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Research article

Drivers of human-megaherbivore interactions in the Eastern and Western Ghats of southern India

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ABSTRACT

The global effort to protect megaherbivore populations is largely dependent on how human-wildlife conflict is identified, prioritized, and remedied. We examined the socio-ecological and landscape-scale factors determining spatial patterns of human-megaherbivore (Asian elephant *Elephas maximus* and gaur *Bos gaurus*) interactions across sixteen Forest Divisions in Tamil Nadu, India. Using a systematic grid-based design, we conducted questionnaire-based surveys of 1460 households at the human-wildlife interface adjacent to Protected Areas, Reserve Forest and Fringe Areas. We specifically collected information on elephant and gaur conflict incidents (*e.g.*, human death/injuries, property damage, and crop-raiding), cropland type, extent of crop area and area lost to crop-raiding, from each household. We found that human-elephant conflict increased with percentage of crop cover, diversity of major and minor crops grown, proximity to water source, flat terrain, and lower rates of precipitation. Human-gaur conflict was greatest with a high diversity of major crops, proximity to water source, moderate precipitation, and more undulating terrain. We identified ca. 7900 km^2 hotspot area of contiguous high-intensity elephant conflict. For gaur, we identified high-frequency conflict hotspot areas covering ca. 625 km^2, which were patchily distributed, highly localised, and attributed mostly to the recent changing land-use patterns. Our findings will help policymakers and park managers in developing landscape-scale human-wildlife conflict mitigation plans in the identified conflict hotspots.

1. Introduction

Megaherbivores have a far-reaching impact on the functioning and balancing of the ecosystem. They are important pollinators and seed dispersers that support ecosystem processes and are proficient in maintaining the forest structure (Danell et al., 2003; Campos-Arceiz and Blake, 2011; Malhi et al., 2016). Among the megaherbivores, the elephant is a critical ‘ecosystem engineer’ that maintains the structure and heterogeneity of the landscape (Campos-Arceiz and Blake, 2011). Their ability to consume and disperse large piles of different varieties of seeds makes them efficient seed dispersers (Schupp et al., 2010; Corlett, 2017; Tan et al., 2021) or rather ‘mega-gardeners of the forest’ (Campos-Arceiz and Blake, 2011). Additionally, they are ‘habitat facilitators’ for various large and small mammal species; as they browse the canopy, the openness of the habitat will be retained with improved grass productivity that provides a safe refuge for the prey species, thereby decreasing their predation risk (Coverdale et al., 2016). Ungulates like gaur have a crucial role in maintaining the grasslands, controlling plant growth and density, and are the major prey for the large carnivores such as tigers (Danell et al., 2003; Asokkumar et al., 2010). Withal, the populations of large mammalian species have experienced a dramatic decline due to habitat alteration, poaching, and other anthropogenic causes, globally (Ceballos and Ehrlich, 2002; Foley et al., 2005). In India, the increasing and related threats of habitat loss and fragmentation (Choudhury, 2004; Kumar et al., 2004) present a grim challenge to maintaining already diminishing migratory and dispersal corridors for wide-ranging species (Tilman et al., 2017). This is noteworthy because India and other tropical countries are considered as the last refuges of many large mammals (Ogutu et al., 2005; Gubbi, 2012). Under the pressures of growing human populations, increasing conflict between

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humans and large terrestrial mammals has emerged as a major modern threat to coexistence (Gubbi, 2012; Okello et al., 2014). However, large mammals are highly sensitive to the effect of habitat degradation (Gubbi, 2012; Tilman et al., 2017) outside Protected Areas (PAs), particularly towards their fringes. Across landscapes where human-large mammal conflict is common, a better understanding of how dynamic land-use changes at these interfaces are critical to large mammal conservation, as is an integrated management approach both inside and outside PAs.

Human-megaherbivore conflict occurs most commonly among the forested landscapes or in their vicinity; it can often be attributed to the changes in local species abundance, rapid shrinkage of natural habitat, and sudden or seasonal food availability inside or on the periphery of the forests (Sukumar, 1989; Ramesh, 1994). Emerging tea and coffee plantations for example, have replaced the natural grasslands in Southern India, which were the crucial ecosystems to mitigating or avoiding human-megaherbivore conflict (Kumar et al., 2004). Elephant and gaur herds are now habituated to open agricultural land (e.g., tea gardens, seasonal crops), where they feed on available lush green crops and grassy patches (Sukumar and Pani, 2016; Indira, 2019). At the southernmost distribution ranges for Asiatic elephant (*Elephas maximus*) and gaur (*Bos gaurus*) in India, the invasion of lantana (*Lantana camara*), wattle *(Acacia* sp.), pine *(Pinus* sp.), and eucalyptus (*Eucalyptus globulus*) into native grasslands and other natural habitat, is reducing natural food availability for these megaherbivores (Ramesh, 1994; Boominathan et al., 2008). Other potential drivers of conflict include seasonal resource variation, whereby the lack of resources during the dry season may force ungulates into agricultural area to compensate for the lower nutritional value of native forest vegetation (Ahrestani et al., 2012). In addition, the habitats of megaherbivores face threats from livestock grazing, wildlife and human competition for water resources, encroachment from woodcutting and the exploitation of bamboo, the collection of minor forest products by local communities, wildfire, and an increase in linear infrastructures, like roads and railways, all of which can displace ungulates and result in more frequent incidents of conflict (Sukumar, 2003; Johnsingh et al., 2010; Ramesh et al., 2012d, 2019; Sukumar and Pani, 2016).

In India, PAs encompass only 22% of elephant habitat, whereas the remaining habitats include highly fragmented forests and agricultural areas (Sukumar, 2006). Large and contiguously forested areas support only 30% of India's elephant populations, whereas the rest are distributed in smaller groups across fragmented landscapes (MoEF, 2010; Naha et al., 2019; Williams et al., 2020). The antagonistic interactions between humans and elephants have increased over the years, causing human fatalities (>400 deaths annually) and extensive crop damage (~330 km^2 every year); ultimately, nearly 500,000 families are affected by crop damage, which leads to approximately 100 elephant deaths each year (MoEF, 2010; Mathur et al., 2015). The situation with gaur populations is similar, and the frequency of human-gaur conflict (HGC) over crop damage is now rapidly rising (Joshi and Madhusudan, 2010; Thomas, 2018). To reduce the number of conflict events involving megaherbivores and enhance their long-term survival, a more focused conservation initiative is required (Johnsingh et al., 2010).

India holds the largest population of the 'Endangered' Asiatic elephant (over 50%) and 'Vulnerable' gaur (over 85%) globally, and very often they share their territories with local communities (Choudhury, 2002; Duckworth et al., 2016). Because of India's high human density even in rural areas, negative human-large mammal interactions are expected to intensify; depletion of food resources, biomass extraction in support of local livelihoods, and habitat degradation caused by the expanding agricultural development and the spread of invasive vegetation, can all facilitate more crop-depredation episodes (Boominathan et al., 2008; Babu et al., 2012). The Western and Eastern Ghats Part of Tamil Nadu (WEGPTN) in southern India are among India's most important elephant and gaur conservation units. This is mostly due to the relatively larger proportion of contiguous forest habitat there, which tend to host relatively higher densities of megaherbivore populations (Sukumar, 1990; Ramesh Kumar, 1994; Daniel et al., 2008; Johnsingh et al., 2010; Ramesh, 2010). However, at present, this landscape has many growing human settlements, accompanied by large cattle herds, which are facilitating the expansion of agriculture and tea/coffee estates within and adjacent to these important forests, including PA buffer zones. (Ramesh Kumar, 1994; Jhala et al., 2010). By better understanding of the landscape and the ecological factors that influence the spatial patterns of human-large mammal conflicts, we can provide better information that is critical in assisting PA managers in their efforts to reduce conflict (Ramesh et al., 2015).

Between 2016 and 2017, the Tamil Nadu Forest Department compensated local communities for 36 elephant-caused and seven gaur-caused human deaths, 2560 crop damages, and 81 household property damages from both the herbivores (Tamil Nadu Forest Department, 2020), although many incidents usually go unreported. The retaliatory killings of these and other large mammals, particularly following crop-raiding events, are among the most serious threats to the conservation of large mammal populations in India (Madhusudan, 2003; Daniel et al., 2008; Gubbi, 2012; Sukumar and Pani, 2016; Ramkumar et al., 2018). Despite several studies on the status, distribution, and habitat utilization of megaherbivores in India and the conflict they cause (Sukumar, 1989; Ramesh Kumar, 1994; Baskaran, 1998; Sankar et al., 2001, 2015; Choudhury, 2004; Ramesh et al., 2012a, 2012b; Goswami et al., 2015; Sukumar and Pani, 2016), knowledge gaps in the critical areas remain as to the ecological drivers of human-megaherbivore conflict in shared human-wildlife interface areas. A potentially useful tool to address conflict is the creation of a large-scale conflict hotspot map that includes important PAs and areas outside PAs, particularly for the WEGPTN. Our goal here was to investigate the effect of socio-ecological and landscape variables on human-megaherbivore conflict patterns at a landscape level with the aim of identifying spatially explicit conflict hotspots for both elephant and gaur. We hypothesised that the availability and types of crops grown in the agricultural land, forest cover, population density, people's livelihood dependence, and village location can be important factors determining human-megaherbivore conflict. We also expect that spatial variation in the availability of water, precipitation, temperature, and landscape features such as slope and elevation play a vital role in driving human-megaherbivore conflict. By understanding the nuances of these spatial variations, we can help policymakers, park managers, and community leadership act more efficiently and effectively to reduce human-megaherbivore conflict risk.

2. Material and methods

2.1. Study area

We conducted our study in 16 forest divisions across the WEGPTN: Kanyakumari Wildlife Sanctuary (WLS), Kalakad-Mundanthurai Tiger Reserve (KMTR), Nellai WLS, Srivilliputhur Grizzled Squirrel WLS, Theni Forest Division (FD), Megamalai WLS, Sathyamangalam Tiger Reserve (STR), Coimbatore FD, Nilgiri FD, Mudumalai Tiger Reserve (MTR), Erode FD, Dharmapuri FD, Kodaikanal WLS, Hosur FD, Cauvery North Wildlife Sanctuary (CNWLS), and Gudalur FD (Fig. 1). Our work was conducted in the Fringe Areas (FAs) of these study sites up to 5 km from forest boundaries. Major forest types in these study areas include evergreen, semi-evergreen, moist mixed deciduous, dry deciduous, dry mixed deciduous, dry thorn, riparian forests, and grasslands (Champion and Seth, 1968). The major crops grown are rice, banana, sugarcane, cotton, groundnut, vegetables, ragi, and pulses (Ramesh Kumar, 1994; Babu et al., 2012; Tamil Nadu Forest Department, 2016). These seasonal crops are important, as they can influence megaherbivore movement outside forested areas, depending on forage available inside the forest (Baskaran et al., 2013). Also, we note that many of our study sites have convoluted and meandering forest boundaries with projections and

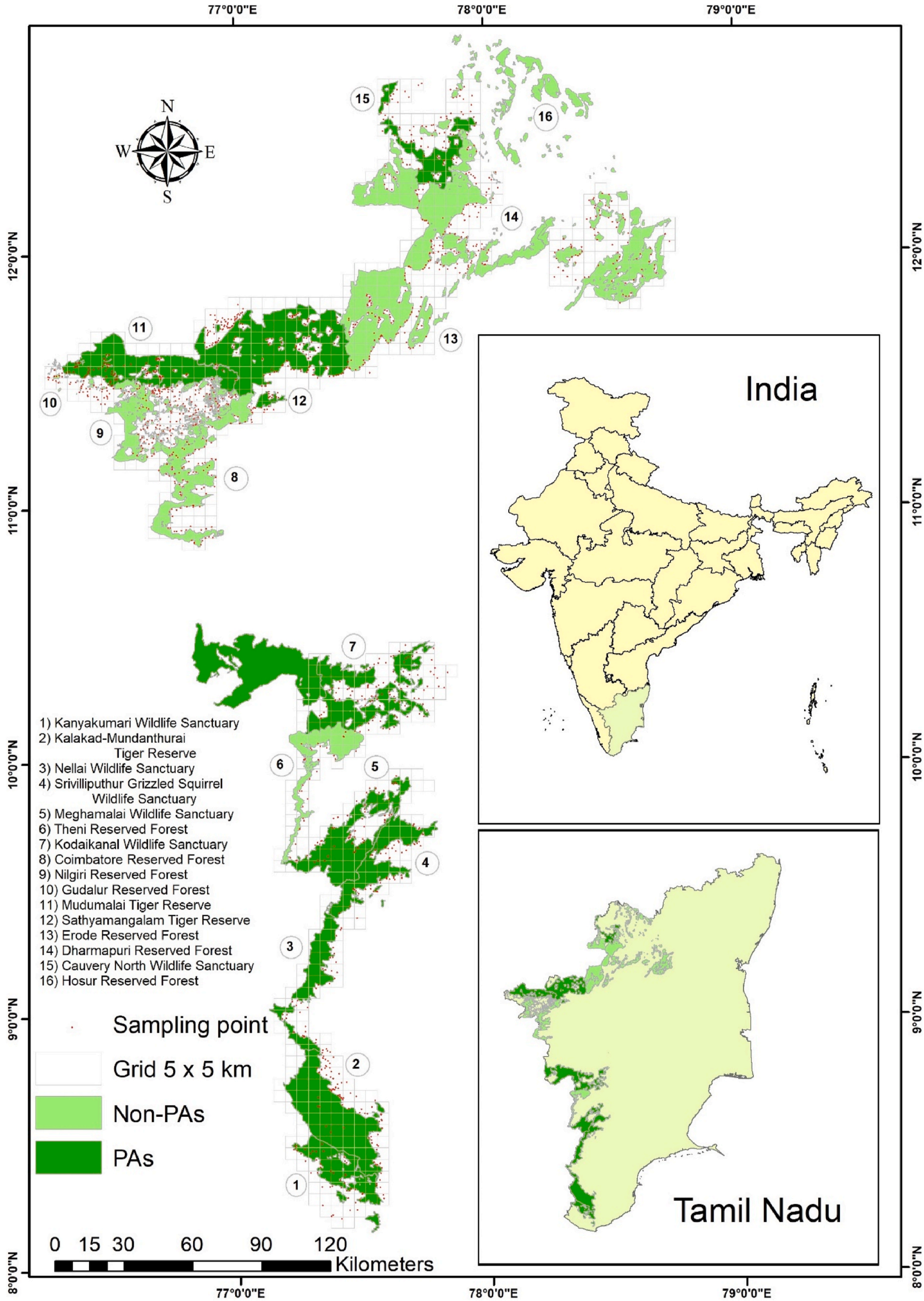

Fig. 1. Study area showing the local questionnaire survey points in the Western and Eastern Ghats part of Tamil Nadu.

indentations adjacent to, and sometimes including, numerous small and large village enclaves within their expanse. Such landscapes at the forest-agriculture-human settlement interface have a high degree of crop-raiding by large herbivores (Babu et al., 2012). For more details on the study area description, refer to Ramesh et al., (2019).

2.2. Semi-structured interviews

Between November 2017 and March 2019, we conducted semi-structured interviews up to 5 km from the boundaries of PAs, Reserve Forests (RFs), and FAs (Fig. 1). We overlaid 5 × 5 km grids (25 km^2) across our entire study area to ensure adequate spatial coverage of households experiencing large mammal conflict. We conducted interviews (Appendix S3) with an average of three independent households per grid and maintained a distance of ca. 0.5–1 km between households, from which proximity to the nearest forest boundary varied. Only interested adult household members with a minimum of five years residency in the area were interviewed (sampled) in the regional language of Tamil. All respondents agreeing to be interviewed represented the views of their entire households. Each questionnaire began with background information which explained the importance and goals of the study. We then noted the age and sex of the respondent's family members and recorded their literacy rate (calculated based on no. of people in a household who read and write Tamil/English), livelihood dependence, the area of cropland they manage, the type of crops grown, and extent (area) to which they have suffered crop loss due to raiding megaherbivores. To help ensure the study accuracy, we also interviewed forest officials and reviewed available media reports to corroborate areas suffering from more conflicts. This includes reviewing compensation data on human-megaherbivore conflict, such as crop damage and human injury/fatalities, which is provided for each forest division by the Tamil Nadu Forest Department. Unfortunately, we found that most of these data are not properly maintained, and that most ground-level conflict incidences are not reported. In addition, we also found that most villagers have little incentive in reporting economic losses to the Forest Department due to the severe delay in processing their compensation claims.

2.3. Predictor variables

We overlaid 1 km^2 subsampling grids across our study area using ArcMap 10.3 (ESRI, 2014). We then reclassified land cover layers from 2006 to 2016 (AWIFS LULC data, Bhuvan, 2017) to 11 designations, including: "built-up", cropland, fallow, plantation, evergreen forest, deciduous forest, degraded/scrub forest, littoral swamp, grassland, wasteland, and water bodies. We considered land as having "natural forest cover" if it included evergreen forest, deciduous forest, and degraded/scrub forest, collectively. All spatial variables we incorporated were assigned to each of the households sampled (interviewed) at a resolution of 1 km^2. We then calculated the percentage of forest cover, and the percentage of crop cover, in each subsampled grid using the tabulate area tool in ArcMap 10.3.

Before assessing differences, we calculated the percentage of forest cover and crop cover separately for both the 2006 and 2016 layers. This allowed us to measure natural forest cover loss and gain, as well as crop loss and gain, by calculating the difference in area of extent of both between 2006 and 2016 layers at a 56 m spatial resolution using a 1 km^2 grid (AWIFS LULC data, Bhuvan, 2017) in ArcMap 10.3. Later, these variables were assigned to household sampling points in the grid. We also gathered information on key spatial variables such as slope, elevation, annual mean precipitation, temperature from WorldClim (Hijmans et al., 2005), and human population density (CIESIN, 2016), at 1 km^2 spatial resolution, and then extracted for each sampling point. We then measured the distance of each household to natural forest cover, nearest water, nearest road, nearest forest boundary of protected and mixed-use areas including Tiger Reserves, Sanctuaries, and RFs using the Euclidean distance tool in ArcMap 10.3. We evaluated the degree of forest dependency by assigning higher scores to households dependent on more categories of forest use, including non-timber forest products (NTFPs), firewood collection, livestock grazing, and miscellaneous activities that ranged from a low of (1) to a high (4). Villages inside PAs (e.g., Tiger Reserves, National Parks) were assigned a "3", those inside RFs a "2", and those located in FAs a "1". For each village, we assumed that higher scores represented greater exposure to HCC, *i.e.*, scores likely reflected a higher abundance or occupancy of megaherbivores in these habitats. Because some farmers grow multiple crops in their farmlands, and this can lead to differential crop loss or loss of crops in varying proportions, we considered households as having "diverse crop types" (*i.e.*, the number of major (primary) crops grown per household) if ≥ 1 acre of each crop was grown per household, and those crops constituted more than 10% of the total landholding (agricultural area) per a household. Any crops not meeting these criteria were considered minor or secondary crops.

2.4. Data analysis

We compared the overall number of conflicts at the household level for each megaherbivore species, different management regimes (land classification), and for different time periods (*i.e.*, morning, afternoon, evening, and night). To identify megaherbivores conflict hotspots, we considered the presence or absence of conflict from each megaherbivore species as the response variable at the household scale. Using a binomial Generalized Linear Model (GLM), we examined the influence of the following potential predictor variables: natural forest cover, natural forest cover change (loss and gain), crop cover type, crop cover change (loss and gain), number of major crops grown, number of minor crops grown, distance to nearest road, village location, human population density, annual mean temperature, annual mean precipitation, distance to nearest forest boundary, distance to nearest natural forest cover, forest dependence, elevation, nearest distance to water, and slope. To develop a crop depredation risk probability map for elephant and gaur, we fitted GLMs assuming a binomial distribution in Program R, version 3.0 (R Development Core Team, 2018).

We first checked for potential multiple correlations among predictor variables using a hierarchical Pearson correlation coefficient test (Graham, 2003) in the *corrplot* package of Program R, version 3.0 (Wei and Simko, 2017). We removed highly correlated ($r > 0.50$) variables (*i.e.*, crop change, distance to natural forest cover, and temperature) before proceeding (Fig. S1.1) and standardized the final variable set using a Z-transformation before final analyses. To check the model fit, we assessed null deviance and residual deviance values, as well as the R^2 value. Model strength of evidence and fitness was based on Akaike's Information Criterion (AIC_c) corrected for relatively small sample sizes. We used relative AIC differences (Δ) and weights (w_i) (Burnham and Anderson, 2002) to identify the best models explaining conflict patterns through predictors. We applied multi-model averaging for all candidate models with $\Delta AIC < 2$ for final inferences (Burnham and Anderson, 2002) using the *MuMIn* package in R (Grueber et al., 2011), and used the AIC_c weight of covariates to evaluate their relative importance from the candidate models (which varied from 0, or "no support", to 1 or "full support") relative to the overall pool of candidate models (Burnham and Anderson, 2002). All analyses were performed using Program R Package, version 3.0 (R Development Core Team, 2018) in the MASS (Venables and Ripley, 2002), *rJava* (Urbanek, 2010), *glmulti* (Calcagno and de Mazancourt, 2010) and *MuMIn* (Bartoń, 2013) packages. We used the R package *effects* (Fox et al., 2014) to plot the response curves of the top model covariates for the dependent variable.

2.5. Hotspot mapping

We applied spatial interpolation (*i.e.*, kriging) to infer incidents of conflict patterns in unsampled areas based on information from the top model for the probability of conflict patterns using the package *gstat* (Pebesma and Graeler, 2019) in Program R, version 3.0 (R Development Core Team, 2018). This methodological approach accounted for uncertainty as distance increased between spatial locations and yielded a semivariogram depicting the spatial correlation among points (Appendix Fig. S1.2; S1.3). We used spherical distribution, an automatic interpolation method, and M. Stein's parameterization models, to explain the patterns of conflict for elephant and gaur, respectively. We then generated conflict hotspot or depredation risk maps for elephant and gaur for the entire landscape, including unsampled areas, using the package *automap* (Hiemstra et al., 2009).

3. Results

3.1. Households, crop damage, injury, and property loss

Overall, we conducted 1460 questionnaires on the presence/absence of elephant and gaur conflict, and consequences of that conflict, *i.e.*, human death/injuries, and/or crop-raiding. Approximately 45% (n = 660) and 10% (n = 140) of households reported elephant and gaur conflict, respectively. Both elephant and gaur mostly caused crop damage (44% and 9.2%, respectively), followed by property damage (6% and 0.41%, respectively) and human injury/death (5.55% and 1.03%, respectively). We found that households inside RFs were most likely to report human-elephant conflict (HEC) (62% of all households), followed by those inside PAs (44% of all households) and FAs (43% of all households). HGC was higher in FAs (11%) than in RFs (6.3%) and PA (5.1%). Human injury and death by elephants (n = 81) were reported much more from PAs and RFs (9.28% and 19.72% respectively) than in FAs (3.11%). The proportion of HECresulting in crop and property damage did not differ much across management systems (PAs: 43.81%, 4.12%; RFss: 35.92%, 3.52%; FAs: 42.17%, 5.34%). Gaur-related conflict resulted in property damage and injury to death ≤1% of the time (n = 15) for all three management categories. Crop damage caused by gaur however was reported in PAs and FAs (8.76% and 9.43%) each more than twice as much as in RFs (4.23%). Nearly all conflict caused by elephants (n = 633) and gaur (n = 134) occurred at night (97.47% and 97.76%, respectively), with little conflict occurring in the morning (4.11%, 7.46% respectively) and evening (1.42%, 10.45% respectively). A total of 17 crops were grown (n = 1137) among all communities, of which the five primary crops most grown were vegetables (predominantly, cabbage, pumpkin, tomato, cauliflower, and beans) (32%), millets (17.50%), banana (16.01%), fruit orchards (predominantly jackfruit, mango, watermelon, and guava) (14.78%), rice paddy (9.23%), and coconut (9.06%) (Fig. 2). The primary crops most involved in HEC (HEC), and more often consumed by elephants (n = 638) were maize (20.69%) and millets (19.75%), followed by banana (13.17%), vegetables (11.60%), sugarcane (7.84%) and rice paddy (6.47%) (Fig. 3). For gaur (n = 135), vegetables were the primary crops (37.04%) most frequently consumed, followed by fruit orchards and banana (11.11% each), and lastly, maize (5.19%) (Fig. 4). Coconuts were the major secondary crop consumed most frequently by elephants (11.44%), whereas all other minor crops combined for <5% of conflict incidents (Fig. 3). Gaur often consumed a greater diversity of secondary crops, including vegetables (13.33%), millets (8.15%), and coffee (5.96%) (Fig. 4).

Among the variables most influencing both elephant and gaur conflict were the percentage of crop cover, distance to nearest water source, number of major crops, mean annual precipitation, and mean slope (Table 1; Table 2; Appendix Figs. S2.1, S2.2, S2.3). The number of minor crops only influenced susceptibility to elephant conflict. The predicted probability of HEC was best explained by a model <Δ2 AIC_c that included these six variables (wt = 0.81). HEC increased with: per cent of crop cover, distance to nearest water source, the number of major crops and minor crops grown, whereas conflict decreased with mean annual precipitation, and mean slope (Fig. 5). The best model predicting conflict with gaurs (<Δ2 AICc; wt = 0.81) also included the five first variables mentioned. HGC increased as: crop cover proportion decreased, distance to the water source increased, more major crops were grown, mean annual precipitation increased, and mean slope increased (Fig. 6). Variables for all the top models contributed substantially, and other variables had relatively minor or no contribution to predicting the probability of conflict for both elephant and gaur; the standard deviation of each model is given in Fig. S1.4.

3.2. Conflict hotspots

The high HEC hotspot areas (0.5–1) we predicted were in and around the FAs (FAs) of Coimbatore FD, MTR, STR, Erode FD, Dharmapuri FD, CNWLS and Hosur FD (Fig. 7). This zone covered a total area of ca. 7000 km^2. The model also predicted additional clusters of 900 km^2 of high HEC in the FAs of Theni FD and Srivilliputhur. The model predicted HGC

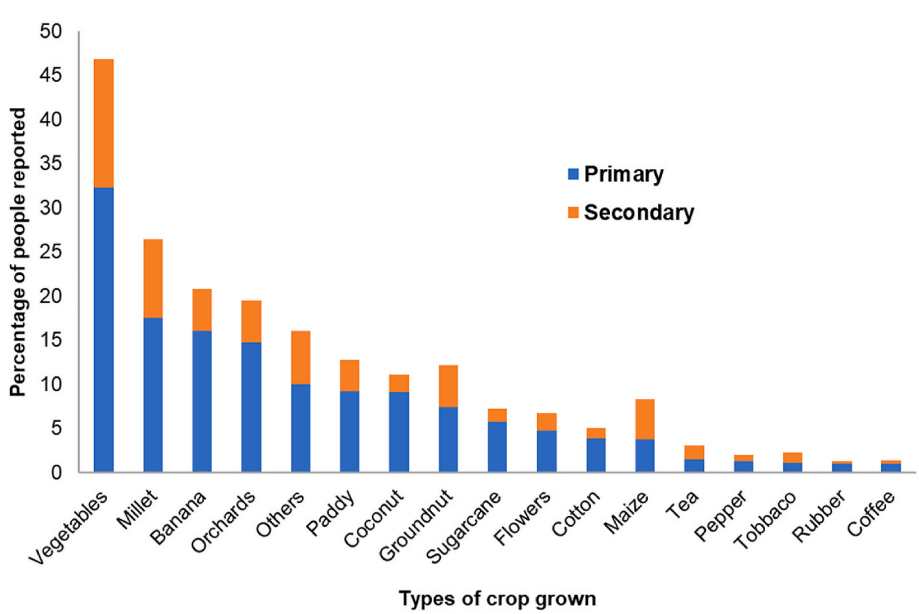

Fig. 2. Different types of primary (major) and secondary (minor) crops grown by local people in the Western and Eastern Ghats part of Tamil Nadu.

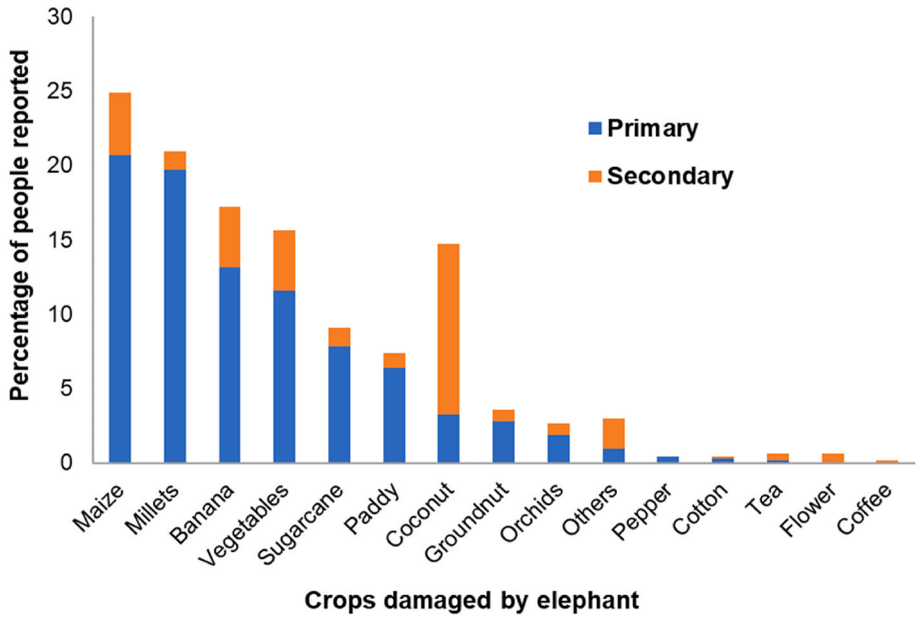

Fig. 3. The primary (major) and secondary (minor) crop varieties damaged by Asian elephant in the Western and Eastern Ghats part of Tamil Nadu.

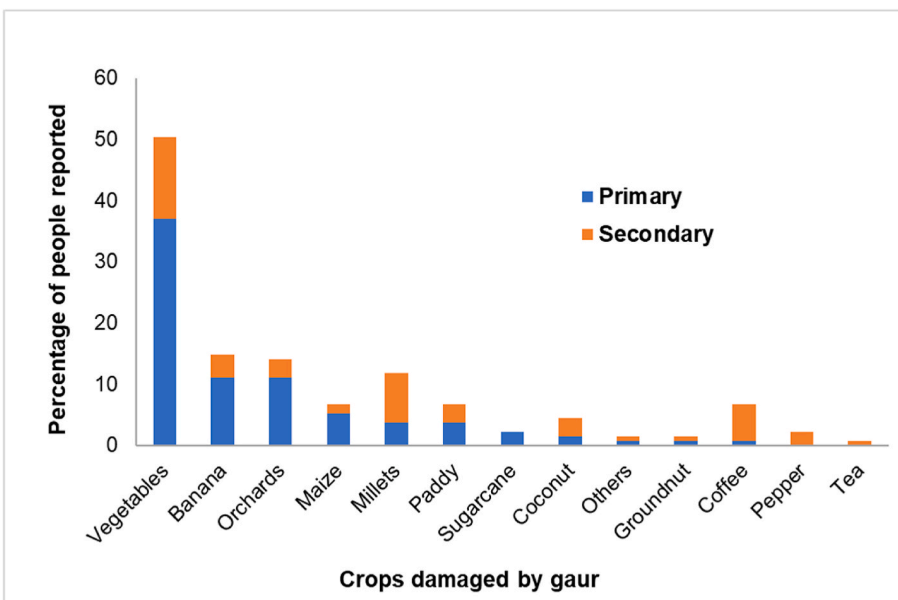

Fig. 4. The primary (major) and secondary (minor) crop varieties damaged by Indian gaur in the Western and Eastern Ghats part of Tamil Nadu.

hotspot areas (0.5–1) as clusters encompassing Nilgiri FD (150 km^2), Kodaikanal FD (225 km^2), parts of Theni FD (125 km^2), STR (75 km^2), Kanyakumari WLS (50 km^2) and Harur FD (50 km^2) (Fig. 7); these areas cumulatively covered 625 km^2. Spatial hotspots areas predicted for HEC were much larger (ca. 40% of the sampled area) than for HGC (ca. 3% of the sampled area), the former being distributed more contiguously along forest divisions, whereas conflict areas predicted for gaur were more patchily distributed.

4. Discussion

Our study has led to practical and actionable information regarding the current spatial patterns and drivers of human-megaherbivore conflicts. For the first time, our study highlights hotspots of this conflict across the human-wildlife interface of a large network of PAs and other land use types in the Western and Eastern Ghats of Tamil Nadu, southern India. Our study outcome benefit farmers from the vulnerable risk area identified by growing alternate crops which are less preferred by megaherbivores that reduce the probability of human-megaherbivore conflict.

Our conflict hotspot map highlighted many households that were vulnerable to elephant and gaur conflict, indicating a need for better land use planning. We found that cropland cover, the number of major and minor crops, proximity to the nearest water source, mean annual precipitation, and mean slope, all predicted the likelihood of megaherbivore conflict hotspots along human-wildlife interface areas of the WEGPTN. HEC hotspots were predicted to occur in lower plain (i.e., flat) terrains characterized by agricultural fields and lower precipitation, whereas HGChotspots were more likely to occur in undulating terrain amidst tea/coffee plantations and other crops. The high elephant and

Table 1
Summary of AIC_c model selection Generalized Linear Models (GLM) explaining factors influencing the predicted probabilityty of human-elephant and human-gaur conflict in the Western and Eastern Ghats part of Tamil Nadu.

Model	df	logLik	AICc	ΔAIC	weight	R^2 Value
Elephant						
CropCov + DistWater + MjCropGrown + MnCropGrown + Precip + Slope	7	−891.19	1796.46	0.00	0.81	0.20
CropCov + DistWater + MjCropGrown + MnCropGrown + Precip	6	−894.37	1800.79	4.33	0.09	0.19
CropCov + ForestDepScore + MjCropGrown + MnCropGrown + Precip + Slope	7	−893.75	1801.58	5.12	0.06	0.19
CropCov + ForestDepScore + MjCropGrown + MnCropGrown + Precip	6	−896.01	1804.08	7.62	0.02	0.19
Gaur						
CropCov + DistWater + MjCropGrown + Slope	5	−413.93	837.89	0.00	0.57	0.16
CropCov + DistWater + MjCropGrown + Precip + Slope	6	−413.78	839.62	1.73	0.24	0.15
CropCov + DistWater + MjCropGrown + MnCropGrown + Precip + Slope	7	−413.32	840.72	2.82	0.14	0.14
CropCov + DistForestBdry + ForestDepScore + MjCropGrown + Precip + Slope	7	−415.47	845.01	7.12	0.02	0.14

df - Residual degrees of freedom, logLik - Log likelihood, AICc - corrected Akaike's Information Criterion, ΔAICc - change in AICc between each model, wi - Akaike weight, CropCov – percent crop cover, DistForestBdry - distance to forest boundary, DistWater – distance to water source, ForestDepScore - local's dependence on forest, MjCropGrown – Number of major crop grown, MnCropGrown - Number of minor crop grown, Precip - mean annual precipitation, Slope – mean slope, R^2 Value – to measure model fit.

Table 2
Estimated beta coefficients for the top ranked models that explain those factors influencing the probability of crop depredation by elephant and gaur in the Western and Eastern Ghats parts of Tamil Nadu.

Models	Estimate	Standard error	P value	Variable contribution
Elephant				
MjCropGrown	0.6631	0.0644	0.0000	1.0000
MnCropGrown	0.3441	0.0578	0.0000	0.9900
DistWater	0.1949	0.0589	0.0009	0.9000
CropCov	0.1336	0.0700	0.0562	0.9800
Slope	−0.1600	0.0642	0.0127	0.8800
Precip	−0.1367	0.0721	0.0580	1.0000
Gaur				
MjCropGrown	0.5002	0.0918	0.0000	1.0000
CropCov	−0.5906	0.1146	0.0000	1.0000
DistWater	0.2858	0.0877	0.0011	0.9500
Slope	0.3655	0.0814	0.0000	1.0000
Precip	0.0526	0.0971	0.5880	0.4300

CropCov – percent crop cover, DistWater – distance to water source, MjCropGrown – Number of major crops grown, MnCropGrown - Number of minor crops grown, Precip - mean annual precipitation, Slope – mean slope.

gaur conflict zones we predicted occurred across ca. 40% and ca. 3% of the total area sampled (22,525 km^2), respectively. Relative to the large area predicted for HEC, we identified proportionally much less area for HGC across reserve networks, which although patchily distributed, suggested a rise in HGC and newly emerging hotspot areas.

4.1. Patterns in human-elephant conflict

Reduction in quality and availability of elephant habitats in the narrow stretch of forested areas of fragmented landscape force elephants to use agricultural areas beyond their natural habitat in the human-wildlife interface areas. During the process, the conflict between human and elephant becomes inevitable which leads to casualties on both sides (Sukumar, 1990; Venkataramana et al., 2017). Therefore, we identified spatial determinants of HEC which are urgently required to develop appropriate mitigation measures. We found that crop cover and diversity of major and minor crops near the forested landscape act as important drivers of HEC in the study area. With the extension of irrigated cultivations near forest boundaries, elephants have become increasingly attracted to forage on nutritious crops like maize, millets, banana, vegetables, sugarcane, and rice paddies. Although cultivated crops have higher digestible energy and are lower in protein and fibre (Sukumar, 1990; Sekar, 2013), increasing crop consumption may reflect fluctuations in availability of natural forage in PAs (Branco et al., 2019). Greater levels of habitat fragmentation and reduction in overall habitat quality in RFs (Ramesh Kumar, 1994; Sivaganesan and Johnsingh, 1995; Sukumar and Ramesh, 1995; Santiapillai, 2003; Babu et al., 2012), could explain the increase in elephant-related conflict compared to situations in PAs and FAs . Over time, the RFs of southern India have shrunk in size and shape to narrow, more linear areas due to increasing deforestation rates and landscape-scale proliferation of human settlements (Puyravaud et al., 2019; Kumar et al., 2004). The forests connecting the Nilgiri hills across the Western and Eastern Ghats are important elephant corridors (Ramkumar et al., 2018), and also areas of high HEC where local communities are dependent on forest resource extraction. Overgrazing by livestock in the forested areas and fuelwood collection from fringe and enclave villages results in a reduction of native trees and forage availability for herbivores and thus overtime their natural habitat witnessed invasion of weeds such as lantana, eupatorium, etc. in a vast area of lower and mid-elevation thorn and dry deciduous forest suppressing the growth of native species including grass (Sekar, 2013; Ramesh Kumar, 1994; Babu et al., 2012; Sivaganesan and Johnsingh, 1995). The loss of food plants and changing cropping patterns with elephant attractive crops drives the elephants into the agricultural areas (Sukumar and Ramesh, 1995; Santiapillai, 2003). Besides, elephant corridors are hindered with human settlements, rising urbanization pressure, and changing land-use patterns from agriculture to housing (Ramkumar et al., 2018).

The intrusion of elephants into human settlements and irrigated croplands in search of water and forage is now common in these regions (Sukumar, 2006). This could at least in part explain the importance of water sources to HEC incidents. Areas with low mean annual rainfall experienced more HEC, possibly because rainfall or lack thereof directly affects the availability of fodder within natural habitats; this drives animals outside such habitats in search of food. Since rainfall pattern had a significant role in controlling the vegetation dynamics and the availability of water, elephants moved accordingly to the most suitable habitats, particularly in the dry seasons of the year (Birkett et al., 2012; Bohrer et al., 2014) which can result in HEC incidents. Several prior studies have reported on HEC patterns during the monsoon (Stewart-Cox and Ritthirat, 2007; Joshi and Singh, 2008; Webber et al., 2011; Chen et al., 2016; Naha et al., 2019), which also coincided with the harvest seasons for maize, sugarcane, wheat, and rice paddies.

Our results depicted that increasing steepness of a landscape reduces the probability of HEC. Slope was a major topographical factor that influences the elephant movement and habitat selection in other studies

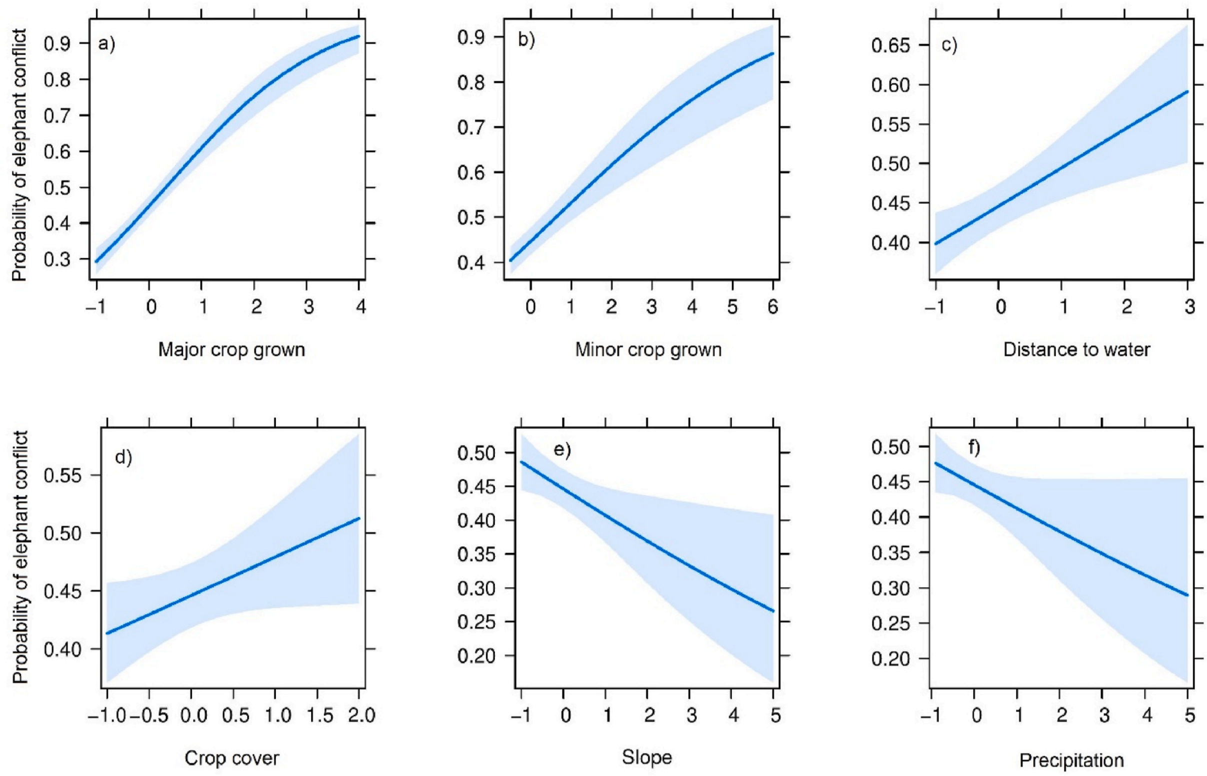

Fig. 5. Top model explaining the predicted probability of conflict by elephant in response to the number of major crops grown (a), number of minor crops grown (b), distance to nearest water (c), percent crop cover (d), slope (e) and mean annual precipitation (f).

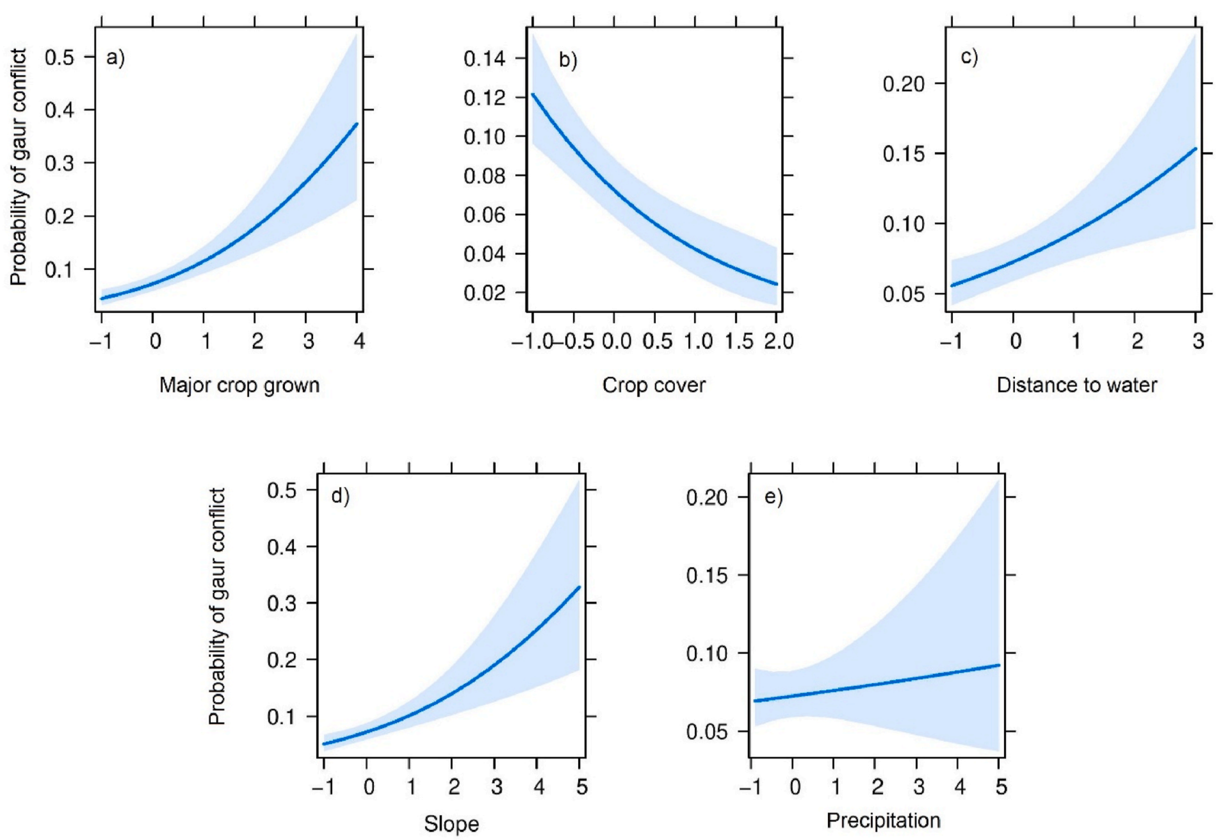

Fig. 6. Top model explaining the predicted probability of conflict by gaur in response to the number of major crops grown (a), percent crop cover (b), distance to water (c), slope (d) and mean annual precipitation (e).

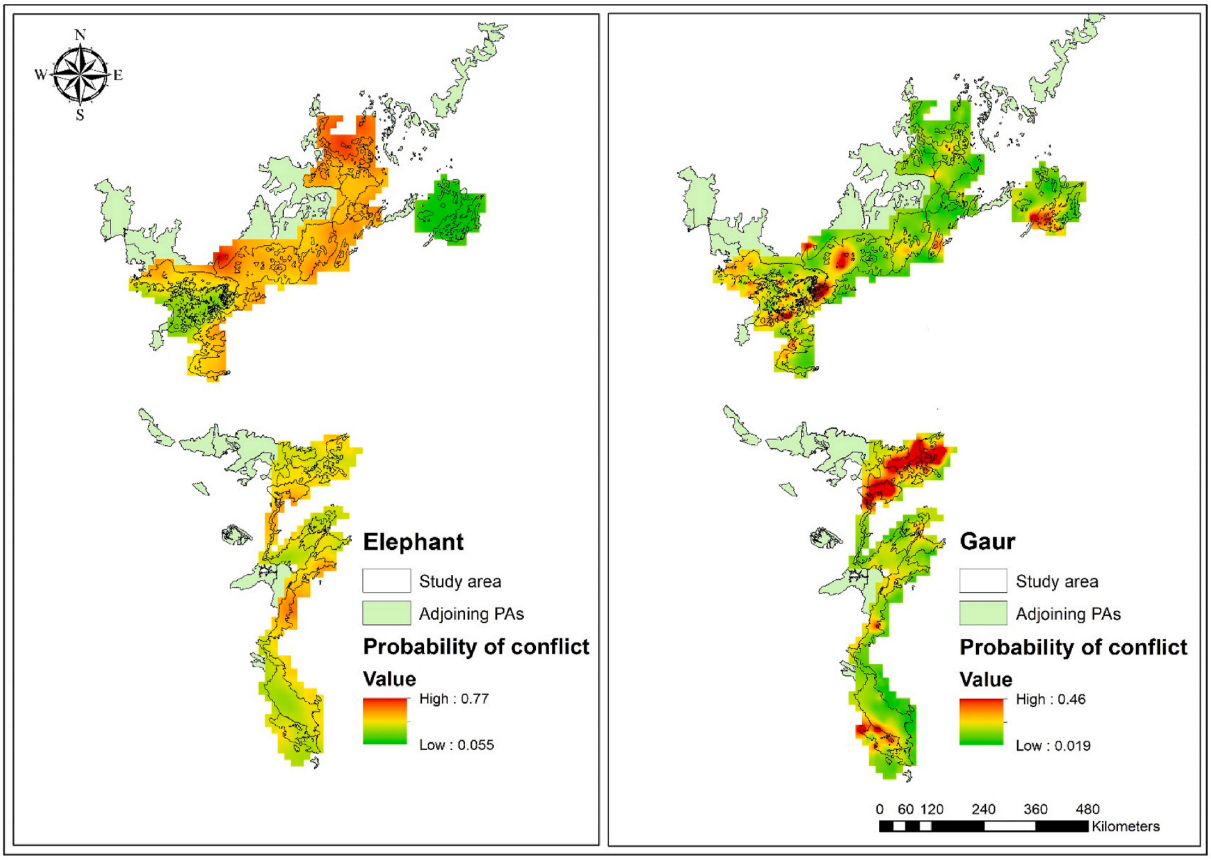

Fig. 7. Predicted conflict hotspots from elephant and gaur in the Western and Eastern Ghats part of Tamil Nadu.

as well (Sappington et al., 2007; Kanagaraj et al., 2019), *i.e.*, landscape steepness probably limited the distribution and behaviour of crop-raiding elephants. Due to better accessibility to food and much effortless movement following their body size, elephants mostly preferred lowland areas. Similar observations of Naha et al. (2019) indicated that even though there were reports of crop-raiding by elephants rarely at even 1000 m high altitude, relatively less incidents of human casualties were reported. Though slope has lesser influence on elephant's habitat selection when compared to other factors (Aini et al., 2015), they try to avoid steep slopes and hills because of overheating of their body, increased fear and risk of injury and limitations in forage and water availability (Wall et al., 2006). Meanwhile, a recent study by Kanagaraj et al. (2019) points out the increased probability of unidirectional range shifts of Asian elephant distribution towards higher elevations in India upcoming years predominantly due to climate changes and increasing anthropogenic pressures.

4.2. Patterns in human-gaur conflict

Overall, we found HGC to be highly localized in WEGPTN. The patchy clusters of HGC were predicted to occur in Gudalur RF, Nilgiris RF, Coimbatore RF, Harur FD, Theni FD, and core regions of STR. A large continuous HGC hotspot area was predicted for Kodaikanal WLS, and a small forest patch in Kanyakumari WLS. With respect to overall spatial area, the HGC hotspots we predicted in the Nilgiri FD, Gudalur FD, and Kodaikanal WLS, were all relatively large. This could be because these Forest Divisions also protect remnant montane and mid-elevation grassland patches on their slopes. In recent years, these have been increasingly converted to plantations of tea and coffee, and are also at increased risk from invasive plant species (Joshi and SankaranRatnam, 2018; Arasumani et al., 2021). Gaurs are grazers and are highly dependent on the availability of grasslands (Schaller, 1967; Chetri, 2003); the extensive loss of grasslands in the Western and Eastern Ghats of Tamil Nadu (Joshi and SankaranRatnam, 2018) may have contributed to low forage availability, forcing gaur to venture into open fringe habitats. Gaur herds and individuals have increasingly been spotted in tea gardens and seasonal croplands at the periphery of PAs, where they have been observed feeding on available understory grass cover in exotic tree plantations (Indira, 2019; Sankar et al., 2020; Chaiyarat et al., 2021). It is in these patch areas that local people have become susceptible to chance encounters with gaur at odd hours (Indira, 2019; Sankar et al., 2020). Encroachment into and cultivation of private forest areas adjacent to the forested landscape are known to escalate the scale of conflict in forest ecosystems of the Nilgiris FD and Kodaikanal WLS. During 2016–18, six human deaths and 36 injuries were attributed to gaur attack, and 31 crop-raiding incidents were reported in the Nilgiris Forest Division alone (Indira, 2019). Such incidents are most prevalent in tea/coffee estates. The increasing localised HGC cases reported in southern India (Joshi and SankaranRatnam, 2018; Sankar et al., 2020) therefore suggest that forested landscapes with undulating, "hilly" boundaries that interface with rural communities need to be regularly monitored so that the change in conflict pattern can be better understood and more effective mitigation measures can be enforced.

The association between HGC and the diversity of major crops at these interface areas further supports the idea that the variety of crops grown at different seasons likely provides more foraging opportunities at a given locality throughout the year. This relationship warrants an in-depth investigation of HGC hotspots to study crop-visitation rates of gaur, and a comparison of nutrient levels between natural and human-modified forage. Such findings could better inform management guidelines for highly degraded grassland patches, or even help to restore grassland habitats and keystone species, in conflict-prone Forest Divisions. One study in Mookambika WLS, Karnataka, reported that the most crop-raiding cases in rice paddy, sugarcane, and ragi fields occurred during summer, particularly in the farms located inside the core area relative to those located in the periphery of the sanctuary (Prashanth et al., 2013).

During the dry season, gaur populations were also attracted to water sources like wells, tanks set up by local villagers, and irrigated crop fields. These conditions often lead to more overlap between gaur and humans, especially at water sources. The annual rainfall pattern also influences HGC, and this could be related to the suitable habitat of gaur in high-altitude undulating slopes (Ramesh et al., 2012c). The presence of disproportionately smaller tiger populations in selected high-altitude areas in Tamil Nadu, and thus lower predation pressure on gaur, may have led to an increase in gaur populations in some Forest Divisions (Ramesh et al., 2012a, 2012c). Sprawling tea estates may have also led to a recent expansion of the gaur population in the Nilgiris Biosphere Reserve (Sankar et al., 2020). In such landscapes, gaur would inhabit small forest pockets interspersed with human habitations.

Wildlife species using human-modified landscapes increase the likelihood of negative human-animal interactions (Madhusudan and Mishra, 2003). These landscapes can disrupt the coexistence balance between people and gaur, changing otherwise empathetic behaviour to hostile behaviour. Gaur populations can also become resident outside of the forest, or take shelter in small insular forest patches, depredating crops, and creating fear and apprehension in local communities. In addition, improper waste disposal in the Upper Nilgiris and Kodaikanal due largely to unregulated touristic activity, is also a major problem; gaur herds have increasingly been observed feeding at these garbage dumps (Sankar et al., 2020). Habituation to such areas however can also lead to greater vulnerability of gaur to human retribution following negative interactions, such as when gaur attack humans and cause severe injury or death. Unlike elephants, HGC seemed to increase in more topographically complex areas, as gaur frequently forage along the hill slopes in fragmented landscapes. Sankar et al. (2013) even noted that gaur used areas with steep slopes more in the monsoon season than in summer and winter in Bandhavgarh.

4.3. Management implications

Our study area supports the largest populations of Asian elephants and Indian gaur in southern India. Not surprisingly, we found significant conflict hotspots for both species across several forest divisions in Tamil Nadu, information that can help in the devising of practical solutions on the ground. Considering the rising conflict, the invasion of weeds, wattle, pine, and eucalyptus species into native grasslands and other natural habitats represent further compromises of elephant and gaur habitat, which of course have potential conflict-related implications. Greater investment in the ecological restoration of such areas therefore has the potential to prevent some conflict in the long-term. We also believe collaborative monitoring among local forest administrative units and responses that include strong mitigation measures could focus time and effort more effectively on priority areas.

Thus far, many major mitigation strategies have been employed by the Tamil Nadu Forest Department to mitigate conflict between rural communities and megaherbivores. These include the provision of compensation, the conducting of awareness programs, and the construction of physical barriers, such as elephant-proof trenches and electric fences; they also include the augmentation of water sources and fodder plantation, use of noise or fire deterrents, deployment of anti-depredation teams, and the use of Kumkis during the translocation of conflict individuals (Baskaran et al., 2006; Milda et al., 2020). The effectiveness of these measures has been mixed, due in part to the failure of local communities to maintain or implement these measures consistently. Other more cost-effective potential mitigation measures, such as bio-fencing of crop fields with unpalatable crops like chilly, ginger, Palmyra, aloe, and citrus plants (Maikhuri et al., 2001; Mehta et al., 2020), bee-hive fencing (King et al., 2011, 2017), spraying cover scents over crops that could mask attractive odour (Santiapillai and Read, 2010), and use of repellents (chilli based, acoustics, olfactory, chemical) (Mehta et al., 2020), can all also reduce crop-raiding by megaherbivores. Early Warning Systems (EWS) using mobile technology and drones might also be applied in high conflict areas to function as deterrents and drive megaherbivores away. Changing crop patterns through sound land-use planning and weed eradication and habitat restoration leading to improved forage availability, particularly in the grasslands that serve as crucial corridors, would be practical and positive management actions. We would also recommend the growth of crops less attractive or palatable to elephants and gaur in those areas identified as at elevated risk of conflict. Proper and regular management of water resources in crucial corridors, particularly inside arid forested areas, might reduce the movements of megaherbivores into fringe and outside PAs. Ultimately however, maintaining the viability of this large elephant and gaur population amidst an increasingly inhospitable landscape, while simultaneously balancing the needs of rural livelihoods, remains a critical but priority conservation challenge for southern India.

CRediT author statement

Tharmalingam Ramesh: Conceived and conceptualization of the ideas, analysed the data and led writing **David Milda:** Collected the data and helped with the writing and revision. **Riddhika Kalle:** Helped with data analysis and revision. **V. Gayathri:** Collected the data. **M. Thanikodi:** Collected the data. **K. Ashish:** Helped with downloading the spatial data and provided editorial input and **Anthony J. Giordano**: Provided advice and editorial input.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jenvman.2022.115315.

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