with small sample sizes, such as ours. We applied a penalty term ( $\lambda$ ) for the likelihood (Clipp et al. 2021) in order to solve boundary estimation problems likely driven by the combination of high naïve occupancy of prey and crop-raiders and our small sampling size ( $n=30$  sites for both seasons). To determine the best penalty term for each season we followed Clipp et al. (2021) approach and used 5-fold cross-validation ( $k=5$ ) and allowed  $\lambda$  to obtain the values  $\{0.01, 0.02, 0.04, 0.08, 0.16, 0.32, 0.64, 1.28, 2.56, 5.12\}$ . We ran 100 iterations of this process and selected the penalty value with the highest frequency ( $\lambda = 1.28$ , for both seasons). Further, we applied 200 bootstraps to generate the variance-covariance matrix and to calculate the 95% confidence intervals of the parameters. Model validation was made through visual inspection of the 24 plots of pairwise-interactions, since, to date no other method exists to explicitly assess model validation within this modelling framework. We used the function *occuMulti* (Rota et al. 2016) in package *unmarked* (version 1.2.3, Fiske and Chandler 2011), implemented in R (version 4.1.2; R Core Team, 2021).

### 3. Results

The dataset used for analysis included 15, 183, 253 and 110 detections of “predators”, “prey”, “crop-raiders” and “humans” during the non-coffee season and 14, 170, 168 and 126 detections during the coffee harvest season, respectively. “Predators” were detected at 11 and 7 sites (naïve occupancy 37% and 23%), “prey” at 30 and 29 sites (naïve occupancy 100% and 97%); humans in 20 and 23 sites (naïve occupancy 67% and 77%), during non-

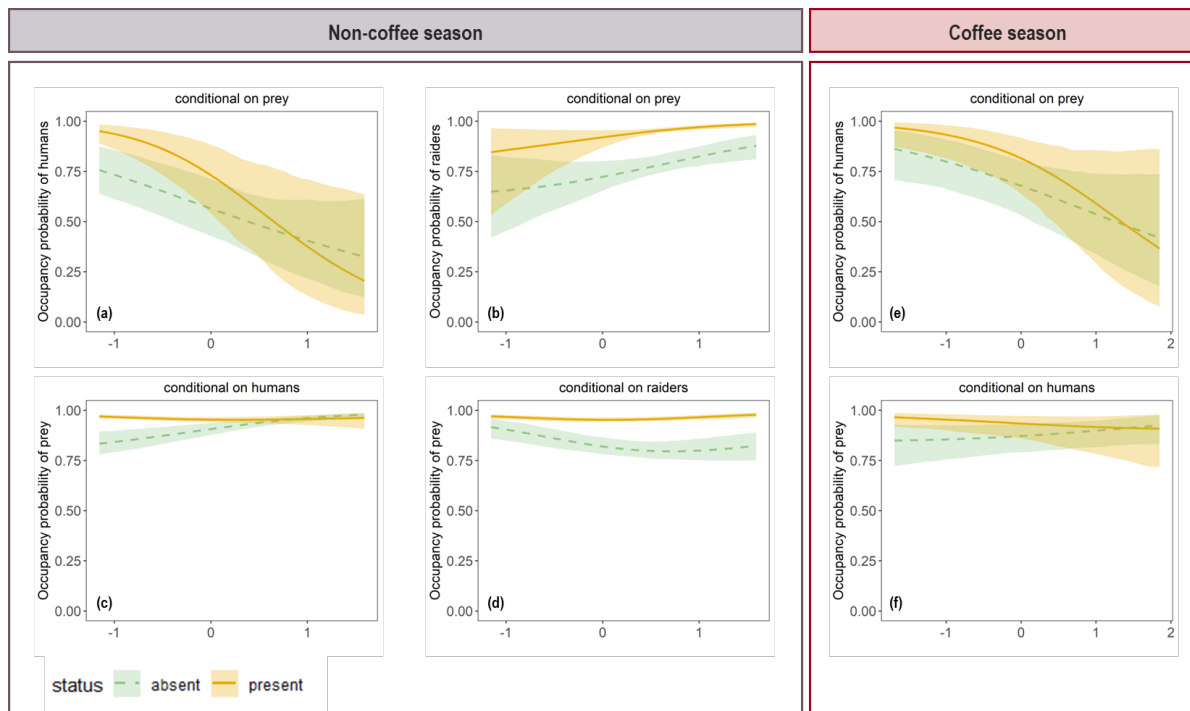
coffee and coffee seasons, respectively. Raiders were detected in 28 sites (naïve occupancy 93%) in both seasons (see supplementary Table A2 for an overview of the datasets).

During the non-coffee season, marginal occupancy probability of humans decreased consistently along the increasing gradient of forest cover (i.e., PCA1, Fig. 3a – grey shading, Table A4). Humans were more likely to be present in sites with more fragmented forest (higher amount of edge and low amount of forest cover) and closer to the forest edge and less likely in sites located towards the forest interior and with high forest cover and low amount of edge. In turn, the marginal occupancy of predators increased along the forest gradient, with predators being more likely to be detected in sites located towards the forest interior and with higher amount of forest cover and less amount of edge (Fig. 3b – grey shading, Table A4). Marginal occupancy probability of prey and raiders was fairly high along the forest integrity gradient (Fig. 3c and 3d - grey shading). We found evidence of interspecific co-occurrence for two pairs of species groups: “humans-prey” and “prey-raiders” and evidence that the co-occurrence of these species-groups varied as a function of the forest gradient. Sites with less forest integrity were more likely to be used by prey if humans were present than if humans were absent (and vice-versa, i.e., humans were more likely to use sites where prey were present than sites where prey were absent) (Fig. 4a, 4c). Likewise, raiders and prey were more likely to co-occur in the presence of each other than in each other’s absence, along the forest integrity gradient (Fig. 4b, 4d, Table A5). We also found minimal evidence that the probability of co-occurrence of “predators-prey” and “predators-raiders” species pairs varied with the forest gradient, with higher likelihood of co-occurrence in areas of high forest integrity (Table A5, Fig. A1). However, despite the statistical support shown by small p-values (Table A5) we consider this evidence as “minimal” only, after visual inspection of the plots which denote substantial overlap in confidence intervals (Fig. A1). Prey and crop-raiders had similar and the highest detection probability estimates (Table A3).



**Figure 3.** Marginal occupancy probabilities for each species group (a) humans, (b) top-predators, (c) prey and (d) crop-raiders, and for each season. Results for the non-coffee season were truncated to the minimum and maximum values of coffee season to improve readability of the plot. Forest integrity gradient: negative values represent areas of fragmented forest, with low amount of forest cover and close to the forest edge, whereas positive values represent areas of high forest cover, low fragmentation and towards the forest interior.

During the coffee-harvest season, marginal occupancy probabilities of humans decreased consistently along the forest gradient, being higher in sites with fragmented forest (high edge amount), closer to the forest edge, and with low forest cover, and decreasing towards areas with high forest cover and towards the forest interior (Fig. 3a – red shading). The marginal occupancy of the remaining species-groups (i.e., predators, prey and crop-raiders) was not driven by the forest gradient (Fig. 3b, c, d – red shading, Table A6). We found evidence of interspecific co-occurrence for “humans-prey” species-pair, with variation along the environmental gradient (Figure 4 e-f) and for “humans-raiders” species-pair (Fig. A2, Table A7). Prey was less likely to occur in sites where humans were absent, than in sites where humans were present (Fig. 4f). Further, the probability that prey and humans co-occurred varied as a function of the gradient of forest cover, such that humans and prey were more likely to co-occur at sites where forest is fragmented, closer to the edge and with low forest cover (Fig. 4e-f, Table A7). Estimates of detection probability were higher for crop-raiders and prey (Table A3).



**Figure 4.** Occupancy probabilities of “humans-prey” during coffee and non-coffee seasons and of “prey-raiders” during the non-coffee season. Shaded areas around the solid and dashed lines represent 95% confidence intervals.

#### 4. Discussion

Promoting the coexistence of wildlife and humans is a challenge facing many biodiversity rich and high-populated areas in tropical regions. Understanding how species interact with each other and the influence of humans in these interactions, can help to inform the development of management strategies that aim to promote coexistence. The effects of human influence on wildlife are often examined using proxies (such as housing density or proximity to settlements (Cavada et al. 2019; Villaseñor et al. 2017) and the use of more explicit indicators of human activity are often overlooked. Here, we use a multispecies occupancy model (Rota et. al. 2016) that accounts for imperfect detection, to explicitly examine fine-scale co-occurrence between humans and different species assemblages along an environmental gradient of forest fragmentation/cover, where humans represent one more species in the ecological system. Our results show (i) signs of co-occurrence between humans and prey during both seasons and between humans and raiders during the coffee season; (ii) signs of co-occurrence between prey and raiders during both seasons; (iii) no evidence of positive or negative co-occurrence

between humans and top-predators; and (iv) no clear evidence of positive or negative co-occurrence between top-predator and prey and top-predators and crop-raiders in both seasons.

During both non-coffee and coffee seasons marginal occupancies of humans (i.e., the probability of people being present regardless of the presence of other species) were associated with the environmental gradient of forest integrity. Marginal occupancy probability of humans was higher at sites with low amount of forest cover and closer to the forest edge, decreasing towards sites located in interior forest, with high forest cover and low amount of edge. This indicates that humans seem to favor the use of more fragmented forest sites and closer to the forest edge when compared to less fragmented and forest interior locations, across seasons. This is a pattern of spatial use that is in line with the results of Beche et al (2022), which show that human-lead forest disturbance in this region of Ethiopia is stronger at the edges and declines with increasing distances from agricultural fields. Further, during the non-coffee season the gradient of forest cover was a strong predictor of the marginal occupancies of top-predators, with high marginal occupancy probabilities found for interior sites with high forest cover and small amount of edge. In contrast, marginal occupancy of prey and raiders was fairly high along the forest gradient, during both seasons, indicating that both species groups are rather common in the surveyed *kebeles* using forest sites along entire gradient.

Contrary to our initial expectation of negative responses by all species groups to human presence (our “human as super-predators” hypothesis), our results show that prey and crop-raiders were more likely to be present in sites also occupied by humans than in sites where humans were absent, during the coffee season. Crop-raiders showed a consistent pattern of use along the environmental gradient, whereas prey showed an increased likelihood of spatiotemporal overlap with humans at sites with fragmented forest and/or located at the edge, only (Fig. 4c – left hand side of x-axis). During the non-coffee season, similar patterns of positive interactions with humans (i.e., overlap in time and space) were found for prey (Fig. 4f). Taken together, these findings lead us to exclude, for both seasons, our null hypothesis of “humans as super-predators” (Darimont et al. 2015).

Recent studies indicate that some mammal species might use humans as shields against predators or competitors. For instance, Atickem et al. (2014) found that mountain nyala (*Tragelaphus buxtoni*) in Ethiopia approached human settlements during the night to shield against predation by spotted hyenas (*Crocuta Crocuta*), whereas Gámez and Harris (2021) show that in urban parks in Chicago (United States) human activity was shielding skunks (*Mephitis mephitis*) against coyotes (*Canis latrans*). The positive co-occurrence that were found between prey and humans during both seasons and raiders and humans during the coffee season indicate that a similar

dynamic might be under way in our system, especially regarding the relationships between prey and humans. However, because we found no evidence of co-occurrence between humans and predators, we only have partial - and not full support - for our alternative hypothesis (i.e., “humans as shields”).

We contend that there are three alternative explanations for our findings. These relate with *(i)* loss of top-control function by predators; *(ii)* species habituation to humans; and *(iii)* limitations in the datasets. First, research is showing that habitat loss and fragmentation is affecting the ability of top predators to persist in the landscape and to exert their ecological role over prey and unsubordinated species (Ripple et al. 2014). Ango et al. (2020) show that forests in the region have been progressively fragmented and converted into farmlands over the past few decades, especially at areas of high altitude. The lack of signs of co-occurrence between top predators and prey and top predators and raiders during the coffee season and the minimal signs found during the non-coffee season may indicate that top predators (such as the leopard) may have been losing, indeed, their ecological function of regulating prey in managed forests, mostly as a result of habitat fragmentation and changes in forest cover.

Second, despite the lack of available official data on bushmeat hunting in the region, knowledge from informal conversations with local farmers indicates that, in general, the pressure resulting from bushmeat hunting is moderate to low in the study area, with some species (such as buffalo, bushduiker and bushbuck) occasionally hunted as bushmeat (co-author, pers. comm.), suggesting that humans do not seem to exert a top-predator force (through direct predation), in the system. It might also explain the very high marginal occupancy of both prey and raiders throughout the forest, which were present in more than 93% of the surveyed sites. In addition, some species, especially crop-raiders, might have become habituated to humans. Focus group discussions with local farmers suggest that crop-raiders (such as baboons) are not afraid of children and women (co-author, pers. comm). In our study area, farmers have few options available to protect against crop-raiding, apart from guarding the fields and chasing animals away (Alemayehu and Tekalign, 2022). Thus, the lack of strong hunting pressure plus the likely habituation to humans might contribute to explaining the positive association registered between humans and prey during both seasons and between humans and raiders during the coffee-season.

A final consideration refers to potential limitations in the datasets, including *(i)* the potential autocorrelation in detections; *(ii)* the relatively small number of survey sites within each season; and *(iii)* the low detection probability of top-predators. We recognize that for species with relatively large home ranges, such as leopards and hyenas, an average distance between cameras of approximately 500 m might be suboptimal. However, the



data used in our study was derived from a survey aiming at assessing the entire medium-large mammal community including species with smaller home ranges (such as hyraxes and porcupines) and a balance between different species home-ranges and logistical constraints had to be made. For this reason, we interpret presence as “habitat use” rather than to “true occupancy”, following (Marescot et al. 2020). We also recognize that a sample size of 30 is relatively small for a method that is relatively data demanding, such as the Rota et al (2016) model. However, we were able to detect signs of co-occurrence between some species groups even with such small sampling sizes, by using the penalization method developed by Clipp and colleagues (2021). Finally, our results show that the detection probability of predators was fairly low (11% and 16% of probability of detecting a top-predator given that it was present, for non-coffee and coffee harvest seasons respectively), which might have prevented the detection of co-occurrence between top-predators and other species groups. To further investigate this, we ran 200 simulations to estimate the obtained statistical power with varying number of sites for different levels of detection probability of predators and prey. Our findings show that if the detection probability of predators was higher, according to our simulations we would be able to detect pairwise relationship between top-predators and prey (see Appendix B).

Understanding how, where and when species co-occur and interact with each other and with humans, and the outcome of those interactions for all the species involved is key to better understand how co-existence between humans and wildlife can be promoted and facilitated. Here, by examining co-occurrence patterns at fine spatial scales we contributed in that direction. By considering humans as one more species in the ecological system we were able to identify signals of co-occurrence between humans and prey, indicating the potential presence of a human-shield effect in managed forests.

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## 7. Competing Interests

The authors declare that they have no relevant competing financial or non-financial interests to disclose.

## 8. Author Contributions Statement

*PR, ID and OG* conceived the idea. *OG* and *PR* designed the methodology. *PR* and *OG* analysed the data; *PR* led the writing of the original draft and all authors contributed critically to the drafts through review and editing. All authors gave final approval for publication.

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## Supporting Information

### Appendix A

**Table A1:** Principal component analysis loadings and variance explained by the first two component (PCA1 and PCA2). Bold values represent the highest loadings on both sides of the axes. The first axis summarizes a joint gradient of forest cover and fragmentation. Only the first axis was used in the modelling framework.

<b>Variable</b>	<b>PCA1</b>	<b>PCA2</b>
Mean patch area	<b>0.492</b>	-0.319
Proportion forest cover	<b>0.471</b>	-0.345
Total amount edge	<b>-0.469</b>	-0.028
Elevation	0.311	<b>0.879</b>
Distance to edge	<b>0.468</b>	0.069
<b>% variance explained</b>	<b>72.8</b>	<b>15.9</b>

**Table A2.** Overview of sampling effort and naïve occupancy for each species group during the non-coffee and coffee seasons.

	<b>Non-coffee season</b>			<b>Coffee harvest season</b>		
Survey period (yr. 2016)	end June – end September			October – end December		
Total number of sites	30			30		
Total number of weeks	14			13		
Species group	Total n. detections	N. sites with detections	Naïve occupancy	Total n. detections	N. sites with detections	Naïve occupancy
top-predators	15	11	37%	14	7	23%
prey	183	30	100%	170	29	97%
crop-raiders	253	28	93%	168	28	93%
humans	110	20	67%	126	23	77%



**Table A3.** Detection probability estimates and corresponding [confidence intervals] for each species group and within each season.

Species group	Detection estimates	
	Non-coffee season	Coffee harvest season
top-predators	0.108 [0.102 – 0.113]	0.164 [0.142 – 0.189]
prey	0.514 [0.487 – 0.540]	0.601 [0.579 – 0.622]
crop-raiders	0.762 [0.749 – 0.774]	0.603 [0.587– 0.618]
humans	0.455 [0.418 – 0.492]	0.542 [0.520 – 0.564]

**Table A4.** Marginal occupancy probability estimates for each species group during the non-coffee season.

		Estimate	Standard Error	p
predators	Intercept	-0.3042	0.178	8.68e <sup>-02</sup>
predators	sPCA1	0.4403	0.134	1.01e <sup>-03</sup>
humans	Intercept	0.0943	0.152	0.534
humans	sPCA1	-0.6759	0.102	4.08e <sup>-11</sup>
prey	Intercept	1.0265	0.079	2.18e <sup>-38</sup>
prey	sPCA1	-0.0740	0.075	0.326
raiders	Intercept	0.6763	0.121	2.53e <sup>-08</sup>
raiders	sPCA1	0.3962	0.153	9.47e <sup>-03</sup>

**Table A5.** Conditional occupancy probability estimates for species pairwise interactions during the non-coffee season. Values highlighted in bolt represent significant relationships.

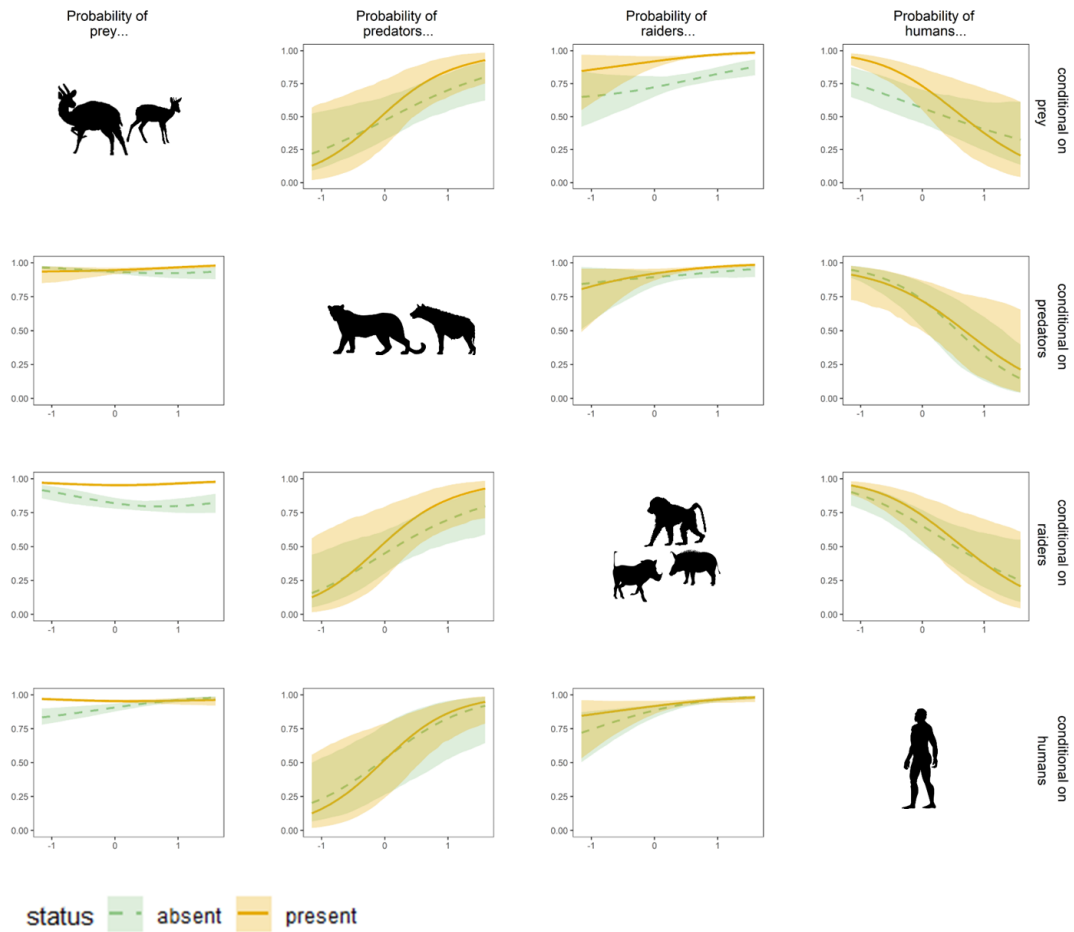
		Estimate	Standard Error	p
predators:humans	(Intercept)	-0.0492	0.2733	0.857
predators:humans	sPCA1	0.3518	0.2908	0.226
predators:prey	(Intercept)	0.1629	0.2112	0.440
<b>predators:prey</b>	<b>sPCA1</b>	<b>0.5906</b>	<b>0.1602</b>	<b>2.28e<sup>-04</sup></b>
predators:raiders	(Intercept)	0.3019	0.2437	0.215
<b>predators:raiders</b>	<b>sPCA1</b>	<b>0.4343</b>	<b>0.1942</b>	<b>2.53e<sup>-02</sup></b>
<b>humans:prey</b>	<b>(Intercept)</b>	<b>0.6901</b>	<b>0.1740</b>	<b>7.28e<sup>-05</sup></b>
<b>humans:prey</b>	<b>sPCA1</b>	<b>-0.8530</b>	<b>0.1409</b>	<b>1.40e<sup>-09</sup></b>
humans:raiders	(Intercept)	0.2643	0.2127	0.214
humans:raiders	sPCA1	-0.2858	0.1985	0.150
<b>prey:raiders</b>	<b>(Intercept)</b>	<b>1.4248</b>	<b>0.1517</b>	<b>5.94e<sup>-21</sup></b>
<b>prey:raiders</b>	<b>sPCA1</b>	<b>0.4116</b>	<b>0.1606</b>	<b>1.04e<sup>-02</sup></b>

**Table A6.** Marginal occupancy probability estimates for each species group during the coffee season.

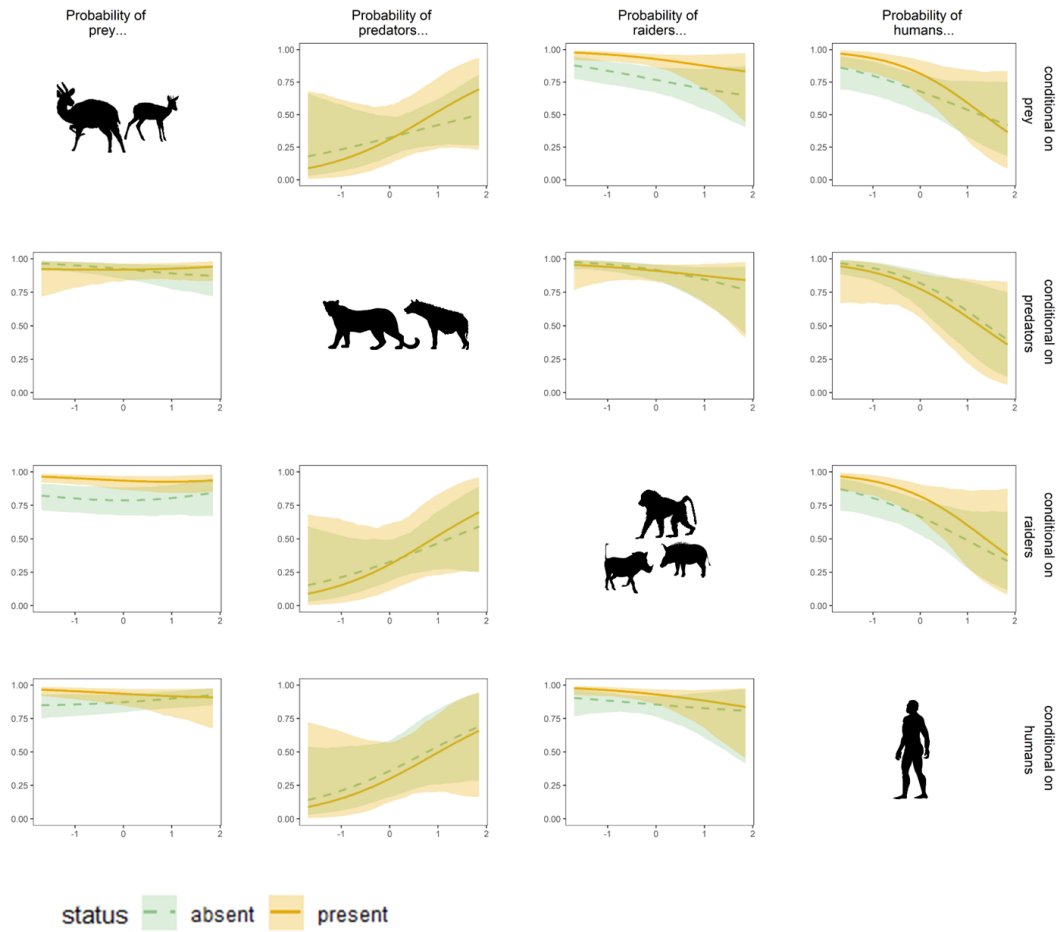
		<b>Estimate</b>	<b>Standard Error</b>	<b>p</b>
predators	Intercept	-0.5320	0.186	4.29e <sup>-03</sup>
predators	sPCA1	0.1736	0.182	0.340
humans	Intercept	0.2994	0.210	0.154
humans	sPCA1	-0.3826	0.147	9.16e <sup>-03</sup>
prey	Intercept	0.9273	0.187	7.07e <sup>-07</sup>
prey	sPCA1	0.2384	0.149	0.110
raiders	Intercept	0.7505	0.182	3.58e <sup>-05</sup>
raiders	sPCA1	-0.2299	0.219	0.293

**Table A7.** Conditional occupancy probability estimates for species group pairwise interactions during the coffee season. Values highlighted in bolt represent significant relationships.

		Estimate	Standard Error	p
predators:humans	Intercept	-0.2639	0.284	0.352
predators:humans	sPCA1	0.0633	0.395	0.873
predators:prey	(Intercept	-0.0223	0.233	0.923
predators:prey	sPCA1	0.4198	0.239	0.079
predators:raiders	Intercept	-0.0394	0.227	0.863
predators:raiders	sPCA1	0.2411	0.207	0.245
<b>humans:prey</b>	<b>Intercept</b>	<b>0.6183</b>	<b>0.257</b>	<b>0.016</b>
<b>humans:prey</b>	<b>sPCA1</b>	<b>-0.4614</b>	<b>0.163</b>	<b>4.74e<sup>-03</sup></b>
<b>humans:raiders</b>	<b>Intercept</b>	<b>0.715</b>	<b>0.308</b>	<b>0.020</b>
humans:raiders	sPCA1	-0.2609	0.193	0.177
<b>prey:raiders</b>	<b>Intercept</b>	<b>1.258</b>	<b>0.249</b>	<b>4.44e<sup>-07</sup></b>
prey:raiders	sPCA1	-0.1779	0.193	0.358



**Figure A1.** Occupancy probabilities of prey, predators, raiders and humans conditional on the presence (yellow solid line) or absence (dashed green line) of each other species groups, during the non-coffee season. The occupancy probability of each species in each column is conditional on the presence or absence of each species group in each row. Shaded areas around the solid and dashed lines represent 95% confidence intervals.



**Figure A2.** Occupancy probabilities of prey, predators, raiders and humans conditional on the presence (yellow solid line) or absence (dashed green line) of each other species groups, during the coffee season. The occupancy probability of each species in each column is conditional on the presence or absence of each species groups in each row. Shaded areas around the solid and dashed lines represent 95% confidence intervals.

## Appendix B

### Simulate data and fit a 2-species static (aka single-season) occupancy model à la Rota et al. (2016)

We consider a two-species static occupancy model. We simulate data from this model, and fit two models, with and without interaction, to these data using Unmarked. See also an old post [here](#). We repeat these steps a large number of times, and estimate statistical power, i.e., the probability of detecting an interaction when there is an interaction, by computing the average number of times the AIC of model with interaction is lower than the AIC of model without interaction over the total number of simulations.

Load the packages we need.

```
library(mipfp)
library(unmarked)
library(tidyverse)
theme_set(theme_light())
```

For reproducibility, we set the seed:

```
set.seed(2021)
```

Let's consider a scenario in which species 2 is a prey of species 1 a predator. To specify this scenario, we will work out the conditional probabilities with a strong signal:

- $\Pr(z_2 = 1|z_1 = 0) = 0.7$ , prey is present with high probability when predator is absent;
- $\Pr(z_2 = 1|z_1 = 1) = 0.2$ , prey avoids predator when predator is present;
- $\Pr(z_1 = 1|z_2 = 1) = 0.7$ , predator likes when prey is present;
- $\Pr(z_1 = 1|z_2 = 0) = 0.4$ , predator is rare when prey is absent.

Now we need to go back to the probabilities of occupancy. Let  $x = \psi_{01}$ ,  $y = \psi_{10}$  and  $z = \psi_{11}$  hence  $1 - x - y - z = \psi_{00}$ , then we have a system of 3 equations with 3 unknowns:

$$0.8 = x/(x + 1 - x - y - z)$$

$$0.1 = z/(z + y)$$

$$0.4 = y/(y + 1 - x - y - z)$$

which can be solved with the [Mathematica online solver](#).

```
(psi01 <- 14/25)
## [1] 0.56
(psi10 <- 4/25)
## [1] 0.16
(psi11 <- 1/25)
## [1] 0.04
```



```
(psi00 <- 1 - (psi01 + psi10 + psi11))  
## [1] 0.24
```

Obtain the marginal occupancy probabilities.

```
psiS1 <- psi10 + psi11  
psiS2 <- psi01 + psi11
```

Simulate data from a multivariate Bernoulli, calculate odds ratios.

```
or <- matrix(c(1, (psiS1*(1-psiS2))/(psiS2*(1-psiS1)),  
              (psiS2*(1-psiS1))/(psiS1*(1-psiS2)), 1),  
            nrow = 2,  
            ncol = 2,  
            byrow = TRUE)  
rownames(or) <- colnames(or) <- c("sp1", "sp2")
```

Get marginal probabilities.

```
marg.probs <- c(psiS1, psiS2)  
marg.probs  
## [1] 0.2 0.6
```

Estimate joint probability.

```
p.joint <- ObtainMultBinaryDist(odds = or, marg.probs = marg.probs)
```

Write function to simulate, fit and test.

```
simul <- function(p_predator, n_sites, n_visits, p.joint){  
  # nb of species  
  S <- 2  
  
  # generate $N$ random samples from bivariate Bernoulli (2 species) w/ relevant parameters  
  z <- RMultBinary(n = n_sites, mult.bin.dist = p.joint)$binary.sequences  
  
  # fix the detection probability for each species:  
  ps <- c(p_predator, 0.8) # predator has low  
  
  # generate detections and non-detections for each species  
  y <- list()  
  for (i in 1:S){  
    y[[i]] <- matrix(NA, n_sites, n_visits)  
    for (j in 1:n_sites){  
      for (k in 1:n_visits){  
        y[[i]][j,k] <- rbinom(1, 1, z[j,i]*ps[i])  
      }  
    }  
  }  
}
```

```

    }
  }
}
names(y) <- c('sp1','sp2')

# format data
data <- unmarkedFrameOccuMulti(y=y)

# specify effects
occFormulas_wi <- c('~1','~1','~1') # w/ interactions
occFormulas_wo <- c('~1','~1','~0') # wo interactions
detFormulas <- c('~1','~1')

# fit models
fit_wi <- occuMulti(detFormulas,occFormulas_wi,data)
fit_wo <- occuMulti(detFormulas,occFormulas_wo,data)

# does model with interaction fit data better (test = 1)
# than model without interaction (test = 0)?
test <- ifelse(fit_wi@AIC < fit_wo@AIC, 1, 0)
test
}

```

Simulate.

```

gridp <- seq(0.1, 0.5, by = 0.1)
nsim <- 200
ind <- 1
res <- matrix(NA, nrow = nsim, ncol = length(gridp))
for (i in gridp){
  for (j in 1:nsim){
    res[j,ind] <- simul(i, 30, 15, p.joint)
  }
  ind <- ind + 1
}
power <- apply(res, 2, mean) # compute stat power
power
## [1] 0.580 0.595 0.755 0.700 0.670

```

Idem with twice as many sites.

```

ind <- 1
res <- matrix(NA, nrow = nsim, ncol = length(gridp))
for (i in gridp){
  for (j in 1:nsim){
    res[j,ind] <- simul(i, 60, 15, p.joint)
  }
  ind <- ind + 1
}
power2 <- apply(res, 2, mean) # compute stat power
power2

```

```
## [1] 0.755 0.870 0.875 0.885 0.880
```

Visualise.

```
df <- tibble(p_pred = c(gridp, gridp),
             power = c(power, power2),
             scenario = c(rep("30 sites", length(gridp)),
                          rep("60 sites", length(gridp))))
df %>%
  ggplot() +
  aes(x = p_pred, y = power, group = scenario, color = scenario) +
  geom_line(lwd = 1.2) +
  labs(x = "detection probability of predator",
       y = "statistical power",
       color = NULL) +
  ylim(0,1)
```

