

Elephants in the neighborhood: Patterns of crop-raiding by Asian elephants within a fragmented landscape of Eastern India

Dipanjana Naha¹, Suraj Kumar Dash¹, Abhisek Chettri¹, Akashdeep Roy¹, Sambandam Sathyakumar^{Corresp. 1}

¹ Endangered Species Management, Wildlife Institute of India, Dehradun, Uttarakhand, India

Corresponding Author: Sambandam Sathyakumar

Email address: ssk@wii.gov.in

Loss of forest cover, rise in human populations and fragmentation of habitats leads to decline in biodiversity and extinction of large mammals globally. Elephants being the largest terrestrial mammal symbolizes global conservation programs and co-occur with humans within multiple-use landscapes of Asia and Africa. Within such shared landscapes, poaching, habitat loss and extent of human-elephant conflicts (HEC) affect survival and conservation of elephants. HEC are severe in South Asia with increasing attacks on humans, crop depredation and property damage. Such incidents reduce societal tolerance towards elephants and increase the risk of retaliation by local communities. We analyzed a 2-year dataset on crop depredation by Asian elephants (N = 380) events in North Bengal (eastern India). We also explored the effect of landscape, anthropogenic factors (area of forest, agriculture, distance to protected area, area of human settlements, riverine patches and human density) on the spatial occurrence of such incidents. Crop depredation showed a distinct nocturnal pattern (22.00-06:00) and majority of the incidents were recorded in the monsoon and post-monsoon seasons. Results of our spatial analysis suggest that crop depredation increased with an increase in the area of forest patches, agriculture, presence of riverine patches and human density. Probability of crop depredation further increased with decreasing distance from protected areas. Villages within 1.5 km of a forest patch were most affected. Crop raiding incidents suggest a deviation from the “high-risk high-gain male biased” foraging behavior and involved proportionately more mixed groups (57%) than lone bulls (43%). Demographic data suggest that mixed groups comprised an average of 23 individuals with adult and sub adult females, bulls and calves. Crop depredation and fatal elephant attacks on humans were spatially clustered with eastern, central and western parts of North Bengal identified as hotspots of HEC. Our results will help to prioritize mitigation measures such as prohibition of alcohol production within villages, improving condition of riverine patches, changing crop composition, fencing agriculture fields, implement early warning systems around protected areas and training

local people on how to prevent conflicts.

1 **Elephants in the neighborhood: Patterns of crop-raiding by Asian elephants within a**
2 **fragmented landscape of Eastern India**

3 Dipanjan Naha¹, Suraj Kumar Dash¹, Abhishek Chettri¹, Akashdeep Roy¹, Sambandam
4 Sathyakumar^{1*}

5 ¹Department of Endangered Species Management, Wildlife Institute of India, Dehradun,
6 Uttarakhand, India

7 Corresponding Author: Sambandam Sathyakumar¹
8 Chandrabani, Dehradun, Uttarakhand, 248001, India
9 Email address: ssk@wii.gov.in

10

11 **Abstract**

12 Loss of forest cover, rise in human populations and fragmentation of habitats leads to decline in
13 biodiversity and extinction of large mammals globally. Elephants being the largest terrestrial
14 mammal symbolizes global conservation programs and co-occur with humans within multiple-
15 use landscapes of Asia and Africa. Within such shared landscapes, poaching, habitat loss and
16 extent of human-elephant conflicts (HEC) affect survival and conservation of elephants. HEC are
17 severe in South Asia with increasing attacks on humans, crop depredation and property damage.
18 Such incidents reduce societal tolerance towards elephants and increase the risk of retaliation by
19 local communities. We analyzed a 2-year dataset on crop depredation by Asian elephants (N =
20 380) events in North Bengal (eastern India). We also explored the effect of landscape,
21 anthropogenic factors (area of forest, agriculture, distance to protected area, area of human
22 settlements, riverine patches and human density) on the spatial occurrence of such incidents.
23 Crop depredation showed a distinct nocturnal pattern (22.00-06:00) and majority of the incidents
24 were recorded in the monsoon and post-monsoon seasons. Results of our spatial analysis suggest
25 that crop depredation increased with an increase in the area of forest patches, agriculture,
26 presence of riverine patches and human density. Probability of crop depredation further
27 increased with decreasing distance from protected areas. Villages within 1.5 km of a forest patch
28 were most affected. Crop raiding incidents suggest a deviation from the “high-risk high-gain
29 male biased” foraging behavior and involved proportionately more mixed groups (57%) than
30 lone bulls (43%). Demographic data suggest that mixed groups comprised an average of 23
31 individuals with adult and sub adult females, bulls and calves. Crop depredation and fatal
32 elephant attacks on humans were spatially clustered with eastern, central and western parts of
33 North Bengal identified as hotspots of HEC. Our results will help to prioritize mitigation
34 measures such as prohibition of alcohol production within villages, improving condition of
35 riverine patches, changing crop composition, fencing agriculture fields, implement early warning
36 systems around protected areas and training local people on how to prevent conflicts.

37 **Keywords:** Asian elephant, conflict, crop-raid, community, conservation, spatial risk

38

39 Introduction

40 Growth in human populations, expansion of agriculture, livestock farming and shared nature of
41 habitats force large mammals to come in conflict with humans. Human-wildlife conflicts also
42 lead to antagonistic relationships between local communities, wildlife managers and
43 conservationists further aggravating the problem of biodiversity conservation (Daskin & Pringle,
44 2016; Tilman et al., 2017). Attacks on humans, depredation of crops and livestock, and damage
45 to property pose significant threat to human livelihoods and safety. Periodic losses reduce
46 societal tolerance of local communities and prompt retaliatory killings, leading to local
47 extinctions with impact on the overall ecosystem (Dickman, 2010; Ogada, 2014). Elephants
48 symbolize large mammal conservation programs and are regarded as landscape engineers in Asia
49 and Africa (Coverdale et al., 2016; Sekar et al., 2017). They range across large areas for dietary,
50 reproductive requirements and forage on a diverse variety of grasses, shrubs, tree leaves, roots
51 and fruits (Sukumar, 2003; Whyte, 2012). Home range size vary based on the abundance and
52 distribution of resources with 100-1000 km² for Asian elephant and 11-500 km² for African
53 elephant herds (Thomas et al., 2008; Alfred et al., 2012). With rising anthropogenic impacts on
54 natural ecosystems, humans and elephants occur in close proximity thus increasing the likelihood
55 of conflicts (Sukumar, 1989; Hoare & Du Toit, 1999; Estes et al., 2011; Liu et al., 2017).
56 Human-elephant conflicts (HEC) are not uniform due to the dynamic nature of ecological and
57 anthropological factors which influence such incidents (DeBoer et al., 2013). Hence, it is
58 important to improve our understanding of HEC to match the dynamic nature of such events.

59 The intensity of HEC differs widely in Africa and Asia alongside variation in environmental
60 factors such as the distribution of natural resources, agricultural practices, seasonal climatic
61 conditions and socio-economic cultural beliefs (Shaffer et al., 2019). Fatal confrontations are
62 relatively rare in Africa, yet increasing in developing regions of Asia (Mumby & Plotnik, 2018).
63 Crop depredation is the most commonly reported form of damage, yet a rise in human injuries
64 and deaths reduce social tolerance towards elephants in Asia and Africa (Sitati et al., 2003; Lenin
65 & Sukumar, 2011; Lamichhane et al., 2018; van de Water & Matteson, 2018). Small scale
66 subsistence farmers are most vulnerable to damage by elephant attacks, crop raids (Riddle et al.,
67 2010) and as a consequence, such low income groups engage in retaliatory killings, help
68 organized poachers or prevent wildlife tourism based activities (Mackenzie & Ahabyona, 2012;
69 Benjaminsen et al., 2013).

70 Asian elephants occupy only 5% of their historic range as a consequence of loss of forest cover
71 and severe anthropogenic impacts on their habitats (Leimgruber et al., 2003). Only 22% of the
72 current Asian elephant habitat is protected and the remaining is a matrix of multiple-use reserve
73 forests, heterogeneous landscapes, crop fields, and human settlements. India has 60% of the
74 global Asian elephant population while the rest are shared between Nepal, Myanmar, Thailand,
75 Sri Lanka, Malaysia, and Indonesia (Sukumar, 2006; Fernando & Pastorini, 2011). An estimated
76 600 humans and 300 elephants die annually in India and Srilanka as a consequence of HEC with

77 additional 600,000 families and 1 million hectares of land affected through crop raiding
78 (Fernando et al., 2008; Pokharel et al., 2018).

79 Crop depredation is regarded as the stimulus of HEC (Webber et al., 2011; Mumby & Plotnik,
80 2018). Thus understanding how, when and where crop raiding occurs help wildlife managers
81 focus on conflict hotspots, safeguard human livelihoods and implement appropriate mitigation
82 measures. Spatial patterns of HEC are somehow positively related to human usage and the
83 presence of settlements, agricultural fields in India, Nepal (Sukumar, 1991; Gubbi, 2012;
84 Acharya et al., 2016), Thailand (Chen et al., 2016; van de Water & Matteson, 2018) and Africa
85 (Hoare & Du Toit, 1999). Conflicts are usually crepuscular and nocturnal with peaks during dusk
86 and dawn (Venkataraman et al., 2005). Crop raiding is generally seasonal and occurs within the
87 periphery of protected areas (Parker & Osborn, 2001; Chiyo et al., 2005). Mean annual rainfall
88 which is considered as a surrogate of primary productivity was found to be positive with HEC in
89 South-east Asia (Webber et al., 2011).

90 Crop raiding is a high-risk foraging behavior demonstrated by elephants especially males. To get
91 easy nutrition, males undertake such risks when raiding crop fields and combined with their large
92 ranging patterns are more likely to get involved in conflicts with humans compared to females
93 (Pokharel et al., 2018). Crop raids can lead to retaliatory killings of elephants by local
94 communities (Sukumar & Gadgil, 1988; Gubbi et al., 2014). Body size hypothesis predicts
95 sexual segregation in bull and cow movement patterns in response to differential nutrient
96 requirements with bulls preferring bulky diets over the quality of vegetation. Such “high risk,
97 high gain” strategy is often adopted by sub-adult, adult males to increase in body size and
98 enhance reproductive success (Sukumar & Gadgil, 1988; Hoare & Du Toit, 1999; Rode et al.,
99 2006; Chiyo et al., 2011). However, female elephants when in large groups also cause significant
100 damage to subsistence farmers and commercial agricultural farms (Sitati & Walpole 2006;
101 Sukumar, 2006). Conflict occurs round the year, with seasonal peaks often coinciding with
102 harvesting time of agricultural crops (Sitati et al., 2003). Elephants show risk avoidance strategy
103 by evading areas of human settlements during the day and thus raid crops mostly at night
104 (Sukumar et al., 2003; Graham et al., 2009; Gunn et al., 2014).

105 North Bengal region situated at the foothills of Eastern Himalaya, India is well known for the
106 severity of human-wildlife conflicts with nearly five-hundred fatal attacks on humans by
107 elephants (Naha et al., 2019) in the last 15 years. Almost twelve to thirteen percent of HEC cases
108 in India occurs within this landscape. The region is highly fragmented with protected areas
109 interspersed with tea plantations, crop fields (Naha et al., 2018) and an increase in area of human
110 settlements in the last decade (Naha et al., 2019). Human drunkenness is a major driver of HEC
111 with tea estate workers and farmers being the primary victims of fatal elephant attacks.
112 Intoxicated people chase/harass elephants near settlements, crop fields and are attacked (findings
113 from Naha et al. 2019). Rice beer (alcohol production) is also frequent within some of these
114 villages and elephants are reported to visit such areas and damage crop, property. As a
115 consequence, an annual sum of USD 67,479 and USD 78,930 was paid by the state forest

116 department for compensating human casualty and crop damage to elephants respectively (Naha
117 et al., 2019). Fatal elephant attacks were documented to be nocturnal with peaks during the
118 monsoon season. The combined threat of a large number of fatal elephant attacks on humans and
119 extent of crop raiding impose a substantial financial burden on wildlife authorities and a serious
120 conservation problem for managing elephants. Though attacks on humans have been recently
121 studied, lack of information on crop raiding remains a serious knowledge gap for mitigation of
122 HEC within this region. It is needless to emphasize that a thorough understanding of crop raiding
123 behavior would help to develop and direct appropriate mitigation measures and reduce the
124 present extent of HEC.

125 Thus, through this present study, we investigate the spatial and temporal patterns of crops raids
126 within a hotspot of HEC in South Asia. We also explore the effects of ecological attributes (tea
127 plantations, agriculture, forest, distance from protected areas, length and extent of riverine
128 patches), anthropogenic variables (human density, human settlements, length of roads) on the
129 risk of crop-raiding by Asian elephants in North Bengal, eastern India. We analyze (1) the
130 temporal and seasonal patterns of crop-raiding, (2) identify the spatial drivers and potential
131 hotspots of crop-raiding, and 3) Understand sex-biased crop-raiding behavior. Based on the
132 review of previous studies on elephant activity (Sukumar et al., 2003; Graham et al., 2009)
133 which suggests nocturnal patterns, we hypothesize that a higher number of crop-raiding events
134 will occur during the night. Considering elephants to be a landscape dependent species (Hoare &
135 Du Toit, 1999; Thomas, Holland & Minot, 2012; Bi et al., 2016), we hypothesize that probability
136 of crop-raiding should be higher in areas with forests (refuge), periphery of protected areas and
137 availability of water. Further, considering the “high-risk foraging behavior” which suggests that
138 crop raiding is sex-biased (Chiyo & Cochrane, 2005), we hypothesize that the majority of crop-
139 raiding incidents will involve lone bulls. Studies on HEC suggest spatial predictability in crop
140 raiding (Ahearn et al., 2001) and our findings will aid in identifying potential crop depredation
141 hotspots within the North Bengal landscape.

142 **Material & Methods**

143 **Study Area**

144 The study site is spread across 5 districts of North Bengal (West Bengal state), eastern India
145 (Darjeeling, Kalimpong, Jalpaiguri, Alipurduar, and Coochbehar) and encompasses an area of
146 12,700 km² (Fig. 1). According to the bio-geographic classification of India by Rodgers, Panwar
147 & Mathur (2000), the study area falls under the two biogeographic zones i.e. the Himalaya and
148 the Gangetic plains. This landscape is also known as Dooars, comprising of alluvial flood plains
149 and intersected by several rivers draining into the Ganga - Brahmaputra delta in Bangladesh. A
150 total of 3 National Parks (NP) i.e. Buxa Tiger Reserve and NP (761km²), Jaldapara NP (220
151 km²), Gorumara NP (80 km²) and 2 Wildlife Sanctuaries (WS) i.e. Chapramari WS and
152 Mahananda WS having an area of 9.5 and 158 km², respectively are located in the foothills of the
153 Dooars landscape. Neora Valley NP (88 km²), Singalila NP (78.6 km²) and Senchal WS (38.6
154 km²), Jorepokhri WS are located above 1000 m altitude in the mountains. North Bengal

155 historically was part of an extensive stretch of terai, alluvial grassland dominated forest
156 extending from Nepal (mechi river in the west) to Assam (north eastern India, sankosh river in
157 the east). Connectivity between the protected areas is poor with the landscape being highly
158 fragmented by tea gardens, villages and urban settlements. The forest types are moist tropical,
159 sub-tropical forests at the foothill region with major endangered large mammals being the Asian
160 elephant (*Elephas maximus*), one horned rhinoceros (*Rhinoceros unicornis*), gaur (*Bos gaurus*)
161 and common leopard (*Panthera pardus*). Elephant population is estimated to be around 500
162 individuals spread across an area of 2000 km² (MoEF&CC Report, 2017).

163 According to the Human Census Data (2011), an average range of (300-700) persons per km²
164 inhabit this region with a total population of 8.5 million. Primary occupation of local
165 communities is agriculture, livestock rearing, and daily wage worker (tea estate). Major crops
166 grown are paddy, jute, potato, maize and mustard with paddy cultivation carried out throughout
167 the year. There are three varieties of paddy grown in the region viz., Aman, Aus and Boro with
168 majority of the annual crop production (80%) derived from Aman and Aus. Harvesting period
169 for this two varieties of paddy occur during monsoon i.e. July-August and winter i.e. November-
170 December.

171 The livestock census 2012 reported a total of 3.5 million livestock in the region including cow,
172 buffalo, goat, sheep, pig, and other with an average of 273 livestock per km². Toto, Rava, Mech,
173 and Bhutia are the major indigenous communities of the North Bengal region whereas the rest
174 (Santhal, Oraon, Bhumij, Munda-Central Indian tribes) were either brought by the British
175 planters or migrated from different regions of India to work in the tea gardens. This region
176 receives an annual rainfall of 3,160 mm with an altitudinal range of 50-3500 m and the major
177 seasons are summer (March-June), monsoon (July-October), and winter (November to
178 February).

179

180 **Data collection**

181 We analyzed data on crop-raiding by Asian elephants between January 2017 to December 2019.
182 Our primary aim was to avoid strong spatial bias and hence we collected data (N = 380)
183 locations from regions that were spatially spread out and not confined to specific localities within
184 the landscape. We had informally constituted community-based village response teams (N = 25
185 teams with 5-7 members from each village) within the entire landscape and one primary task of
186 such teams was to record and report incidents of HEC. To avoid exaggeration of losses (Siex &
187 Struhsaker, 1999) we didn't record data on the extent of crop damage. Once an incident was
188 reported by the local community members, data collection was done by a team of researchers.
189 Each researcher had a predefined area to be surveyed and a team of researchers allowed us to
190 effectively sample the entire landscape. The research team recorded the GPS coordinates of the
191 crop-raiding site, type of agricultural crops damaged, herd demographics, time spent during
192 crop-raiding and time of raids (Appendix 1). Each crop-raiding incident was related to an
193 occurrence of elephants within a particular locality (village) at a specific time. When our
194 research team reached a particular village and elephants had left, data on the same parameters

195 were collected through interviews with the local community members. There was also forest
196 staff who were engaged by the local wildlife department to drive elephants from villages, crop
197 fields and they also helped during data collection. These staff members visited the specific areas
198 to confirm extent of damage and drove elephants from the crop fields. We verified the exact
199 number of elephants involved within each event from the compensation records and also through
200 direct communication with the staff members. The involvement of local community members,
201 field researchers, and forest staff helped reduce bias and exaggeration of facts related to crop-
202 raiding incidents. All field data were cross-checked at the Wildlife Institute of India, GIS lab and
203 then imported to a geodatabase.

204

205 **Conflict Risk Mapping**

206 Data were analyzed as previously described in a study conducted on fatal elephant attacks on
207 humans (Naha et al., 2019). We examined the seasonal and temporal patterns of crop depredation
208 using the chi-square test ($\alpha = 0.05$) (Zar, 2010) in R 3.4.0. We also examined difference in crops
209 raided and human behavior, activity during crop raids using chi-square test in R 3.4.0. Monthly
210 rainfall and crop damage frequencies (Perace & Smith, 1999) were also explored using spearman
211 correlations (IMD <http://www.imd.gov.in>) in R 3.4.0. The study area was overlaid with 2,780
212 grids and 600 grids each with an area of 5 and 25 km² respectively using Arc GIS 10.2.2. The
213 cell size was selected as 5 km² and 25 km² based on an earlier study (Naha et al., 2019) to
214 compare spatial patterns of crop damage and fatal elephant attacks on humans. We evaluated
215 spatial autocorrelation among crop damage events within the cells (5 km²) using function
216 `moran.test` (Moran's I) in package (`spdep`) in R 3.4.0. We selected a total of 10 predictor
217 variables based on their ecological importance to model HEC risk (Table S1). Land use data
218 were categorized into 5 types (area of agriculture, forest, tea plantation, sand bed, riverine
219 patches in m²). Distance from protected areas (m) was tabulated using the Euclidean distance
220 tool for every grid. Data on anthropogenic variables such as length of roads (m), human density
221 (per km²), and area of human settlements (km²) were extracted from the Digital Chart of the
222 World (CIESIN, Columbia University), online human census data (Human Census Data, 2011)
223 and supervised vegetation map (Naha et al., 2019). We omitted slope, aspect and elevation, from
224 the predictor variables since majority of the crop damage events occurred in flat lands. Our
225 primary aim was to identify landscape predictors of HEC and hence we discarded distance to
226 villages and considered area of human settlements (an artifact of human presence within rural,
227 urban clusters) in a grid/cell (Pozo et al., 2017; Mukeka et al., 2019). After all predictor variables
228 were compiled, they were extracted to the predefined grids and converted to raster files (ASCII
229 format) using Arc GIS 10.2.2. The locations of crop raids were projected into UTM coordinates
230 in Arc GIS 10.2.2 for all spatial analyses. The relationship between crop-raiding and the spatial
231 variables was explored statistically using Arc GIS 10.2.2 and Maxent program. Maxent is an
232 open access based species distribution program which is used to generate distribution of certain
233 species/events based on a set of environmental/predictor variables (Phillips et al., 2006). A total

234 of (N = 380) locations were used as sample data to run presence only species distribution models
235 and model human-elephant crop depredation risk for the North Bengal landscape.

236 Maxent program calculated probability of conflict (crop depredation) based on the ecological
237 predictors. Twenty-five percent of the locations were used as random test data or training to
238 evaluate final model performance. We generated response curves for all individual variables and
239 204 jackknife estimator was used for computing final model output. We used 5 replicates to
240 derive 205 model outputs with a total of 500 iterations. Accordingly, Maxent generated pseudo
241 absence 206 points (10000) from the entire study region (Elith & Leathwick, 2009). Details of
242 the analytical procedure is provided as supporting information files (File S1).

243 **Results**

244 **Seasonal and temporal pattern of crop-raiding**

245 In total, we recorded 380 crop-raiding incidents in the North Bengal region between 2017 to
246 2019. Crop-raiding events had major distinct peaks with 45% of the incidents recorded in winter
247 between November to February, followed by 43% between July to October and rest twelve
248 percent between March to June ($\chi^2 = 19.86$, $df = 2$, p -value < 0.05). Such crop raids coincided
249 with harvesting of Aman and Aus varieties of paddy. There was a negative correlation between
250 total number of crop raids and monthly rainfall ($r = -0.306$, $p < 0.05$) (Fig. 2). There was a
251 distinctive nocturnal pattern with majority 89% of the incidents recorded between 10 PM – 6
252 AM and the rest between 2 PM – 10 PM ($\chi^2 = 139.77$, $df = 2$, p -value < 0.05). Majority of the
253 crops raided were paddy (65%), maize (11%) and rest 25% comprised of seasonal vegetables,
254 potatoes, cabbage, lentils, cauliflower, spinach, banana, jackfruit ($\chi^2 = 45.42$, $df = 2$, p -value $<$
255 0.05). Elephant crop raids occurred in flat areas with an average elevation of 117 m (SE 35).

256

257 **Demography of crop-raiding elephants**

258 The mean group size was 23 SE 14.1 (range 2-150). Fifty-seven percent of the crop-raiding
259 events involved mixed groups whereas 43% of the incidents involved lone bulls (sub-adult to
260 adult males). Mixed groups composed of adult females, sub adult females, bulls and calves.

261

262 **Time spent in crop-raiding**

263 Elephants spent an average of 308 mins i.e. 5 hrs (SE 167 mins) during crop-raiding range (15
264 mins to 15 hrs).

265

266 **Human behavior and activity during crop-raiding**

267 During crop-raiding, 61% of the people in the neighborhood were busy guarding agricultural
268 fields, 30% were sleeping, 6% of the local community members were chasing the elephants
269 whereas rest were engaged in household work ($\chi^2 = 178.74$, $df = 2$, p -value < 0.05). An average
270 of 6 persons (range 1-20) were present in crop fields chasing elephants. From interviews with the

271 local community members, we recorded that 75% of the localities raided by elephants had
272 presence of locally brewed rice beer “haaria” production units’/storage chambers. Rice beer
273 production units were concentrated around forest edges and periphery of protected areas (Fig. 3).
274

275 **Distance of crop depredation sites to nearest forest patches**

276 We recorded that crop depredation sites were located within close proximity of forest patches.
277 The average distance of a crop field raided by elephants was estimated to be 1.6 km (SE 1.5)
278 (range 0 – 18.5 km) from the nearest forest patch. Thirty-five percent of the villages were located
279 within 500 m of a forest patch whereas overall 63% of the incidents occurred within 1.5 km.
280

281 **Influence of landscape, anthropogenic variables on crop-raiding by elephants**

282 Moran’s I identified spatial clusters of crop depredation within the North Bengal landscape. The
283 z value (13.148), Moran’s Index (0.174) and (p value < 0.01) indicate that there was less than 1
284 percent likelihood that this pattern was due to random chance. The threshold distance was
285 estimated to be 2,236.42 m. Maxent program used a total of 228 locations for training whereas
286 76 locations were used for testing. Based on this training and testing data set, final crop
287 depredation risk maps and predictions were generated. A total of 5 replicates were used for
288 model averaging and convergence.

289 Probability of crop depredation by elephants within a 5 km² grid were best explained by a
290 combination of ecological, anthropogenic attributes such as i) area of riverine patches, ii) area
291 of agricultural fields, iii) length of rivers, iv) distance from protected areas, and v) Human
292 density. Receiver operating characteristic curve (ROC) value was estimated to be 0.89 (S1 Fig).
293 Area of riverine patches which indicates availability of water within a grid was identified as the
294 most important predictor of crop depredation.

295 Within a 5 km² grid, crop raiding risk increased initially with an increment in area of agricultural
296 fields (< 5 km²) and then declined rapidly. Probability of crop raiding were highest in areas with
297 water (> 600 m²), forests (refuge), tea plantations (4,000 m²) and vicinity of protected areas
298 (refuge). Anthropogenic variables such as human density (< 40 persons/km²) and area of human
299 settlements (< 1,500 m²) were positively related to probability of crop depredation whereas such
300 incidents decreased with increase in presence of roads (700 m) within a grid.

301 For 25 km² grids, risk of crop damage increased with an increment in area of agricultural fields
302 (> 13,000 m²), tea plantations (> 10,000 m²), forest patches (> 20,000 m²) and human density (>
303 42 persons/km²). Risk of crop raiding decreased with increase in distance from protected areas (>
304 1 km), area of riverine patches (> 6,000 m²), length of rivers and length of roads. Probability of
305 crop depredation were best explained by a combination of ecological, anthropogenic variables
306 such as i) distance from protected areas, ii) area of forest patches, iii) area of tea plantation, iv)
307 area of riverine patches, v) length of roads, vi) area of human settlements, and vii) area of
308 agriculture fields. At a landscape scale, distance from protected areas was identified as the most

309 important predictor of crop depredation. Receiver operating characteristic curve (ROC) value for
310 the 25 km² grid-based final model was estimated to be 0.83.

311

312

313 **Hotspots of conflict**

314 The predictive maps based on the maxent models indicate eastern, central, and western parts of
315 the North Bengal region as HEC hot spots (Fig. 4). Crop raiding probability increased near the
316 periphery of protected areas (Mahananda WS, Gorumara NP, Jaldapara NP and Buxa NP), major
317 forested corridors and the tea growing belt within the landscape.

318 **Discussion**

319 Our analysis of crop-raiding data together with predictor variables generated new information on
320 the potential drivers and spatial distribution of HEC in South Asia. Analysis of the temporal
321 patterns supports the hypothesis that crop-raiding by elephants was nocturnal in nature which
322 exhibits avoidance behavior of peak human activity. In line with our 2nd hypothesis, our model
323 also confirms that elephants being a landscape dependent species, probability of crop-raiding are
324 higher in areas with a matrix of agriculture, forests, riverine patches, tea plantations and
325 periphery of protected areas. Contrary to our 3rd hypothesis, crop-raiding incidents involved both
326 mixed groups and lone bulls.

327 Our results also suggest that the probability of crop-raiding increased with increasing human
328 density (till a critical threshold of 40 persons/km²). Elephant raids peaked in areas located within
329 a distance of 1,500 m from forested areas. Local community members proactively guarded their
330 crop fields and chased elephants from the neighborhood. Villages located at the periphery of
331 protected areas and forest refuge were the most affected by HEC. Attacks by Asian elephants on
332 humans were recorded outside protected areas near human settlements and in the vicinity of crop
333 fields in Nepal and India (Acharya et al., 2016; Naha et al., 2019). Results suggest seasonal
334 variation in crop raids with eighty-eight percent of the incidents recorded in the monsoon and
335 post monsoon seasons i.e. between July-February. Unlike in parts of South-east Asia where crops
336 raids are positively correlated with monthly rainfall (Webber et al., 2011), we did not document
337 any positive association of rainfall and crop raiding frequencies in the North Bengal region.

338 The most interesting finding of our study was that elephants raided villages where alcohol
339 production (haaria- rice beer) was prevalent. Alcoholism (human drunkenness) is a major driver
340 of fatal elephant attacks in this region and people intoxicated with rice beer have been reported to
341 harass and chase elephants from villages, crop fields (Naha et al., 2019). As a consequence, more
342 than five hundred people have been killed by elephants in the past 10 years (Naha et al., 2019).
343 Similar patterns have been reported from Assam (India) and terai region of Nepal where HEC

344 victims were drunk and chasing elephants (Lahkar et al., 2007; Lenin & Sukumar, 2011;
345 Neupane, Johnson & Risch, 2013). Rice beer production is a community based activity and this
346 alcoholic drink is produced from par boiled rice (paddy), ivy gourd and other locally available
347 herbs. Once all raw ingredients are gathered, small tablets are prepared and dried in the sun.
348 Dried tablets are kept within gunny bags for incubation which takes 2-6 days depending on the
349 weather condition. Once the tablets are ready they are mixed with boiled rice, mixed with water
350 and transferred to a fermenter within the village. The total incubation period for this preparation
351 is 3-5 days and subsequently the fermented stock emits a strong pungent smell which attracts
352 elephants (Ghosh & Das, 2004). Hence, such rice beer (alcohol) breweries should be relocated
353 from the vicinity of villages to avoid frequent visitation by elephants and reduce the current
354 extent of HEC.

355 Though spatial drivers of HEC are influenced by land-use patterns and anthropogenic factors,
356 seasonality of such events are governed by the agriculture calendar. Seasonal patterns of crop
357 raids coincide with monsoon and winter months when maize and paddy are ready to be
358 harvested. Crop raiding has been widely documented to coincide with the harvesting pattern of
359 major agricultural crops in Africa and Asia (Sitati et al., 2003; Chen et al., 2016). There are three
360 varieties of paddy grown in this region i.e. Aman, Aus and Boro. Crop raiding has two distinct
361 peaks which coincide with the harvesting of Aus and Aman varieties of paddy. Such patterns are
362 similar to the adjoining Assam region where crop depredation occurred between August to
363 December (Wilson et al., 2015). Female elephants are reported to be in peak sexual activity
364 during monsoons which could be another major driver of crop-raiding peaks in monsoon months
365 (Sukumar et al., 2003; Webber et al., 2011). Seasonal patterns of crop-raiding and fatal elephant
366 attacks on humans also exhibit a similar trend with peaks during monsoon and winter months
367 (Naha et al., 2019). Hence, we recommend intensification of mitigation measures during these
368 two major crop raiding periods.

369 Data on the demography of crop-raiding elephants suggests that incidents involved an equal
370 proportion of mixed groups and lone bulls. Our results are similar to findings from the
371 neighboring region of Assam where crop-raiding involved smaller mixed groups comprising of
372 adult females, sub-adult individuals and calves. The average herd size for crop-raiding elephants
373 was 23 which is similar to the herd size of 18 elephants reported from the Assam region (Wilson
374 et al., 2015). This foraging behavior is different from the male-biased crop-raiding behavior
375 reported from other regions of South Asia and Africa (Sukumar, 1991; Graham et al., 2009;
376 Goswami et al., 2015). Bulls, in general, are reported to use marginal habitats (Hoare & Du Toit,
377 1999) and crops constitute 10% of their overall diet as compared to 2% for herds (Sukumar et al.,
378 2003). With the current loss of forest cover (>30%) in the region during the past few decades,
379 elephants have been forced to rely on agricultural crops and the surrounding anthropogenic
380 landscape for access to food and water (Lenin & Sukumar, 2011; Wilson et al., 2015). Unless the
381 functionality, quality of existing elephant habitats, and dispersal corridors are revived, the
382 present extent of crop-raiding and attacks on humans will increase (Lenin & Sukumar, 2011;

383 Wilson et al., 2015). Appropriate mitigation measures such as restoring existing forest patches,
384 increasing natural forage within protected areas and regulated crop cultivation should be the
385 topmost conservation priority (Wilson et al., 2015).

386 Our results suggest that a matrix of landscape elements such as the area of agriculture,
387 distribution of protected areas, availability of water and tea plantations are major drivers of HEC.
388 North Bengal was once a contiguous elephant habitat extending from Nepal in the west to
389 Myanmar in the east (Choudhury et al., 1998). In recent times, the landscape has been severely
390 fragmented with the construction of dams, linear infrastructure, human settlements apart from the
391 presence of agriculture lands and tea plantations (Sukumar et al., 2003). Forest cover is primarily
392 restricted to the protected areas, major wildlife corridors and reserved forests. Though there are
393 numerous tea plantations in this region, they don't provide forage and only act as temporary
394 refuge for elephants (Chartier, Zimmermann & Ladle, 2011). Probability of crop raiding
395 increased with area of agriculture fields within 25 km² grids which was similar to findings of an
396 earlier study on crop depredation by African elephants in Trans Mara area of Kenya (Sitati et al.,
397 2003) and Asian elephants in north-eastern India (Wilson et al., 2015). Risk of human injuries
398 and deaths to elephant attacks were also documented to be higher in such areas with presence of
399 forest patches and agriculture fields (Naha et al., 2019). Thus, risk of crop raiding and human
400 injuries, deaths were spatially clustered within specific land use types and such areas should be
401 completely avoided by local communities during night.

402 The probability of crop-raiding was largely restricted to 1.5 km surrounding forested regions
403 (refuge) and hence local communities residing within such areas were at the highest risk. Our
404 results also highlight that crop raiding risk was highest within close proximity of protected areas
405 and increased with human density. Local communities residing at the edge of forests, protected
406 areas here are a combination of ethnic tribes (Rajbanshi, Mech, Rava, Gorkha, Tamang) and
407 immigrants (tribes from central India such as Santhals, Oraon, Munda) who are either employed
408 as tea estate workers or involved with subsistence agriculture. The major victims of elephant
409 attacks are also such community members (tea estate workers and marginalized farmers) (Naha
410 et al., 2019). Elephants are part of the local folklores and form an important part in the socio-
411 cultural beliefs of tribal communities. Studies on HEC suggests that such incidents increase
412 within close proximity to protected areas, forests (Nyhus, Tilson & Sumianto, 2000; DiFonzo,
413 2007; Lahkar et al., 2007; Riddle, 2007) and are generally confined within 1 km of the protected
414 area (Sukumar, 1989). Previous studies in south, south-east Asia, and Africa have reported a loss
415 of forest cover and rising human densities as major drivers of HEC (Leimgruber et al., 2003;
416 Neupane, Johnson & Risch, 2013; Hoare, 2015). HEC show a positive relationship with human
417 density, and research in Zimbabwe suggests that African elephants will adapt to humans till a
418 critical threshold is reached which is 15-20 persons/km² (Hoare & Du Toit, 1999). Our results
419 also confirm that the probability of crop-raiding increases with human density and then decreases
420 (threshold value 40 persons/km²) which is an artifact of elephant avoidance of dense human
421 settlements. Human density in North Bengal was fairly high (range 200-700 persons/ km²) and

422 large settlements also act as barriers to elephant movement (Fernando et al., 2006). Majority of
423 conflicts happen when they traverse such human used areas (Lenin & Sukumar, 2011).
424 Mitigation measures should be focused on specific crop depredation zones within the landscape
425 such as commercial agricultural farms and human settlements within close proximity of
426 protected areas.

427 Our results confirm previous findings that HEC increases with an increment in crop fields.
428 Studies on HEC in north-eastern India (Wilson et al., 2015) reported conflicts to be positively
429 related to distribution of villages and refuge areas whereas in Kenya conflicts were positively
430 related to the location of agricultural fields and their proximity to towns and roads (Sitati et al.,
431 2003). Primary productivity has been identified as a major driver of HEC in Africa because dry
432 arid savannahs are generally devoid of crops. The problem intensifies with an increase in crop
433 production (Sitati et al., 2003; Wilson et al., 2015) such as in Asia where crop fields, human
434 settlements provide food and forage, whereas forest patches, plantations act as day refuges
435 within anthropogenic landscapes.

436 Distribution of water plays a major role in movement of large mammals within an ecosystem.
437 Numerous studies in Asia and Africa have highlighted availability of water, swamps, streams
438 and rivers as crucial drivers of habitat use by elephants within a landscape (Fernando et al., 2006;
439 Duffy et al., 2011). Limited literature on Asian elephants suggests that forage, water (Sukumar,
440 1989) and anthropogenic impacts are significant predictors of resource use (Desai & Baskaran,
441 1996). Presence of water also influences the extent of a rice-based agricultural system, human
442 settlements which further explains the importance of riverine patches as major spatial drivers of
443 crop raids and fatal elephant attacks in North Bengal (Naha et al., 2019). Our results thus
444 confirm that in a fragmented landscape, access and availability of water is a major spatial driver
445 of HEC.

446 To safeguard elephants and humans within heterogeneous landscapes, multiple sociological
447 factors should be addressed for developing successful conservation programs (Shaffer et al.,
448 2019). Mitigation strategies should focus on keeping elephants out of crop fields and human
449 settlements rather than confining them within fenced reserves. Elephants are dependent on forest
450 patches, protected areas for movement, resting, forage and hence maintaining connectivity within
451 such patches should be the topmost priority (Goswami & Vasudev, 2017). Forest patches in the
452 vicinity of human settlements should be restored and encroachment of riverine patches should be
453 minimized. There should be a prohibition on rice beer production and instead breweries should
454 be relocated from the vicinity of villages to nearby urban centres. Breweries should be
455 constructed with durable material to avoid any damage by elephants. The district administration
456 should provide financial support/loan to the village communities to set up these breweries,
457 shops/counters within the urban centres and commercialise production and sale of bottled
458 traditional “North Bengal” rice beer. Such a program will provide local employment, generate
459 revenue and reduce the present extent of HEC. Such programs should be integrated with
460 conservation awareness camps for the local communities regarding spatial, seasonal and

461 temporal patterns of crop-raids, human drunkenness and impact on HEC. Village elders and
462 community leaders should also discourage human drunkenness and provocative behavior such as
463 harassing or chasing elephants within their respective localities. Solar and electric fences can be
464 set up around crop fields, human settlements (Hedges & Gunaryadi, 2009; Davies et al., 2011;
465 Wijayagunawardane et al., 2016) and their effectiveness to deter elephants should be evaluated
466 within such areas. Traditional crop guarding measures should be integrated with early warning
467 systems (seismic and motion sensor triggered proximity alarms) and beehive fencing around
468 identified hotspots (Fernando et al., 2008; King et al., 2017). Flash lights should be put up
469 around crop fields, farmers can be provided with torchlights and fences can be covered with
470 chili-oil soaked rags (Hoare, 2015; Gunaryadi et al., 2017). Villagers can also be trained to
471 prepare chili powdered bombs and use guard dogs to deter elephants near settlements (Hoare,
472 2015). Unpalatable yet economically beneficial crops such as ginger, garlic, chillies, lemongrass
473 should be grown in fields regularly visited by elephants (Gross et al., 2017). Such cash crops
474 could act as deterrents as well as provide income for the local communities (Fernando et al.,
475 2008). Timely compensation of crop damage incidents should also be provided as such measures
476 will improve societal tolerance towards elephants (Gross et al., 2017). Small-scale community
477 based tourism initiatives should also be explored within the hotspots to reduce extensive crop
478 cultivation and generate economic benefits from wildlife (Ogutu, 2002). Radio-telemetry studies
479 should be undertaken to understand the activity and resource utilization patterns of elephants at
480 the interface between protected areas and the surrounding human-dominated landscape
481 (Venkatraman et al., 2005; Buchholtz et al., 2019).

482 **Conclusion**

483 Our study helps to untangle the relations between crop depredation, cropping pattern, land use
484 type and human behavior, activity within a multi-use landscape of South Asia. We recommend
485 further research on quantification of property damage, evaluation and comparison of multiple
486 (long and short term) mitigation measures, age and gender specific elephant movement behavior.
487 Studies should also be undertaken to understand the effect of crop fields, fragmentation and
488 human presence on nocturnal habitat utilization by elephants. Long term monitoring of the HEC
489 hotspots should be carried out to examine any changes in seasonal, temporal patterns of crop
490 raids.

491 HEC remains a serious conservation challenge for managers, conservationists in Asia and Africa
492 threatening safety, livelihoods of rural communities and survival of elephant populations.

493 Considering the limitations to animal dispersal, gene flow, and financial investments in fencing
494 protected reserves, current strategies to physically separate elephant and humans as is done in
495 parts of southern Africa cannot be advocated for rest of the elephant populations. Moreover, size
496 of protected areas is comparatively smaller in Asia than Africa. Efforts should be prioritized to
497 monitor HEC hotspots, maintain connectivity between populations, invest in HEC mitigation
498 measures and provide economic incentives to local communities for coexistence. With three-
499 fourth of the present Asian elephant habitat fragmented as a result of anthropogenic impacts,

500 future of Asian elephants depends on habitat improvement and reduction in HEC within larger
501 heterogeneous landscapes.

502 **Additional Information and Declarations**

503 **Competing Interests**

504 The authors declare there are no competing interests

505 **Author contributions**

506 Dipanjan Naha conceived and designed the experiment, analyzed the data and authored drafts of
507 the paper.

508 Suraj Kumar Dash collected data, did preliminary data analysis and approved the final draft.

509 Abhishek Chettri collected data, did preliminary data analysis and approved the final draft.

510 Akashdeep Roy collected data, did preliminary data analysis and approved the final draft.

511 Sambandam Sathyakumar authored or reviewed drafts of the paper, approved the final draft.

512 **Funding**

513 This study was supported under the National Mission on Himalayan Studies by the Ministry of
514 Environment, Forest & Climate Change, Government of India. The funders had no role in study
515 design, data collection, and analysis, decision to publish, or preparation of the manuscript.

516 **Acknowledgments**

517 We are grateful to the Principal Chief Conservator of Forests and Chief Wildlife Warden of West
518 Bengal for granting permission for research in North Bengal. We thank the tea garden authorities
519 and local community heads, non-governmental organization members for their support during
520 fieldwork.

521 **Reference**

522 Acharya KP, Paudel PK, Neupane PR, Köhl M. 2016. Human-wildlife conflicts in Nepal:
523 Patterns of human fatalities and injuries caused by large mammals. *PLoS ONE* 11:1–18.
524 DOI: 10.1371/journal.pone.0161717.

525 Ahearn SC, Smith JLD, Joshi AR, Ding J. 2001. TIGMOD: an individual-based spatially explicit
526 model for simulating tiger/human interaction in multiple use forests. *Ecological Modelling*
527 140:81–97. DOI: 10.1016/S0304-3800(01)00258-7.

528 Alfred R, Ahmad AH, Payne J, Williams C, Ambu LN, How PM, Goossens B. 2012. Home

- 529 Range and Ranging Behaviour of Bornean Elephant (*Elephas maximus borneensis*)
530 Females. *PLoS ONE* 7:e31400. DOI: 10.1371/journal.pone.0031400.
- 531 Benjaminsen TA, Goldman MJ, Minwary MY, Maganga FP. 2013. Wildlife Management in
532 Tanzania: State Control, Rent Seeking and Community Resistance. *Development and*
533 *Change* 44:1087–1109. DOI: 10.1111/dech.12055.
- 534 Bi Y, Roy A, Bhavsar D, Xu J, Wang M, Wang T, Yang X. 2016. Kamala tree as an indicator of
535 the presence of Asian elephants during the dry season in the Shivalik landscape of
536 northwestern India. *Ecological Indicators* 71:239–247. DOI:
537 10.1016/j.ecolind.2016.07.011.
- 538 de Boer WF, van Langevelde F, Prins HHT, de Ruiter PC, Blanc J, Vis MJP, Gaston KJ,
539 Hamilton ID. 2013. Understanding spatial differences in African elephant densities and
540 occurrence, a continent-wide analysis. *Biological Conservation* 159:468–476. DOI:
541 10.1016/j.biocon.2012.10.015.
- 542 Buchholtz E, Fitzgerald L, Songhurst A, McCulloch G, Stronza A. 2019. Overlapping landscape
543 utilization by elephants and people in the Western Okavango Panhandle: implications for
544 conflict and conservation. *Landscape Ecology* 34:1411–1423. DOI: 10.1007/s10980-019-
545 00856-1.
- 546 Chartier L, Zimmermann A, Ladle RJ. 2011. Habitat loss and human-elephant conflict in Assam,
547 India: Does a critical threshold exist? *ORYX* 45:528–533. DOI:
548 10.1017/S0030605311000044.
- 549 Chen Y, Marino J, Chen Y, Tao Q, Sullivan CD, Shi K, Macdonald DW. 2016. Predicting
550 hotspots of human-elephant conflict to inform mitigation strategies in Xishuangbanna,
551 Southwest China. *PLoS ONE* 11:e0162035. DOI: 10.1371/journal.pone.0162035.
- 552 Chiyo PI, Cochrane EP. 2005. Population structure and behaviour of crop-raiding elephants in
553 Kibale National Park, Uganda. *African Journal of Ecology* 43:233–241. DOI:
554 10.1111/j.1365-2028.2005.00577.x.
- 555 Chiyo PI, Cochrane EP, Naughton L, Basuta GI. 2005. Temporal patterns of crop raiding by
556 elephants: A response to changes in forage quality or crop availability? *African Journal of*
557 *Ecology* 43:48–55. DOI: 10.1111/j.1365-2028.2004.00544.x.
- 558 Chiyo PI, Lee PC, Moss CJ, Archie EA, Hollister-Smith JA, Alberts SC. 2011. No risk, no gain:
559 effects of crop raiding and genetic diversity on body size in male elephants. *Behavioral*
560 *Ecology* 22:552–558. DOI: 10.1093/beheco/arr016.

- 561 Chowdhury S, Khalid MA, Roy M, Singh, AK, Singh RR. 1998. Management of elephant
562 populations in West Bengal for mitigating man-elephant conflicts. Dehradun, India: Wildlife
563 Institute of India.
- 564 Coverdale TC, Kartzinel TR, Grabowski KL, Shriver RK, Hassan AA, Goheen JR, Palmer TM,
565 Pringle RM. 2016. Elephants in the understory: opposing direct and indirect effects of
566 consumption and ecosystem engineering by megaherbivores. *Ecology* 97:3219–3230. DOI:
567 10.1002/ecy.1557.
- 568 Daskin JH, Pringle RM. 2016. Does primary productivity modulate the indirect effects of large
569 herbivores? A global meta-analysis. *Journal of Animal Ecology* 85:857–868. DOI:
570 10.1111/1365-2656.12522.
- 571 Davies TE, Wilson S, Hazarika N, Chakrabarty J, Das D, Hodgson DJ, Zimmermann A. 2011.
572 Effectiveness of intervention methods against crop-raiding elephants. *Conservation Letters*
573 4:346–354. DOI: 10.1111/j.1755-263X.2011.00182.x.
- 574 Desai A, Baskaran N. 1996. Impact of human activities of the ranging behaviour of elephants in
575 the Nilgiri biosphere reserve, South India. *The journal of the Bombay Natural History*
576 *Society*. 93:559–569.
- 577 Dickman AJ. 2010. Complexities of conflict: the importance of considering social factors for
578 effectively resolving human-wildlife conflict. *Animal Conservation* 13:458–466. DOI:
579 10.1111/j.1469-1795.2010.00368.x.
- 580 Difonzo, MMI. 2007. Determining correlates of human–elephant conflict reports within fringe
581 villages of Kaziranga National Park, Assam. MSc thesis, University of London, UK.
- 582 Duffy KJ, Dai X, Shannon G, Slotow R, Page B. 2011. Movement Patterns of African Elephants
583 (*Loxodonta africana*) in Different Habitat Types. *South African Journal of Wildlife*
584 *Research* 41:21–28. DOI: 10.3957/056.041.0107.
- 585 Elith J, Leathwick JR. 2009. Species Distribution Models: Ecological Explanation and Prediction
586 Across Space and Time. *Annual Review of Ecology, Evolution, and Systematics* 40:677–
587 697. DOI: 10.1146/annurev.ecolsys.110308.120159.
- 588 Estes JA, Terborgh J, Brashares JS, Power ME, Berger J, Bond WJ, Carpenter SR, Essington TE,
589 Holt RD, Jackson JBC, Marquis RJ, Oksanen L, Oksanen T, Paine RT, Pikitch EK, Ripple
590 WJ, Sandin SA, Scheffer M, Schoener TW, Shurin JB, Sinclair ARE, Soulé ME, Virtanen
591 R, Wardle DA. 2011. Trophic Downgrading of Planet Earth. *Science* 333:301–306. DOI:
592 10.1126/science.1205106.
- 593 Fernando P, Kumar AM, Williams CA, Wikramanayake E, Aziz T, Singh SM. 2008. *Review of*
594 *human-elephant conflict mitigation measures practiced in South Asia*.

- 595 Fernando P, Pastorini J. 2011. Range - wide Status of Asian Elephants. *Gajah* 35:15–20. DOI:
596 10.5167/uzh-59036.
- 597 Fernando P, Wikramanayake E, Weerakoon D, Jayasinghe LKA, Gunawardene M, Janaka HK.
598 2005. Perceptions and patterns of human-elephant conflict in old and new settlements in Sri
599 Lanka: Insights for mitigation and management. *Biodiversity and Conservation* 14:2465–
600 2481. DOI: 10.1007/s10531-004-0216-z.
- 601 Ghosh C, Das A. 2004. Preparation of rice beer by the tribal inhabitants of tea gardens in Terai
602 of West Bengal. *Indian Journal of Traditional Knowledge (IJTK)* 03:373–382.
- 603 Goswami VR, Medhi K, Nichols JD, Oli MK. 2015. Mechanistic understanding of human-
604 wildlife conflict through a novel application of dynamic occupancy models. *Conservation*
605 *Biology* 29:1100–1110. DOI: 10.1111/cobi.12475.
- 606 Goswami VR, Vasudev D. 2017. Triage of Conservation Needs: The Juxtaposition of Conflict
607 Mitigation and Connectivity Considerations in Heterogeneous, Human-Dominated
608 Landscapes. *Frontiers in Ecology and Evolution* 4:1–7. DOI: 10.3389/fevo.2016.00144.
- 609 Graham MD, Douglas-Hamilton I, Adams WM, Lee PC. 2009. The movement of African
610 elephants in a human-dominated land-use mosaic. *Animal Conservation* 12:445–455. DOI:
611 10.1111/j.1469-1795.2009.00272.x.
- 612 Gross EM, Drouet-Hoguet N, Subedi N, Gross J. 2017. The potential of medicinal and aromatic
613 plants (MAPs) to reduce crop damages by Asian Elephants (*Elephas maximus*). *Crop*
614 *Protection* 100:29–37. DOI: 10.1016/j.cropro.2017.06.002.
- 615 Gubbi S. 2012. Patterns and correlates of human-elephant conflict around a south Indian reserve.
616 *Biological Conservation* 148:88–95. DOI: 10.1016/j.biocon.2012.01.046.
- 617 Gubbi S, Swaminath MH, Poornesha HC, Bhat R, Raghunath R. 2014. An elephantine challenge:
618 human–elephant conflict distribution in the largest Asian elephant population, southern
619 India. *Biodiversity and Conservation* 23:633–647. DOI: 10.1007/s10531-014-0621-x.
- 620 Gunaryadi D, Sugiyo, Hedges S. 2017. Community-based human–elephant conflict mitigation:
621 The value of an evidence-based approach in promoting the uptake of effective methods.
622 *PLOS ONE* 12:e0173742. DOI: 10.1371/journal.pone.0173742.
- 623 Gunn J, Hawkins D, Barnes RFW, Mofulu F, Grant RA, Norton GW. 2014. The influence of
624 lunar cycles on crop-raiding elephants; evidence for risk avoidance. *African Journal of*
625 *Ecology* 52:129–137. DOI: 10.1111/aje.12091.
- 626 Hedges S, Gunaryadi D. 2010. Reducing human–elephant conflict: do chillies help deter
627 elephants from entering crop fields? *Oryx* 44:139. DOI: 10.1017/S0030605309990093.

- 628 Hoare R. 2012. Lessons from 15 years of human–elephant conflict mitigation: Management
629 considerations involving biological, physical and governance issues in Africa Richard.
630 *Pachyderm* 51:60–74.
- 631 Hoare RE, Du Toit JT. 1999. Coexistence between people and elephants in African savannas.
632 *Conservation Biology* 13:633–639. DOI: 10.1046/j.1523-1739.1999.98035.x.
- 633 King LE, Lala F, Nzumu H, Mwambingu E, Douglas-Hamilton I. 2017. Beehive fences as a
634 multidimensional conflict-mitigation tool for farmers coexisting with elephants.
635 *Conservation Biology* 31:743–752. DOI: 10.1111/cobi.12898.
- 636 Lahkar BP, Das JP, Nath NK, Brahma N, Sarma PK, Dey S. 2007. *A study of habitat utilization*
637 *patterns of Asian elephant (Elephas maximus) and current status of human elephant conflict*
638 *in Manas National Park within Chirang-Ripu Elephant Reserve, Assam. A technical report*
639 *prepared by Aaranyak.*
- 640 Lamichhane BR, Persoon GA, Leirs H, Poudel S, Subedi N, Pokheral CP, Bhattarai S, Thapaliya
641 BP, de Iongh HH. 2018. Spatio-temporal patterns of attacks on human and economic losses
642 from wildlife in Chitwan National Park, Nepal. *PLoS ONE* 13. DOI:
643 10.1371/journal.pone.0195373.
- 644 Leimgruber P, Gagnon JB, Wemmer C, Kelly DS, Songer MA, Selig ER. 2003. Fragmentation
645 of Asia’s remaining wildlands: implications for Asian elephant conservation. *Animal*
646 *Conservation* 6:347–359. DOI: 10.1017/S1367943003003421.
- 647 Mackenzie CA, Ahabyona P. 2012. Elephants in the garden: Financial and social costs of crop
648 raiding. *Ecological Economics* 75:72–82. DOI: 10.1016/j.ecolecon.2011.12.018.
- 649 MoEF. 2017. Synchronized Elephant Population Estimation India. Ministry of Environment,
650 Forest and Climate Change, Government of India. Available at
651 <http://www.indiaenvironmentportal.org.in/files/file/Synchronized%20Elephant%20Populati>
652 [on%20Estimation%20India%202017.pdf](http://www.indiaenvironmentportal.org.in/files/file/Synchronized%20Elephant%20Populati). (Accessed on 05 January 2020)
- 653 Mukeka MJ, Ogutu OJ, Kanga E, Røskoft E. 2019. Human wildlife conflicts and their correlates
654 in Narok County, Kenya. *Global Ecology and Conservation*. 18:e00620. DOI:
655 10.1016/j.gecco.2019.e00620
- 656 Mumby HS, Plotnik JM. 2018. Taking the Elephants’ Perspective: Remembering Elephant
657 Behavior, Cognition and Ecology in Human-Elephant Conflict Mitigation. *Frontiers in*
658 *Ecology and Evolution* 6:1–8. DOI: 10.3389/fevo.2018.00122.
- 659 Naha D, Sathyakumar S, Dash S, Chettri A, Rawat GS. 2019. Assessment and prediction of
660 spatial patterns of human-elephant conflicts in changing land cover scenarios of a human-
661 dominated landscape in North Bengal. *PLOS ONE* 14:e0210580. DOI:

- 662 10.1371/journal.pone.0210580.
- 663 Neupane D, Johnson RL, Risch TS. 2013. Temporal and spatial patterns of human-elephant
664 conflict in Nepal. In: *2013 International Elephant & Rhino Conservation & Research*
665 *Symposium Proceedings*. 1–11.
- 666 Nyhus PJ, Tilson R, Sumianto. 2000. Crop-raiding elephants and conservation implications at
667 Way Kambas National Park, Sumatra, Indonesia. *ORYX* 34:262–274. DOI: 10.1046/j.1365-
668 3008.2000.00132.x.
- 669 Ogada DL. 2014. The power of poison: Pesticide poisoning of Africa’s wildlife. *Annals of the*
670 *New York Academy of Sciences* 1322:1–20. DOI: 10.1111/nyas.12405.
- 671 Ogutu ZA. 2002. The impact of ecotourism on livelihood and natural resource management in
672 Eselenkei, Amboseli Ecosystem, Kenya. *Land Degradation & Development* 13:251–256.
673 DOI: 10.1002/ldr.502.
- 674 Parker GE, Osborn F V. 2001. Dual season crop damage by elephants in the Eastern Zambezi
675 Valley, Zimbabwe. *Pachyderm*:49–56.
- 676 Pearce EA, Smith CG. 1998. *The Hutchinson world weather guide*. Hutchinson.
- 677 Phillips SJ, Anderson RP, Schapire RE. 2006. Maximum entropy modeling of species
678 geographic distributions. *Ecological Modelling* 190:231–259. DOI:
679 10.1016/j.ecolmodel.2005.03.026.
- 680 Pokharel SS, Singh B, Sukumar R. 2018. Lower levels of glucocorticoids in crop-raiders: diet
681 quality as a potential ‘pacifier’ against stress in free-ranging Asian elephants in a
682 human-production habitat. *Animal Conservation* 22:177-188. DOI:10.1111/acv.12450
- 683 Pozo RA, Coulson T, McCulloch G, StronzaAL, Songhurst AC. 2017. Determining baselines for
684 human-elephant conflict: A matter of time. *PLoS ONE* 12(6): e0178840. [https://doi.org/](https://doi.org/10.1371/journal.pone.0178840)
685 10.1371/journal.pone.0178840
- 686 Riddle H. 2007. Elephant Response Units (ERU). *Gajah* 26:47–53.
- 687 Riddle HS, Schulte BA, Desai AA, Meer L van der. 2010. Elephants - a conservation overview.
688 *Journal of Threatened Taxa* 2:653–661. DOI: 10.11609/JoTT.o2024.653-61.
- 689 Rode KD, Chiyo PI, Chapman CA, McDowell LR. 2006. Nutritional ecology of elephants in
690 Kibale National Park, Uganda, and its relationship with crop-raiding behaviour. *Journal of*
691 *Tropical Ecology* 22:441–449. DOI: 10.1017/S0266467406003233.
- 692 Rodger WA, Panwar HS, Mathur VB. 2000. Biogeographical classifications of India. In:
693 *Wildlife protected area network in India: a review*. Dehradun: Wildlife Institute of India.

- 694 Sekar N, Lee C-L, Sukumar R. 2017. Functional nonredundancy of elephants in a disturbed
695 tropical forest. *Conservation Biology* 31:1152–1162. DOI: 10.1111/cobi.12907.
- 696 Shaffer LJ, Khadka KK, Van Den Hoek J, Naithani KJ. 2019. Human-Elephant Conflict: A
697 Review of Current Management Strategies and Future Directions. *Frontiers in Ecology and*
698 *Evolution* 6:1–12. DOI: 10.3389/fevo.2018.00235.
- 699 Siex KS, Struhsaker TT. 1999. Colobus monkeys and coconuts: A study of perceived human-
700 wildlife conflicts. *Journal of Applied Ecology* 36:1009–1020. DOI: 10.1046/j.1365-
701 2664.1999.00455.x.
- 702 Sitati NW, Walpole MJ, Smith RJ, Leader-Williams N. 2003. Predicting spatial aspects of
703 human-elephant conflict. *Journal of Applied Ecology* 40:667–677. DOI: 10.1046/j.1365-
704 2664.2003.00828.x.
- 705 Sitati NW, Walpole MJ. 2006. Assessing farm-based measures for mitigating human-elephant
706 conflict in Transmara District, Kenya. *Oryx* 40:279–286. DOI:
707 10.1017/S0030605306000834.
- 708 Sukumar R, Gadgil M. 1988. Male-female differences in foraging on crops by Asian elephants.
709 *Animal Behaviour* 36:1233–1235. DOI: 10.1016/S0003-3472(88)80084-8.
- 710 Sukumar R. 1989. Ecology of the asian elephant in southern india. i. movement and habitat
711 utilization patterns. *Journal of Tropical Ecology* 5:1–18. DOI:
712 10.1017/S0266467400003175.
- 713 Sukumar R. 1991. The management of large mammals in relation to male strategies and conflict
714 with people. *Biological Conservation* 55:93–102. DOI: 10.1016/0006-3207(91)90007-V.
- 715 Sukumar R, Venkataraman A, Cheeran JV, Mujumdar PP, Baskaran N, Dharmarajan G, Roy M,
716 Madhivanan A, Suresh HS & Narendran K. 2000. Study of the elephants in Buxa Tiger
717 Reserve and adjoining areas of northern West Bengal and preparation of conservation action
718 plan. Final Report. Bangalore: Centre for Ecological Sciences, Indian Institute of Science.
- 719 Sukumar R. 2003. *The Living Elephants: Evolutionary Ecology, Behavior, and Conservation*.
720 New York: Oxford University Press (OUP).
- 721 Sukumar R. 2006. A brief review of the status, distribution and biology of wild Asian elephants
722 *Elephas maximus*. *International Zoo Yearbook* 40:1–8. DOI: 10.1111/j.1748-
723 1090.2006.00001.x.
- 724 Sukumar R. 2011. *The Story of Asia's Elephants*. The Marg, Mumbai.
- 725 Thomas B, Holland JD, Minot EO. 2008. Elephant (*Loxodonta africana*) Home Ranges in Sabi
726 Sand Reserve and Kruger National Park: A Five-Year Satellite Tracking Study. *PLoS ONE*

- 727 3:e3902. DOI: 10.1371/journal.pone.0003902.
- 728 Thomas B, Holland JD, Minot EO. 2012. Seasonal home ranges of elephants (*Loxodonta*
729 *africana*) and their movements between Sabi Sand Reserve and Kruger National Park.
730 *African Journal of Ecology* 50:131–139. DOI: 10.1111/j.1365-2028.2011.01300.x.
- 731 Tilman D, Clark M, Williams DR, Kimmel K, Polasky S, Packer C. 2017. Future threats to
732 biodiversity and pathways to their prevention. *Nature* 546:73–81. DOI:
733 10.1038/nature22900.
- 734 Venkataraman AB, Saandeeep R, Baskaran N, Roy M, Madhivanan A, Sukumar R. 2005. Using
735 satellite telemetry to mitigate elephant-human conflict: An experiment in northern West
736 Bengal, India. *Current Science* 88:1827–1831.
- 737 van de Water A, Matteson K. 2018. Human-elephant conflict in western Thailand: Socio-
738 economic drivers and potential mitigation strategies. *PLOS ONE* 13:e0194736. DOI:
739 10.1371/journal.pone.0194736.
- 740 Webber CE, Sereivathana T, Maltby MP, Lee PC. 2011. Elephant crop-raiding and human-
741 elephant conflict in Cambodia: crop selection and seasonal timings of raids. *Oryx* 45:243–
742 251. DOI: 10.1017/S0030605310000335.
- 743 Whyte IJ. 2012. The elephant management dilemma. In Schmidt D, Willott E, ed.
744 *Environmental Ethics: What Really Matters, What Really Works*. New York: Oxford
745 University Press, 71–84.
- 746 Wijayagunawardane MPB, Short R V., Samarakone TS, Nishany KBM, Harrington H, Perera
747 BVP, Rassool R, Bittner EP. 2016. The use of audio playback to deter crop-raiding Asian
748 elephants. *Wildlife Society Bulletin* 40:375–379. DOI: 10.1002/wsb.652.
- 749 Wilson G, Desai AA, Sim DA, Linklater WL. 2013. The influence of the invasive weed *Lantana*
750 *camara* on elephant habitat use in Mudumalai Tiger Reserve, southern India. *Journal of*
751 *Tropical Ecology* 29:199–207. DOI: 10.1017/S0266467413000205.
- 752 Wilson S, Davies TE, Hazarika N, Zimmermann A. 2015. Understanding spatial and temporal
753 patterns of human-elephant conflict in Assam, India. *ORYX* 49:140–149. DOI:
754 10.1017/S0030605313000513.
- 755 Zar JH. 2010. *Biostatistical analysis*. Upper Saddle River, New Jersey: Pearson Prentice-Hall.
756 <https://www.census2011.co.in/census/district/1-darjiling.html>. Accessed February 2020.
757 <https://www.census2011.co.in/census/district/2-jalpaiguri.html>. Accessed February 2020.
758 <https://www.census2011.co.in/census/district/3-koch-bihar.html>. Accessed February 2020.
759 <http://www.imd.gov.in> . Accessed April 2020
760

761 Figure 1. Study Area with the distribution of protected areas, rivers and towns
762 Figure 2. Graph displaying relationship between crop raiding frequencies by elephants and monthly
763 rainfall in North Bengal
764 Figure 3. North Bengal landscape with the distribution of protected areas, rice beer production units and
765 elephant crop depredation locations
766 Figure 4. Hotspot of human-elephant conflicts with locations of crop depredation events
767 Table 1. List of all variables considered for spatial risk mapping of human-elephant conflicts
768 Appendix 1. Questionnaire sheet used for recording data on crop depredation by elephants
769 File S1. Details of the analytical procedure for HEC risk mapping
770 Supplementary Figure 1. Receiver operating curve (ROC) for 5 km² Maxent models
771

Figure 1

Study Area with the distribution of protected areas, rivers and towns

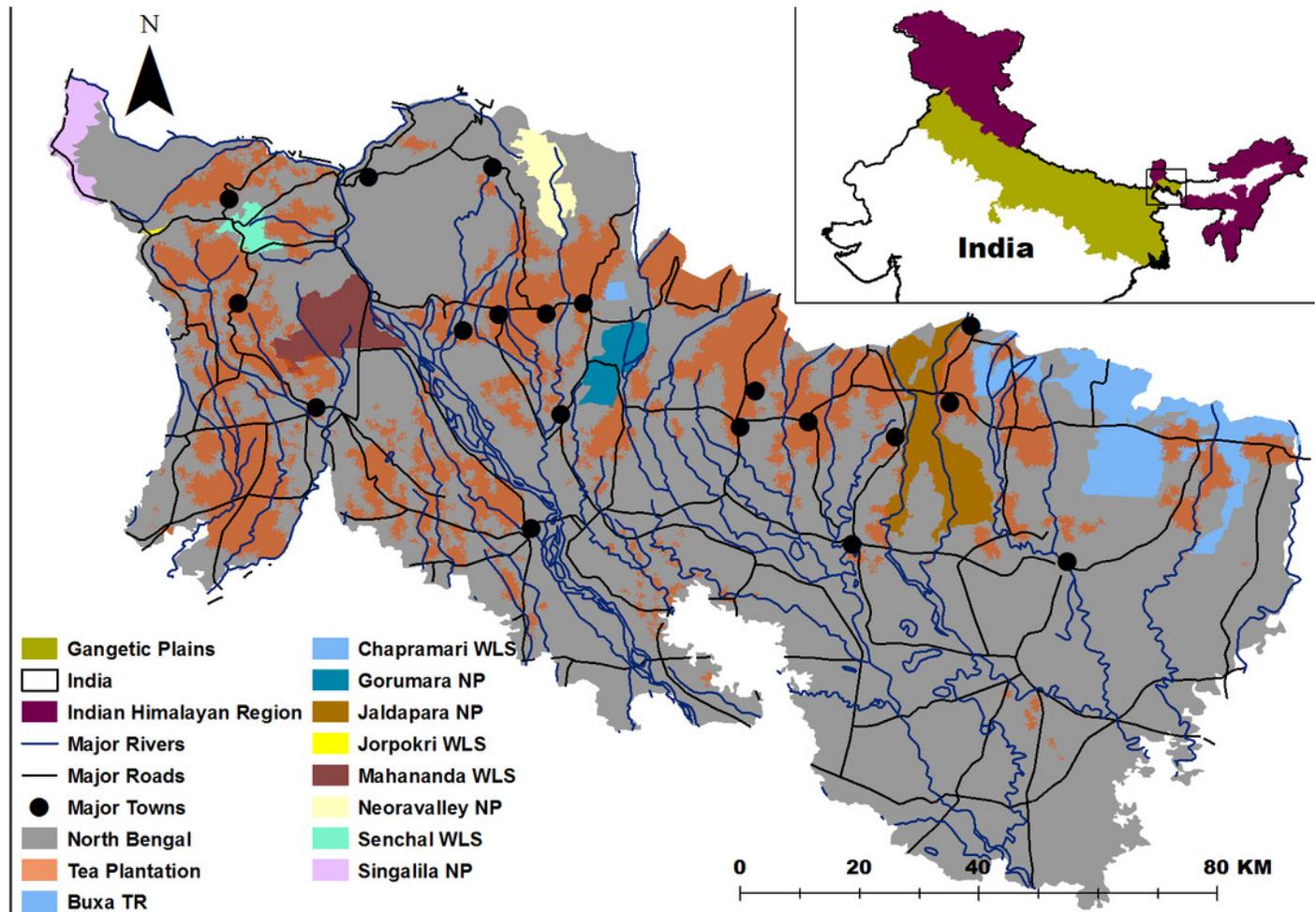


Figure 2

Graph displaying relationship between crop raiding frequencies by elephants and monthly rainfall in North Bengal

Bars denote number of crop depredation events by elephants and line denotes monthly rainfall in North Bengal

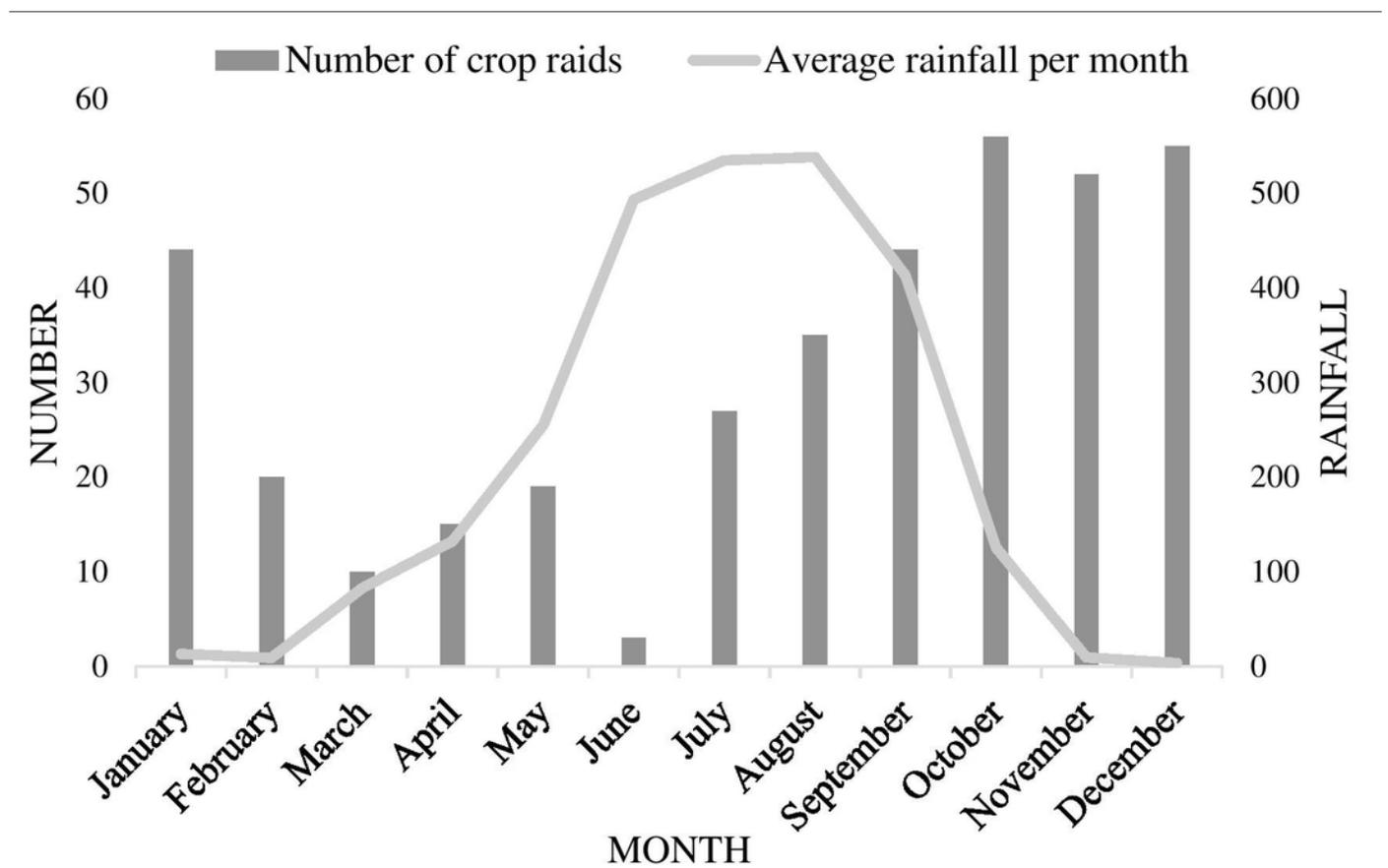


Figure 3

North Bengal landscape with the distribution of protected areas, rice beer production units and elephant crop depredation locations

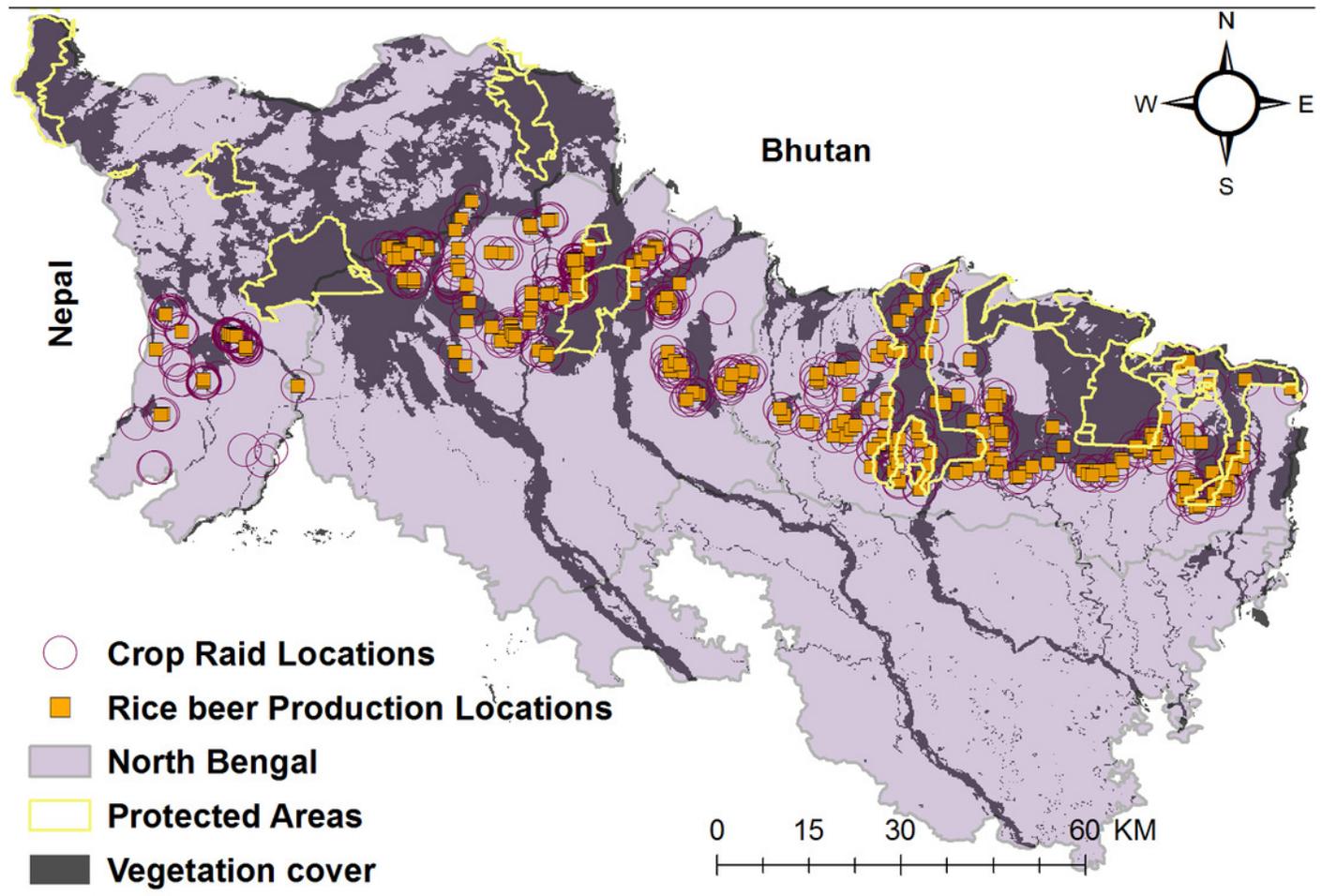


Figure 4

Hotspot of human-elephant conflicts with locations of crop depredation events

