

Article

The Influence of Habitat Changes on Elephant Mortality Associated with Human–Elephant Conflict: Identifying Areas of Concern in the North Central Dry Zone of Sri Lanka

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Abstract: Human–wildlife conflict (HWC) is becoming increasingly prevalent as human activity expands, and monitoring the impact of habitat quality on wildlife mortality related to HWC is critical for the well-being of wildlife and people. Using ten years of necropsies from free-ranging Asian elephants in the Northwestern Wildlife Region (NWR) of Sri Lanka, we quantified the effect of habitat quality on human–elephant conflict (HEC) (i.e., human-caused elephant mortality), hypothesizing that both artificial (e.g., forest cover loss) and natural (e.g., water availability, temperature) changes would be associated with elephant mortality. We collated necropsies from 348 elephants that died due to human activity from 2009 to 2018, comparing the results with data on forest cover loss, perennial water, rainfall, temperature, and human population sizes. Over the study period, we found that forest cover loss was significantly correlated with human-caused mortality in a district-specific manner. Similarly, access to perennial water and precipitation levels appeared to influence mortality, but not temperature, human population density, or percent land cover used for agriculture. We conducted emerging hot spot analyses to identify areas within the NWR that should be prioritized for protection, which included landscapes that are not currently protected (approximately 43% of the hot spots we identified). Similarly, areas that we identified as cold spots included many areas with minimal forest cover loss. Together, our results emphasize the impact that human activity can have on the measurable outcomes of HEC. We suggest that adaptive HWC management strategies that use retrospective analyses should inform any potential changes to the protection of vital wildlife habitats, such as the north central dry zone of Sri Lanka.



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Keywords: anthropogenic activities; Asian elephant; crop-raiding; forest cover loss; emerging hot spot analysis; human–elephant conflict; spatiotemporal statistics

1. Introduction

Negative interactions between humans and wildlife (human–wildlife conflict, HWC) are practically ubiquitous, forming a multi-dimensional problem threatening the well-being of people and the sustainability of many wildlife populations [1–5]. As human activity expands, fewer natural resources are available for wildlife, and HWC worsens in scope and magnitude. Changes in the physical environment can exacerbate this conflict, and so it is imperative that we explore environmental factors that may be associated with HWC.

One factor that may influence HWC is changes to habitat quality, including the physical structure of the environment, access to food and water, and anthropogenic influences. Even in protected landscapes, habitat quality changes over time [6,7], and wildlife managers may monitor variations in habitat availability and quality to predict the extent of HWC in a given area [8]. In this regard, habitats in tropical dry forests are of special concern

because of imminent anthropogenic threats and their high biodiversity value [9,10]. Sri Lanka has been identified as a biodiversity hot spot due to its high degree of species endemism inhabiting its dry forests and its growing human population [11]. Approximately 72% of Sri Lanka is comprised of the “dry zone”, where dry forest vegetation harbors much biodiversity [12–14]. However, Sri Lanka has one of the highest rates of deforestation in Asia [15], largely driven by the clearing of dry forests for farming [16], and more recently by infrastructure enhancement [17]. Land utilized for agriculture as a percentage of total land area ranges from 9% to 61% in the north central dry zone [18]; a significant proportion of agriculture here is slash and burn or shifting cultivation [19]. This involves the cutting and burning of forests at the end of the dry season to create ephemeral agricultural lands that are abandoned after a few years of consecutive use, perhaps enriching available habitats for wildlife because abandoned fields revert to scrub through succession [19]. The transformation of dry forests has been identified as a driver of HWC in Sri Lanka, and Asian elephants (*Elephas maximus*) are predominantly implicated [20,21], commonly causing human–elephant conflict (HEC).

HEC in Sri Lanka encompasses a wide range of negative interactions between humans and elephants, including crop-raiding (perhaps the most common form of HEC), retaliatory killing of elephants by people, and vehicle collisions [22]. All of these forms of HEC involve humans and elephants vying for the same resource(s), namely land, water, and/or food. Asian elephants are endangered [23], and HEC is often fatal for the animals involved, further exacerbating their dire conservation status. Habitat loss and fragmentation further threatens Asian elephants throughout their range [24], exacerbating HEC and compromising local communities that live alongside elephants. Due to their preference for forest edge habitats [25], and because protected areas are reaching their carrying capacities, many elephants regularly come into contact with human activity [26]. While Asian elephants are afforded a high level of protection in Sri Lanka and throughout their range, HEC-related mortality commonly occurs due to the potential negative consequences of elephant activity around people if no action is taken. For example, a single group of elephants can eat and/or destroy an entire year’s yield of a subsistence farming family; these communities thus may be motivated to engage in potentially fatal conflict with elephants if their own safety and/or livelihood is at risk. Human responses to HEC range from intentional persecution (e.g., gunfire, improvised explosives, poisoning) to unintentional reactions (e.g., vehicle collisions). The intentionality of some human responses that are fatal to elephants can vary based on context. For example, electric fences are widely used in Sri Lanka throughout protected and unprotected areas to discourage elephants to move towards people and/or agriculture [25]. While not all electric fences are installed to kill elephants (the consequences for those with dead elephants found on their property are severe according to Sri Lanka’s long-standing Fauna and Flora Protection Ordinance), structures may be connected to power lines and erected by farmers who have been negatively impacted by weaker fences. These structures may become deadly as elephants move across them [27,28]. Elephants can be expected to exhibit short- and long-term behavioral and ecological responses to the whole spectrum of human influences, which reflects the prevalence of HEC [29–32].

Traditionally, conflict with elephants was minimized with land use systems that facilitated cohabitation, including shifting cultivation practices, limited cropping areas, and communal land use patterns [20]. The conversion of forests into “edge habitats” through anthropogenic activities (e.g., agriculture, infrastructure development), other environmental modifications (e.g., artificial water bodies), and human population growth have exacerbated the conflict [21,26,33,34]. For example, elephants are frequently drawn to man-made water bodies in human settlements [33], increasing the chances of human–elephant interaction. In our recent analysis of causes of elephant mortality in the Northwestern Wildlife Region (NWR) of Sri Lanka (predominantly comprised of dry forests), we found that approximately 70% of all elephant deaths were directly or indirectly related to humans [28]. Furthermore, we revealed significant spatial variation in mortality patterns; districts with higher proportions of protected areas also experienced high rates of human-

caused elephant mortality. In addition to differences in human activity in this region, variations in habitat quality may also contribute to the spatial variation in elephant mortality. Because of the Asian elephant's endangered status, it is important to understand how the characteristics of the environment can influence the frequency of HEC and, thus, elephant mortality.

While the existing system of national parks and reserves in the dry zone is integral to the conservation of the Asian elephant, there are a large proportion of habitats with high elephant densities outside this network designated as "Other State Forests" (OSFs) [25]. OSFs are forests that have not been legally declared as protected areas. The governance of these forests was formerly under the Forest Department of Sri Lanka, but recently this has been shifted to regional governments so that they can be utilized for economic development if necessary [35]. Critics of this move suggest changes to OSFs will have negative repercussions for humans and elephants, with a concomitant increase in HEC. To predict the extent of this conflict, it is important to assess historical changes to forested areas outside the existing system of national parks and reserves. Hence, the purpose of this study was to investigate the effect of habitat quality (including natural and anthropogenic factors influencing habitat quality) within and outside protected landscapes on human-caused elephant mortality in a region of the dry zone of Sri Lanka. We combined data on annual elephant mortality in four districts that comprise the NWR with spatial information on forest cover loss, temperature, access to water, precipitation, and human activity to relate spatial variation to the incidence of HEC (i.e., human-caused elephant deaths) over a 10-year span. Any of these factors may be linked to food availability (both natural food sources and human crops), and so we expected they may also influence the frequency of HEC. We hypothesized that both engineered habitat enrichment (such as converting forests for agriculture or other human uses) and physical factors of the environment are correlated with HEC in this region. We also used spatiotemporal statistics (i.e., emerging hot spot analysis) to identify areas of increasing or decreasing concern for HEC based on forest cover loss in the study area from 2009 to 2018. A novel tool for geospatial analyses, emerging hot spot analysis (EHSA) is a spatial tool that can accurately characterize spatiotemporal data [36–38], and we apply it here to mark areas for further protection to promote human cohabitation with elephants. While this analysis did not incorporate elephant mortality data, it complements our other analyses by providing wildlife managers and other stakeholders with predictive tools for habitat management based on recent changes in habitat quality (i.e., forest cover loss). EHSA may be indispensable to identifying areas that have high levels of HEC in the future, indicating places that require management intervention to ensure human cohabitation with elephants.

2. Materials and Methods

2.1. Study Area

The NWR is one of seven wildlife regions recognized by Sri Lanka's Department of Wildlife Conservation (DWC) and experiences some of the highest rates of HWC on the island [39] (Figure 1). There are four districts in the NWR that vary in human population density: Anuradhapura (area = 7343.87 km², human density = 117.18 people/km²), Kurunegala (4702.32 km², 344.21 people/km²), Mannar (729.90 km², 136.40 people/km²), and Puttalam (3210.54 km², 248.18 people/km²) [40]. The area is composed of land devoted to human activity—primarily agriculture—and protected landscapes. In 2009, approximately 3304.74 km² of Anuradhapura was protected (45% of the total area of the district), 611.30 km² of Kurunegala (13%), 452.54 km² of Mannar (62%), and 898.95 km² of Puttalam (28%). In 2012–2013, the Department of Census and Statistics in Sri Lanka estimated that 33.0% of Anuradhapura is used for agriculture, 60.5% of Kurunegala, 9.2% of Mannar, and 37.4% of Puttalam [18].

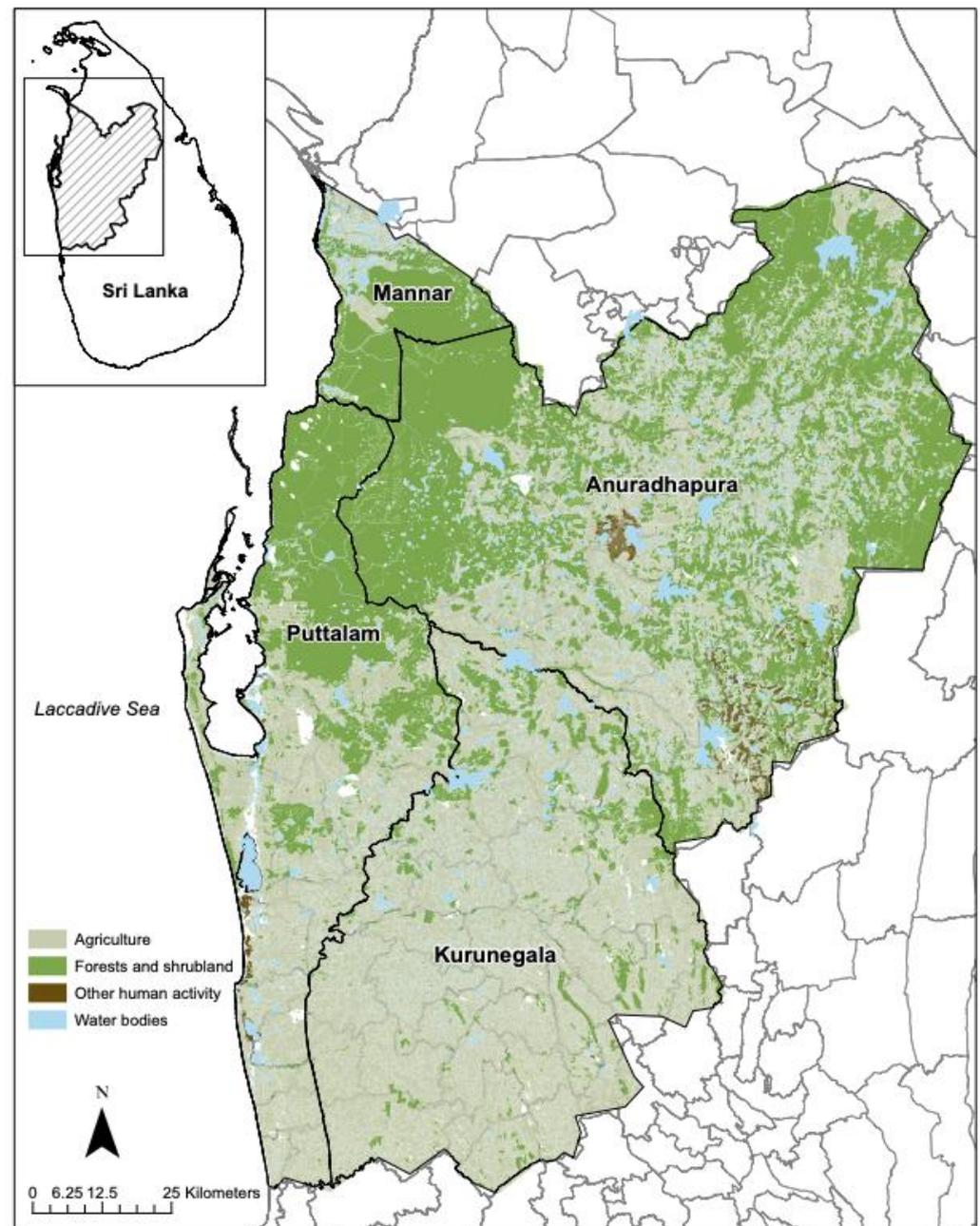


Figure 1. Map of study area, Northwestern Wildlife Region (Sri Lanka), with major patterns of land use indicated. Major forms of agriculture include rice paddies, tea farms, chena cultivation, and coconut plantations. “Other human activity” includes human usage not directly related to agriculture, such as community areas, homesteads and residential areas, and commercial and industrial areas. The Northwestern Wildlife Region encompasses all of Anuradhapura, Kurunegala, and Puttalam districts, and much of Mannar district. Land use data were obtained from the Urban Development Authority of Sri Lanka.

There are two inter-monsoon seasons in the NWR (March to April, and October to November), and between 1000 and 1500 mm of precipitation are recorded annually. Annual temperatures fluctuate between 22.5 and 30.0 °C, and elevation ranges from 8 m to 120 m (Department of Meteorology, Sri Lanka). Forests in the NWR are predominantly dry semi-evergreen forests. The most accurate estimate for the number of elephants inhabiting this region during the study period is 1189 [41].

2.2. Elephant Mortality

It is standard practice in Sri Lanka for veterinarians from the DWC to carry out necropsies on all elephants discovered dead. We collected and collated necropsy information for 498 elephants that died in the NWR from 2009 to 2018, using the detailed methods in LaDue et al. [28]. We could only ascertain the location of each death at the district scale (Anuradhapura, Kurunegala, Mannar, or Puttalam), and we could assign definitive causes of death for 482 elephants. We further classified deaths as human-related mortality events ($n = 348$ elephant deaths) if they were caused intentionally (i.e., by gunshot, improvised explosives, or poisoning; $n = 256$ elephant deaths) or even unintentionally (i.e., electrocution, train or vehicle collisions, landmines, or snares; $n = 92$ elephant deaths) by people.

For this study, we only included human-caused elephant mortality, as we assumed this would reflect the changing levels of HEC over the study period. Additionally, we combined intentional and unintentional mortality into one measure (human-caused elephant mortality) because their annual frequencies were strongly correlated (Spearman's rank correlation test between annual intentional and unintentional mortality events: $\rho_8 = 0.611$, $p = 0.030$), and because unintentional mortality events were less common [28], making quantitative analyses difficult to conduct on their own.

2.3. Environmental Datasets

All spatial datasets were analyzed in ArcGIS Pro v.2.7 (ESRI, Redlands, CA, USA). Data were obtained for the NWR in Sri Lanka using the "Select By Location" tool and selecting the features that partially intersected the NWR boundary. The latest dataset for world protected areas was downloaded from ProtectedPlanet (<https://www.protectedplanet.net/en>, accessed on 1 December 2020). All spatial datasets used the projected coordinate system WGS 1984 Web Mercator Auxiliary Sphere.

2.3.1. Forest Cover Loss

The latest forest cover loss—defined as "stand-replacement disturbance"—raster dataset created by [42] was obtained from Global Forest Watch (<https://www.globalforestwatch.org>, accessed on 1 December 2020) at a 30 m spatial resolution. These datasets are commonly used to accurately map global forest loss [42]. We estimated forest cover loss per year from 2009 to 2018 in the portion of each district that fell within the NWR boundary using the Google Earth Engine, loading the raster dataset into ArcGIS Pro and using the conversion tool "Raster to Point" to obtain representative point data of forest cover loss. We removed any points with a grid code of 0, representing no forest cover loss. A new time field was created from the grid code field using the data management tool "Convert Time Frame" in order to aggregate points into space-time bins for the emerging hot spot analysis. Points were aggregated using the space-time pattern mining tool "Create Space Time Cube By Aggregating Points". We selected "Fishnet Grid" for Aggregation Shape Type and "1 Year" for the Time Step Interval. All other defaults of the tool were accepted.

2.3.2. Water Bodies

The world water bodies ArcGIS layer package was obtained from The World Bank Data Catalog (<https://datacatalog.worldbank.org/home>, accessed on 1 December 2020). This dataset contains open water rivers, lakes, dry salt flats, seas, and oceans, as indicated by the "TYPE" field. Pastorini et al. [33] found that elephants elsewhere in Sri Lanka showed a preference for perennial water bodies. Therefore, we only include perennial inland water bodies in our analysis. The number and area of perennial water bodies in each district are: Anuradhapura ($n = 228$, area = 214.2 km²), Kurunegala ($n = 26$, area = 51.5 km²), Mannar ($n = 6$, area = 14.4 km²), and Puttalam ($n = 63$, area = 66.9 km²).

2.3.3. Rainfall and Temperature

Monthly precipitation, maximum temperature, and minimum temperature datasets were obtained for each of the four districts from Sri Lanka's Department of Meteorology (<http://www.meteo.gov.lk/index.php?lang=en>, accessed on 1 December 2020). For each district, we found the average annual values for each of these statistics using monthly summaries, as the forest cover loss dataset available provided information at this temporal scale.

2.3.4. Human Population and Agriculture

Human population estimates and agriculture prevalence data were obtained from Sri Lanka's Department of Census and Statistics [18,40]. Accurate population census information was only available for 2012 and was obtained at the district level for each of the four districts that comprise the NWR. Similarly, only estimates for the percent of land cover in each district used for agriculture were available during the 2013–2014 growing season. Other measures of human activity (e.g., extent of roads and railroads) were strongly related to human population density and so were excluded from analysis.

2.4. Data Analysis

2.4.1. Correlates of Human-Related Elephant Mortality

For factors related to forest cover loss and perennial water bodies, we standardized measures by the area of each district in km². We investigated inter-district differences in annual forest cover loss with analyses of variance (ANOVAs), elucidating significant differences with Tukey's honestly significant differences (HSD) test. Further, for each district, we analyzed relationships between annual rates of human-related elephant mortality and annual forest cover loss, average annual precipitation, and average annual maximum and minimum temperatures, as we expected any of these factors to be related to HEC. To describe these relationships, we used the non-parametric Spearman's rank correlation coefficient. Due to low sample sizes within each district, we could not use integrative models (e.g., a linear model approach) to analyze the potential interactive effects of these factors. Similarly, only single data points ($n = 4$) in each district for the number/area of perennial water bodies and human-related factors (human population density and percent of land used agriculture) were available over the entire study period, so inter-district differences in elephant mortality related to each of these variables were described qualitatively.

The above statistical analyses were conducted using R version 3.6.3 [43], and plots were generated with the package ggplot2 [44]. p -values ≤ 0.05 indicated statistical significance.

2.4.2. Emerging Hot Spot Analysis

After finding that forest cover loss is correlated with human-caused elephant mortality within the NWR, we carried out emerging hot spot analysis (EHSA) to identify areas undergoing forest cover loss that should be prioritized to mitigate HEC. EHSA is a relatively new analysis method in ArcGIS Pro, and is used to determine spatiotemporal trends within a dataset by identifying statistically significant new, intensifying, diminishing, and sporadic hot and cold spots. The analysis uses the Getis-Ord G_i^* statistic [45] to measure the intensity of the clustering of points, while the Mann–Kendall trend test [46,47] is used to evaluate temporal trends. Studies have used EHSA to determine emerging hot spots of forest loss in threatened landscapes [38], to detect spatiotemporal sentiment/emotion hot spots using geotagged photos [37], and to analyze disease distribution patterns in vulnerable areas [36]. We used EHSA to determine significant hot and cold spots and their underlying patterns of forest cover loss across the NWR in Sri Lanka (Table 1). Hot spots indicate regions of forest cover loss, while cold spots indicate regions of diminishing forest cover loss. p -values ≤ 0.05 indicate statistical significance.

Table 1. Emerging hot spot analysis category definitions for classifying patterns of annual forest cover loss in the Northwestern Wildlife Region of Sri Lanka (2009–2018). Definitions adapted from ArcGIS Pro documentation (pro.arcgis.com, accessed 1 December 2020).

Category Name	Definition
Hot spots	
New hot spot	Statistically significant hot spot only for the year 2018.
Intensifying hot spot	Statistically significant hot spot for 90% of the years, including 2018. The intensity of the clustering of increased forest cover loss within each year is significantly increasing overall.
Consecutive hot spot	Statistically significant hot spot for consecutive run at the end of the study period. This location has never been a statistically significant hot spot prior to the series, and less than 90% of all years are statistically significant.
Sporadic hot spot	On-again then off-again hot spot. Less than 90% of the years have been statistically significant hot spots and none of the years have been a statistically significant cold spot.
Oscillating hot spot	Statistically significant hotspot for the year 2018 that has also been a statistically significant cold spot in a previous year(s). Less than 90% of the years were statistically significant hot spots.
Diminishing hot spot	Statistically significant hot spot for 90% of the years, including 2018. The intensity of the clustering of increased forest cover loss each year is significantly decreasing overall.
Cold spots	
New cold spot	Statistically significant cold spot only for the year 2018.
Intensifying cold spot	Statistically significant cold spot for 90% of the years, including 2018. The intensity of the clustering of decreased forest cover loss within each year is significantly increasing overall.
Consecutive cold spot	Statistically significant cold spot for consecutive run at the end of the study period. This location has never been a statistically significant cold spot prior to the series, and less than 90% of all years are statistically significant.
Sporadic cold spot	On-again then off-again cold spot. Less than 90% of the years have been statistically significant cold spots and none of the years have been a statistically significant hot spot.
Oscillating cold spot	Statistically significant cold spot for the year 2018 that has also been a statistically significant hot spot in a previous year(s). Less than 90% of the years were statistically significant cold spots.
Diminishing cold spot	Statistically significant cold spot for 90% of the years, including 2018. The intensity of the clustering of decreased forest cover loss each year is significantly decreasing overall.

Using the space time cube previously created, we ran the “Emerging Hot Spot Analysis” tool in ArcGIS Pro, accepting all defaults. We used the default neighboring distance (9.63 km) and the default distance interval (1.85 km), resulting in a bin size of approximately 3 km²; this relatively small bin size is appropriate to capture changes in habitat quality even within the smallest home range size reported for elephants in Sri Lanka [48,49].

3. Results

3.1. Correlates of Human-Related Elephant Mortality

Forest cover loss in each NWR district over the 10-year study period is provided in Table 2. There were no inter-district differences in overall annual forest cover loss per km² ($F_3 = 1.172, p = 0.334$). However, when analyzing each district separately over the study period each year, there were significant positive correlations between annual forest cover loss and human-caused elephant mortality in Anuradhapura ($\rho_8 = 0.631, p = 0.050$) and Mannar ($\rho_8 = 0.675, p = 0.032$), but not in the other two districts (Kurunegala: $\rho_8 = 0.015, p = 0.967$; Puttalam: $\rho_8 = 0.192, p = 0.596$) (Figure 2a). These inter-district differences may have been driven by losses of forests within protected areas, as annual forest cover loss

within protected areas differed between the four districts ($F_3 = 1.804$, $p = 0.005$); Tukey's HSD revealed significant differences between Anuradhapura and Mannar ($p = 0.011$), Kurunegala and Mannar ($p = 0.011$), and Puttalam and Mannar ($p = 0.045$). There was a similar significant positive correlation between this annual loss of protected forests and human-caused elephant mortality in Anuradhapura ($\rho_8 = 0.675$, $p = 0.032$) and Mannar ($\rho_8 = 0.651$, $p = 0.042$), and these patterns were not found in the other districts (Kurunegala: $\rho_8 = 0.086$, $p = 0.814$; Puttalam: $\rho_8 = 0.062$, $p = 0.865$).

Table 2. Percent of annual forest cover loss within each of the four districts within the Northwestern Wildlife Region (NWR), Sri Lanka. Percent of overall forest cover loss that was protected is given in parentheses.

Year	Anuradhapura Total % (% Protected)	Kurunegala Total % (% Protected)	Mannar Total % (% Protected)	Puttalam Total % (% Protected)
2009	7.7 (5.2)	1.9 (13.4)	1.0 (45.4)	1.2 (18.8)
2010	1.3 (13.2)	0.4 (8.5)	4.3 (25.9)	2.5 (40.1)
2011	7.0 (6.3)	1.1 (12.8)	3.2 (14.8)	2.0 (27.6)
2012	3.2 (9.0)	5.9 (10.1)	3.8 (58.2)	2.6 (22.7)
2013	2.6 (10.3)	3.3 (12.2)	3.6 (54.4)	2.1 (24.0)
2014	3.2 (11.4)	9.7 (6.5)	5.0 (75.9)	1.6 (15.5)
2015	1.7 (13.5)	1.3 (14.4)	3.4 (41.0)	0.9 (36.0)
2016	5.0 (10.8)	4.8 (13.0)	1.9 (33.3)	3.7 (16.7)
2017	1.2 (20.9)	3.3 (7.7)	0.8 (19.4)	3.1 (17.5)
2018	2.9 (17.1)	4.1 (9.3)	0.3 (40.2)	1.9 (23.2)

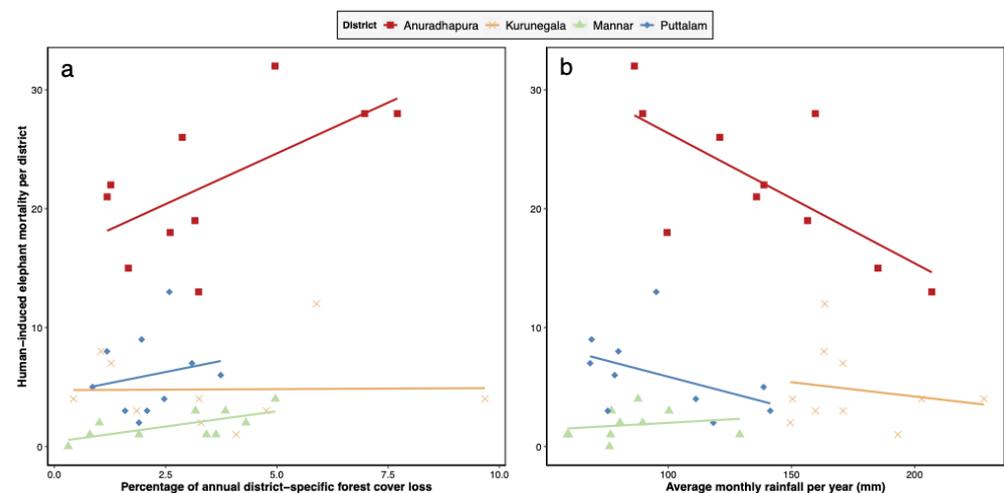


Figure 2. Relationships between (a) annual forest cover loss and human-induced elephant mortality, and (b) average rainfall per year and human-induced elephant mortality, for the four districts that comprise the Northwestern Wildlife Region, Sri Lanka. Points show observed values, with lines showing linear regressions for each district over 2009–2018.

Access to water appeared to be strongly correlated to human-related elephant mortality in one district in the NWR. The average monthly rainfall per year was negatively correlated with human-related elephant mortality in Anuradhapura ($\rho_8 = -0.713$, $p = 0.021$), but not in any of the other districts (Kurunegala: $\rho_8 = -0.184$, $p = 0.611$; Mannar: $\rho_8 = 0.595$, $p = 0.192$; Puttalam: $\rho_8 = -0.452$, $p = 0.190$) (Figure 2b). While there are not enough data to analyze the correlation between the number or area of perennial water bodies and human-related elephant mortality, qualitative comparisons suggest that elephant mortality was highest in the district with the most water bodies (Anuradhapura) and lowest in the district with fewest water bodies (Mannar).

Other environmental factors we suspected may be related to HEC had no strong correlation with human-related elephant mortality. For example, we found no significant correlation between maximum annual temperature (Anuradhapura: $\rho_8 = 0.221$, $p = 0.539$; Kurunegala: $\rho_8 = -0.082$, $p = 0.822$; Mannar: $\rho_8 = -0.125$, $p = 0.731$; Puttalam: $\rho_8 = -0.013$, $p = 0.971$) or minimum annual temperature (Anuradhapura: $\rho_8 = 0.438$, $p = 0.205$; Kurunegala: $\rho_8 = -0.299$, $p = 0.402$; Mannar: $\rho_8 = -0.491$, $p = 0.150$; Puttalam: $\rho_8 = 0.280$, $p = 0.434$) and human-related elephant mortality in any of the four districts across the 10 years of this study. Additionally, while the sample size was low, there was also no apparent relation between human population density in each district and elephant mortality, or between the amount of agriculture in each district and elephant mortality.

3.2. Areas of Concern Revealed by Emerging Hot Spot Analysis

Because forest cover loss was correlated with human-caused elephant mortality, we employed separate EHSA to identify areas of particular concern for HEC mitigation strategies. The data can be found in the Supplementary Material. EHSA revealed 3004 bins (approximately 9012 km²) that were statistically significant oscillating hot spots (38.00%), new hot spots (0.60%), sporadic hot spot (0.03%), sporadic cold spots (9.89%), oscillating cold spots (9.45%), diminishing cold spots (0.27%), intensifying cold spots (0.10%), new cold spot (0.03%), and consecutive cold spot (0.03%) (Figure 3). Additionally, 1250 (41.60%) bins detected no pattern. Of the bins that were significant, 692 (23.00%) fell completely or partially within protected areas. In total, 43.79% of hot spots ($n = 303$) are currently unprotected, compared to 19.36% of cold spots ($n = 134$). Two protected areas contained new hot spots: Kahalla Reserved Forest and Hurulu Forest Reserve. The largest clusters of statistical significance were comprised of oscillating hot spots followed by sporadic cold spots and oscillating cold spots.

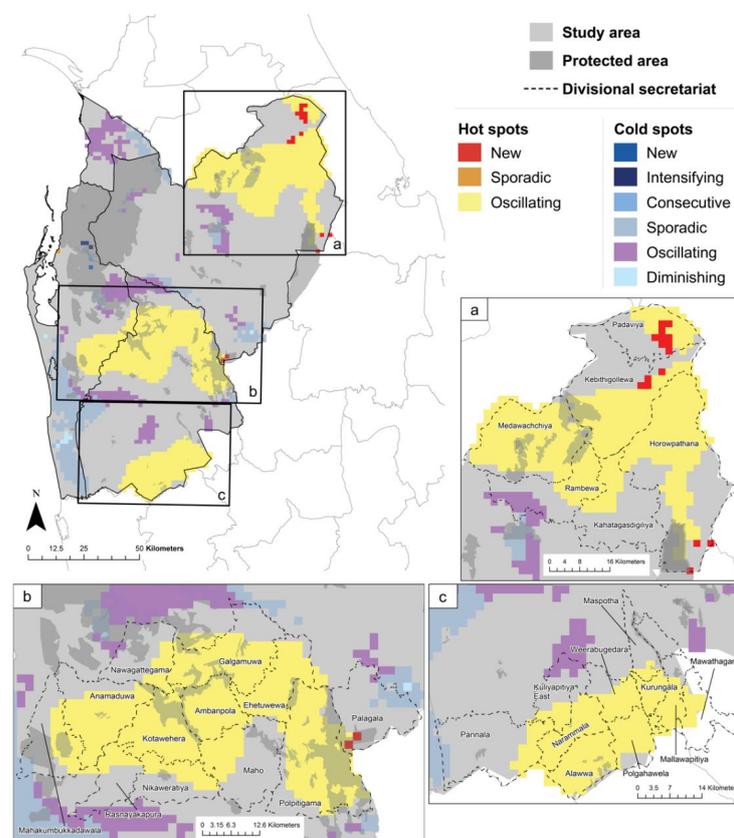


Figure 3. Results of emerging hot spot analysis for Northwestern Wildlife Region of Sri Lanka from 2009–2018, with areas of interest labeled in panels (a–c). Refer to Table 1 for definitions of hot and cold spot categories.

All new hot spots fell within Anuradhapura ($n = 18$, approximately 54 km²). Kurunegala had the most bins categorized as a hot spot ($n = 570$, 1710 km²) followed by Anuradhapura ($n = 516$, 1518 km²) and Puttalam ($n = 109$, 327 km²). However, Mannar had no bins categorized as a significant hot spot. Clusters of oscillating hot spots within Anuradhapura ($n = 498$, 1494 km²) are composed of the following areas: Padaviya, Kebetigollewa, Medawachchiya, Horowpathana, Rambewa, and Kahatagasdigiliya. The oscillating hot spot cluster that exists in Puttalam ($n = 108$, 324 km²) and Kurunegala ($n = 570$, 1710 km²) was found primarily in Galgamuwa, Ehetuwewa, Anamaduwa, Kotawehera, Nikaweratiya, and Polpitigama. The southern cluster of oscillating hot spots within Kurunegala was found primarily in Narammala, Alawwa, Weerabugedara, Polgahawela, Kurungala, and Mallawapitiya.

4. Discussion

Our results suggest that habitat quality, including changes by humans, affects HEC in the NWR of Sri Lanka. These retrospective analyses indicate that future habitat modifications—such as those that may occur with shifting governance of OSFs in this area of Sri Lanka [35]—could exacerbate the problem of HEC. While fine-scale spatial records of elephant mortality were unavailable, inter-district differences in human-caused mortality (an indicator of HEC) from 2009 to 2018 support this claim. For example, in Anuradhapura and Mannar—but not Kurunegala or Puttalam—forest cover loss was correlated with human-caused elephant mortality. These inter-district differences could have been driven by the loss of forest cover in protected areas (forest cover loss within protected areas was also correlated with elephant mortality in these two districts), indicating that maintaining protected habitats is critical to reducing HEC. Still, the ranging patterns of elephants are large, and the boundaries of protected areas are often porous. As a result, elephants navigate landscapes that encompass both natural and human-dominated areas [26,50], resulting in HEC. Crop type, availability, and seasonality can result in temporal variation in HEC where agriculture borders protect areas [51–53].

Additionally, inter-district differences in the number of water bodies within the NWR appeared to be linked to rates of HEC. Access to water has been shown to strongly influence elephant movement patterns [33,54–58]; water availability may also drive elephants closer to people, thus promoting HEC. For instance, both the number and area of perennial water bodies in each district strongly predicted rates of human-caused elephant mortality. Much of the agriculture that takes place in the NWR also depends on these water bodies for irrigation [59], and so this result may suggest that human-caused elephant mortality is more prevalent around agricultural areas. Similarly, elephant mortality was more common in Anuradhapura during years with less precipitation. If natural vegetation and water sources used by elephants are less available during years with low precipitation, this could mean that elephants may have relied on crop-raiding and utilized manmade perennial water bodies during these years, resulting in higher mortality rates. Other studies have found opposite effects of rainfall on HEC in other areas. While droughts can change the vegetation structure available to elephants and even cause starvation in some populations [60,61], these events may also intensify elephants' propensity to raid crops [62]. Sri Lanka does not experience intense droughts, but contextualizing our findings with other studies indicates that changes in water availability may impact HEC in unpredictable ways. This study and others like it that investigate the environmental correlates of HWC serve to inform mitigation strategies by relating long-term patterns of HWC to spatial and temporal variations in habitat quality.

We employed EHSA to complement our other analyses based on elephant mortality patterns, revealing particularly concerning areas for forest cover preservation. There was clustering of cold spots around some protected areas, illustrating that the protection of these landscapes resulted in overall decreased forest cover loss during the study period. However, there were also larger areas of clustered oscillating hot spots spanning the Anuradhapura, Kurunegala, and Puttalam districts, indicating that habitat preservation in

these locations should be prioritized. The majority of these bins were not within protected areas; this pattern of forest cover loss is nevertheless disturbing, as the majority of these hot spots surround protected areas that may act to connect protected habitats, and elephants in Sri Lanka frequently utilize these non-protected habitats [26,33]. The further degradation of these habitats—which also act as buffer zones between elephants and humans—would be detrimental to all stakeholder groups in the region if HEC increases. The areas that we identified as hot spots for forest cover loss closely mirror other studies that have identified particular locations in Sri Lanka where HEC is most prevalent [26,39], further illustrating their importance in HWC mitigation strategies. Combined with our other results, we suggest that this evidence links habitat modification to rates of HEC in Sri Lanka's NWR, and further modifications in the interest of agriculture and/or development at the expense of habitat quality will result in increased HEC. We suggest that EHSA may be a useful tool for wildlife managers in Sri Lanka and elsewhere so that they can identify areas of concern for HWC based on spatiotemporal changes in habitat quality.

The results of this study also underscore the importance of adaptive wildlife management strategies that consider regional variation. It is clear that inter-district environmental variability is associated with variations in human-induced elephant mortality between districts in this study. Accurate estimates of human population density and agricultural activity within each district at fine spatial and temporal scales were unavailable, but approximations suggest that neither human population density nor proportion of land devoted to agriculture are alone predictive of total human-caused elephant mortality. Further, the causes of mortality (e.g., gunfire, electrocution, poisoning, vehicle or train collisions) did not differ between the NWR districts over the study period [28]. Instead, the indirect impacts of human activity (including forest cover loss and perennial water bodies that may include artificial sources) are sufficient to have measurable effects on wildlife mortality from increased HEC. Therefore, changes in the physical structure and/or the protection status of landscapes in Sri Lanka and elsewhere are likely to impact the prevalence of HWC in the future.

The global trend in the prioritization of economic development over the protection of natural resources complicates efforts to reduce HWC, further jeopardizing the conservation of threatened species [4]. While we do not advocate abandoning the well-being and prosperity of local people in the interest of wildlife, ignoring the needs of native animal populations will certainly increase the frequency and/or intensity of HWC, ultimately incurring a cost for people. True coexistence of people and wildlife—whereby each party can consume resources without interference from the other—may be unfeasible in Sri Lanka [26,63]. In this regard, a “national park strategy” that seeks to separate wildlife from people is insufficient to reduce HWC. However, adaptive management strategies that afford certain degrees of protection to surrounding habitats may function to complement national parks and address HWC in specific localities, such as those we identified with EHSA. This investigation provides both an example of how habitat quality and human activity can impact HWC, and a call to more effectively manage elephants in Sri Lanka in light of recent changes in land governance. Most notably, shifting the oversight of OSFs to local governments [35] may negatively impact both elephants and humans through increased HEC for reasons we have illustrated here, and indeed, it is counterproductive to sustaining elephant populations through the efforts outlined in Sri Lanka's 2019 National Policy on the Conservation and Management of Wild Elephants. Instead, we suggest that studies such as this one, which predict the impact of habitat modifications on elephants and other wildlife, should guide policy that addresses HWC. OSFs seem to be important tools for mitigating HWC in Sri Lanka (e.g., by creating buffer zones between undisturbed habitat and areas of human activity). “Conservation spaces” may be formed with a combination of protected areas, OSFs, and abandoned habitations, leaving regions outside of these spaces for human development. Without OSFs and similar buffers, national parks and other protected areas become isolated, limiting dispersal options for wildlife and thereby

increasing HWC. Our study underscores the importance of these areas; eliminating OSFs limits wildlife management options that can curb HWC.

Supplementary Materials: The EHSA GIS layers we created during our analyses are available online at <https://www.mdpi.com/article/10.3390/su132413707/s1>.

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