

**SOCIO-ECOLOGICAL FACTORS DRIVING THE
POPULATION OF STRIPED HYAENA (*HYAENA HYAENA*)
IN THE WESTERN AND EASTERN GHATS PART OF
TAMIL NADU, SOUTHERN INDIA**

**Thesis submitted to Bharathiar University in partial fulfillment of the requirements for
the award of the degree of**

DOCTOR OF PHILOSOPHY IN ZOOLOGY

by

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(Reg. No: 22710/B1/ 2019)

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TAMILNADU, INDIA

December 2024

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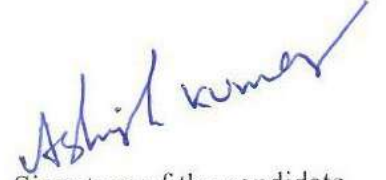
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Glossary

GLOSSARY

AITM	All India Tiger Monitoring
BTR	Biligiri Ranganathaswamy Tiger Reserve
CCMB	Centre for Cellular and Molecular Biology
CNWLS	Cauvery North Wildlife Sanctuary
DistRiver	Distance to River (in meters)
ESA	Extensive Study Area
FEC	Faecal Egg Count
FGC	Faecal Glucocorticoids
GBH	Girth at Breast Height
GCs	Glucocorticoid
GPS	Global Positioning System
HCC	Human-Carnivore Conflict
HFP	Human Footprint
HPA	Hypothalamic-Pituitary-Adrenal
ISA	Intensive Study Area
IUCN	International Union for Conservation of Nature
LULC	Land Use Land Cover
MDA	Mean Decrease Accuracy
MTR	Mudumalai Tiger Reserve
mtry	Number of variables randomly sampled at each split (Random Forest)
NA	Not Applicable
NBR	Nilgiri Biosphere Reserve
NSAIDs	Non-Steroidal Anti-Inflammatory Drugs
nTree	Number of Trees (Random Forest)
OOB	Out Of Bag
PAs	Protected Areas
PDP	Partial Dependency Plot
RFs	Reserve Forests
ROC	Receiver Operating Characteristics
RSGRs	Region-specific Global Responses
SNS	Sympathetic Nervous System
STR	Sathyamangalam Tiger Reserve

UNESCO	The United Nations Educational, Scientific and Cultural Organization
UTM	Universal Transverse Mercator
WEGPTN	Western and Eastern Ghats part of Tamil Nadu

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Summary

Summary

Western and Eastern Ghats part of Tamil Nadu (WEGPTN) is an important area of “Nagarhole-Bandipur-Wayanad-Mudumalai-Sathyamangalam-Biligiri Ranganathaswamy Tiger Reserve complex” identified for the conservation of large mammals in Southern India. This is the largest contiguous forest in the Western Ghats that supports significant populations of tiger (*Panthera tigris*), leopard (*Panthera pardus*), dhole (*Cuon alpinus*), and their prey species. Many studies have been conducted on these species from the WEGPTN but detailed studies on the striped hyaena (*Hyaena hyaena*) are lacking while there are large patches of suitable habitat available for the species in this landscape. Striped hyaena is one of the least studied carnivores, and only meagre information is available on its ecology and current population distribution. The landscape has drastically changed over time due to the rise in human activities. This human-wildlife interaction often results in livestock predation by carnivores and subsequent retaliatory killing of predators. Such interactions have emerged as pressing threats to the existence of carnivores in this landscape. While minimal information is available on hyaena-human interactions from other regions, there is little information available on this crucial aspect of this landscape. Human-induced changes and stochastic changes in the ecosystem can also have an impact on habitat selection and distribution of species. Over time, the distribution of hyaenas has been shrinking in the landscape, hence a complete understanding on the patchy distribution patterns of the species is much needed from this landscape. Therefore, realizing the need for critical information on the species from Protected Areas (PAs) and Non-PAs of WEGPTN, this comprehensive study was conducted with the following three distinct objectives 1) Examine the role of socio-economic characteristics and livestock predation on the prospect of striped hyaena conservation in a high human-carnivore conflict landscape, 2) Assess co-predator interaction in the breeding habitat of striped hyaenas, and 3) Prioritize potential suitable habitats for striped hyaena conservation.

Prior to the collection of objective specific data, the first potential habitats available in WEGPTN were identified based on the occurrence records of the species from secondary sources such as forest department census data, newspaper reporting, and published-unpublished literature. Subsequently, potential hyaena distribution areas were marked as an Extensive Study Area (ESA), predicted through a preliminary species distribution model, calibrated using secondary data. The identified ESA includes Mudumalai Tiger Reserve (MTR), Sathyamangalam Tiger Reserve (STR), Cauvery North Wildlife Sanctuary as well as

Gudalur, Nilgiris, Coimbatore, Erode, Dharmapuri, and Hosur Forest Divisions. The ESA was further surveyed through camera traps in conjunction with indirect sign surveys, and current distribution ranges were ascertained in the landscape. The entire study area was divided into 5x5 sq km grids and 2.5x2.5 sq km sub-grids to stratify our sampling efforts systematically throughout the ESA identified. During the field survey, 248 grids on 2 km trails were covered to collect information on current species occurrence along with its co-predators and prey species through indirect sign surveys. The current occurrence record of the species was supported by photographic evidence from 194 camera traps placed across seven forest divisions of ESA, with an effort of 4975 trap nights. We recorded a small population of the species in this landscape which is confined to a small geographic area (314 sq. km). The current distribution of the species majorly lies in the Sigur and Moyar valleys comprising Bhavanisagar range of STR, and Masinagudi, Sigur, and parts of the Nilgiri Eastern Slope ranges of MTR deemed to be intensive study area (ISA) for further detailed studies.

To assess the temporal variation in livestock depredations by striped hyaenas, 197 open-ended semi-structured questionnaire surveys were conducted in and around the delineated ISA areas. The surveys were conducted in Tamil with the help of local field assistants to collate information on the incidences of livestock predation by striped hyaena. Information on the socio-economic attributes of people, details on conflict with other carnivores, and people's perceptions towards hyaena were also collected at the household scale. Overall, 69.54% (n=137) of people were uncertain about the predatory behavior of hyaenas whereas 07% (n=14) of respondents perceived hyaenas as a threat to their livestock and 23% did not perceive hyaena as a threat. Hyaena was alleged in only eight cases for depredation (six goats, two dogs) while 237 separate incidences of depredations by other large carnivores were reported. Despite the low level of livestock depredation by hyaena, 20.81% of the respondents were found to be not in support of hyaena conservation in their vicinity, and had negative conservation attitudes towards the species. Such an unjustified intolerance for this small population is really a matter of concern. Similarly, such intolerance has been reported for many less-inflicting carnivores throughout the globe. So far, there was no cogent justification present for such unproportionate intolerances. This is presumably because perception in this domain has been predominantly understood as a function of socio-economic status of people and associated cost-benefit with the species. Human cognition also plays a seminal role in such decision-making which has been merely explored. Furthermore, fear-induced generalization of threats to non-inimical stimuli is a common behavioral tendency of humans that seeks

minimizing exposure to potential threats. It is evident that people generalize fear of predation and subsequent intolerance to non-obligate carnivores despite the disparity in predation rate by species in human-carnivore conflict zones. The threat-generalization was investigated as an effect of a perceived threat of livestock depredation by obligate large predators on the tolerance level and perception towards striped hyaena in a human-carnivore conflict hotspot. Tolerance levels of people were modeled as a function of loss to livestock predation, livestock disease, perceived threat of predation by hyaena, and other socio-economical attributes at the household scale, through a random forest algorithm. The study established the interplay between threat generalization and economic instability mainly articulated with livestock predation, occupation, and cattle mortality due to disease and also underscored the role of ambiguous perception (uncertainty) in the ill-generalization. The study documented the prevalence of fear-induced generalization over a non-obligate predator like hyaena. The economic loss due to livestock predation by carnivores was the most important variable in explaining the conservation attitude of people and the same was reflected in measures of variable importance. The partial dependency graph of the random forest model showed a decreasing trend in the conservation attitude of people toward hyaena with the increase in economic loss to livestock predation by co-occurring large carnivores. The variable importance showed other top variables of the model were livestock dependency, number of people employed, annual income, age, loss to disease, and the threat to hyaena.

Through 248 sign survey trails and camera trapping with an effort of 4975 trap nights, the population of hyaena was found to be confined to the Moyar Valley and Sigur plateau in a large landscape of WEGPTN. The restricted distribution of hyaena limited the potential of the third chapter to study intricate phenomena like species interaction which data-hungry endeavor with the limited dataset. Therefore, to get a better understanding of spatial interaction between the species the objective was extended to Shivalik, Central India-Eastern Ghats, and Western Ghats landscapes designated under all India Tiger Monitoring exercise. These landscapes are the tiger conservation landscapes where hyaena along with tiger and leopards are found. The primary aim of the extension was to gain a more comprehensive understanding of spatial avoidance or co-existence using a large data set available from All India Tiger Monitoring reports and also under if hyaena response to predators are stationary in nature or vary with the landscape. Under this objective data on presence-absence of hyaena, chital, leopard, and tiger were digitized from All India Tiger Monitoring reports in ArcGIS from all three landscapes. At the country level, the digitization resulted in presence-absence data from 14,064 locations for each species.

Candidate random forest models were calibrated for each landscape separately as a function of prey, predators and other biogeoclimatic variables identified through literature surveys. Apart from regional candidate models, a global random forest model was trained on the combined dataset from all the landscapes and with consistent parameters as of the regional model. There is an increase in macroecology to study ecological spatial patterns and the global random forest model was fit to test if the model can accurately predict regional response of hyaena to independent variables. Hyaena occurrence in space was found to be independent from the occurrence of tigers and leopards as no significant relationships between hyaena and predators were observed across the landscapes. However, a weak positive relationship between Hyaena and leopard was observed in Central India. Instead of top-down control, the spatial occurrence of hyaena was differentially determined by other biogeoclimatic variables such as population density, mean diurnal range, precipitation seasonality, etc across the landscapes. Despite finding no overall effect of predators on the scavenger space selection, significant differences in the statistical properties of scavenger responses (non-stationarity) were observed across the landscapes. This is the first study to examine the top-down effects on hyaenas at such a broad scale. Additionally, it also heuristically demonstrates the effectiveness of a global random forest model in predicting context-dependent species-environment responses using a region-specific global response approach (RSGRs). This underscores the critical role of variable interactions in addressing non-stationarity in ecological studies. As such, the study calls for reconsidering criticisms of the random forest model's presumed static behavior, which inherently accounts for variable interactions. This study also further advocates for methodological advancements that allow for the prediction of differential limiting factors within a single modeling framework, addressing a key limitation of existing approaches. Such advancements would make the algorithm more robust in addressing non-stationary ecological phenomena, such as habitat selection and top-down control, ultimately enabling more efficient wildlife management by addressing data deficiencies at the micro-scale and non-stationarity at the macro scale.

The fourth chapter assesses available suitable habitats for hyaena conservation by analyzing hyaena occurrences as a function of biogeoclimatic factors, prey, and predators. Presence-absence data for hyaenas, tigers, leopards, dholes, and their prey were collected through 248 sign survey trails and 4975 trap nights of camera trapping. Using a random forest algorithm, hyaena distribution was modeled locally as a function of key ecological variables, including climate, prey abundance, and the predicted occurrence probabilities of other large carnivores.

About 21% of the study area was identified as a highly suitable hyaena habitat. Elevation, Bio3, cattle density, and probabilities of chital and dhole occurrences were influential in determining hyaena distribution. In these contiguous forested landscapes, striped hyaenas were confined to relatively small, discrete areas compared to the other three predators, likely a mechanism for coexistence at smaller spatiotemporal scales and continued persistence at larger scales. The most supported model suggested that hyaenas tended to avoid areas where other large predators were more likely to occur. Relatively more arid conditions, complex topography, and differences in the relative abundance of potential prey were primary drivers of these “opportunity gaps” for hyaenas. Striped hyaenas were also observed at relatively lower abundances than their co-predators, likely balancing the trade-offs between optimizing carcass acquisition and managing risks associated with living alongside larger carnivores. Furthermore, hyaenas chose to coexist in areas with low to medium relative abundances of co-predators. We found that “altitudinal heterogeneity” in plateau regions between mountain ranges may provide more denning opportunities or refugia for hyaenas, facilitating coexistence. The association between striped hyaenas and sub-optimal thorn forests probably contributes to landscape-scale sympatry, as other large predators are less common in these habitats. Predicted areas such as Masinagudi and the Coimbatore Forest Division were identified as priorities for hyaena conservation, as they are contiguous with the current hyaena distribution range and have a high protection status.

In the research work, the population of hyaenas was found to be confined to a small region of Moyar Valley, and hyaena habitat was characterized by dry arid climatic, scrubland, close to human settlements and undulating mountain slopes. Mountain ridges and suboptimal dry habitats provide competition refugia to hyaenas and facilitate the co-existence of the species with other co-predators in the landscape. However, the empirical results of the study suggest no impact of large predators on space selection by hyaena and propose the need for detailed study through abundance data. The study also suggested the impact of limiting factors on habitat selection by hyaena can also be nonstationary in space, analyzing country-level data, and recommended that its consideration in further studies on hyaena. Hyaenas in WEGPTN were found to be also vulnerable to ill generalization of threat under high economic stress caused by cooccurring large predators like tiger and leopard. The generalization is a potential threat to the species and the study recommends more awareness programs, and quick compensation schemes as mitigation measures. Furthermore, the population is confined and vulnerable to the threat of extinction, and therefore, close and regular monitoring of the species, their dens, and further detailed studies would be key to their conservation.

Chapter 1

Chapter 1: Introduction



The Western and Eastern Ghats part of Tamil Nadu (WEGPTN) is an important area of the "Nagarhole-Bandipur-Wayanad-Mudumalai-Sathyamangalam-Biligiri-Ranganathaswamy Tiger Reserve (BRT) complex," identified for the conservation of large mammals in Southern India (Qureshi *et al.* 2023). This is the largest contiguous forest patch in the Western Ghats that supports significant populations of tiger (*Panthera tigris*), leopard (*Panthera pardus*), dhole (*Cuon alpinus*), striped hyaena (*Hyaena hyaena*), and their prey species (Jhala *et al.* 2020). There are few studies available on habitat suitability, den-site selection, and species interaction based on few records on hyaena from other parts of India but detailed studies on the striped hyaena from WEGPTN were lacking (Bopanna 2013; Wagner 2006). The striped hyaena, which is predominantly a scavenger species, is one of the least studied carnivores, and only meager information is available on its ecology and current population distribution (Wagner 2006). The landscape conformation has drastically changed over time due to the rise in human activities. This human-wildlife interaction often results in livestock predation by carnivores and subsequent retaliatory killing of predators (Karanth & Madhusudan 2002). Such interactions have emerged as pressing threats to the existence of carnivores in this landscape (Ramesh *et al.* 2020). Some information is available on Hyaena-human interactions from other regions (Wanger 2006; Bopanna 2013), while there was no information available on this crucial aspect from this landscape. Human-induced changes, large predator-centric forest management, and stochastic changes in the ecosystem can also have a severe impact on habitat selection and distribution of species. Such alterations, coupled with the high risk of negative interspecific interaction with recovering populations of its super ordinates like tiger, leopard, and dhole, may be strongly associated with the decreasing population of the species throughout its distribution ranges. However, most of the observed decline in the species population has been mostly attributed to anthropogenic threats, and there were no systematic studies available assessing the effect of top-down control on the scavengers (Alam *et al.* 2009). Furthermore, there are few field observations available indicative of the potential negative impact of large predators, and therefore, considering the knowledge gap as well as supportive field observations, this study explored the role of sympatric carnivores in the conservation of Hyaenas.

The focal population of the species is the last remaining major breeding population of Southern India, and since the population is confined to a small geographic area, it is highly vulnerable to extinction due to inbreeding depression and any unpredictable catastrophic events. Therefore, it is crucial to understand the relationship of the population with the different biogeoclimatic components constituting its habitat so that suitable habitats for the species can be identified. Realizing the need for critical information on the species from Protected Areas (PAs) and Non-PAs of WEGPTN, this comprehensive study was conducted.

1.1 Literature Review

1.1.1 Evolution and history of hyaenas

Hyaenas have dominated the Miocene and are believed to be the most diverse group in the order Carnivora. Evolutionary genetic studies suggest that hyaenas stemmed from feliforms about 25 million years ago in the Oligocene (Werdelin & Solounias 1991; Koepfli *et al.* 2006). In the late Miocene, the family had radiated into 20-30 species occupying a major portion of the globe including Australia, Asia, Africa, Europe, and North America (Werdelin & Solounias 1991). Later, Hyaenidae experienced a precipitous decline and turned out to be the least diverse family of Carnivora with only four living extant. These four extant are Spotted hyaenas (*Crocuta crocuta*), Brown hyaenas (*Parahyaena brunnea*), Aardwolves (*Proteles cristata*) and Striped hyaenas (*Hyaena hyaena*) (Figure 1.1). Both Spotted hyaenas and Brown hyaenas are monotypic species and found only in Africa. Spotted hyaenas are widely distributed in sub-Saharan Africa and Brown hyaenas are confined mostly to South African countries. There are two subspecies of Aardwolf classified into East African Aardwolf and South African Aardwolf (Figure 1.1). Analogous to its name the East African Aardwolf is distributed in the eastern part of Africa while another one to the southern part of Africa. Striped hyaenas are the most widely distributed species among the family and paleontological evidences suggest that it was also present in Britain and the Pyrenees (Ewer 1955). Striped hyaenas are found outside Africa and native to 41 countries, distributed in the northern and eastern parts of Africa extending to India including some important areas of the Middle East like Syria, Arabs, and Israel (AbiSaid & Dloniak 2015; Castelló 2020) (Figure 1.2). The species is further classified into five species namely Barbary striped hyaena, East African striped hyaena, Syrian striped hyaena, Arabian striped hyaena, and Indian striped hyaena (Figure 1.1). Among these Barbary striped hyaena and East African striped hyaena are distributed in the Northern and eastern parts of Africa.

While Syrian striped hyaena and Arabian striped hyaena are found in the Middle Eastern countries, Indian striped hyaenas dominate the scavenging niches in India and Pakistan (AbiSaid & Dloniak 2015).

1.1.2 General description of striped hyaenas

Striped hyaena was the foremost species that was described in the family by Linnaeus as *Canis hyaena* in 1758. Because of its eco-morphological resemblance with canids, preliminarily it was categorized under the Canidae family. Subsequent studies after the description ascertained the proximity of the hyaenas more towards felids than canids but the species was categorized in a new genus *Hyaena* of the Hyaenidae family in 1762 by Brisson (Jenks & Werdelin 1998). The striped hyaenas are the least studied species of the family. The weight of an adult individual of the species varies from 30– 35 kilograms (Watts & Holekamp 2007) weighing less than a spotted hyena. The species shows no anthropometrical sexual dimorphism, particularly with body weight and size (Rieger 1981), although Watts & Holekamp (2007) suggest that males are larger in body size compared to their female counterparts. Striped hyaenas are primarily scavengers of flesh and bones from carcasses but are also known to raid farmlands occasionally. The dentition and well-developed sagittal crests have evolved to crush hard and dry bones. With due time, the species adopted specific physiological mechanisms, like specialized digestive and enhanced immune systems that help them to digest pathogen-rich old and decaying carcasses (Blumstein *et al.* 2017; Westbury *et al.* 2021). These adaptations probably have evolved in a dearth of fresh food availability or under high interspecific competition. Selection pressures in such a circumstance may have pragmatically also led to olfactory specialization in the species that aids in locating carcasses.

Hyenas of the World

From Felids and Hyenas of the World
José R. Castelló, Princeton University Press, 2020

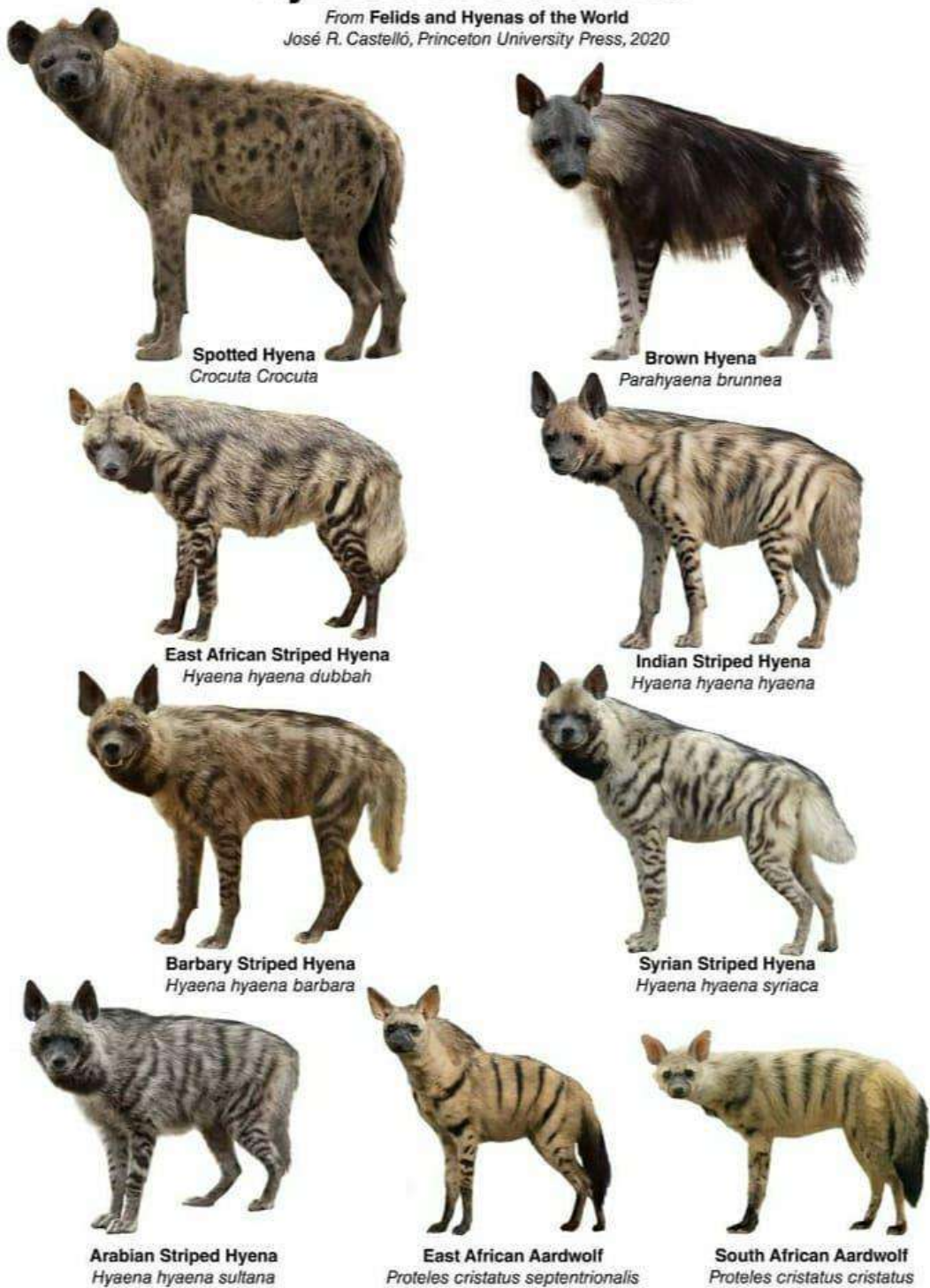


Figure1. 1 Hyenas of the world (Castelló 2020)

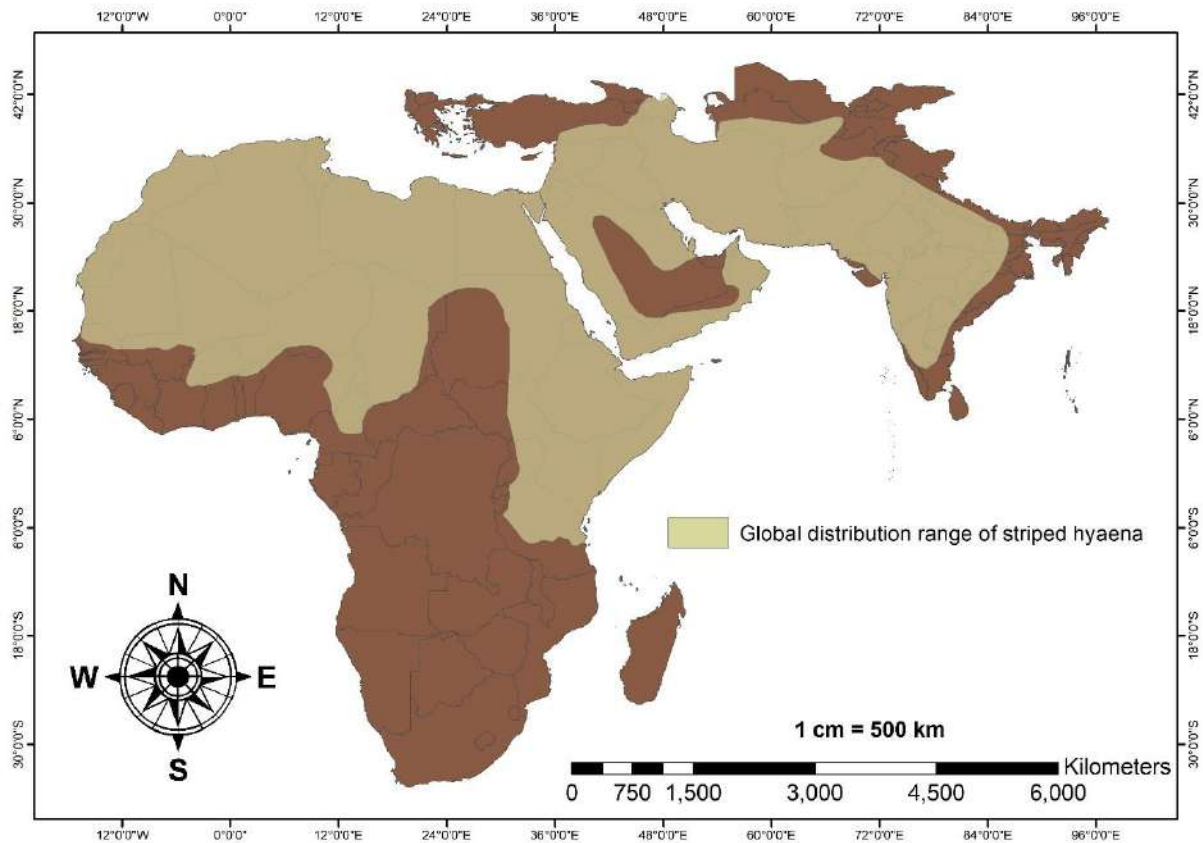


Figure1. 2 Global distribution range of striped hyaena (IUCN, 2015).

1.1.3 Ecology and Habitat selection

Striped hyaenas are cryptic and occur in very low density throughout their distribution ranges. This could be a suit of the reasons that it is the least studied hyaena species. The social behavior of the species is one of the poorly understood aspects while the social structure of other sister species like spotted hyaena is well explored (Wagner 2006; Watts & Holekamp 2009; Holekamp *et al.* 2012; Turner *et al.* 2018). Conventionally, the species has been deemed as a solitary animal acknowledging the rare assemblage of few individuals (Finn 1929; Kruuk 1976). But subsequent studies suggest that though the species is a solitary forager it exhibits a complex shared space-use pattern by sharing space with multiple individuals but not at the same time (Tichon *et al.* 2020). Furthermore, hyaenas were also observed to form a group of one female and two to three male but shows less interaction between them (Watts & Holekamp 2007; Bopanna 2013; Mandal 2018).

A habitat is a Latin word meaning an ecological and environmental area that provides the appropriate level of biotic and abiotic features required by a species to sustain itself, propagate, and complete all stages of its life cycle. Odum defined a habitat as a place where an animal lives (Odum, 1971). Habitat suitability modeling can be defined as a method to predict the potential habitat of a species by assessing the empirical relationship between species occurrence and potential environmental variables. The concept of habitat suitability began with the development of the Habitat Evaluation Procedure by the U.S. Fish and Wildlife Service in 1981 (Imam and Kushwaha 2013). Advancements in geospatial technology, such as GIS and machine learning, have opened up new paradigms in spatial ecology, enabling better wildlife management (Worah *et al.* 1989). These tools are cost-effective and can be implemented at macroecological scales, accommodating a large array of potential variables (Areendran 2007; Hara and Seiki, 1996). Information from such modeling is used to assess the impact of biogeoclimatic factors on species occurrence, helping prioritize conservation efforts in a time- and cost-effective manner (Kushwaha *et al.* 2004).

Hyaenas prefer dry and open habitats from arid and semi-arid zones, tropical dry, and moist deciduous forests in India (Rosevear *et al.* 1974; Kruuk 1976; Prater 1980; Karanth 1986; Leakey *et al.* 1999; Singh 2008; Chourasia *et al.* 2012). Hyaena prefers habitat within a 10 km radius of water sources (Rieger 1981). Throughout their distribution ranges, hyaenas occur with their co-predators like wolves, tigers, leopards, and lions (Arivazhagan *et al.* 2007; Harihar *et al.* 2010; Alam *et al.* 2014; Singh *et al.* 2014; Jhala *et al.* 2020). Undulating terrain provides safe denning refugia for the species (Nikunj *et al.* 2009; Singh *et al.* 2010; Bopanna 2013; Alam *et al.* 2014; Singh *et al.* 2014; Khanal *et al.* 2017; Mandal 2018). Co-occurrence with sympatric species provides abundant scavenging opportunities from carcasses. Furthermore, the species also prefers undulating terrain which provides safe denning refugia for the species (Singh *et al.* 2010). Most of the studies suggest that hyaenas occur more abundantly near human settlements which offer anthropogenic waste for scavenging (Kruuk 1976; Prater 1980; Mills & Hofer 1998; Singh *et al.* 2010; Sharma *et al.* 2011; Alam *et al.* 2015; Mukherjee *et al.* 2021; Panda *et al.* 2022). Home ranges of the species were reported to vary from 60-125 km² from Kutch, India (Bopanna 2013) while from Kenya the range was found relatively smaller (44 to 72 km²) (Wagner 2006).

1.1.4 Human Hyena conflict

Apart from scavenging, hyenas have been alleged to predate on small to medium-sized prey species (Prater 1980; Watts & Holekamp 2007) and are also known to feed on insects and vegetable matter (Kruuk 1976). These include small vertebrates, sheep, goats, dogs, donkeys, horses, and poultry (Kruuk 1976; Rieger 1981; Qarqaz *et al.* 2004; Nikunj *et al.* 2009 Chourasia 2012; Alam *et al.* 2015; Alam & Khan 2015). However, despite being solitary and morphologically evolved as scavengers, available anecdotal records suggested a long history of misbeliefs and the perception of people for hyenas. In 1936 people identified hyenas as group living predators and alleged for killing and attacking humans in Mainpuri District of Uttar Pradesh, India (The Times of India, 11th July 1936). A similar historical account reported hyenas as ugly predators accused of preying on cattle and children (The Times of India, 20th October 1864). There are some other contrasting historical accounts of the predatory behavior of the species. Hyenas have been alleged of child lifting which eventually results in retaliatory killing of the species (AbiSaid & Dloniak 2015), though such incidents are low when compared to other large carnivores. For example, it was reported that the hyena killed 221 people from 1875 to 1881 while the tiger alone caused casualties for around 5845 people during the same period (Balfour 1885). Apart from these, hyenas have been also associated with traditional superstitious beliefs and practices across their distribution ranges. Through its distribution in the Middle East and North Africa, the species is considered as grave robbers and loathed with many superstitious fears which also leads to subsequent persecution of the species (Mills *et al.* 1998; Bopanna 2013). In Middle Eastern countries like Israel, it is also perceived as a demonic creature. In India, different body parts of hyena are believed to have medical properties. For example, people are reported to use blood and fat of hyena for their believed medicinal properties in Kutch (Gupta 2003). In a few parts of India like Rajasthan and Maharashtra people are also reported to use hyena's brain and fat to cure diseases like epilepsy and arthritis (Sharma 2002; Patil 2003). Hyenas are also believed to be a symbol of productivity and to possess aphrodisiac properties in their different body parts (Mills *et al.* 1998; Dadashi-Jourdehi *et al.* 2020). These beliefs also lead to the persecution of species in different parts of its distribution ranges particularly reported from the Middle East and some parts of India. Tourani *et al.* in 2012 reported the removal of genital parts from striped hyena carcasses in central Iran, probably for traditional practices.

Persecution of hyaenas for their traditional beliefs is very limited and might have turned anachronistic while, human hyaena perceived and real conflict has emerged as a looming threat to hyaena conservation. Hyaenas are one of the least studied species and there is meager information available on the status of human hyaena conflict. Some contemporary studies support historical accounts as there are only sporadic reports of livestock depredation by hyaena. Human hyaena conflict plays a key role in shaping people's perception other than socio-economic attributes like sex, income, age, ethnicity, beliefs, and cognitive factors. There is no verified information about human-hyaena conflict in studies conducted from its current distribution ranges (Bhandari & Bhusal 2017). Despite the negligible amount of conflict with humans, the species is often persecuted by people. For example, eight hyaenas were killed in Nepal between 2015-2016, and seven hyaenas were brutally persecuted in Agra, India, out of which two died of injury (Bhandari & Bhusal 2017; Ilayaraja *et al.* 2018). Mills & Hofer (1998) attributed persecution of hyaena as a major reason for the observed population decline throughout its distribution ranges. People's perception plays a very important role in determining the antagonistic behaviour of people towards hyaenas. A study by Bhandari and Rijal (2015) investigating people's perceptions showed mixed opinions of people towards hyaena conservation in Nepal but most of them were against hyaena conservation due to the potential threat of livestock predation by the species. Similarly mixed responses were also observed in Kutch, India where 35% of people perceived hyaena as a threat while only 18 verified incidences of hyaena were reported in a study conducted from 2006 to 2011 (Bopanna 2013). In Sawai Mansingh Wildlife, Rajasthan, India despite having no reported conflict with hyaenas and acknowledging the ecological role in cleaning the environment 25% of people were found to have a negative attitude toward hyaena. Despite the negligible real conflict, no cogent justification has been postulated for this unproportionate antagonism towards the species such understanding is critical to conserve the species which mostly occurs in close proximity to human settlements. But in some of the regions, intolerance for hyaenas was reported to be linked with superstitious beliefs particularly in the Middle East (Abi-Said 2006). Road accidents are also considered as one of the reasons that aggravated the population decline in many regions. Hofer (1998) also highlighted the impact of change in agro-pastoralist practices and the decrease in the population of sympatric predators on the hyaena population as such change can affect carcass availability for the species. Poaching for the skin is also a major threat to the conservation of hyaena (AbiSaid & Dloniak 2015). In Morocco, the species is commercially poached for the presumed medicinal value of various body parts like a brain.

Furthermore, reducing livestock carcass availability due to changes in agro-pastoralist practices has also emerged as one of the major threats to the hyaenas.

1.1.5 Ecosystem services by hyaena

Humans and scavengers have been closely related to each other since the late Pliocene when early humans (Hominins) were highly dependent on meat as a prominent food source. The early relationship between humans and scavengers was highly competitive in nature as early humans were predominantly confrontational scavengers. It has been widely argued that this confrontational competition over the procurement of carcasses with scavengers and other potential competitors has augmented human progress during the course of evolution. Procuring meat through confrontational scavenging was a risky endeavor but number of members could minimize the involved risk of injury or casualty. Therefore, this arguably would have acted as one of the major selective pressures for the evolution of intra-specific cooperation aided by the development of primitive language, and importantly, defensive arsenals in the stone age (Bickerton & Szathmáry 2011; Moleon *et al.* 2014). Undoubtedly, scavengers also played an important role in early human development apart from other important factors which were involved. Paleontological evidence suggests that during the Pleistocene striped hyaena had established its current distribution ranges around the globe (Rohland *et al.* 2005). Striped hyaena has been an important terrestrial scavenger since its evolution and played a seminal role in the development of early human cooperation, and vocal languages, and has evoked the need for primitive arsenals. During this phase of human evolution, scavengers also helped in locating carcasses of early humans and Moleon *et al.* (2014) stated that this is probably the first ecosystem service to humans that must have been facilitated by scavengers.

Apart from this fundamental and indispensable role that hyaena arguably must have played in early human development, hyaena has many other far-reaching ecological services that are generally overlooked. Hyaenas scavenge on carcasses of a wide variety of animals ranging from domestic cattle to wildlife species. Hyaenas evolved with formidable jaws, and enhanced digestive and immune system that helps to extract bone marrow by crushing bones and even to digest putrefied meat (Horwitz & Smith 1988; Zhou *et al.* 2020). The robust digestive system helps hyaenas to digest every part of the carcass except hair. Carcasses contain a plethora of nutrients and consuming carcasses helps in transferring energy from one trophic level to another and also in the nutrition cycle (Wilson & Wolkovich 2011; Inger *et al.* 2016). Putrefying unscavenged carcasses are the reservoir of harmful bacteria and pathogens (Vass

2001; Morales-Reyes *et al.* 2015; Inger *et al.* 2016). Research work by Inger *et al.* (2016) showed that the presence of scavengers in an ecosystem can increase depletion rate of carcasses by approximately 14 percent. Being opportunistic scavengers, hyaenas decrease the risk of outbreak of diseases by clearing 23.13 tons of livestock carcasses which are potentially replete with pathogens and toxins from surrounding (Panada *et al.* 2023). Furthermore, the absence or a reduction in the population of scavengers like hyaena can impose a high fiscal penalty. For example, a severe decline in vulture populations from India is suspected to impose a fiscal burden of around £10 billion annually on the Indian health sector (Markandya *et al.* 2008). Keeping the importance of hyaena in view, it is imperative to conduct possible studies on data-deficient species so that promising conservation management strategies can be devised.

1.1.6 Status of hyaenas from India

India was once the stronghold for hyaenas. Paleontological evidence from Siwalik suggests that there were at least eight species of Hyaenidae present in this region (Werdelin & Solounias 1990). The fossil record of spotted hyenas from the Madras presidency of colonial India also confirms the historical presence of the species at least from peninsular India (Prater 1935). At present, only striped hyaenas are found in the part of Indian sub-continent. Historical accounts of the species from India suggest that the species was common in the countryside and even in the forested regions. These regions covered most of the important biogeographical zones of India like Gangetic plain, Semi-arid biogeographic zones, Central highlands, Deccan plateau, and Eastern-Western Ghats (Edward 1885; O'Malley 1911; Prater 1935; Salim *et al.* 1985; Krishna Raju *et al.* 1987; Tehsin 1987). The species has experienced unprecedented decline from most of its distribution ranges. For example, a study comparing past and present distribution ranges confirmed mass extirpation of the species from its historical ranges of current Bengal (Akash *et al.* 2021). The authors also raised their concerns over the decline of the species despite it being the least prized among the hunters. But later also ascribed those declines as a combined ensue of persecution, habitat loss, prey loss, and road kills, which might be exacerbated by game hunting. The striped hyaena is already extinct in many localities because of the same reasons (Kruuk 1976; Mills & Hofer 1998; Wagner 2006; Khorozyan *et al.* 2011). Now it has been categorized as Near Threatened by the IUCN (Arumugam *et al.* 2008; AbiSaid & Dloniak 2015), whereas in India the species is placed in schedule-III and hunting is prohibited (The Indian Wildlife (Protection) Act 1972). Despite this categorization and conservation status, the population of the species is under severe threat due to its

persecution as a result of real and perceived threats on livestock by species, poaching, road or rail accidents, and habitat loss (Mousavi 2010; Mandal 2018; Akash *et al.* 2021). The striped hyaena is a data-deficient species and in-depth ecological information is needed to address conservation issues in its distribution ranges (Qarqaz *et al.* 2004; Wilkinson *et al.* 2024).

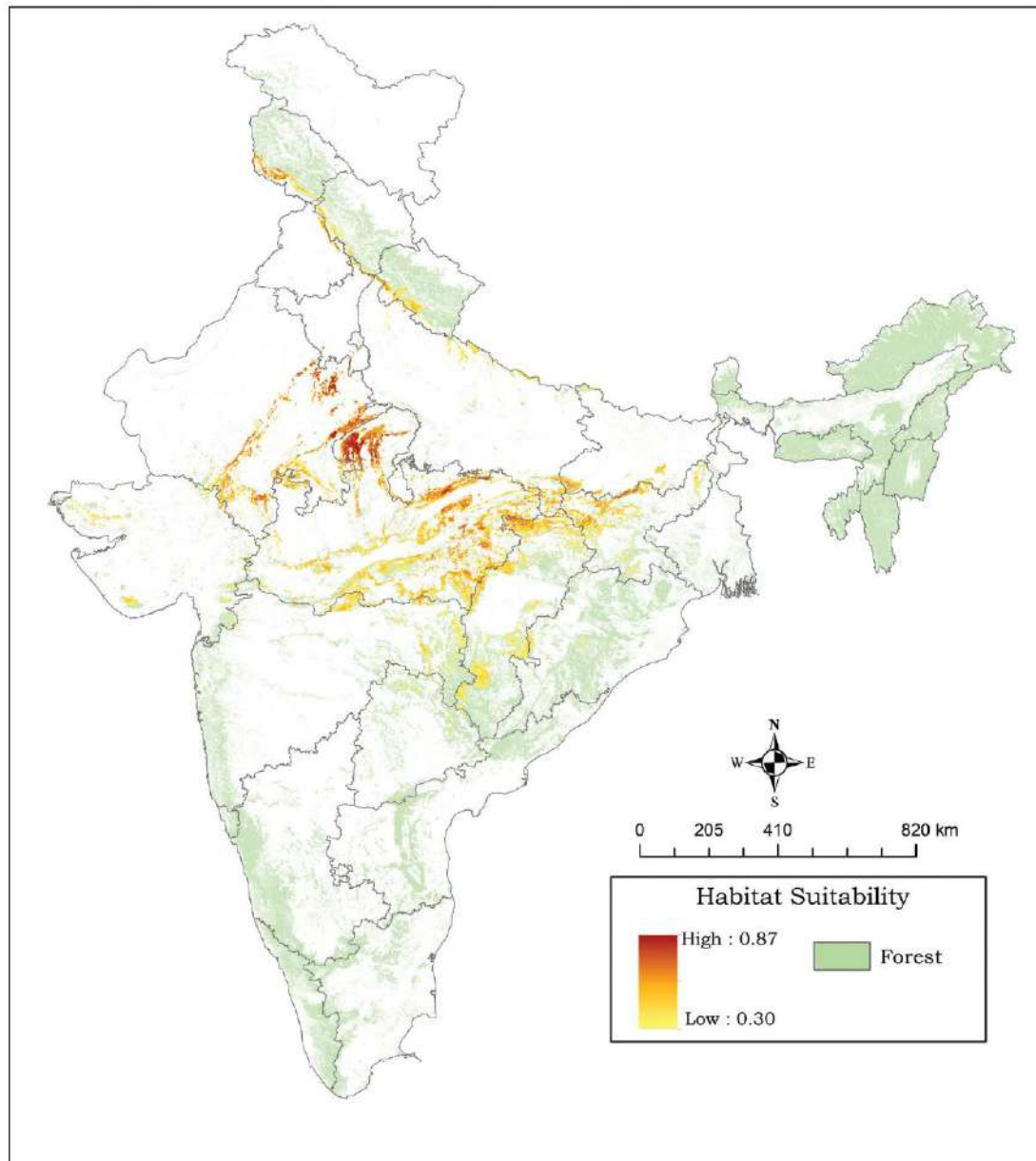


Figure1. 3 Current presence records of hyaena from India (Jhala *et al.* 2021).

1.2 Rationale of the study

Peninsular India has been the citadel of the stronghold population of striped hyaenas and recorded hyaenas occurrences from Eastern and Western Ghats (Prater 1935). There are historical reports of hyaenas from many areas of southern India like regions of Hyderabad, Nagarhole, Papikonda Hills of Eastern Ghats, Mudumalai Tiger Reserve, Sathyamangalam Tiger Reserve, Bandipur Tiger Reserve and even in Ooty region above 3000 to 8000 ft elevation (Salim *et al.* 1985; Krishna Raju *et al.* 1987; Aditya & Ganesh 2017). Atkinson & Bashir (1988) have also mentioned common occurrences of the species from the Masinagudi region in 1988. The Masinagudi region is part of the study area in Mudumalai that covers the Western Eastern Ghats part of Tamil Nadu (WEGPTN). The WEGPTN is marked as an important tiger conservation landscape under the All-India Tiger Monitoring program and a part of Nilgiri Biosphere Reserve declared in 1986. As a part of the All India Tiger Monitoring program, Jhala *et al.* (2020) have mapped the occupancy of tigers, their co-predators, and prey species. The species has experienced unprecedented rates of decline over the last few decades due to human persecution (poisoning), diseases, and habitat loss. Furthermore, the occupancy map (Jhala *et al.* 2020) from the study elucidated that the WEGPTN holds the last remaining major population of striped hyaenas in entire southern India. Notwithstanding this decline, hyaenas are still accused by the local farming community as they purportedly inflicted damages to livestock. Deep-rooted antagonism and fears in rural areas are responsible for the negative public attitude towards this species. This causes continuous conflicts between the farming local communities and the carnivores. Although there are several studies available on spotted hyaenas, brown hyaenas, and even on striped hyaenas (Gupta *et al.* 2009; Harihar *et al.* 2010; Singh *et al.* 2010; Singh *et al.* 2014; Alam *et al.* 2015) but there are a very few available on interspecific interaction and people perception on hyaena (Wilkinson 2024). However, there are some detailed long-term studies on habitat use, ranging patterns, and food habits of striped hyaena (Alam 2011; Bopanna 2013; Mandal 2018). But practically no information is available with reference to the human-hyaena conflict, Interspecific competition and spatial distribution of species especially from the WEGPTN, southern India. Although, all these aspects of the species ecology are imperative to comprehend fully for better and sound scientific management of this last remaining major population.

Human-carnivore conflict is a serious issue in the conservation of large carnivores and depends on various local and landscape factors. However, in this region, the human population pressure

has continued to grow with agriculture, livestock grazing, tourism and other developmental activities, and carnivore–livestock conflict is likely to increase. To avoid the establishment of population “sinks” in surrounding reserves, in which human-caused mortality limits survival of predators dispersing from the reserve (Woodroffe and Ginsberg 1998), livestock depredation and the resulting persecution of carnivores must be minimized through appropriate research studies that the study proposed here to implement. The rates of livestock depredation by large carnivores can be influenced by local environmental conditions that include an abundance of natural prey, livestock husbandry practices and livestock enclosures (Madhusudan 2003; Ogada *et al.* 2003; Woodroffe and Frank 2005). However, there is no information available on the rate of livestock depredation by hyaena from this region and there is no clue about the factors and pattern of depredation by the species. Therefore, it is important to study the factors that affect livestock predation by hyaena.

The striped hyaena coexists with large predators such as tigers and leopards across a significant portion of its distribution in forested landscapes. The abundance and distribution of these carnivores are argued to have significant implications for scavengers like hyaenas, through both interspecific competition and carcass facilitation. The impact of these intricate interactions can vary depending on resource availability, environmental conditions, interacting species, and their abundance, all of which fluctuate over time and space. This dynamic nature of interactions further adds complexity to an important topic that remains largely unexplored. In India, conservation policies are primarily focused on reviving the populations of large carnivores, while overlooking the disappearing open habitats that serve as crucial refuges from competition for scavengers like hyaenas. As the population of big cats recovers and critical open habitats continue to deteriorate, the potential for increased resource overlap may intensify competitive interactions, posing a threat to hyaena conservation. Despite the significance of these interactions, there is a lack of comprehensive understanding, particularly regarding their spatial dynamics, which is crucial for effective wildlife management in India. Although some studies have examined interspecific interactions at carcasses, their implications for the spatial ecology of hyaenas remain largely unknown. This doctoral research also assesses the top-down impact of large predators on the spatial ecology of hyaenas.

Recent developments in the knowledge about striped hyaena as well as older literature stress the importance of secondary forest habitat in species conservation (Jhala *et al.* 2011; Jhala *et al.* 2020). A considerable population of the species is present in the secondary forest habitat that is surrounded by human settlements and most of the areas fall outside the Protected Areas

(PAs). The ecological integrity of both PAs and non-PAs is severely affected by anthropogenic pressure exerted on natural resources and habitats. The increase in fragmentation of carnivore habitat for agriculture and other developments warrants an understanding of the ecological factors, including various forms of human disturbances that influence movement decisions by large carnivores. These kinds of data sets are critical for guiding park management in assessing extinction risk and the response of wildlife populations to disturbance (Kolowski & Holekamp 2009; Ramesh *et al.* 2015) would guide the balance between optimal resource use and risk of persecution (Ramesh *et al.* 2015). Therefore, resources within human-altered environments influence carnivore responses to disturbance and the costs associated with these responses. An understanding of these costs and trade-offs increases the ability to predict the consequences of disturbance and the functional losses of carnivore habitat associated with human disturbance. Several studies have demonstrated carnivore avoidance of areas exposed to intense human activity (Carter *et al.* 2012; Oriol-Cotterill 2015; Ramesh *et al.* 2015), few studies have attempted to quantify disturbance response decisions (Gibeau *et al.* 2002; Kolowski & Holekamp 2009). Large carnivores, like striped hyaenas (*Hyaena hyaena*) frequently share their landscape with livestock and the latter often graze closely, guarded by herders. These are expected to serve as a disturbance to carnivores and alter their patterns of distribution in response to livestock grazing. A study on the disturbance and ecological factors influencing the distribution of hyaena in the landscape can help in understanding the distribution pattern of the species with respect to anthropogenic and ecological factors in the landscape.

1. Examine the role of socio-economic characteristics and livestock predation on the prospect of striped hyaena conservation in a high human-carnivore conflict landscape.
2. Assess co-predator interaction in the breeding habitat of striped hyaenas.
3. Prioritize potential suitable habitats for striped hyaena conservation.

Organization of the Thesis

The current chapter (Chapter I) informs the ecology and evolution of striped hyaenas, literature review and the background of the study, and the research objectives. Chapter II discusses about geo-climatic features and biodiversity of the study area, provides an account of past distributional records, highlights the importance of the study area, and discusses the selection of an intensive study area. Chapter III addresses my first objective and encompasses details on the human hyaena conflict, people's perceptions of hyaena and major allied problems of

conservation in this region. Chapter IV addresses my second objective and discusses the spatial interaction of hyaenas with their sympatric carnivores and associated variations across the tiger conservation landscapes of India. Data from my field investigation lacked enough observations on interactions due to the restricted distribution of hyaena WEGPTN. Therefore, to have a better understanding of the crucial aspect of hyaena ecology the study was extended to other tiger conservation landscapes. Chapter V deals with the spatial distribution of the species in WEGPTN. Summarizing the findings of the study chapter VI provides a detailed conclusion and way forward.

Chapter 2



Chapter 2: Study Area

Nilgiris is the chain of mountains that converge between the Eastern and Western Ghats mountain ranges of peninsular India. The Nilgiris is the largest contiguous forested landscape of peninsular India and is situated at the tri-junction of Karnataka, Kerala, and Tamil Nadu. The Nilgiris is recognized as a biodiversity hotspot in the Western Ghats and has 150 endemic vertebrates out of 730 as well as ca. 150 angiosperms endemic to this region (Anon 1983; Atkinson & Bashir 1988; Puyravaud & Davidar 2013). This includes 100 mammalian species, 550 species of avian fauna, and 80 species of reptiles and amphibians (Atkinson & Bashir 1988). The Nilgiris is also a very important landscape for elephant conservation and holds the highest population of the species in Asia (Baskaran & Sukumar 2015). The importance of this vast landscape for the conservation of its endemic and emblematic wildlife species of peninsular India has been well recognized since Imperial India. Madras Wild Elephant Preservation Act of 1873 and Nilgiris Game and Fish Preservation 1879 were among the important acts enacted to conserve the valuable biodiversity of the region. Post-independence, Nilgiris was proposed to be declared as a Biosphere reserve in August 1984 following the acceded participation of three states Karnataka, Kerala, and Tamil Nadu (Atkinson & Bashir 1988). After 12 years of the proposal, on 1st September 1986, Nilgiri was declared the first Biosphere Reserve of India and recognized by The United Nations Educational, Scientific and Cultural Organization (UNESCO) in 2000 (Daniels & Vijayan 1996). To strengthen the Protected Area (PA) network within the Nilgiris Biosphere Reserve (NBR), constituting states have taken certain initiatives like the inclusion of more forest land under PAs and also upgrading the existing conservation status and newly recognized PAs. Johnsingh *et al.* (2010) suggested the extension of the existing Protected Area through the inclusion of adjacent reserved forest patches of NBR. Following, the Tamil Nadu government undertook remarkable efforts in accord to extend the Mudumalai Tiger Reserve (MTR) merging Sigur, Singara, Nilgiris Eastern Slope Ranges and part of Gudalur Forest divisions; declaration of Satyamangalam Tiger Reserve (STR) and even planning to update the conservation status of Coimbatore Reserve Forest to Protected Area. Currently, Tamil Nadu is one the most tiger-bearing states of the Western Ghats (Jhala *et al.* 2021)

The study was conducted in the Western and Eastern Ghats part of Tamil Nadu (WEGPTN) (Figure 2.1 and Figure 2.2) which is an important wildlife conservation area and includes central as well as north-eastern part of the NBR. The study area is a vast multi-use landscape covering an area of 7319 sq. km and stretched between 10.85° to 12.86° in the north and 76.24° to 78.74° in the east. It includes a diversity of habitats, PAs, Reserved Forest, and mixed-use forests across a large and mostly contiguously-forested landscape, including STR, MTR, Cauvery North Wildlife Sanctuary (CNWLS), as well as the Gudalur, Nilgiris, Coimbatore, Erode, Dharmapuri, and Hosur Forest Divisions. This huge landscape connects to Wayanad forest division (Kerala) in the west, Bandipur Tiger Reserve (Karnataka) in the north-west, Biligiri Ranganathaswamy Tiger Reserve (BRT) (Karnataka) in the north, Silent Valley National Park in the south, and also connects the Eastern Ghats to the Western Ghats of India (Figure 2.1). The Sigur plateau and the Moyar valley together constitute a prime passage to the Eastern Ghats from the Western Ghats (Puyravaud & Davidar 2013). Cauvery, Doddahalli, Chinnar, Moyar, and Bhavani are the major streams flowing through the study area. Moyar is the perennial water source transecting the driest part of the study area (Moyar Valley) of the Sigur Plateau, a unique part of the study area. The valley is characterized by a narrow strip of arid habitat stretched between two mountain chains running parallel to each other and the river draws an administrative boundary between Mudumalai-Sathyamangalam and Bandipur Tiger Reserves.

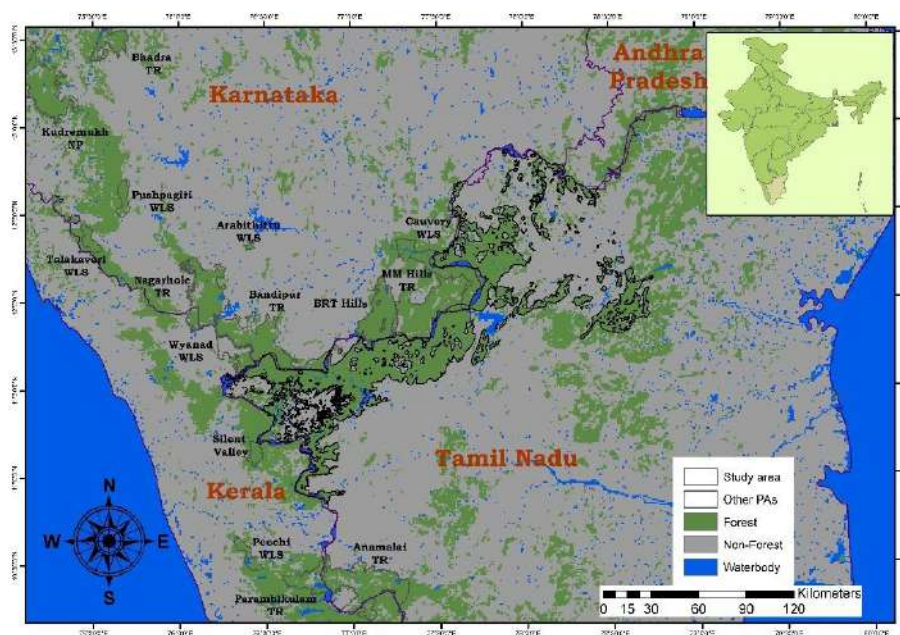


Figure 2.1 Landscape map of study area

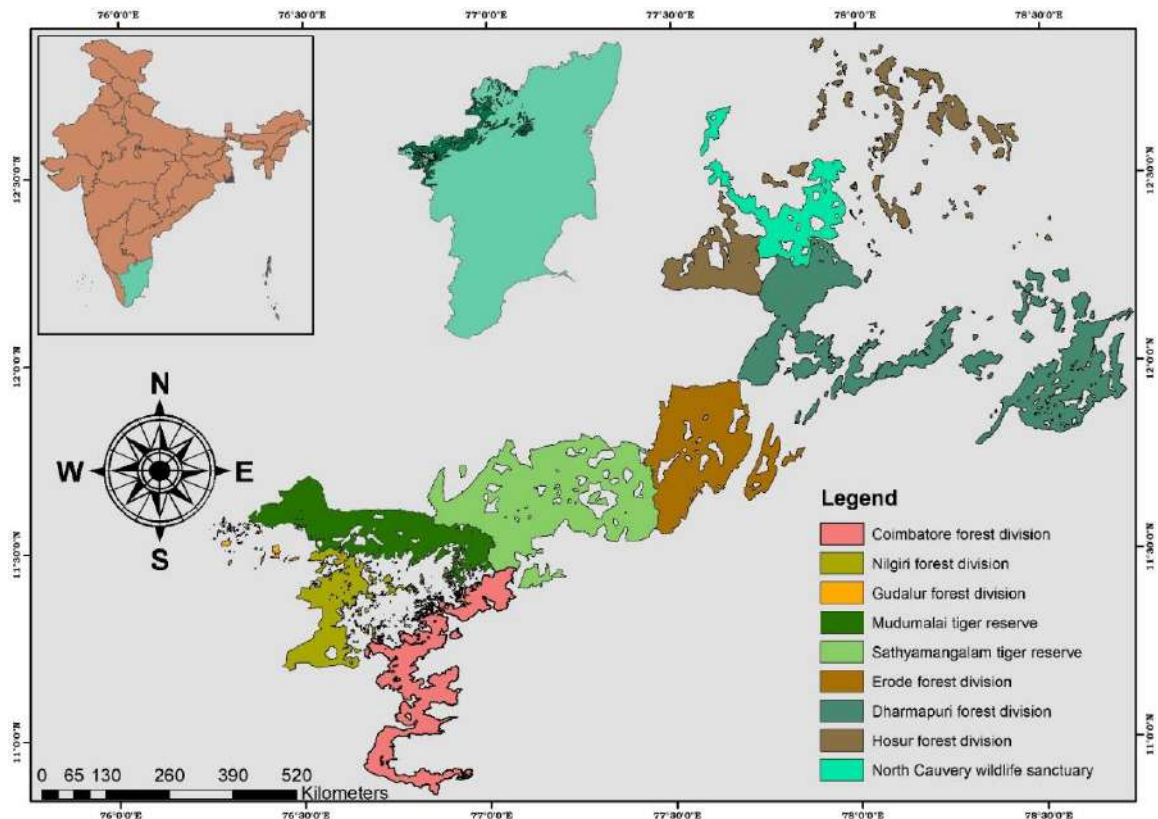


Figure 2. 2 The study area with administrative boundaries of Protected Areas and Forest Divisions in the Western and Eastern Ghats part of Tamil Nadu.

2.1 Geo-climatic characteristic of WEGPTN

The topography of the landscape varies extremely and elevation in the study area ranges from 207 to 2530 m asl. (Figure 2.2) The Dodabetta is the highest peak of the landscape while Moyar Valley to the plains of Coimbatore are the low-lying areas whose elevation ranges from 186 to 708 m asl. The landscape has three distinct climatic regimes which vary with topographical characteristics within the area (Gadgil & Sukumar 1986; Atkinson & Bashir 1988). Warm and wet tropical climatic zones prevail in the mid-elevation range below 1400m in north-west regions. While geographical precincts above that range and a portion of Talamalai plateau of the Eastern Ghats experience cold and wet tropical climate; and rest of the areas below 1400 are characterized by warm and dry tropical climatic conditions. Overall, the mean annual temperature ranges from 12.77 to 27.92 degrees centigrade across the WEGPTN as shown in figure 2.3.

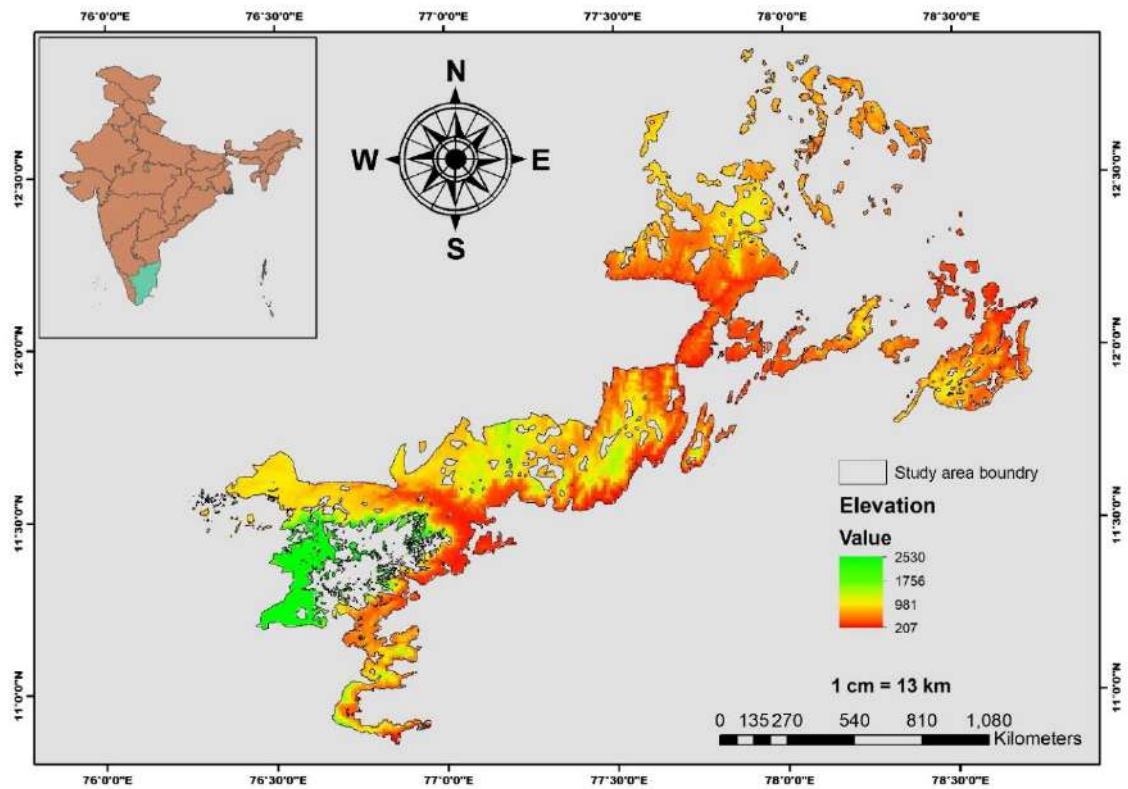


Figure 2. 3 Elevation map of the study area.

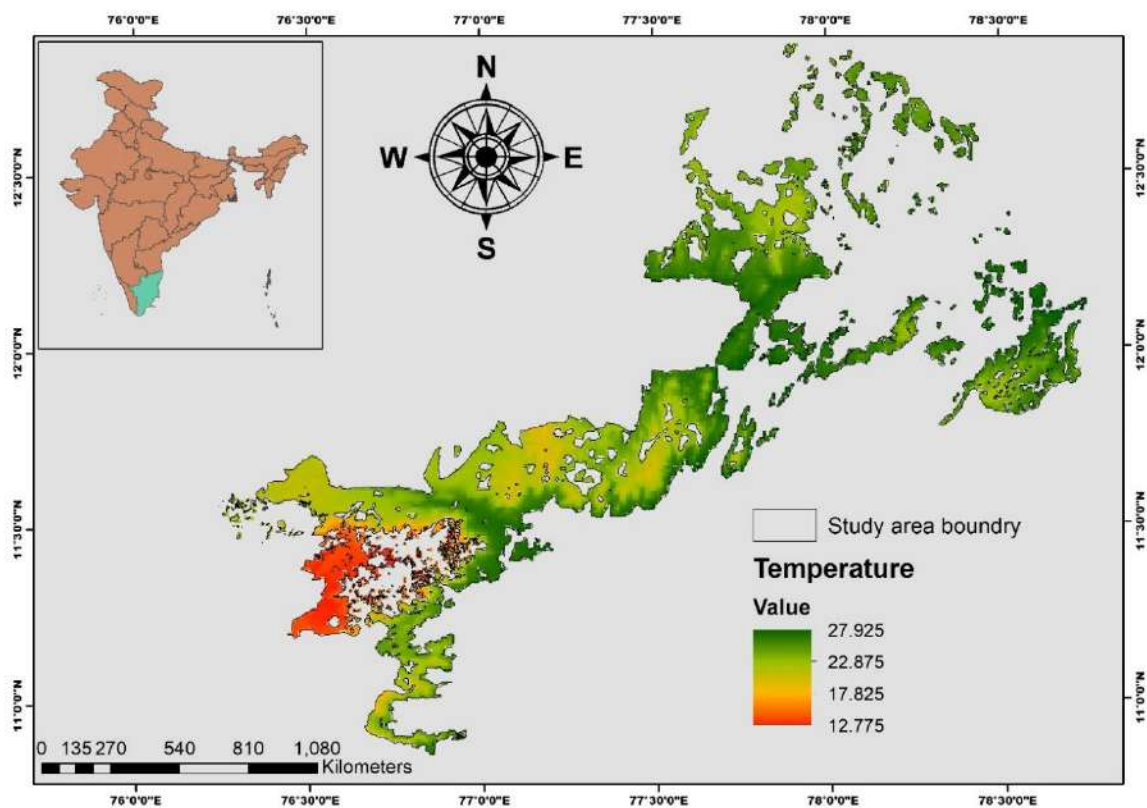


Figure 2. 4 Temperature of the study area.

2.2 Flora of WEGPTN



The altitudinal heterogeneity along with varying allied geo-climatic conditions harbor diverse vegetation types in this region. This vast contiguous landscape is predominantly comprised of four vegetation types namely, 1) Tropical Mountain evergreen forest, 2) Tropical moist deciduous, 3) Dry deciduous forest, and 4) Open dry thorn (Champion & Seth 1968). The major forest types from the study area are shown in Figure 2.4. The Tropical montane evergreen forest occurs in upper Nilgiris above 1,500 m. Sholas are mainly confined to the valley and high hill mountains fold. The major tree species found in this region are *Cinnamomum wightii*, *Elaeocarpus* spp., *Gordonia obtuse*, *Meliorma* spp., *Liquortrum voxburghii*, *Litroea* spp., *Schefflera* spp., *Symplocos* spp. and *Syzygium arnottianum*. Southern Tropical moist deciduous forest is present in the mid-elevation ranges (Atkinson & Bashir 1988) of MTR, a portion of Talamalai plateau of STR, and the Erode Forest division which receives ca. rainfall between 1600mm and 2000mm. *Tectona grandis*, *Lagerstomia microcarpa*, *Butea monosperma*, *Terminalia crenulata*, and *T. tomentosa* are the dominant tree species grow in this vegetation type. Southern tropical dry deciduous forests are found in the region that receive an average rainfall of between 100mm and 1200mm. This forest type mainly dominates low to mid-elevated plateaus and *Grewia tilifolia*, *Anogeissus latifolia*, *Tectona grandis*, and *Kediya calycina* are major trees that characterize this vegetation type. Southern Tropical dry thorn forests are present in the low-lying areas (foothills of Nilgiris) receive an average annual rainfall of 600mm and are best represented in the Sigur plateau and Moyar valley. This habitat is characterized by stunted tree species like *Acacia catechu*, *A. chundra*, *A. suma*, *A. leucophloea*, *Anogeissus latifolia*, *Ziziphus xylopyrus*, *Ziziphus zuzuba*, *Ziziphus enophilia*, *Sapindus emarginatus*, *Phyllanthus emblica*, *Erythroxylon monogynum*, *Canthium parviflorum* and *Capparis* species.

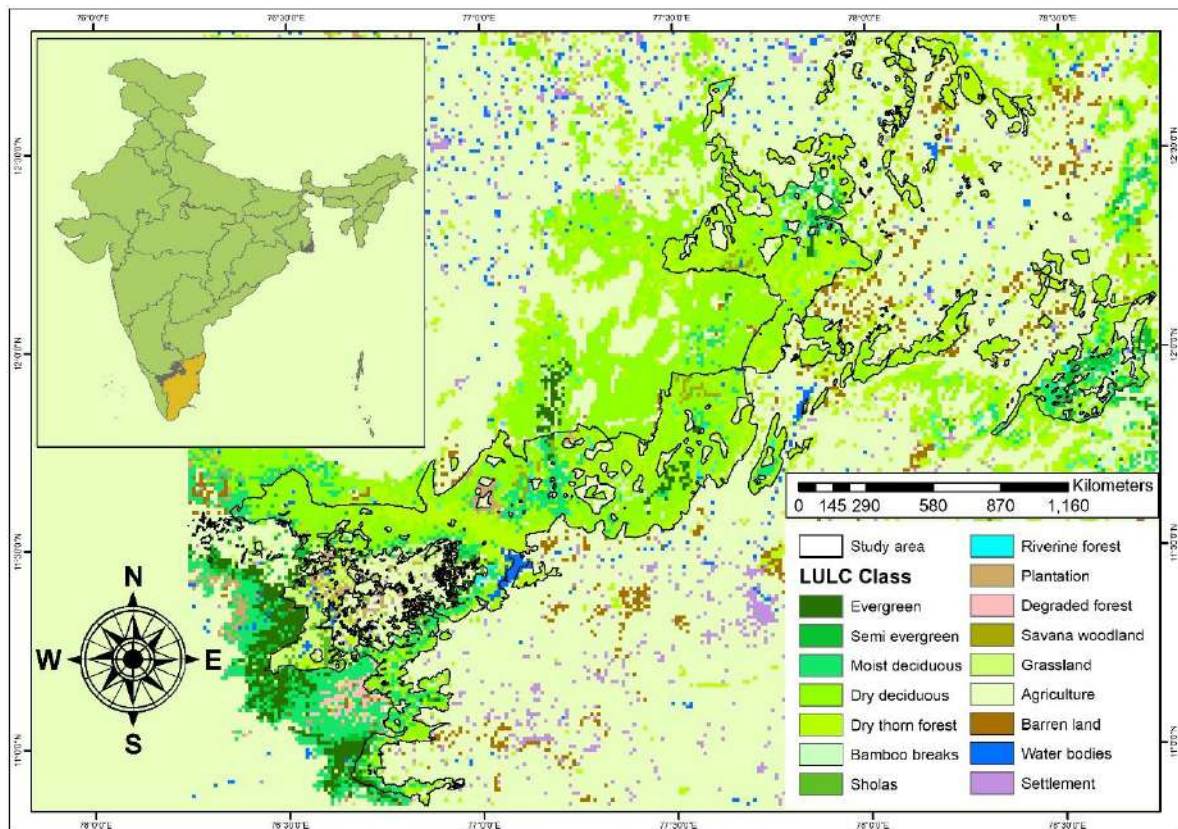


Figure 2.5 Land use land cover of the study area.

2.3 Fauna of WEGPTN

The WEGPTN is an important area of “Nagarhole-Bandipur-Wayanad-Mudumalai-Sathyamangalam- complex” identified for the conservation of the large mammal in the Western Ghats. This forested landscape complex is extended till the Cauvery North Wildlife Sanctuary and is the largest contiguous tiger conservation landscape in the world. Recent country-level tiger monitoring conducted in 2018 suggested that this complex supports 724 individuals of tiger which is the largest continuous population in the world (Jhala *et al.* 2020). Forest land of Tamil Nadu state constitutes an important part of this complex and holds a population of 264 tigers in the state. The landscape connects the Eastern Ghats and is very important for the maintenance of viable populations of the species and its co-predators like dhole and leopard. The contiguous landscape of the WEGPTN supports a major population of important species like leopard, dhole, elephant, and gaur in India (Figure 2.5 & 2.6 show the picture of major fauna present in the landscape). These species are abundant in areas like MTR, STR, Bandipur Tiger Reserve, and BRT. Healthy populations of these species are also present in other

important areas from the point of wildlife conservation like Coimbatore, Erode, Dharmapuri, and North Cauvery Forest divisions. For example, tiger reserves like MTR as well as Bandipur hold more than 100 individuals of leopards making this landscape the most abundant in leopard population in the entire Western Ghats (Jhala *et al.* 2021). This complex also holds the most extensive stronghold population of key species like gaur and elephant (Choudhury 2002; Sukumar 2006; Ramesh *et al.* 2012a). Large carnivores found in the WEGPTN are tiger (*Panthera tigris*), leopard (*Panthera pardus*), dhole (*Cuon alpinus*), and hyaena (*Hyaena hyaena*) supported by major prey species like chital (*Axis axis*), sambar (*Rusa unicolor*), gaur (*Bos gaurus*), four-horn antelope (*Tetracerus quadricornis*), wild pig (*Sus scrofa*), barking deer (*Muntiacus muntjak*), and black buck (*Antelope cervicapra*). The blackbuck is confined to the Moyar Valley which has a more diverse prey base in the landscape. Furthermore, this unique habitat was also home to other open habitat species like Wolf *Canislupus*, Nilgai *Boselaphus tragocamelus*, and Chinkara *Gazellabennettii* (Nicholson 1887; Pythian-Adams 1951).



Figure 2.6 Key herbivores found in the landscape: Elephant (a), Gaur (b), Sambar (c), Chital (d), Barking deer (e), Blackbuck (g), Four horn antelope (f) and Mouse deer (h).

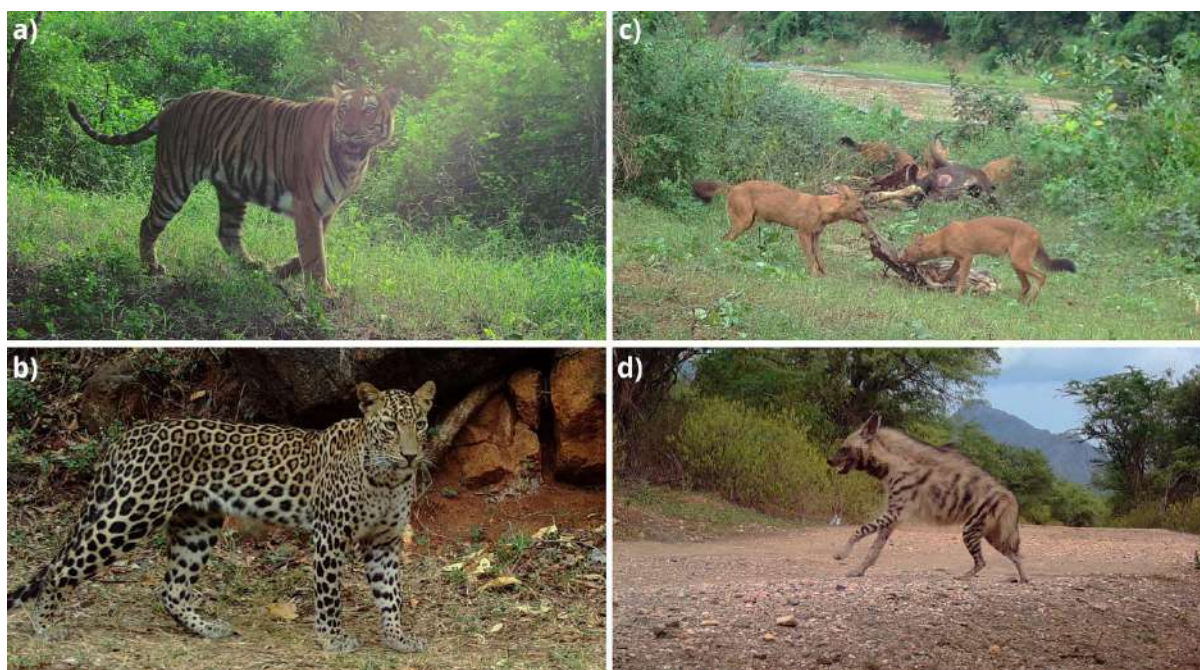


Figure2. 7 Major carnivores present in the landscape: Tiger (a), Leopard (b), Dhole (c) and Hyaena (d)

2.4 Threats and conservation issues

The colonization of India coincided with a sudden increase in demand for natural resources to meet the needs of then spurring industrialization. Throughout Imperial India, the natural ecosystems were immensely disturbed for hydroelectricity, commercial plantation, mining, bamboo extraction for the paper industry, and timbers for the construction of railways as a prime means of transportation. The fragile forest ecosystem of both the Western and Eastern Ghats also experienced extensive alteration for tea, coffee, eucalyptus, cinchona, wattle, rubber, and clove plantations (Jhala *et al.* 2020). In 1820, the Nilgiri plateau had become the functional administrative and military base for the Britishers. After the colonization of Nilgiris, they indiscriminately cleared natural forests and introduced many exotic species into the area (Hockings 1989). The major exotic tree species commercially planted in this region were wattle (introduced in 1832), eucalyptus (1842), conifers, fruiting trees, alder, coffee, and tea (Figure 2.7 shows pictures human-wildlife interface due to intensive deforestation). Furthermore, the part of the study area that has been recently designated as STR was intensively exploited for bamboo during imperial rule (Tamil Nadu Forest Department 2010). STR was replete with bamboo patches and was known to



widely spread across the forest landscape. The indiscriminate harvesting of bamboo has led to the distribution of bamboo in a few pockets in the Moyar Valley and Hassanur Range. Such undesirable changes in land use and land cover in the area led to habitat fragmentation and seriously threatened large-ranging species like tiger, leopard, elephant, and gaur (Figure 2.8 shows pictures of human-wildlife interaction at interface areas). Other than this organized encroachment over the natural habitat, high anthropogenic pressure in the form of livestock grazing and increasing human population has been a major concern of the region (Figure 2.9). Cattle rearing was one of the major occupations of the people and large herds of cattle were harbored for manure. By 2010, there were 25,000 cattle competing with the wildlife for forage, and water was reported alone from the sanctuary area of STR (Tamil Nadu Forest Department 2010). 10000-20000 cattle have been reported from the Masinagudi and Moyar areas (Salim *et al.* 1985) and overgrazing has led to habitat degradation in this area. In the past, the area was subjected to the construction of a series of hydroelectricity power stations which caused a mass influx of people, mostly of landless labourers seeking employment opportunities. Job opportunities during the construction of dams in areas like Singara, Masinagudi, and Moyar led to an increase in human population by 143% between 1961 and 1991 (Silori & Mishra 2001). The immigration of people to Masinagudi regions was accompanied by a rise in large cattle for cattle dung which was high in demand in tea and coffee estates as manure. Silori & Mishra (2001) revealed that about 2100 tons of dry dung were sold only between 1992-1993. Such reliance of people on cattle for livelihood throughout the study exerted extreme pressure on forest resources and caused forest fragmentation in many areas. Forest fragmentation and competition between humans and wildlife over depleted resources often become reasons for human-wildlife conflict in the study area leading to bilateral damage. For example, elephant herds from the Dharamapuri-Hosur forest division were reported to move out from their degraded habitat which led to aversive interaction with people (Baskaran *et al.* 1995). Many parts of the study area like the Moyar Valley were also a hunting ground for British people (Jhala *et al.* 2010). Even after the stringent prohibition and wildlife legislations implemented, hunting of prey species is still a persistent threat to wildlife in this region. The study area is mostly dominated by indigenous tribes like Irulas, Kurumbas, Sholaga, Kattunaickers, and Paniyas. These tribal communities are highly dependent on agro-pastoralist forms of economy, collection, and selling of non-timber forest products like honey, medicinal plant roots, aromatic gum resins, bamboo rice, *Zizyphus* spp. Fruits, *Phyllanthus emblica* fruits, and firewood (Ramesh *et al.* 2019). These tribes also hunt species like chital, hare, and sambar for food which needs to be checked immediately (Tamil Nadu Forest Department 2010). Kattunaickers and

Kurumba are reported to be mostly dependent on employment provided by forest departments while others rely on labour-based opportunities for their livelihood. Other than ethnic groups, Mountain Chetties are the non-tribal dominant community and reported own large number of cattle from MTR (Ramesh *et al.* 2019). The study by Ramesh *et al.* (2019) based on the socio-economy data collected in 2010 also highlighted the extreme biotic pressure on forests and reported that around 96% of the households were depended on firewood and other non-timber forest products. However, Kodandapani *et al.* (2014) highlighted the decline of people's dependency on forests, and no further encroachment on forest land has been reported (Tamil Nadu Forest Department, 2010). The decline in dependency on forests mostly occurred in designated PAs while in Reserve Forests (RFs) like Coimbatore, Erode, Dharmapuri, and Hosur forest divisions still, the pressure accounts in high proportion. A recent large-scale study from this landscape indicated that 58% of the households are still dependent on herding sheep and goats which is considerably higher than PAs where it was only 40% (Ramesh *et al.* 2020). Likewise, people residing in RFs are reported to be more dependent on cow/buffalo than people from PAs. Overall anthropogenic activities synergistically have already increased in the human-wildlife interface area. An increase in interface areas often results in aversive interaction in the form of livestock predation by carnivores and crop raiding by species like wild pigs, elephants, and other ungulates. Such aversive interaction not only causes retaliatory killing of conflict species but also imperils the existence of other less inflicting species like hyaena. Incidences such as elephant poaching are rare but elephant causality to electrocution is an important concern for the conservation of the species in this landscape. Furthermore, forest fire particularly in drier regions of foothills, burgeoning tourism, increasing biotic pressure, and proliferation of exotic species like *Opuntia dellini*, *lantana camara*, and *Prosopis* *sp.* are serious issues in the region that require immediate managerial interventions (Johnsingh *et al.* 2010).



Figure2.8 Human-wildlife interfaces from the study area.



Figure2.9 Human-wildlife interactions from the study area.



Figure 2.10 Livestock grazing pressure in the forests adjacent to the human-wildlife interface areas

2.5 Intensive study area and methods

The WEGPTN is very diverse in its habitat type and conformed by various vegetation types that vary across the landscape (please see representative pictures of major forest types in Figure 2.10 and landscape pictures in Figure 2.11). Available studies on the striped hyaena stress that it is a species of dry and open habitat, and occupies arid zones in a landscape. Therefore, to align the research efforts with its objectives precisely, the identification of potential hyaena habitats was very crucial before carrying out intensive fieldwork. The potential habitat available in the WEGPTN was identified based on the occurrence records of the species from secondary sources like forest department census data, newspaper reporting, and published-unpublished literature. Post identification, potential hyaena distribution areas were marked as an extensive study area (ESA), predicted through a preliminary species distribution model calibrated using secondary data collated. The ESA was further surveyed through camera trapping in conjunction with indirect sign surveys and current distribution ranges were

ascertained from the landscape. The entire study area was first divided into 5x5 sq km grids and 2.5x2.5 sq km sub-grids to stratify the sampling efforts systematically throughout the Extensive Study Area (ESA) identified. A total of 248 grids on trails of 2km length were covered and current occurrence records of the species along with its co-predators and their prey species were recorded through indirect sign surveys. The current occurrence record of the species was supported by photographic evidence from 194 camera traps placed across seven forest divisions of the ESA, with an effort of 4975 trap nights. A small population of the species was found in the landscape confined to a small area of approximately 314 sq. km. The current distribution of the species majorly lies in the Sigur and Moyar valleys of the region and was deemed as an intensive study area (ISA) for further detailed studies.

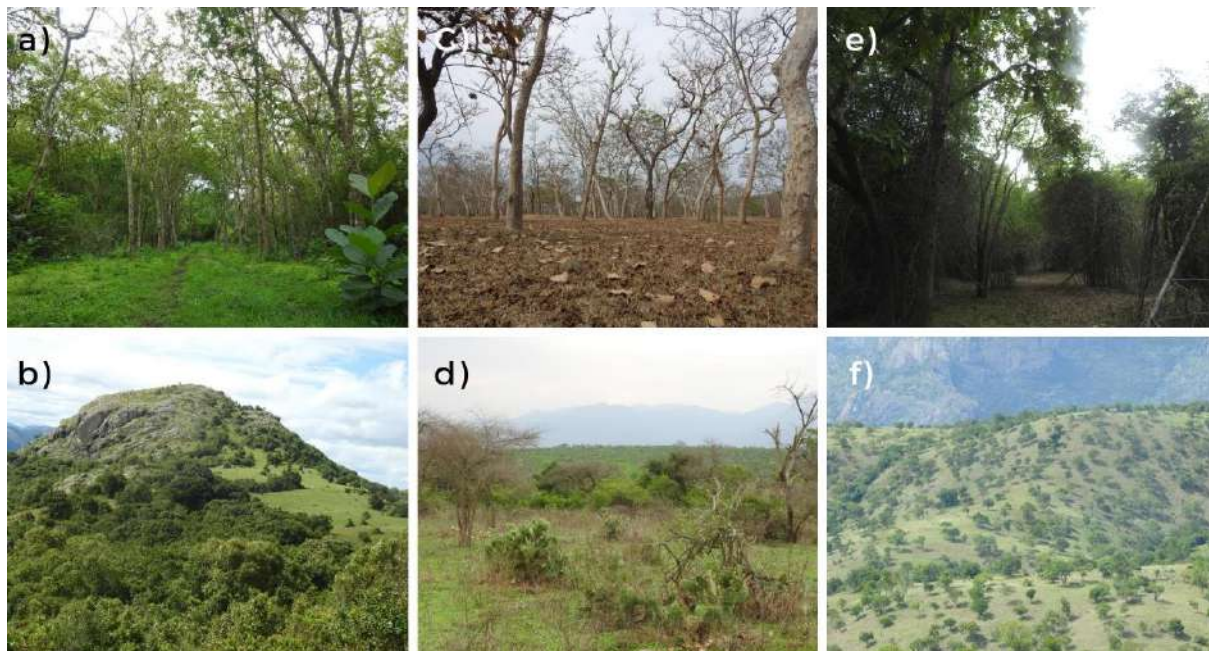


Figure 2.11 Different habitat types of the study area: Moist deciduous forest (a), Evergreen forest (b), Dry deciduous (c), Scrub forest (d), Bamboo break (e) and Savana type grassland (f).



Figure 2.12 Different landscape views of the study area.

Chapter 3



Chapter 3: Examine the role of socio-economic characteristics and livestock predation on the prospect of striped hyaena conservation in a high human-carnivore conflict landscape

3.1. Introduction

Global carnivore population inhabits a proximate association with humans (Ripple *et al.* 2014) and recurring inimical human-carnivore interactions at such interfaces as livestock-depredation (Khorozyan *et al.* 2015), and human fatality (Ripple *et al.* 2014), spur retaliatory killing of species in conflict (Karanth & Madhusudan 2002). Such counterproductive encounters are generally pronounced as human-carnivore conflict (HCC) (Madden 2004). The impoverished economy of the people susceptible to high HCC makes the losses owing to livestock depredation unaffordable, which further increases negative conservation attitude towards predators which is also generally hailed as intolerance (Graham *et al.* 2005; Gusset *et al.* 2009). Retaliation is a manifestation of intolerance that has led to a population decline of many key species like spotted hyaena (*Crocuta Crocuta*), tiger (*Panthera tigris*), lion (*Panthera leo*), condor (*Vultur gryphus*), wild dog (*Lycaon pictus*), cheetah (*Acinonyx jubatus*), wolves (*Canis lupus*), and cougar (*Puma concolor*) (Marker *et al.* 2003; Gusset *et al.* 2009; Cailly Arnulphi *et al.* 2017). Moreover, the negative conservation attitude that is exhibited in the form of social repugnance may not only defy the established conservation policies but may also worsen governance through a protracted effect. Political outrage against wildlife conservation is an ostensible form of the collective and protracted effect of social repugnance. Hazzah *et al.* in 2014 reported the killing of 161 lions in Kenya from 2003-2011 out of which 50% of kills were retaliatory and the rest were the victims of political outrage. Ecological havoc like “The Great Sparrow Campaign” which had led to the extirpation of sparrows from entire China and the extirpation of the wolf and cougar from Mexico and Washington state (Moctezuma *et al.* 2004; Woodroffe *et al.* 2005; Chapron *et al.* 2014) exemplifies the impact such outrage may have. If social repugnance may not prompt an impromptu and direct response it may encourage to allow an outsider to poach the problematic species (Liu *et al.* 2011). Hereby, negative conservation attitude imparts a huge and grim impact on conservation practices in the form of both retaliation and social repugnance though their relative impact may be debatable.

Tolerance is a personality trait and also a function of perception which is not only determined by experienced loss but also significantly varies across demographic properties like gender, ethnicity (culture and religion) and age, etc (Bhatia *et al.* 2017; Ballejo *et al.* 2020). In conservation science, the term perception has relevance as a positive or negative appreciation for wildlife (Cailly-Arnulphi *et al.* 2017). Different studies have been conducted to understand the appropriative mechanism of negative perception towards carnivores (Marker *et al.* 2003; Nawaz *et al.* 2016; Bhatia *et al.* 2017; Mogomotsi *et al.* 2020). Out of these, most have explored only the direct impact of socio-economical attributes on the perception towards carnivores. However, such apprehending approaches generally fail to provide very cogent justifications for negative attitudes and persecutions of mere inflicting carnivores. All co-occurring carnivores don't affect the people's economy equally (Trajçe *et al.* 2019). Nonetheless, the soaring unsustainable economic loss elicited by a group of species or a species overgeneralizes the predation-induced fear of damage-causing species (Farhadinia *et al.* 2017). Although higher antagonism towards more problematic species is evident, a vivid increase in intolerance for co-occurring species along with predation rate by prior was also recorded (Gusset *et al.* 2009). This underpins the prevalence of generalization of a perceived threat to the entire functional guild. While, such over-perceived threats, contradict the actual damage caused (Ballejo *et al.* 2020), and jeopardize the co-occurring lesser-known carnivores (Marker *et al.* 2003). The over-generalization of perceptual fear, coherently, might occur due to high economic stress and to increase sustainability in high-conflict hotspots. The process of generalization over different species could be well understood by the universal law of generalization proposed by Shepard (1987). According to the law, the distance between a pair of items in psychological space determines whether they will be perceived as similar. Following the theory, the current study was designed to assess the generalization of perceived fear and attitude of intolerance over the striped hyaena, *Hyaena hyaena* as a result of high HCC in the Western and Eastern Ghats part of Tamil Nadu (WEGPTN), India. The leopard which is proximate to hyaena in terms of body size and weight inflicts high livestock loss in landscape and may preclude “discriminative cognition” under high economic stress. Furthermore, apart from predation, livestock ailments also cause huge losses to the agro-pastoralist economy and often exceed the loss from HCC in most of the HCC hotspots (Harihar *et al.* 2014). Such bilateral losses from depredation and diseases may curtail the victim's sustainability and exacerbate the intolerance towards carnivores further. Therefore, the impact of livestock ailments on the people's tolerance towards the species was also assessed in the chapter.

Striped hyaena is predominantly a solitary scavenger (Wagner *et al.* 2008). Its global geographic range includes the Middle East, Caucasus region, Central Asia, and the Indian subcontinent, with its southern and western limits in Africa (Mills & Hofer 1998). The species has experienced a sheer decline in its population throughout its global distributional range due to persecution for meat or traditional belief, deliberate poisoning, competition from co-existing carnivores, and reduction in livestock carcasses owing to the alteration in agro-pastoral practices (Kruuk 1976; Wagner 2006; Alam 2011; Ilayaraja *et al.* 2018). Such pervasive threats have already led to the extinction of the species from many places (Kruuk, 1976; Mills & Hofer 1998) and species have become critically endangered in some of their distributional ranges (Kasperek *et al.* 2004). These have also caused a drastic decline of the striped hyaena population in the WEGPTN (Arumugam 2012) and presently a small breeding population is confined in the Moyar valley of the Mudumalai-Sathyamangalam landscape which is a high HCC hotspot zone (Ramesh *et al.* 2020). The precise information on the reason behind the generalization of fear and intolerance can minimize the vulnerability of mere damage-causing species. As the striped hyaena (henceforth called “hyaena”) is predominantly a scavenger, the priori assumption in the study was that hyaena would have a negligible contribution to the total livestock depredation caused by the functional guild. In this chapter, I have studied the socio-economic status of villagers and tested whether the collective economic stress elicited by large sympatric carnivores generalizes the fear of livestock predation among local communities and their intolerant attitude towards hyaena. This chapter examined the following research questions: i) Does high economic stress caused by obligate predators curtail people’s tolerance towards mere inflicting species like hyaena? ii) Does loss of livestock due to disease also play a role in such ill-generalizations?

3.2 Methods

3.2.1 Socio-economic survey

The socio-economic survey was conducted in the Intensive Study Area (ISA) identified based on the current local distribution of hyaena in the WEGPTN (Jhala *et al.* 2020). Initially, potential hyaena distribution areas were marked as Extensive Study Area (ESA), predicted through a species distribution model calibrated using secondary data available. The ESA was further surveyed through camera trapping (Figure 3.1 & 3.2) in conjunction with the indirect sign surveys. Based on the recorded evidence of the species occurrence, the ISA was delimited. The ISA majorly encompasses Sathyamangalam Tiger Reserve (STR) and Mudumalai Tiger

Reserve (MTR). Semi-structured questionnaire surveys were conducted to collect the socio-economic data in the language of Tamil. Households practicing agro-pastoralist lifestyle were selected and one the interested members of households who were above 18 years old were interviewed. In the survey, 197 households (Figure 3.1) were interviewed covering 32 different settlements situated within and in the immediate proximity of hyaena distribution range.

Before carrying out the field survey, it was assumed that fear cum expectations, incompetency, and false memory (Roediger & McDermott 1995) of respondents are the most probable causes that may embody disparity in the data. Therefore, considering the threats of error that may be induced advertently and inadvertently, a “quadruple check mechanism” to maximize the fitness of the data was developed. In the first step, the academic purpose of the survey to the villagers was explained and it was clarified that it has no immediate managerial implication, to minimize the fear cum expectation lured biases in their responses. Secondly, only the heads of households who had experienced living in the interface areas for more than five years were interviewed assuming they were well accustomed to carnivores and competent in ascertaining their kills. As a third step, each interviewee was explained about the signature pattern of kill of all four carnivores like laceration of flanks and hind legs in dhole while strangulation with throat bites in cats. Moreover, injury marks, scats, tracks, and rakes of all four carnivores were shown which were developed in a print format for training field frontline staff from over 15 years of in-depth field experience working on large carnivores (Ramesh 2010; Ramesh *et al.* 2012b). At last, the aim, to minimize the effect of false memory attempted by taking the account of predation for only the last two years.

The questionnaires had three broad sections: the socio-economic status, HCC, and people's attitudes towards hyaena. Under the first section, socio-economic attributes were gathered (Table 3.1) wherein, the annual income is cumulative earnings from farming, wages, non-timber forest products, and dairy and cattle rearing of a family were recorded. Under the second section, details on livestock lost in attacks by four carnivores (Tiger, Leopard, Dhole, and Hyaena) and of those who died of ailment in the last two years were collected. Finally, respondents were asked whether hyaena is a potential threat to their cattle and also inquired about their willingness to conserve the species in their vicinity.

3.2.2 Selection of variables for analysis

Initially, 13 explanatory variables (Table 3.1) were selected based on the understanding developed through relevant literature and open-end interaction with villagers, to test their impact on the conservation attitude towards the species (Gusset *et al.* 2009; Farhadinia *et al.* 2017; Harihar *et al.* 2014; Bhandari & Bhusal, 2017; Ballejo *et al.* 2020; Castillo-Huitrón *et al.* 2020). Pearson correlation test was applied to all explanatory variables in program R version, 3.0 (R Development Core Team, 2018), and among the highly correlated variables ($r > 0.60$) only the most ecologically sensible was retained (Figure S3.1). The total number of attacks on livestock and economic loss to predation were the only variables found to be highly correlated and the variable attacks on livestock was discarded (Figure S3.2).

3.2.3 Data analysis

A social system is a very complex organization and exhibits intricate and non-linear interactions that result in uncertainty in any allied phenomenon. While linear models are pragmatic and hold many assumptions that seldom stand true in a socio-economic framework, they usually fail to recognize complex interactions. Here, I used the Random Forest classifier (Breiman 2001) which is a non-linear model, to understand the importance of variables and their complex interaction in explaining the conservation attitude of villagers (Cutler *et al.* 2007). The binary response variable (conservation attitude) was class imbalanced (the number of cases of one class was substantially higher than another). Initially, more data were synthesized for minority class using the Majority Weighted Minority Oversampling Technique (Barua *et al.* 2012), in program R. Several random forest models were calibrated using the random forest package (Liaw & Wiener 2002) with a different number of trees to check prediction stability and grew 19000 trees as computational time was not a limitation. To determine the optimal number of variables randomly to be sampled as candidates at each split (mtry), I ran several models with different values and found the model's highest accuracy at mtry equal to 4, and the same was maintained for the final model. The tree depth that is node size was kept the same as default which was 1. Two measures of variable importance, 1) mean minimal depth which is the depth of the node that splits on that variable and is the closest to the root of the tree and 2) Gini index (Lerman & Yitzhaki, 1984) was calculated. Wherein, a lower value of mean minimal depth is commensurate to the higher importance of the variable in the model whereas a high Gini index implies greater importance in the model. In this chapter,

I also identified protagonist interactions of variables explaining the conservation attitude based on conditional mean minimal depth (Seifert *et al.* 2019).



Figure 3.1 Photographs of preliminary field efforts taken to delimit Intensive Study Area: Camera trapping (a & b), Sign survey (c & d).

Table 3.1 Variables used in the model and their properties.

Sl No.	Name of co-variates	Understanding	Variable type	Class-level
1.	Age	Age of the respondent	Numeric	-NA-
2.	Sex	Sex of the respondent	Binomial	Male, Female
3.	Community	Whether the respondent is a tribal or a non-tribal	Binomial	Tribal, non-tribal
4.	Literacy	Whether any of a household member is literate	Binomial	No, Yes
5.	Annual income	Annual income of the family	Numeric	-NA-
6.	Number of people employed	Total number of people employed in the family	Numeric	-NA-
7.	Livestock dependency	Proportion of the family dependent on dairy or livestock rearing for livelihood	Numeric	-NA-
8.	Forest dependency	Proportion of the family dependent on working with forest department for livelihood	Numeric	-NA-
9.	Threat by Hyaena	Whether respondent perceive hyaena as a threat for their livestock	trinomial	No, Yes, not sure
10.	Loss to disease	Sum of estimated value of livestock died due to disease in last two years	Numerical	-NA-
11.	Loss to predation	Sum of estimated value of livestock killed by carnivores in last two years	Numerical	-NA-
12.	Livestock vaccination	Whether family is a beneficiary of any government sponsored livestock vaccination scheme	Binomial	No, Yes
13.	Total attack	Total number of attacks on livestock by a wild predator in last 2 years	Numeric	-NA-

(*NA-Not Applicable)

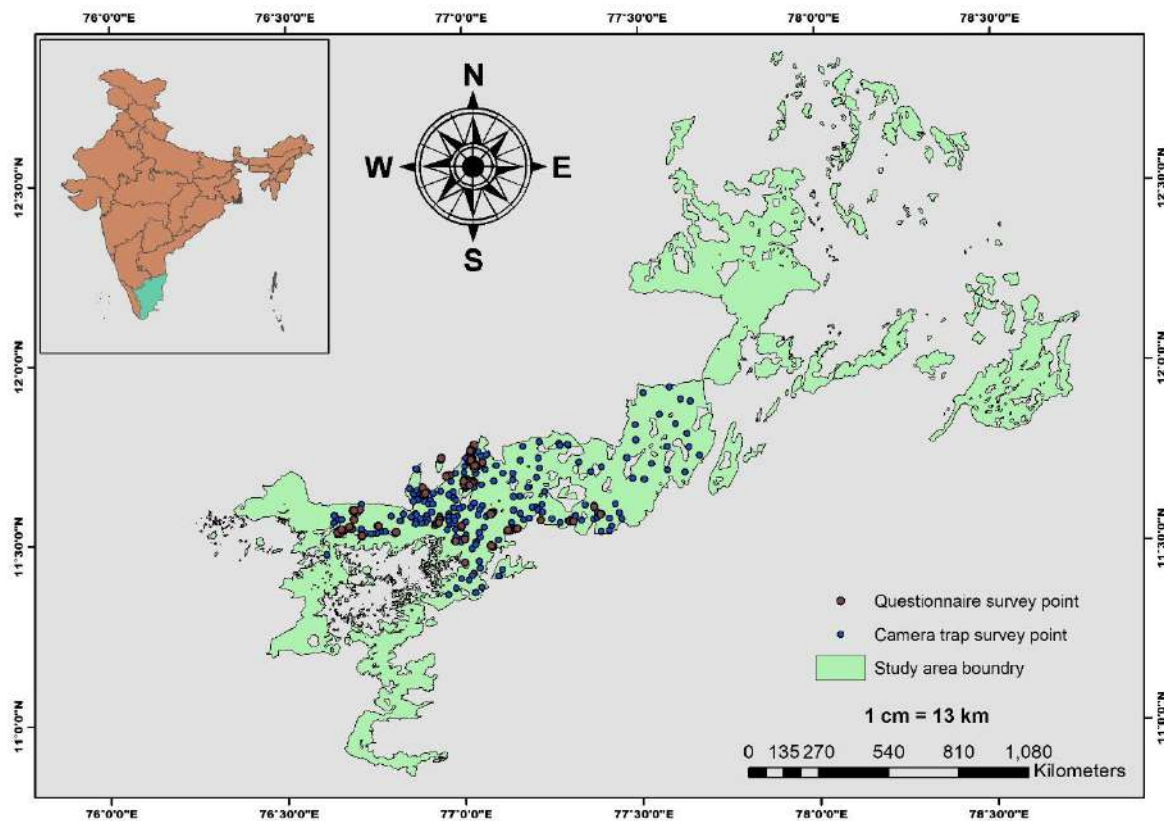


Figure 3.2 The figure illustrates the location of 197 semi-structured questionnaire camera trap survey points displayed over the boundary map of the Western and Eastern Ghats parts of Tamil Nadu. The camera traps were operated 24hrs for a minimum of 20 days in a location for detecting hyaena and other co-occurring species.

3.3. Results

For this chapter 45.69% tribal and 54.31% non-tribal communities were interviewed and the proportion of males and females who appeared in the interview was 81.73% and 18.27% respectively (Figure S3.3 & S3.4). Overall, 86.3% of families were found to be literate, however, the literacy rate of tribal was found to be 75.4% and in non-tribes was 82% (Figure 3.3). People's economy was heavily reliant on agro-pastoralism, and wages-based work wherein annual mean dependency on animal husbandry was 26.68% of their livelihood. Dependency on forest department-sponsored opportunities ranged from 18% to 85 % of people's total annually but only 3.55 % were found to be beneficiaries of such opportunities. Overall, 69.54% (n=137) of people were uncertain about the predatory behavior of hyaenas whereas seven percent (n=14) of respondents perceived hyaenas as a threat to their livestock

and 23% did not perceive hyaena as a threat (Figure S3.5). Analogous responses were observed across the socio-ecological affiliations of the respondents (Figure S3.5 to S3.9). Furthermore, 23.36% of people who were uncertain about the predatory behavior of species respondents were intolerant towards hyaena (Figure S3.10). 79.18% of respondents were interested in conserving hyaenas, while 20.81% were found to be reluctant to conserve the species in their vicinity. The respondents belonging to the non-tribal community, female gender class, and illiterates showed higher relative intolerance for the species than their respective counterparts (Figure S3.11 to S3.13). Economic loss due to cattle disease was 60.53% of the total economy of people while predation caused only a 39.95% loss of people's economy. In total, 245 instances of livestock predation were reported by 40% of people interviewed. Out of which hyaena was alleged for only eight cases and those include predation on six goats and two dogs.

The calibrated model underscored the loss to livestock predation as the most important in explaining the conservation attitude of the respondents (Figures 3.4, 3.5 & 3.6). The mean minimal depth and Gini index for the variable loss to predation were found to be 1.31 and 30.87 respectively. In both of the indices, livestock dependency was the second most important variable followed by the number of people employed, annual income, age, loss to disease, the threat by hyaena, community, sex, literacy, livestock vaccination, and forest department dependency (Figure 3.5 & 3.6; Table S3.1). Based on the conditional mean minimal depth, the 30 most influential variable interactions were identified (Figure 3.6) wherein consortium of loss to predation and livestock dependency placed at the root and subsequent node of a tree respectively showed the lowest conditional mean minimal depth. This implies the best interaction to predict conservation attitude which reaffirms their firm significance in the model. Partial dependency graphs of the seven most pivotal variables of the model were plotted. Following, loss to predation, livestock dependency, annual income, and loss to predation exhibited a negative relation with the conservation attitude of people. This implies that it is less likely to have a positive conservation attitude if the respondent is associated with a higher limit of these variables. Older respondents (> 40 years) were more likely to possess a positive conservation attitude than their younger counterparts. Similarly, a higher value of the total number of people employed corresponded with a positive conservation attitude. The negative conservation attitude was found firmly associated with perceptual uncertainty about the predatory behavior of hyaena. This implies that it is more likely to have a negative attitude if the respondent is uncertain. The overall error rate of the model based on the Out of Bag (OOB) (data points from the dataset that were not used in model calibration but left out for the model

validation.) estimate was 12.62% while the false positive rate was found to be 13.79 % and false-negative 11.53% (Figure 3.6).

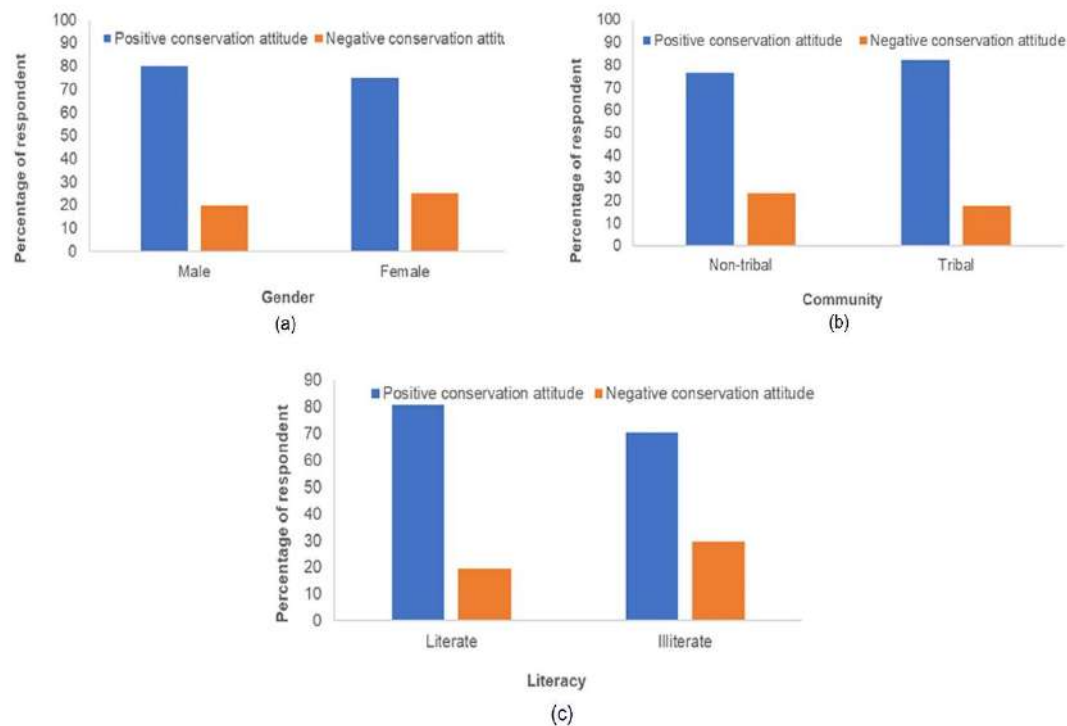


Figure 3.3 (a) Frequency of male and female respondents corresponding to conservation attitude towards hyaena. Those who supported the conservation of hyaena were higher for males 80.12% (n=129) and 75% (n=27) for females. Figure 2 (b). Frequency of tribe and non-tribe corresponding to conservation attitude towards hyaena. Non-tribe were found to possess a higher percentage of intolerance than tribes, 23.36% (n=25) and 17.78% (n=16) respectively. Figure 2 (c) Frequency of literate and illiterate corresponding to conservation attitude towards hyaena. Illiterate were found to possess a higher percentage of intolerance than literate, 29.63% (n=8) and 19.41% (n=33) respectively.

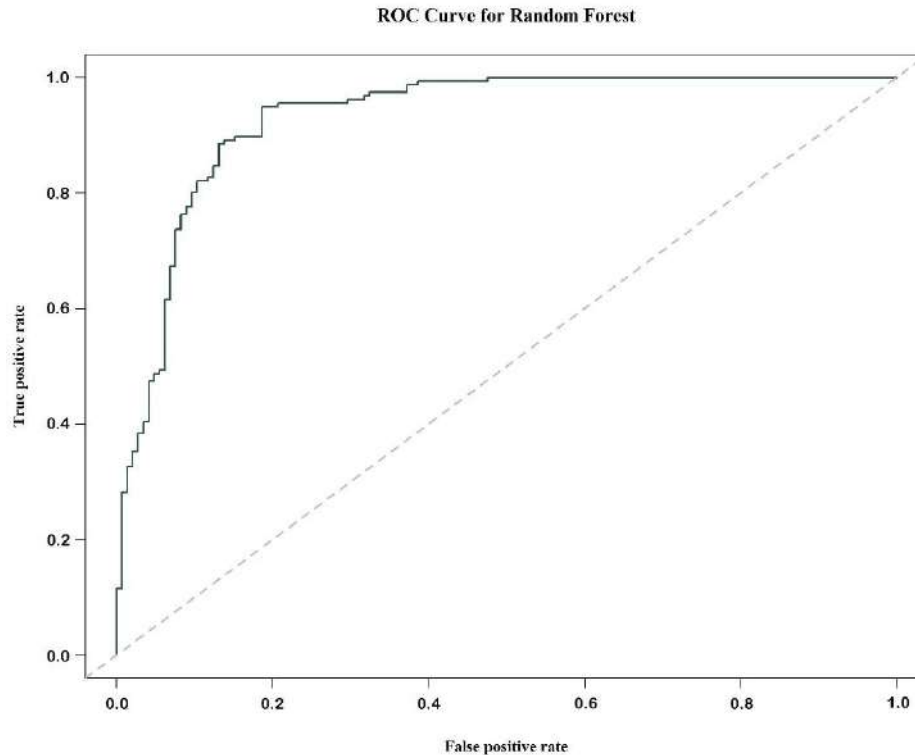


Figure 3.4 The accuracy of the calibrated model was checked by plotting the Receiver Operating Characteristics (ROC) curve which is a trade-off between the proportion of correctly identified positive conservation attitude (True positive rate) and wrongly identified negative conservation attitude (False positive rate) from a dataset. These proportions are based on the number of predictive classifications made on Out of Bag (OOB) data modulating different class thresholds on the probability predicted for positive conservation attitude by the model. Therefore, the low value of False-positive conservation attitude on the X-axis and high value of True positive rate on the Y-axis corresponds to a high likelihood of correct classification if any test data ran through the calibrated model. Following, the graph depicts about 90% of predictions made on OOB data have less than a 0.4 false-positive rate which means these predicted classes are highly likely to be correct. Here the term Out of Bag data refers to the data points from the dataset that are not used in model calibration but left out for the model validation. OOB data are the unused data points from the dataset in model calibration and are used for model validation.

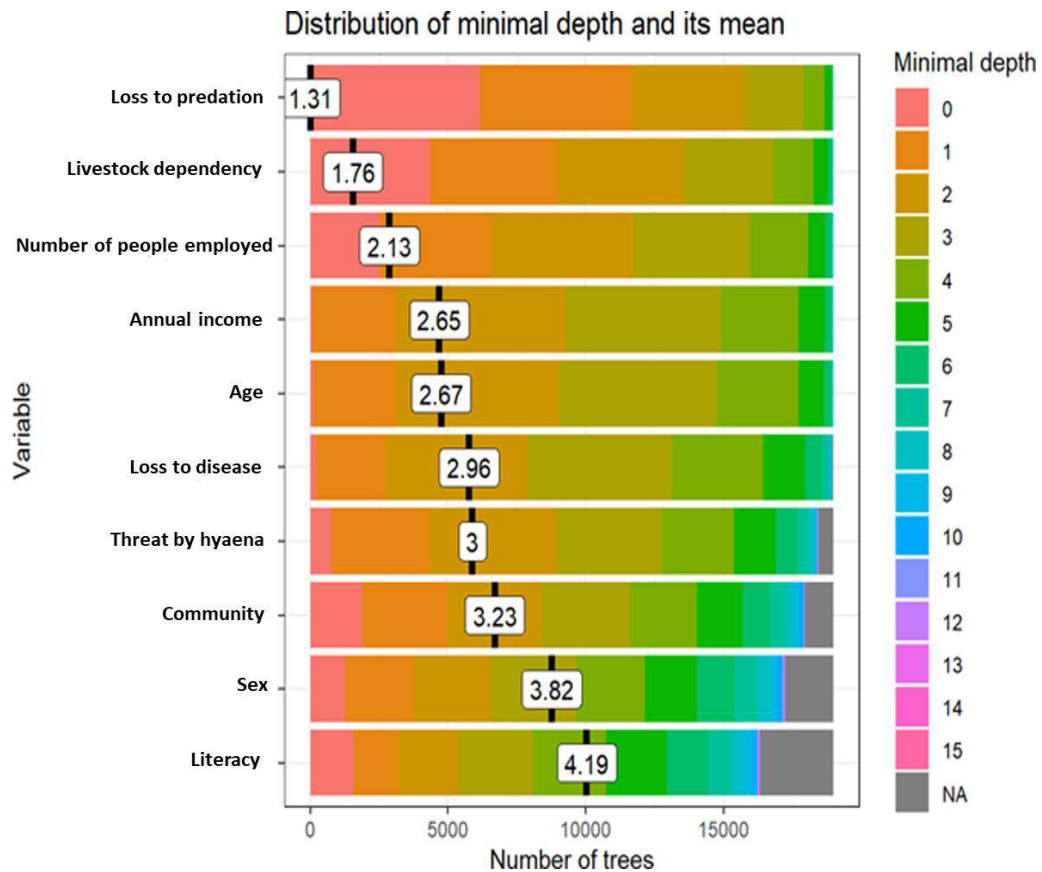


Figure 3.5 Variable importance graph represents the 10 most important variables in determining the people's attitude towards hyaena using mean minimal depth as a parameter. Importance of a variable in the model was assessed by the mean of minimal depth attained by every node split on that particular variable. Here the mean minimal depth is an average of minimal depth for a variable and minimal depth stands for the distance between decision node and the node that splits on that particular variable in a tree. Lower the value of minimal depth for a variable higher the robustness of the variable in making binary decisions by achieving intra-class homogeneity with minimal subsequent splits. In the graph mean minimal depth of a variable is labelled on the colour scale stretched parallel and corresponds to the X axis which is the number of trees grown in the model. The graph represents the mean minimal depth of most 10 variables out of 12 and within which variable loss to predation appeared to be most important variable in determining the people's attitude. NA in the minimal depth of some variables means no data as no trees were split on these variables for the corresponding ranges of numbers of trees present at X axis. Occurrence of NA in minimal depth of week variables further also suggests that weaker variables appear in a smaller number of trees in comparison to their stronger counterparts.

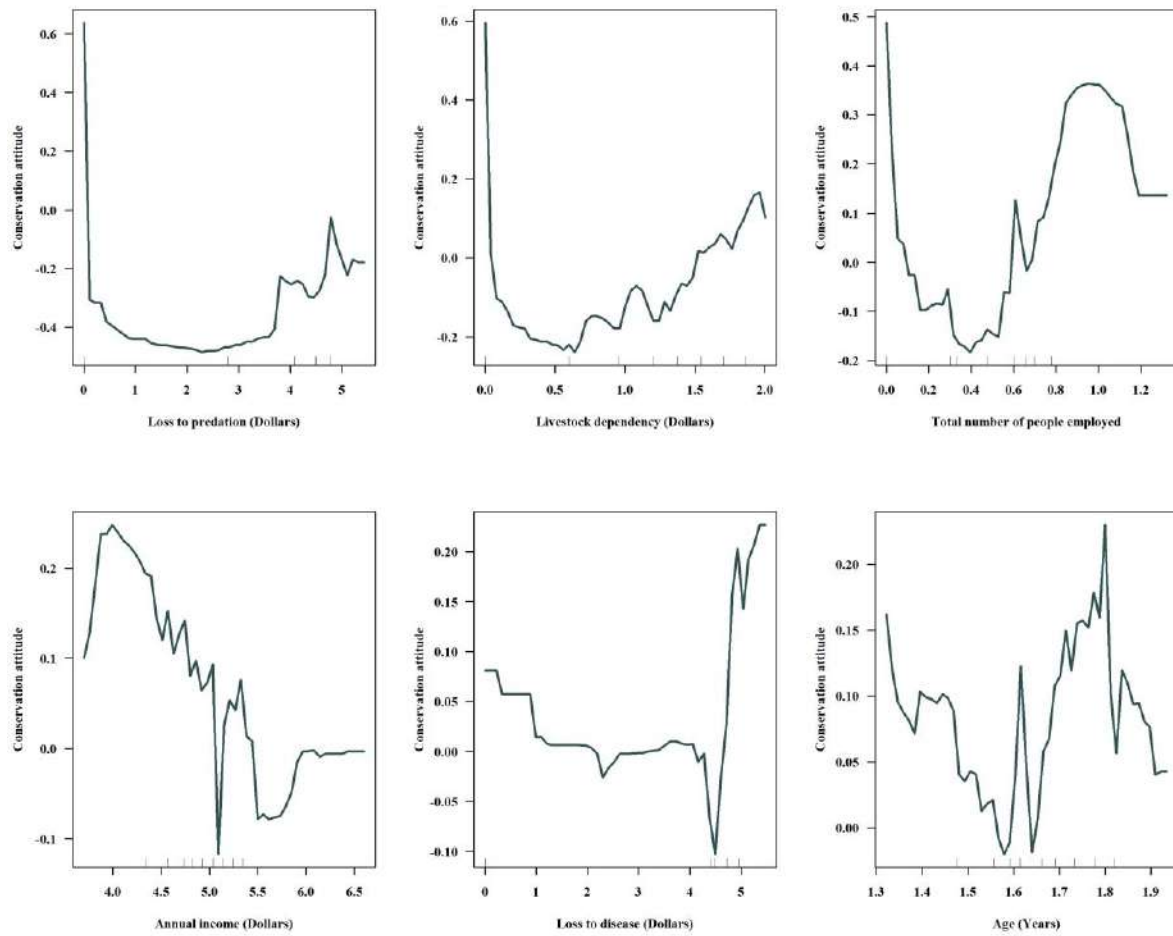


Figure 3.6 Partial dependency graphs of six most important variables show their marginal effect on the conservation attitude of respondents. Here, marginal effect refers to how changes in the value of a variable keeping others at a constant value affect the likelihood of a positive conservation attitude of people. These graphs cogently show the decline in the likelihood of positive conservation with an increase in values of important variables like loss to predation and livestock dependency.

3.4 Discussion

Worldwide, mesocarnivores are being persecuted by villagers for their perceived threats of livestock predation while those conjectural threats rarely match the actual damage caused. Striped hyaena which is a victim of such persecution (Wagner 2006; Bhandari & Bhusal 2017; Ilayaraja *et al.* 2018), accounts for minimal livestock loss that is almost negligible in comparison to the damage caused by its sympatric species (Bopanna 2013; Farhadinia *et al.* 2017; Srivathsa *et al.* 2019). Analogously, in this study, only a few cases of livestock predation by the species were recorded but conversely, the majority of respondents (70%) were uncertain of the predatory efficiency of hyaena. Further, perceptual uncertainty was found to be sheerly articulated with a negative conservation attitude in the random forest model. Such intolerance to uncertainty is not novel but a known tendency to perceive uncertainty as prejudicial (Carleton 2016). Here, perceptual uncertainty could be a result of the elusive and nocturnal behavior of hyaena that can reduce “discriminative cognition” and may coerce to perceive two proximates as similar. Leopards, which are proximate to hyaena in body size were reported to have the highest livestock-predation rate from this landscape (Ramesh *et al.* 2020) (Figure 3.7). This morphological proximity probably subjected hyaena to be perceived as a threat, particularly by the people who found the predatory behaviour of hyaena uncertain. A similar case where irrespective of the damage inflicted, jackals were regarded as a threat by people who perceived leopards as problematic, (Marker *et al.* 2003). Such stress-induced generalization of fear is ubiquitous (Shin & Liberzon 2010) and a contemporary domain in human psychology that regards such “perpetual enveloping” as a dispositional defensive tendency that minimizes threat exposure. Generalization was not only found limited to the perceived threat but about 21% of people were found to be intolerant to the species in disproportionate to the number of people who perceived hyaena as a threat. Such discrepancy already has been evident in a study where the cheetah was persecuted in the area where people had a largely positive attitude towards the species (Marker *et al.* 2003). Further, Marker *et al.* (2003) attributed such indiscriminate removal of cheetahs as a traditional attitude irrespective of contemporary conflict status with the species. The presence of secondary stimuli like a play tree in farmland that attracts other cheetahs could also affect the evaluation of primary stimuli and may be another alternative reason for the reported removal. Furthermore, in this study, collective economic stress to predation was found to be a protagonist factor in determining the intolerance and showed a positive relation with the cumulative loss inflicted by sympatric species. A similar pattern was observed by Farhadinia *et al.* (2017) where a negative view

towards leopards was strongly associated with the amount of loss caused by wolves. The observed generalization of intolerance articulated with predation-induced economic stress is a survival strategy and aligns with an increase in generalization with stress levels in both human and non-human animals observed by Dunsmoor *et al.* (2017). In a lucid term, the studied generalization is a defense mechanism that prefers “fear over tears” seeking economic sustainability grappling under the high stress of livestock predation. The economic stability was also found to be undercut by loss to livestock disease more than predation does and was also discerned as an important driver of generalization. Loss to disease was another essential axis of economic stability that needs due managerial attention, especially in the human-carnivore interface.

In the study, it was observed that acute intolerance for hyaena conservation due to over-generalization of fear elicited under high economic stress remarkably articulated with livestock predation, livestock loss to disease, people’s livelihood, and importantly perpetual uncertainty on predatory efficiency of species. This generalization is situational and heavily conditioned by economic instability so it does hold a leeway for its modulation with both ancillary and auxiliary befitting managerial interventions. Thus, to reduce intolerance, it is imperative to offset the economic stress elicited by livestock predation with prompt compensation programs. Auxiliary veterinary support should be reinforced (Nawaz *et al.* 2016) in the study area and also people should be acquainted with the scavenging behavior of the species. Compensation endures high managerial expenditure particularly in poor governance (Nyhus *et al.* 2003), and may cost dearly if improvised management fails to support the compensation in the future (Treves *et al.* 2009). Therefore, modulating people’s perception through community involvement (Treves *et al.* 2009) along with the ancillary and auxiliary managerial interventions may prove a “golden mean approach”. Analogously, high-income countries' practices are more inclusive policies providing community involvement and a firm place in conservation management apart from strong legislation (Woolaston *et al.* 2021). Such efficient strategies have not only successfully shifted the people’s anger from the wolf for depredation to management marking the loss as a managerial lacuna in Washington (Anderson 2021). However, efficient governance with strong legislation has also helped in reviving the carnivore population that who once extirpated through persecution in the US, Mexico, and one-third of the European host mainland (Chapron *et al.* 2014; Castillo-Huitrón *et al.* 2020; Anderson 2021). Education and awareness are the key tools that increase the social acceptance of carnivores by modulating the perception of the whole community (Baruch-Mordo *et al.* 2011).

Therefore, the findings suggest that the curriculum of primary and secondary education should also have a component of wildlife education primarily in the interface areas which will act as a precautionary measure to relegate to human-carnivore conflict. Following, this may be done under the “appraise-appraise” feedback framework for management which will not only appraise the effectiveness of awareness programs in curtailing the existing intolerance for hyaena but will also establish a firm place of perceptual uncertainty in HCC management. On the other hand, pastoralist community grazes their cattle inside the forest which often results in livestock depredation by other predators like the tiger, leopard, and dhole. Managerial interventions like the arrangement of stall feeding for their cattle will reduce such aversive interaction and will help assuage the negative attitude towards carnivores in the landscape. Reducing their dependency by providing different alternative opportunities in the form of eco-tourism and small-scale handicraft industry in the area will also be helpful in the long-run conservation of this last remaining major breeding population of hyaena in southern India. Furthermore, there is a dire need for demographic study of the population and identification of alternative suitable habitats for the population. So that the befitting managerial interventions can be taken to conserve this small and confined population.

The study is probably the first designed avant-garde investigated fear-induced generalization of predation risk by non-obligate predators although generalization is a common behavior in humans. The study established the interplay between generalization and economic instability and also underscored the importance of uncertainty in such ill-generalization. However, the study manifested the prevalence of fear-induced generalization over the non-obligate predators of a carnivore guild, only less than one-fourth population reported a negative conservation attitude towards the species. There could be several reasons for this underrepresentation but in the discrete data exploration, it was realized that 245 incidences of conflict that was reported by only 40 percent of people. This would be a proximate reason for the less reported negative conservation attitude but it may exacerbate with conflict rate. Even though, if 20.81% negative conservation attitude is considered just as a sinister of threat generalization then the empirical model confirms the daunting pattern firmly. This implies that if the HCC continues to increase it can severely imperil the existence of the last remaining major population of carnivores in southern India. Furthermore, the study did not investigate species-dependent variance in generalization due to the absence of other sympatric species like fox and jackal from the study area. Again, in this study, only the body size of hyaena was assumed as an index of perceptual proximity to obligate predator leopard in this case but it is not yet established empirically that

how morphology and ecology of non-obligate predators will determine the species-specific generalization (perceptual proximity). This conundrum can be hammered-out with the theory of generalization and will help to prioritize conservation urgency based on the degree of perceived proximity of a species to obligate predators (generalization). In the regime of increasing HCC, this study can be very efficient to check or predict if any wildlife species is prone to such intolerance currently or in the future with some methodological optimization like the inclusion of ecology and behavior of the species as a predictor. Moreover, the efficacy of the “quadruple check mechanism” to minimize both advertently and inadvertently induced disparity in questionnaire surveys should be checked further for its wider applicability to ensure the fidelity of data in such studies.



Figure 3.7 Livestock depredation by leopard and scavenging by hyaena in the landscape.

Chapter 4



Chapter 4: Assess co-predator interaction in the breeding habitat of striped hyenas

4.1 Introduction

Top predators occupy the foremost place in food webs and serve as indicator species in conservation biology, as they are highly sensitive to environmental dysfunction (Landres *et al.* 1988; Lindenmayer *et al.* 2015; Marneweck *et al.* 2022). Environmental perturbations at lower trophic levels, resulting from climate change or anthropogenic pressure, often translate into subsequent changes in the behavior and demography of apex predators (Morrison *et al.* 2007; Hazen *et al.* 2019). Due to their acute sensitivity to habitat alteration, high energy demands, and low fecundity, apex predators face a high threat of extinction throughout their distribution under high anthropogenic pressure. (Weaver *et al.* 1996; Carbone *et al.* 2007; Sergio *et al.* 2008; Ripple *et al.* 2014; Abrahms *et al.* 2022). At the same time, as keystone species they structure a large component of their habitat by exerting a disproportionate top-down impact on the ecosystem relative to their abundance (Terborgh *et al.* 2001; Ritchie & Johnson, 2009; Maslo *et al.* 2016). Predation is a crucial evolutionary component of an ecosystem, and its absence may allow the unchecked population of primary consumers to temporarily exceed the carrying capacity, potentially resulting in the complete devastation of the ecosystem. The trophic cascade effect of apex predators is widespread and observed across different habitats, ecosystems, and regions. For example, the deterioration of kelp forests followed by the eradication of otters along the Pacific coast of North America (Estes *et al.* 1998). A reduction in the population of top predators below an optimal level or their eradication from a multipredator guild can induce entropy in the ecosystem, also by triggering an outbreak of mesopredator populations (a phenomenon known as “mesopredator release”), which may lead to unchecked predation on smaller prey species and a simultaneous increase in population large ungulate (Ritchie *et al.* 2009).

Recognizing their important roles and large home range, large carnivores have been indiscriminately leveraged as flagship or umbrella species in wildlife conservation policies to extend patronage to larger taxonomic groups and conservation regimes (Wilmers *et al.* 2003; Ripple & Beschta, 2006; Thorne *et al.* 2006; Sergio *et al.* 2008; Jhala *et al.* 2021). Such large carnivore-centric policies garner high public support, owing to the aesthetic value of large

predators and their close association with human culture, curated through a long history of interactions (Gittleman 2001; Lundberg & Arponen 2022). However, the purported advantages of such top predator-centric policies may not be uniform across different taxa, ecosystems, and conservation regimes. There is a growing body of literature that cautions against this conservation approach, highlighting its caveats over the conservation of sympatric meso-carnivores or subordinates of flagship predators (Gese *et al.* 1996; Helldin *et al.* 2006; Ritchie & Johnson 2009).

In a synthesis, Prugh and Sivy (2020) attributed one-third of mesocarnivore mortality to intraguild killing by their larger counterparts. The proportion of such competitive elimination may also reach very high levels, potentially influencing community assemblages and their structure. For instance, the cheetah population declined by 73% due to intraguild killing by lions (Laurenson 1994). Similarly, an increase in the population of large predators such as lions and wolves has already led to the extinction of wild dogs and coyotes from Serengeti National Park and Isle Royale, respectively (Creel & Creel, 1998; Lindström *et al.* 1995; Peterson, 1995; Smedshaug *et al.* 1999). Additionally, interference competition also imposes more severe and long-term consequences on subordinates by restricting their movement and distribution outside resource-rich habitats (Sergio & Hiraldo 2008). Competition for habitat may further intensify the negative impact of predation, as access to limited resources and fear of large predators impede the growth, reproduction, and survival of subordinates (Creel & Christianson 2008; Ritchie & Johnson 2009). It is very difficult to precisely quantify intraguild predation in the field (Ritchie & Johnson 2009); therefore, the existing understanding of competition has primarily relied on spatiotemporal changes in occupancy and/or distribution of meso-predators with respect to their superordinates.

Spatiotemporal congruence or avoidance between top and meso-predators is dependent on prevailing environmental conditions, and may vary significantly over time, region, and interacting species, both in strength and direction. Such context dependence is complex, non-linear, pervasive, and highly dynamic; in short, it exhibits non-stationary patterns, with the same interacting species responding strikingly different across regions (Krefting 1962; Smith *et al.* 2003; Ritchie & Johnson, 2009; Karanth *et al.* 2017;). Such non-stationarity of environmental effects notwithstanding, studies investigating species interactions at the macroecological level often ignore the potential for varying underlying responses.

Non-stationarity refers to deviations in the statistical properties of a model due to changing interactions of variables driven by environmental variability, over time, or in space (Rollinson *et al.* 2021). It is an implicit assumption of any attempt to predict from a statistical model to new data. For example, macroecological analyses of occupancy (i.e., species distribution models) are based on data from different regions, yet they tacitly assume a static statistical model across ecological contexts (Kupfer & Farris 2007 Finley 2011, Thorson *et al.* 2023, Doser *et al.* 2024). Managerial inferences drawn from such studies, especially for complex phenomena such as species interactions, may mislead context or site-specific management and potentially have long-term negative impacts on wildlife conservation. A series of studies have demonstrated non-stationary response of animals to habitat parameters and potential mis-implications of large-scale stationary models on wildlife conservations (Liang *et al.* 2020; Pan *et al.*, 2024; Rana *et al.* 2024). However, the impact of violated stationarity on interspecific interactions is still underexplored. Therefore, this study explores non-stationarity in species interaction by examining top-predator control over hyaena and jackal in different landscapes of India.

Apart from identifying non-stationarity in ecological systems, its efficient incorporation into analytical frameworks would aid in wildlife management using big data. Non-stationarity is a long-known statistical phenomenon yet approaches accounting for it, such as Spatial Varying Coefficient Models have been employed in fewer than 10% of large-scale studies using SDMs (Rollinson *et al.* 2021; Thorson *et al.* 2023).

Variation in the importance and direction of effects across regions is in itself no sufficient evidence for non-stationarity. As many predictors change with region (e.g. population density, climatic conditions, dominant land cover), so can the effect of biotic interactions which they moderate. The question of non-stationarity in non-spatial model can thus be explored by evaluating regional predictions of a global model, for example, by adjusting context through region-specific means of interacting variables during Partial Dependence Plot (PDP) calculations. However, this potential remained unexplored in such studies. Therefore, this study assesses non-stationarity in the top-down control of lesser-known species such as the hyaena and jackal, and in addition, explores the robustness of the Random Forest model in recognizing and predicting nuanced regional patterns through post-model specification of context to address nonstationarity.

Studies on interspecific competition are geographically and taxonomically biased, with Asian ecosystems accounting for less than 14% of the total global research (Prugh and Sivy 2020). The few studies available on the topic from the Indian subcontinent mostly cover flagship species such as tigers, leopards, and dholes, overlooking the critical role of top-down control on key scavenger species (Karanth *et al.* 2017; Kumar *et al.* 2019). Striped hyaena is a meso-carnivores that is predominantly a scavenger and a species of secondary forest habitat (Kruuk 1976). Hyaena occupies much of its available habitat throughout the tiger conservation landscape competing for resources with tiger and leopard, except in the moist region of northeast and the southernmost tip of India. Interspecific interaction is an intricate ecological phenomenon that requires a large number of observations for thorough study. However, during data collection, the distribution of hyaenas was found to be confined to a very limited geographical range within the Moyar Valley. This restricted distribution in the Western Eastern Ghats of Tamil Nadu (WEGPTN) limited the scope for drawing meaningful inferences or conclusions about interspecific competition between hyaenas and their sympatric species, tigers, and leopards. Therefore, the study on interspecific interactions was expanded to include other tiger conservation landscapes: the Shivalik Hills, Central India, and the Western Ghats, where hyaenas are also present. Expanding the study area to these regions provided not only an opportunity to examine species interactions more broadly but also the potential to investigate non-stationarity in interaction patterns across different regions. This broader scope addresses the following research questions: (i) whether scavengers exhibit varying responses to predators and other environmental variables across the three regions, and (ii) with the prior understanding that Random Forest models can account for local variation and variable interactions, whether the global Random Forest model is non-stationary and capable of predicting reliable, region-specific responses.

4.2 Methods

4.2.1 Study area

All India Tiger Monitoring (AITM) is an intensive field exercise that began in 2006 and is carried out every four years to assess the abundance of tigers, their prey, co-predators, and the health of forests in all potential tiger-carrying forests of India, covering approximately 395,379 km². This survey provides the most reliable account of the distribution of the target species through a robust field sampling framework. The vast sampling area greatly varies in

geoclimatic conditions, anthropogenic pressure, prey density, and genetic diversity of predators. Therefore, the areas have been divided into five tiger conservation landscapes (also called complexes) in such a way that each landscape shares higher homogeneity in biogeoclimatic features within each landscape and differences among each other, simultaneously facilitating field sampling.

Across the five landscapes, the study focuses on three: i) Shivalik and Gangetic Plain (hereafter referred to as Shivalik), ii) Central India and Eastern Ghats (hereafter referred to as Central India), and iii) Western Ghats, where hyaenas are confined (Figure 4.1). The Shivalik landscape covers the lower hills of the Himalayas and its Terai region, spanning a sampling area of approximately 35,100 km², while Central India covers 86,5200 km² and Western Ghats cover 155,800 km². Despite the small landscape, the Shivalik landscape sustains the highest concentration of tigers, representing 54.7% of its total sampled area, followed by Western Ghats (25.67%) and Central India (12%). Furthermore, Central India is the largest landscape among the three and serves as a link between the forests of Shivalik and Western Ghats. Central India is the most fragmented landscape and has experienced several events of local extinctions and subsequent reintroductions of wild animals. Western Ghats represent the southern part of India's tiger range and are a biodiversity hotspot. Though the landscape faces threats of elevating anthropogenic pressure and is fragmented, it harbors a high density of both prey and predators. The significant differences in biogeoclimatic features between the landscapes will alter the interactions between the availability of these features and predators, resulting in varying contexts across the landscapes. Hence, this provides a suitable environmental setting to test for context-dependent non-stationarity in top-down control by predators.

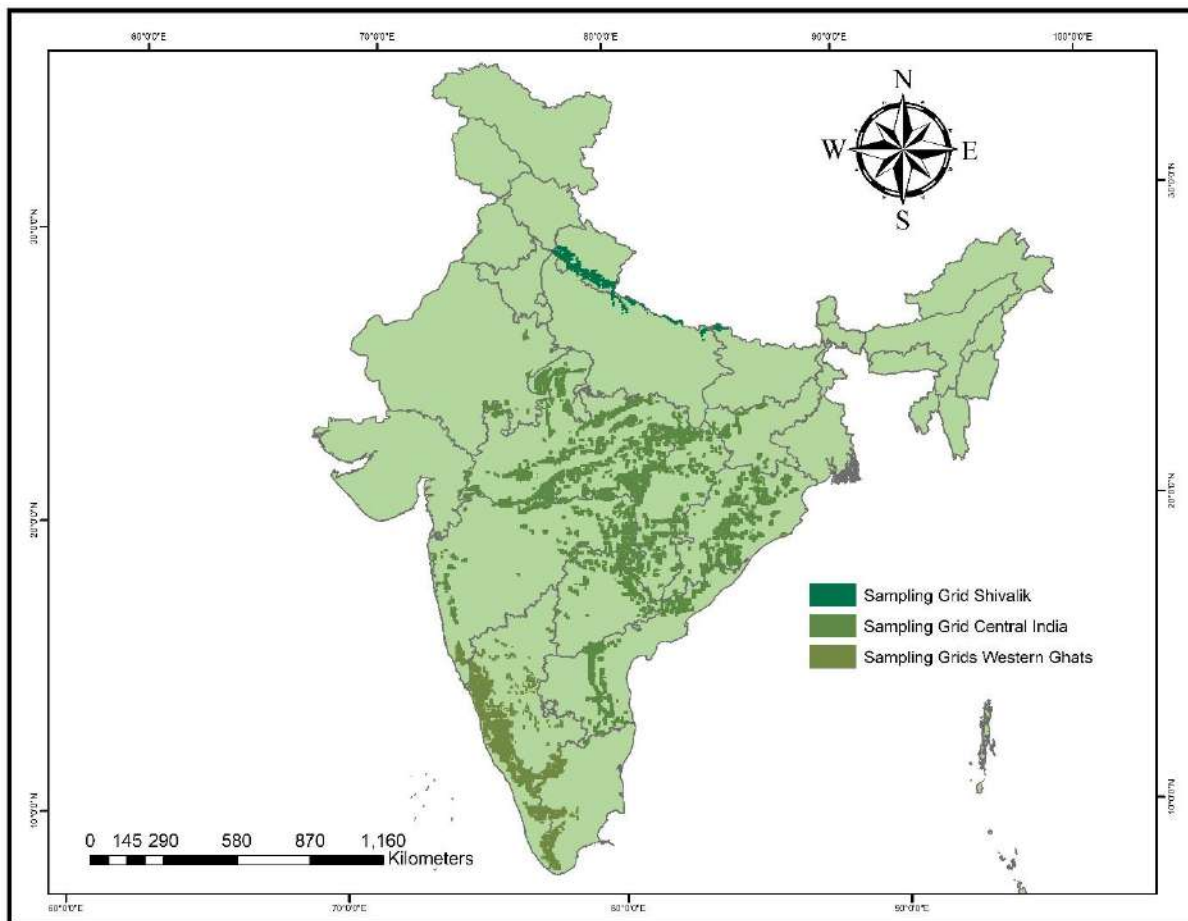


Figure 4.1 Presence-absence data for Tiger, Leopard, Chital, Sambar, and Hyaena were digitized from three tiger conservation landscapes in India: The Shivalik Range, Central India, and the Western Ghats, as depicted in the study area maps. The Shivalik Range, situated at the foothills of the Himalayas, is the smallest of these landscapes, contributing 5% of the total observations in the pooled data. Central India, located between the Shivalik and the Western Ghats, is the largest tiger conservation landscape in India and accounted for 75% of the total observations. The Western Ghats, representing the southernmost tiger distribution range and the second-largest landscape, contributed 20% of the data.

4.2.2 Data collection

A total of 14,064 data points on the presence-absence of hyaenas, tigers, and their two major prey species, chital and sambar, across the three tiger conservation landscapes in India were digitized from distribution maps published in the All India Tiger Monitoring Report, 2022 (Qureshi *et al.* 2023). Leopard data, available in a separate 2018 report, were digitized from Jhala *et al.* (2021). To minimize autocorrelation, a minimum distance of 5 km was maintained between observations by recording data at the centroid of 5x5 km² grids. Of the 14,064 observations, 75%, 20%, and 5% were from Central India, the Western Ghats, and the Shivalik

range, respectively. Presence records for chital (n=7,600), sambar (n=6,418), tiger (n=4,309), leopard (n=5,891), and hyaena (n=4,962) were recorded at the country level and digitized using ArcMap 10.8.

4.2.3 Variable selection and data preprocessing

To comprehend the distribution patterns of hyaena as a combined effect of bottom-up and top-down forces, information on 27 broad environmental variables were collected that could potentially drive the distribution of hyaena. These variables were identified based on existing research hyaenas (Alam *et al.* 2009; Gupta *et al.* 2009; Harihar *et al.* 2010; Jhala *et al.* 2011; Sankar *et al.* 2010; Jhala and Moehlman 2013; Pillay *et al.* 2011; Chourasia 2015; Hoffmann *et al.* 2018; Kumar *et al.* 2022). They encompassed two topographic factors: elevation and its derivative, the terrain ruggedness index calculated in ArcGIS. Additionally, various climatic variables from WorldClim (www.worldclim.org/current), along with landscape-level anthropogenic and biotic factors such as cattle density (Robinson *et al.* 2014), human population density (GPW 2018), land cover (Roy *et al.* 2015), tree cover (Hansen *et al.* 2013), human footprint (Key *et al.* 2021), and land use/land cover (LULC) (Roy *et al.* 2016), were initially identified.

The 'Human Footprint' (HFP) variable serves as a surrogate and synergetic measure of human-induced pressure on Earth through various anthropogenic activities (Key *et al.* 2021), indexed from 2001 to 2019. However, the discrete index for each independent year does not inform changes (increase or decrease) in human pressure in a particular area. Therefore, the Human Footprint Composite Index was calculated by multiplying the change in HFP (from 2001 to 2019) by their respective cell values of HFP in 2019. These calculated composite values were envisaged to provide more weight to the cells that experienced more drastic changes over the 18 years, potentially aiding in impact assimilation of increases or decreases in human-induced pressure on the target species.

Shivalik and Western Ghats are heterogeneous landscapes, characterized by variations in landscape features at fine spatial scales. Therefore, to represent this fine-scale variation, all response variables were resampled to the finest scale of 1km, at which most of the response variables were procured. Furthermore, raster data downloaded for India were reprojected to the WGS UTM projection system and all data preprocessing was executed in ArcMap 10.8.

After preprocessing, the values of all variables were extracted at the centroids of the common grid used during the digitization of presence-absence data on prey (sambar and chital), predators (tiger and leopard), and hyaena at the India level, covering all three tiger conservation landscape complexes. These extracted values were then used to test pairwise correlations between potential variables using Pearson correlation analysis in R. Highly correlated variables were identified at the threshold of $|r| > 0.7$ and the ecologically more significant variables were retained for further analysis (Table 1).

Table 4.1. Variables used in the models and their properties.

Sl No.	Name of co-variates	Variables	Variable type	Class-level	Data source
1	Bio1	Annual Mean Temperature	Numeric	-NA-	Bioclim
2	Bio2	Mean Diurnal Range			
4	Bio3	Isothermality	Numeric	-NA-	Bioclim
5	Bio9	Mean Temperature of Driest Quater	Numeric	-NA-	Bioclim
6	Bio11	Mean Temperature of Coldest Quater	Numeric	-NA-	Bioclim
7	Bio14	Precipitation of Driest Month	Numeric	-NA-	Bioclim
8	Bio18	Precipitation of Warmest Quarter	Numeric	-NA-	Bioclim
9	TRI	Terrain Ruggedness Index	Numeric	-NA-	Calculated on ASTER
10	FootPrint	An index of Human pressure	Numeric	-NA-	Forest department data achieve 2021.
11	FootPrint_Composite	Weighted Human Foot Print	Numerical	-NA-	
12	Tree cover	Percentage of pixel covered by tree	Numeric	-NA-	NASA Land Data Products and Services

13	LULC	Land use and forest type	Nominal	19 classes	Roy et al. 2015
14	Cattle density	Number of cattle per sq. km.	Numeric	-NA-	Robinson et al. 2014
15	Population density	Human population density	Numerical		SEDAC
16	Tiger	Probabilistic estimate of tiger occurrence	Numerical	-NA-	AITMR
17	Leopard	Probabilistic estimate of leopard occurrence	Numerical	-NA-	AITMR
18	Chital	Probabilistic estimate of Chital occurrence	Numeric	-NA-	AITMR
19	Sambar	Probabilistic estimate of Sambar deer occurrence	Numeric	-NA-	AITMR

4.2.3 Data analysis

To assess the top-down control over the focal scavenger and associated non-stationarity in patterns among the landscapes in India, random forest model was fit for all three landscapes separately (i.e., landscape models) and a global model on the pooled data. In random forest, presence absence of hyaena were modelled as a function of noncorrelated variables and digitized presence-absence records of co-predators and their prey (i.e., tiger, leopard, chital, and sambar). Random Forest is a robust, nonlinear, and non-parametric predictive model that does not rely on data assumptions and can recognize complex patterns. The relative importance of prey-predator along with the other 16 variables and the responses of scavenger species to them were compared across different landscapes using Partial Dependency Plots (PDPs) to test the hypothesis of nonstationarity in top-down control. The relative importance that is the strength of a variable in a model was calculated using Mean Decrease Accuracy (MDA) measure. Furthermore, the evaluation of nonstationarity was facilitated by assessing the uncertainty around predicted PDPs, which could potentially be induced by the dominant and differential impact of individual observations, signifying nonstationarity in the training dataset.

To assess this uncertainty, the infinitesimal jackknife approach was implemented in the model and calculated 95% confidence intervals for PDP predictions (Wager et al., 2014).

The concepts of Partial Dependency Plots (PDPs) and the infinitesimal jackknife were further leveraged to assess the assumed efficiency of the global Random Forest model in learning and predicting underlying regional patterns. The precision of PDPs predicted by the global model on regional data (i.e., a subset of the global model's training data), hereafter referred to as the '**Region-Specific Global Responses (RSGRs)**', was evaluated. Unlike Cushman et al. (2024 b), which compares individual and global responses directly, the RSGRs describe the accuracy of the global model in recognizing patterns within subsets of its training dataset. The RSGRs were predicted by holding all other variables at their respective regional means defining regional context and predicting the global model's response for the target variable at its unique observed values within each region. Furthermore, the overlap between the variance calculated around both regional patterns and RSGRs was analyzed, expecting higher congruence and lower uncertainty around the latter, in support of the hypothesis regarding the robustness of the global Random Forest model in recognizing underlying regional patterns.

In the random forest analysis 3,000 trees were grown, and the mtry value, which is the optimal number of variables to be randomly selected, was set to the default value of the square root of the number of variables used in each model. In addition to measuring variance through infinitesimal jackknife in the models, overall model accuracy was checked using the OOB error rate (Breiman, 2001). To optimize the accuracy of the regional model for the Shivalik and Western Ghats, where substantially absence inflated (imbalanced; see the imbalance ratio in appendix S4.1) records of hyaena were observed, an upsampling correction method was implemented (Johnson et al., 2012). The upsampling method increases the representation of the minority class (i.e., the presence of scavengers) in the model by random resampling, without deleting or adding new observations (McCarthy et al., 2005). The objective of the upsampling was to maintain the overall OOB error for all models below 20%, which was achieved (see Appendix S4.2).

The data analysis was performed in R using the ranger package, which provides a faster and more memory-efficient implementation of Random Forest, suitable for big data analysis as used in this study (Wright et al., 2019).

4.3. Results

4.3.1 Top-down Control and non-stationarity

Variable importance determined by Mean Decrease Accuracy (MDA) scores suggests, that instead of presence absence of predators, the distribution of Hyaena was majorly limited by other geoclimatic factors which greatly varied across the regional models (Appendix S4.3). The distribution of hyaena was found to be limited by population density only in Shivalik range but not in other landscapes. Aligning with MDA, no significant difference in the PDP values for hyaenas in both the presence and absence of predators was recorded, suggesting indifferent response of scavengers across any of the three landscapes (Figure 4.2). However, an ostensible positive response of Hyaena for leopard was observed in Central India but was ultimately found to be insignificant due to overlapping confidence intervals (CIs). In contrast to the observed insignificant impact of predators across the landscapes, hyaenas exhibited a significant negative relationship with chital in the Central India landscape, while showing insignificant negative to no relationship in the Shivalik and Western Ghats, respectively. However, no relation between Hyaena and sambar across the regions was observed. Apart from insignificant variation in the trend of hyaena response for prey and predator, both first-order and second-order nonstationarity in Hyaena response was observed between the landscapes (Figure 4.3). The first-order nonstationarity as observed between Shivalik and Western Ghats is characterized by overlap variance but differential mean values of PDPs. Strong and second-order nonstationarity was observed in Hyaena responses between Central India and the other two landscapes with no overlap in any statistical properties (mean and variance) of PDPs.

Overall, no significant impact of predators on hyaena in any of the landscapes or in the global models was observed. However, consistent with the first hypothesis, first- and second-order non-stationarity in scavenger responses were observed, characterized by variations in mean, and in both mean and variance of PDP, respectively, across the landscapes. Furthermore, the consensus and differences in the statistical properties of patterns across landscapes varied by scavenger species, prey-predators, and other environmental variables.

4.3.2 Region specific global responses (RSGRs)

The global models demonstrated high efficiency in predicting RSGRs in all three regions: Shivalik (I:S), Central (I:C) and Western Ghats (I:W). RSGRs varied in their trends and values according to defined regional contexts, aligning with the responses observed in the candidate models for each respective region. For categorical variables, such as the presence or absence of prey and predators, the response of hyaenas to chital serves as a fitting example, signifying the robustness of region-specific global responses (Figure 4.2). The global model predicted a negative relationship in Shivalik and Central India, and an indifferent response in the Western Ghats, all of which were consistent with the respective candidate regional models. Similarly, the efficiency of RSGRs was found to be robust across variables and landscapes. Furthermore, RSGRs were observed to reduce uncertainty by curtailing the confidence interval around pdps which was particularly observed in the case of Shivalik range (Figure 4.4). However, the confidence intervals, indicating uncertainty around RSGRs, varied depending on both the variable and the region.

Similarly, a reduction in uncertainty was observed in the Central India-specific global response for precipitation of the driest month and precipitation of the warmest quarter. (Appendix S4.4) Furthermore, Central India, which had the highest number of observations, showed some degree of dominance in global model predictions. For instance, high uncertainty in the precipitation of the warmest quarter observed in central India influenced the Western Ghats-specific global response (I:W) for hyaenas, inducing higher uncertainty (Appendix S4.5). The mean diurnal range, an important factor for hyaenas in both the Western Ghats and Central India, was similarly influenced by Central India in the global response for the Western Ghats, leading to a significant deviation from the regional model in a small data gradient.

Despite the dominance, such deviations of the regional model from the global model were found to be rare. Thus, the global random forest model produced nonstationary responses that varied across regions when corresponding contexts were defined by holding other variables at their regional means, and it provided reliable regional predictions despite some tolerable anomalies.

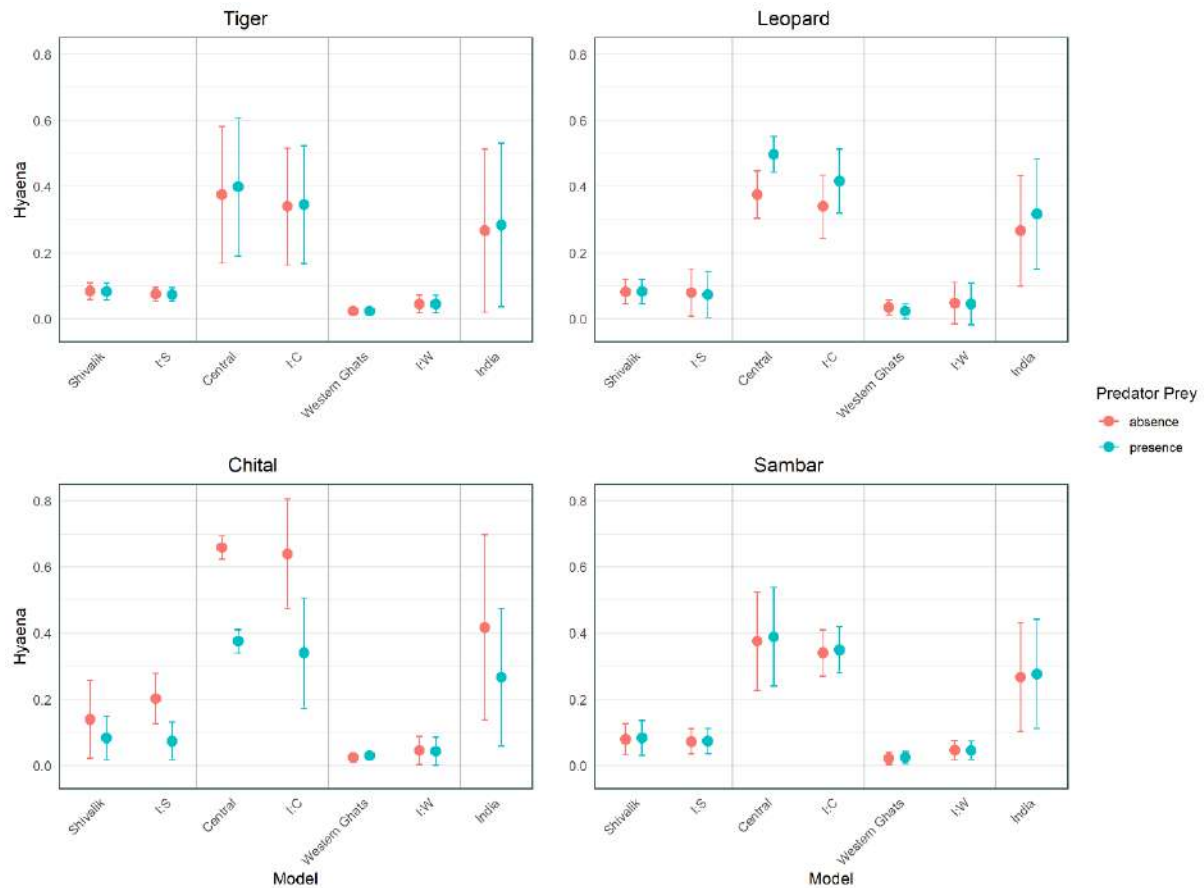


Figure 4.2 Partial dependency graphs represent the regional and Region specific global responses of Hyaena across the regions (I:S for Shivalik, I:C for Central India and I:W for Western Ghats), as well as the global model's (India) predictions in the presence or absence of prey and predators. The plots include 95% confidence intervals calculated through the infinitesimal jackknife method, indicating both the strength and uncertainty of the predicted trends. No significant influence of prey or predator presence/absence was observed across the landscapes, except for a positive relationship between prey (chital) and predator presence in Central India. Despite of no trend, significant nonstationarity in statistical properties of prediction was observed between Central India and other two landscapes but the Region specific global responses (I:S, I:C and I:W) showed demonstrated high efficiency in predicting nonstationary regional responses across the regions as shown in the figure.

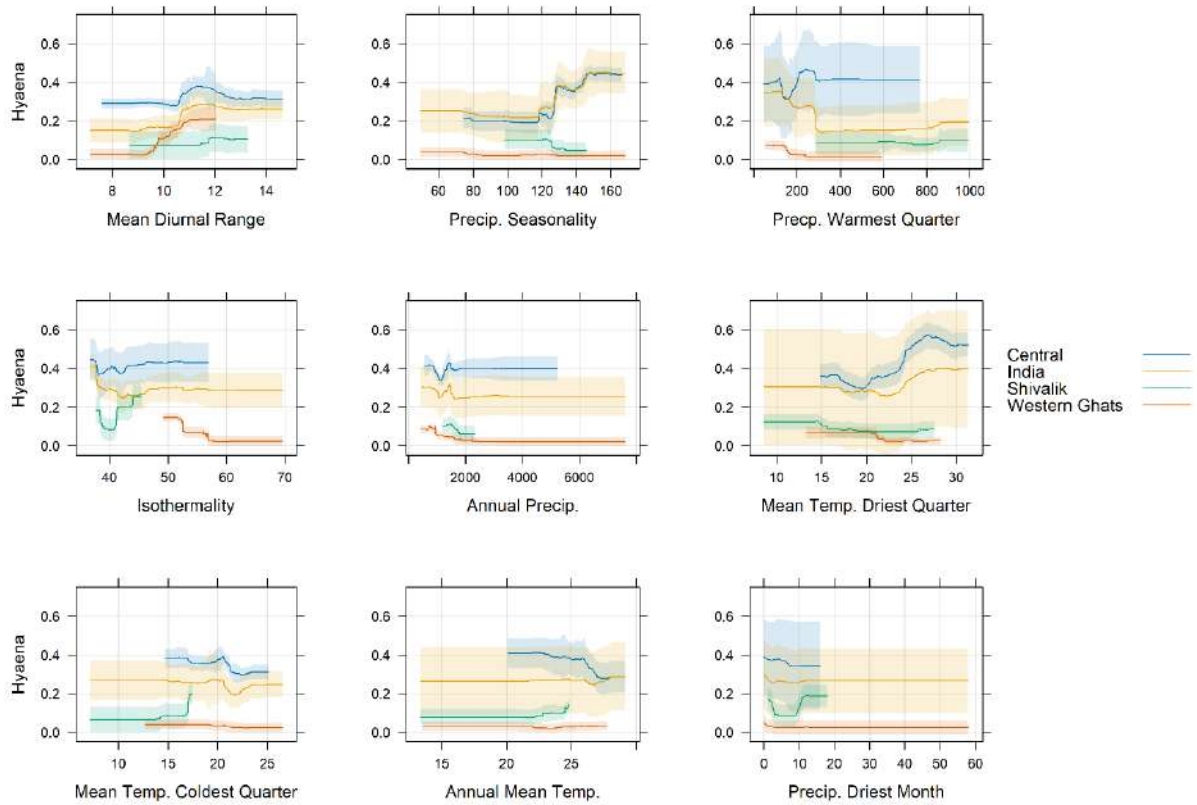


Figure 4.3 The Partial Dependency Plot (PDP) responses for the most important limiting factors of *Hyaena*, derived from the global model, indicate overall first-order nonstationary responses between the Shivalik Range and Western Ghats, with overlapping confidence intervals along common gradients of most of the variables. In contrast, the Central model exhibits strong second-order nonstationarity in their responses with both Shivalik and Western Ghats, with no overlap in any statistical properties of the PDP responses.

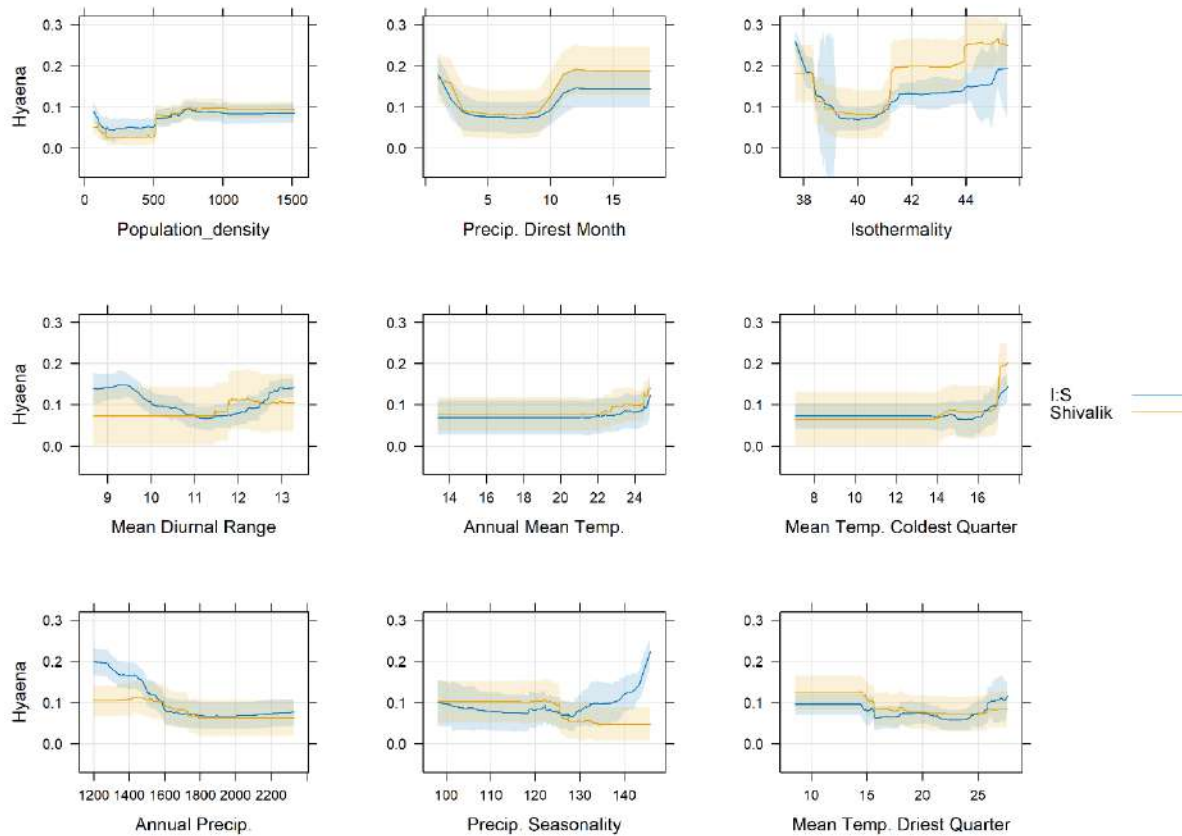


Figure 4.4 The graph compares the Region-Specific Global Responses (RSGRs = I:S) of hyaenas in the Shivalik region with the corresponding regional model responses for the nine most important limiting factors affecting the species. The RSGRs improved local prediction accuracy without significant deviations from trends in the Shivalik-specific model, except for a tolerable deviation in precipitation seasonality and annual precipitation over a short gradient.

4.4. Discussion

4.4.1 No Absolute Spatial Avoidance to Predators

Interspecific interaction is complex and occurs in various forms, ranging from facilitative interactions to interspecific competition, and varies with interacting species, their life histories, and the productivity of the surrounding environment. However, most studies investigating intraguild interactions presume suppressive competition. In this study, which assessed the context-dependent response of scavengers to their superordinate predators across three regions and in a global analysis, no negative impact of large predators on scavenger space selection was observed. Instead, an indifferent response from hyaena across regions and in the global analysis was observed, signifying no absolute spatial avoidance of predators. This result aligns with the findings of Karanth *et al.* (2017), where they found no dominant spatial trend when

analyzing co-occurrence among tiger, leopard and dhole with detection, and non-detection data. Furthermore, scavengers are known to depend on kills made by large predators for a significant portion of their dietary requirements. A review by Prugh and Sivy (2020) suggested that large predators can provide substantial scavenging opportunities, facilitating up to 1,351 kg of carcasses per year, which act as loci for meso-carnivore attraction. Such attraction becomes even more compelling in the absence of alternative feeding opportunities or under stressful resource conditions, potentially precluding absolute spatial segregation or even leading to strong positive associations. However, hyaenas are also known to rely equally, if not more, on anthropogenic food subsidies, such as cattle carcasses (Raichev *et al.* 2013; Panda *et al.* 2023). For instance, hyaenas have been reported to consume up to 1,461 kg of livestock waste per year (Panda *et al.* 2023). Therefore, the indifferent response observed in this study, rather than an absolute positive or negative association, could represent a nuanced spatial strategy, allowing scavengers to maximize scavenging opportunities while minimizing the potential risks of direct competition with larger predators, particularly when alternative scavenging sources are available. The indifferent response of hyaenas to predators across regions and in global models was consistently significant, despite an ostensible but insignificant positive relationship between hyaenas and leopards, particularly in the Central India model. Hyaenas and leopards, being similar in body size, the positive association aligns with the “body size ratio” hypothesis, which predicts less aversive interactions between similarly sized animals capable of launching counterattacks (Donadia & Buskirk 2006). In contrast, the indifferent responses observed in large-scale global models contradict the scale-dependent hypothesis proposed by Sivy *et al.* (2017) and later endorsed by Prugh & Sivy (2020), which predicts emergent negative associations at larger scales as a result of interspecific killing.

Furthermore, intraguild interactions are density-dependent, and their suppressive or facilitative impacts may become more evident at specific density thresholds, which were overlooked in this study due to a lack of the required data. As a result, the interactive responses based on presence-absence data presented here only confirm the absence of absolute predator avoidance, but they also highlight the need for detailed studies investigating the density-dependent responses of scavengers for a more comprehensive understanding. Such studies are urgently needed, especially considering the recovering populations of tigers in many regions (Jhala *et al.* 2021) and the limited empirical research on this subject. Data unavailability/hegemony, despite India’s world-record achievements in ecological data collection, remains a significant

challenge for proactive wildlife management and hinders the potential for deeper ecological insights. Increased data availability would greatly encourage more studies on complex phenomena, such as top-down control, and would promote more comprehensive wildlife management in India.

4.4.2 Nonstationarity in Scavenger Responses

Furthermore, significant variation in the statistical properties (mean and variance) of scavengers' responses across variables was observed, despite the consistent trend in top-down control observed across the landscape. The impact of a response variable is known to be gradient-dependent, and the unavailability of a decisive gradient in a landscape may relegate its importance, leading to spatially varying limiting factors (Osborne *et al.* 2007). The environmental gradients, widely varied across the selected landscapes (Shivalik, Central India, and the Western Ghats) in the presence absence data (Figure 4.3). For example, significant variation in annual precipitation not only alters the availability of variables but also influences the spatial context by changing interactions between them. This variability can lead to differences in statistical properties, as observed in the responses of scavengers across landscapes, and used as a key to recognizing nonstationarity between models in this study.

In this chapter both first order and second order nonstationarity was observed which signifies the strength of divergent responses of the scavenger, accounting for overlap between the predicted variance (Rollinson *et al.* 2021; Figure 4.3). Furthermore, overlap between Western Ghats and Shivalik which are not adjacent to each other calls for validation of the efficiency of Spatially Varying Coefficient models (SVCs) for addressing nonstationarity, particularly for such cases which violate the assumption autocorrelations (Thorson *et al.* 2023). Despite the significant nonstationarity observed, the global random forest model predicted the regional patterns precisely across the landscapes, and variables, when corresponding context were defined properly by other variables at their regional mean (Figure 4.2, & 4.4; Appendix S4.4-S4.5). Change in global model response with change in the mean value of other holdout variables also very strongly reaffirms the high relevance of variable interaction in determining nonstationarity in ecological patterns. Hereby, the findings from this chapter support the proficiency of the Global random forest model in handling nonstationary data as assumed by Evans *et al.* (2010) and found consistent with Cushman *et al.* (2024a).

4.4.3 RSGRs a Robust Approach to Address Nonstationarity

Macroecology has been widely criticized based on the assumptions of inefficiency for identifying spatially varying coefficients of responses from a global model and which is particularly true if the modeling approach is linear and fails to account for inherent interaction between variables. This means, the global model only identifies a broad and uniform relation per variable that might not be relevant across the space and may deceive local wildlife management through ecological fallacy (Osborne *et al.* 2007; Liang *et al.* 2020; Cushman *et al.* 2024 c). Acknowledging the limitation, site level (microecology) or Spatially Varying Coefficient (SVC) models have been encouraged exclusively for better explanatory power of local responses (Osborne *et al.* 2007; Liang *et al.* 2020). However, both approaches may fail under some circumstances which Global Forest model with regional specific global responses was found to overcome them in this study as discussed below based on observations. 1) **Data deficiency:** The local data often tend to be small or class imbalanced which can substantially impact the performance of local models as observed in Shivalik and Western Ghats which aligns with findings of other research work (Appendix S4.1). ii) **Violation of spatial autocorrelation:** SVC models allow a smooth transition in correlation coefficient by assigning a higher weight to spatially proximate observation assuming spatial autocorrelation (Osborne *et al.* 2007; Thorson *et al.* 2023). However, spatial correlation does not always explain proximate ecological relations (Cushman *et al.* 2024 c), as also signified by significant variance overlap between Shivalik and Western Ghats which are not adjacent to each other (Figure 4.3). The methodological framework of SVC models might hinder its performance in such cases, which not was evident in the region-specific global prediction.

Despite this, Random Forest is often regarded as a stationary modeling framework by overlooking the potential of region-specific global responses and only focusing on broad responses on aggregated data. While this research work heuristically demonstrated the nonstationary behavior of Global random forest model which serves the purposes of both global as well as regional models, under a single modeling framework through region-specific global predictions. Furthermore, the examined approach also showed improvement in the precision of response for class imbalance (small) data which is often the case for small regions and also not constrained by the assumption of autocorrelation. Therefore, the result suggests that the efficient use of macroecology under the demonstrated methodological framework can be an advantage over microecology without obscuring local species-environment relationships.

4.4.4 Does RSGR completely outsmart the local models?

Efficient wildlife management not only relies on the identification of reliable trends in interspecific interaction or animal environmental relations but also on the right identification of limiting factors. In the results, dramatic differences in limiting factors across the regional models were observed which is in concordance with other research works conducted on nonstationarity (Shortbull *et al.* 2011; Vergara *et al.* 2017; Cushman *et al.* 2024d). For example, while exhibiting differential response, hyaena habitat selection was characterized by population density only in Shivalik range. Unlike SVCs, random forest only provides global estimates of variable importance which could lead to misidentification of region-specific limiting factors. This is a major limitation of the approach as variable importance aids in the prioritization of managerial or scholarly attention to empirically important animal environment relationships. Therefore, RSGR does not completely outsmart the regional model and the global model still lacks in befitting methodological mechanism to identify differential limiting factors.

Additionally, the global variable importance was observed to be dominated by limiting factors from Central India and Western Ghats due to high observation from these regions in pooled data. Despite the bagging nature, the random forest remains slightly biased to the central tendency of the input data and which was also sometimes observed in region-specific global predictions, though tolerable. The slight deviation in region-specific global responses can be rectified further by assigning a higher weight to observations from data deficit regions to balance their representation in the global model. However, this would not address the problem of misidentification of region-specific limiting, and further methodological advancement to addressing the limitation in a single modeling framework would benefit well-informed conservation decisions.

This chapter explored non-stationarity in top predator control by analyzing the impact of tigers and leopards across three major tiger conservation landscapes in India. Despite finding no overall effect of predators on the scavenger space selection, significant differences in the statistical properties of scavenger responses (non-stationarity) were observed across the landscapes. This is the first study to examine the top-down effects on hyaenas at such a broad scale. Additionally, this chapter also heuristically demonstrated the effectiveness of a global random forest model in predicting context-dependent species-environment responses using a region-specific global response approach (RSGRs). This underscores the critical role of

variable interactions in addressing non-stationarity in ecological studies. As such, the study calls for reconsidering criticisms of the random forest model's presumed static behavior, which inherently accounts for variable interactions. This chapter also further advocates for methodological advancements that allow for the prediction of differential limiting factors within a single modeling framework, addressing a key limitation of existing approaches. Such advancements would make the algorithm more robust in addressing non-stationary ecological phenomena, such as habitat selection and top-down control, ultimately enabling more efficient wildlife management by addressing data deficiencies at the micro-scale and non-stationarity at the macro scale.

Chapter 5



Chapter 5: Prioritize potential suitable habitats for striped hyaena conservation

5.1 Introduction

The striped hyaena is one of the most important and widely distributed species among the four extant members of the Hyaenidae family. Despite its extensive range, studies on the striped hyaena contribute only 16% of all research conducted on hyaena species (Wilkinson *et al.* 2024). However, the population of the striped hyaena is reported to be continuously declining across its range, except in Israel, where a recent study recorded a 68% increase in population trends (AbiSaid & Dloniak 2015; Hadad & Yosef 2023). Striped hyaenas inhabit open, arid habitats like grasslands, scrublands, and secondary forests near human settlements. These open habitats face high extinction risks due to their conversion to other land uses, such as woodlands, leading to a 31% decline in India from 2005 to 2015 (Lahiri *et al.* 2023). The loss of critical habitat, combined with roadkill, interspecific interactions, and antagonistic human actions such as den site destruction and retaliatory killing has been identified as a major threat to hyaena conservation (Kruuk 1976; Hofer & Mills 1998; Wagner 2006; Wilkinson *et al.* 2024; AbiSaid & Dloniak 2015; Jhala *et al.* 2021). These threats have led to the extinction of hyaenas in many areas globally and from several historical ranges in India (Wagner 2006; Arumugam *et al.* 2008; Akash *et al.* 2021). A recent study from the eastern Indian state of West Bengal showed that hyaenas have been extirpated from nearly every part of the region except the western part of the state. Historically, hyaenas were widely distributed across southern India, particularly in regions like Hyderabad, Nagarhole, the Papikonda Hills of the Eastern Ghats, Mudumalai Tiger Reserve, Sathyamangalam Tiger Reserve, Bandipur Tiger Reserve, and even the Ooty region at elevations of 3,000 to 8,000 feet (Salim *et al.* 1985; Krishna Raju *et al.* 1987; Eagan 1916; Aditya & Ganesh 2017). However, hyaenas have experienced an unprecedented decline throughout this region, including in Masinagudi of the Western Ghats, which once served as a stronghold for the population (Atkinson & Bashir 1988). Currently, a very small population remains in the Western Ghats, which represents the last major breeding population in southern India. This population is critical for hyaena conservation in southern India and requires immediate conservation efforts.

Protection and efficient management of crucial habitats, followed by their identification, are key to the conservation of threatened species (Leston *et al.* 2024). Habitat suitability analysis has emerged as an important and cost-effective method for identifying critical habitats for biodiversity conservation. This method analyzes the relationship between species occurrence and surrounding environmental factors to predict suitable habitat availability in both space and time (Hirzel & Lay 2008). While there are a few habitat suitability studies on hyaenas from India, they primarily focus on the western and northern parts of the country, and there is no specific study available on this critical population (Alam *et al.* 2009; Gupta *et al.* 2009; Harihar *et al.* 2010; Sankar *et al.* 2010; Jhala *et al.* 2011). Furthermore, existing studies only account for the fundamental niche, analyzing occurrence merely as a function of habitat features, while ignoring crucial factors like interspecific competition and den site selection (Wilkinson *et al.* 2024). This chapter explores habitat suitability for the hyaena as a function of both top-down and bottom-up processes to identify critical habitats for hyaena conservation within the landscape.

Today, interspecific competition plays a deterministic role in shaping the composition of carnivore communities. This happens both through the active displacement of competitors, and by shaping the adaptations of other species in the community (Dröge *et al.* 2017; Elbroch & Kusler 2018). A synthesis by Prugh & Sivy (2020) suggested that about 30% of the mortality of mesopredators is caused by larger predators, which in turn affects mesopredator distribution, habitat use, prey preference, and abundance in a shared landscape. Conversely, even in resource-rich habitats, greater pressure from large carnivores may increase food acquisition costs for smaller carnivores, which can negatively impact their reproduction, growth, and viability even more than interspecific predation (Gorman *et al.* 1998; Creel 2001; Creel & Christianson 2008; Palomares *et al.* 2016; Elbroch & Kusler 2018). Successful coexistence between predators over time may be facilitated by species-specific behavioral traits, and/or scale-dependent spatiotemporal partitioning and avoidance, which can balance the trade-offs between resource acquisition and predation/encounter risk (Heithaus 2001; Vanak *et al.* 2013). Active avoidance at a fine scale, whereby subordinate predators are more aware of the movements of large predators, can also facilitate successful occupation of the same habitats and ultimately coexistence (Sollmann *et al.* 2012; Vanak *et al.* 2013). In previous studies for example, puma, cheetah, African wild dog, leopard, and dhole tend to avoid areas where large apex predators, like jaguar, lion, tiger, and spotted hyaena, are present in high numbers or were

highly active (Rabinowitz & Nottingham 1986; Gorman *et al.* 1998; Creel & Creel 1996; De Azevedo & Murray 2007; Hayward & Slotow 2009).

Ecological attributes like habitat structure and cover, prey abundance, behavior, and seasonality, may also influence coexistence by differentiating or partitioning resource use patterns over time. In Africa, although painted dogs avoided areas with relatively high lion density, they still showed significant overlap with lions in the wet season; high vegetative cover and pronounced seasonality of wild dog movements, likely facilitated coexistence with lions by minimizing negative interactions (Vanak *et al.* 2013). Other behaviors used by smaller carnivores to facilitate coexistence with larger species in their guild include reducing or optimizing movements, use of fine-scale habitat “refuges,” and aggression or the deployment of chemical repellents (Krebs *et al.* 2004; Ritchie & Johnson 2009; Vanak *et al.* 2013; Allen *et al.* 2016; Dröge *et al.* 2017). Reproductive behavior, including the timing of births, as well as the selective location and security of dens, may be effective strategies to reduce intraguild predation of young, an important source of mortality for many smaller African carnivores (Mills 1993; Mills & Mills 2014). Despite the potential obvious importance of den site selection to carnivore coexistence, this topic has rarely been explored empirically as a strategy by one or more species for mitigating competition and ultimately facilitating persistence among larger carnivores.

Hyaenids are among those carnivore species that nearly always occur with other larger or similarly-sized carnivores. They first evolved during the Oligocene from feliform ancestors during a time of great competition for large prey (Werdelin & Solounias 1991; Westbury *et al.* 2021), subsequently radiating into a diversity of species and specialized ectomorphs. Optimized digestive and enhanced immune systems help the hyaenids leverage pathogen-rich food sources otherwise not exploited by other carnivores, an advantage that may have allowed them to become the most diverse carnivore group in the late Miocene (Benbow 2015; Westbury *et al.* 2021).

Of the four extant hyaenids, the striped hyaena has the widest distribution. Unlike spotted hyaenas, which are effective predators, striped hyaenas, which range from North Africa to the Indian subcontinent, are predominantly scavengers (Mills & Hofer 1998; AbiSaid & Dloniak 2015; Alam & Khan 2015). Across their range, striped hyaenas co-occur with many other large predators, including tigers, leopards, dholes, lions, and wolves, frequently occurring near human settlements (Arivazhagan *et al.* 2007; Singh *et al.* 2014). All these predators, as well as

humans through their livestock and other anthropogenic waste, can increase scavenging opportunities for striped hyaenas; in turn, hyaenas can negatively affect the energetic balance of other carnivores by kleptoparasitizing kills and forcing them to hunt and kill more prey (Mattisson *et al.* 2016; Mellard *et al.* 2021). As ecosystems become more impacted by people through development and agriculture, one consequence may be the disruption of this relationship between hyaenas and other carnivores, whereby hyaenas are forced into more direct “confrontations”, and thus limiting mechanisms for coexistence across a shared landscape.

To date, a few studies have investigated the factors influencing the persistence of striped hyaenas in these competitive contexts but their distribution across large areas, or the impact that large carnivore activity and abundance on the species have been not studied. Some prior studies across five Indian Tiger Reserves have indicated that striped hyaena occupancy changes in response to the presence of other large carnivores (Alam *et al.* 2009; Gupta *et al.* 2009; Harihar *et al.* 2010; Sankar *et al.* 2010; Jhala *et al.* 2011). In Sariska and Achanakmar Tiger Reserves, where tiger populations are low relative to historical densities, the local striped hyaena population density appeared high; conversely, hyaenas were found at lower population densities in reserves, where more tigers were present. Despite these apparent top-down pressures, declines in hyaena populations have thus far only been ascribed to anthropogenic factors, like habitat destruction (Alam *et al.* 2009). Moreover, other large predators help facilitate striped hyaena persistence and coexisting through the provisioning of prey carcasses.

This chapter investigates the effects of habitat characteristics and other predators on the presence of striped hyaenas as well as predicted potential habitat in the Western and Eastern Ghats part of Tamil Nadu (WEGPTN). This chapter also examined the potential role of den sites as part of strategies to facilitate coexistence with southern India’s other large carnivores, including tigers, leopards, and dholes, with which hyaenas occur sympatrically. I hypothesized that in the study area, fine-scale space use by hyaenas, including the use of habitat and denning refugia, will help facilitate the trade-offs between risk and opportunity related to the predators that striped hyaenas likely depend on for their survival. It was also noted that this region encompasses the only major breeding population of striped hyaenas in Tamil Nadu, one that would serve as a critical source for the potential recovery of the species more widely across the southern subcontinent.

5.2 Material and Methods

5.2.1 Data collection and analysis

Data on the presence-absence of striped hyaenas, all three co-occurring obligate predators (i.e., tigers, leopards, and dholes), and major prey species (Chital, Sambar and domestic cattle) was collected from across the study area (Figure 4.2 & 4.3). Both indirect sign (track/scat) and camera-trapping surveys were conducted to gather location and date/time data of these species. A total of 248 trails of 2km in length were sampled, including management roads from all representative habitats and forest divisions, covering most of the forest ranges. Indirect evidence of different predator and prey species was confirmed based on distinct characteristics unique to each respective species, including track morphology, fecal material (scat) size and shape, and scrape marks (Kolipaka 2014). Camera- traps at 194 sites across seven forest divisions were installed and accrued a total sampling effort of 4975 trap nights to complement the sign surveys with photographic evidence (Figure 5.1). Cameras relied on motion and infrared detection to record target species; they were installed in locations optimal for detecting the presence of passing mammals, including water holes, the junction of game trails, walking transects created by the forest department, and area management roads. Sampling occurs throughout the year except for the rainy season when visibility inside forests decreases due to rapidly-growing vegetation in the forest undergrowth.

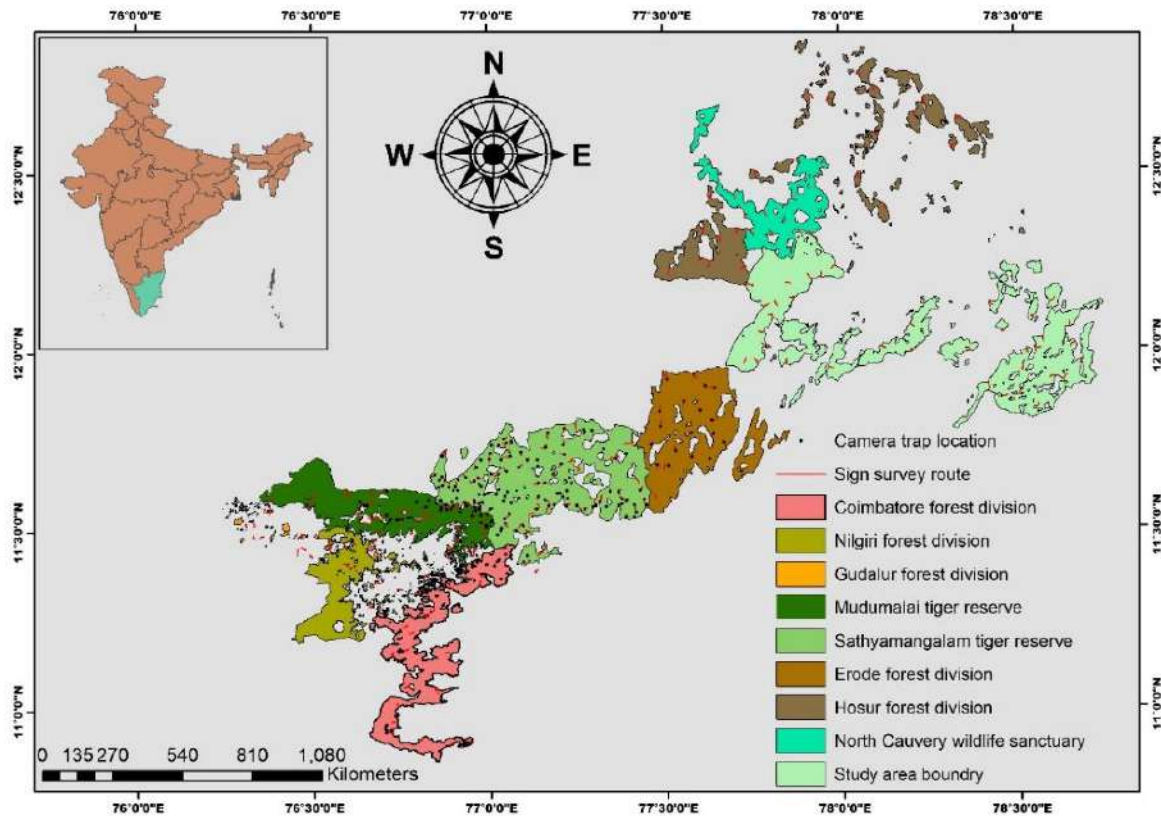


Figure 5. 1 Study area map showing managerial boundary of different forest divisions and Protected Areas. Camera trap location and survey route of 2km show the sampling effort that was put for data collection from the study area.

First key literature was reviewed to understand the den site selection in carnivores and other mammals, to identify the best approaches for this study (Vroom *et al.* 1980; Boydston *et al.* 2006; Nikunj *et al.* 2009; Singh *et al.* 2010; Bopanna 2013; Jackson *et al.* 2014; Singh *et al.* 2014; Davies *et al.* 2016; Majumder *et al.* 2016; Khanal *et al.* 2017; Mandal 2018; Mukherjee *et al.* 2018; Chourasia *et al.* 2020). Furthermore, data on the attributes of potential den sites and microhabitat features of striped hyaenas dens were collected. After identifying the core habitat of the striped hyaena in the landscape for example, hyaena dens were located by exploring potentially suitable sites like mountain slopes and rifts, the junction between mountain ranges and dry riverbeds, and any natural foothold refuges, like modified porcupine (*Hystrix indica*) dens, as has been reported from the literature (Bopanna 2013; Alam *et al.* 2014; Singh *et al.* 2014). Hyaena dens were confirmed based on direct signs of recent hyaena denning activity in the form of fresh tracks or scats outside of suspected dens, or the hoarding of bones inside or outside of the entrance, as is often characteristic of hyaena behavior (Kruuk 1976; Bopanna 2013; Stewart *et al.* 2021). The identification of den sites was also relied on the experiences of and sightings by local forest department staff and villagers. In addition to

occurrence surveys, camera-traps were also used to confirm activity at suspected hyaena den sites.

To determine the distribution patterns of striped hyaena across the study area, I collected information on 25 important explanatory variables that could potentially influence the distribution of hyaena prey (Table 4.1). Many of these variables were initially identified based on their relevance to striped hyaenas based on prior research (Alam *et al.* 2009; Gupta *et al.* 2009; Harihar *et al.* 2010; Sankar *et al.* 2010; Jhala *et al.* 2011). Among other topographic variables, they included elevation, slope, and terrain ruggedness. They also included all climatic variables from Worldclim (www.worldclim.org/current) and other landscape variables, such as land cover (Roy *et al.* 2015), tree cover (Sexton *et al.* 2013), distance from the nearest settlement, and proximity to streams. A raster layer of variable tree cover was also downloaded from NASA Land Data Products (Townshend 2016) at a 30 m spatial resolution, which allowed us to quantify the proportion of land in each pixel covered by woody vegetation > 5 m in height. To account for the effect of stream and settlement over the distribution of the species their shape files were procured from the state forest department and were rasterized using Euclidean distances tool in ArcGIS (ESRI 2014). After procuring these datasets, all raster layers were projected into WGS 1984 UTM (Universal Transverse Mercator) projection system using reproject tool in ArcGIS. Afterward, the reprojected data were resampled at 1 km spatial resolution and clipped to the extent of the study area in ArcGIS. After pre-processing of raster layers, terrain slope and ruggedness were calculated for the study area from the elevation layer downloaded from Earth Explorer (NASA/METI/AIST/Japan Spacesystems and U.S./Japan ASTER Science Team 2019). The original 28 discrete classes of the land use/ land cover (LULC) layer were reclassified into 16 broad categories (Table S5.1, Figure S5.1). All raster layers were then resampled at 1 km² in ArcGIS.

To test all variables for potential pairwise correlation, Pearson correlation test was applied (Figure 5.4) and ultimately only non-correlated variables were retained (i.e., $r < 0.6$) for the final analyses (Table 5.1). Habitat suitability of target species (Hyaena, tiger, leopard, dhole, chital and sambar) were analyzed using Random Forest algorithm which is a non-linear and non-parametric model (Breiman 2001). The random forest model was implemented using randomForest package in R (R Development Core Team 2018; Breiman *et al.* 2020). Presence/absence points (GPS location) of each target species were plotted over 1 sq km grid in ArcGIS map after reprojecting those locations into UTM. For analysis, only one point per grid indicating only presence/absence of species in a grid was retained. Afterwards, values of

all predictor layers were extracted for those points and using the binary decision analytical framework, the presence-absence of species were analyzed as a function of selected environmental variables. The model stabilized after growing 5000 trees, at which point the optimal number of variables to be randomly sampled (mtry) was determined by running and comparing several models with different values. An mtry value of 4 produced the highest accuracy and was therefore assigned to all final models; additionally, the default tree depth of '1' at each node was retained. All these optimizations were kept consistent for all four carnivores while for chital and sambar 6000 and 5000 trees were grown respectively. The value of mtry was also optimized for both prey species based on model stabilization, model for chital the mtry was assigned 2 while model for sambar was stabilized at mtry=3.



Figure 5.2 Indirect evidence of major prey species: gaur (a), sambar (b), chital (c) and cattle (d)

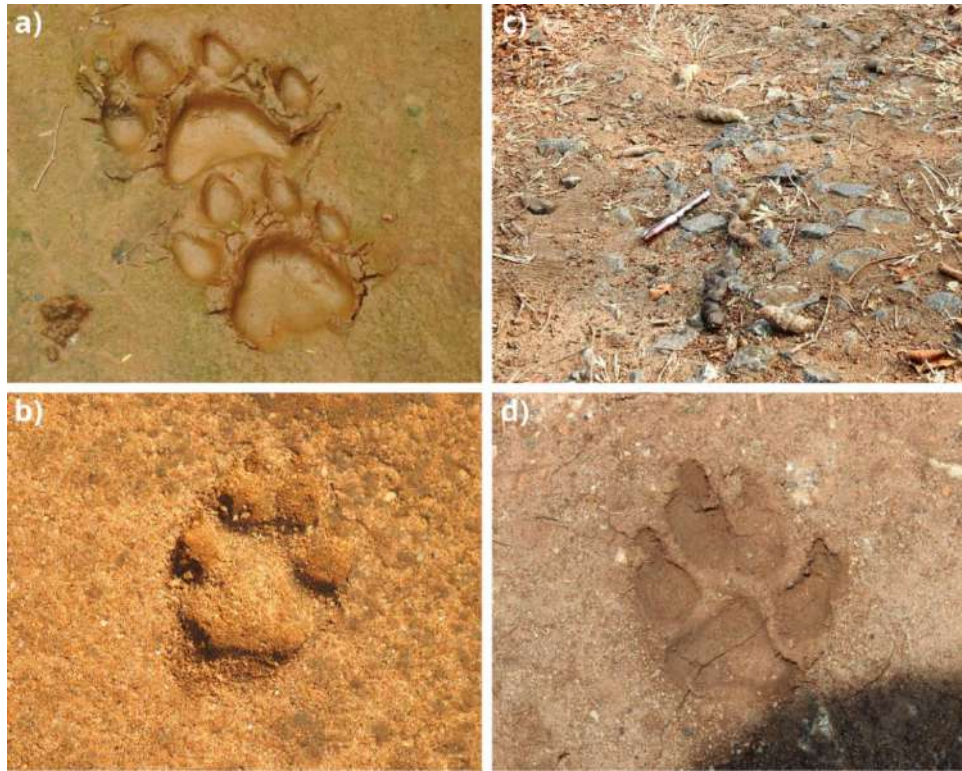


Figure 5.3 Indirect evidence of major carnivores: tiger (a), leopard (b), dhole (c) and hyaena (d)

The accuracy of the models was checked from out-of-bag data, the data points from our dataset that were not used in model calibration but left out for the model validation. True skill statistic was applied to calculate the True positive rate and False positive rate and plotted ROC curve for model validation. The overall variable importance for each species was assessed using two metrics: (1) the mean minimal depth of the tree node, and (2) the Gini index (Lerman & Yitzhaki 1984). The lower value of mean minimum depth corresponds to the relative higher importance of a variable in the model for tree nodes; a high Gini index implies greater relative importance for a given model. Furthermore, the impact of independent variables on species occurrence probability was checked through partial dependency plots.

Table 5.1 Variables used in the models and their properties.

Sl No.	Name of co-variates	Variables	Variable type	Class-level	Data source
1	Bio2	Mean diurnal Range	Numeric	-NA-	Bioclim
2	Bio3	Isothermality	Numeric	-NA-	Bioclim
3	Bio12	Annual precipitation	Numeric	-NA-	Bioclim
4	Bio14	Precipitation of driest Month	Numeric	-NA-	Bioclim
5	Dem	Elevation in meter	Numeric	-NA-	ASTER
6	Slope	Slope of terrain in degree	Numeric	-NA-	ASTER
7	Stream	Distance from nearest stream	Numeric	-NA-	Lin <i>et al.</i> 2021
8	Settlement	Distance from nearest human settlement	Numeric	-NA-	Forest department data achieve.
9	Tree cover	Percentage of pixel covered by tree	Numeric	-NA-	NASA Land Data Products and Services
10	LULC	Land use and forest type	Nominal	16 classes	Roy <i>et al.</i> 2015
11	Cattle density	Number of cattle per sq. km.	Numeric	-NA-	Robinson <i>et al.</i> 2014
12	Tiger	Probabilistic estimate of tiger occurrence	Numerical	-NA-	Field data
13	Leopard	Probabilistic estimate of leopard occurrence	Numerical	-NA-	Field data
14.	Dhole	Probabilistic estimate of dhole occurrence	Numeric	-NA-	Field data
15.	Chital	Probabilistic estimate of chital occurrence	Numeric	-NA-	Field data
16.	Sambar	Probabilistic estimate of sambar occurrence	Numeric	-NA-	Field data

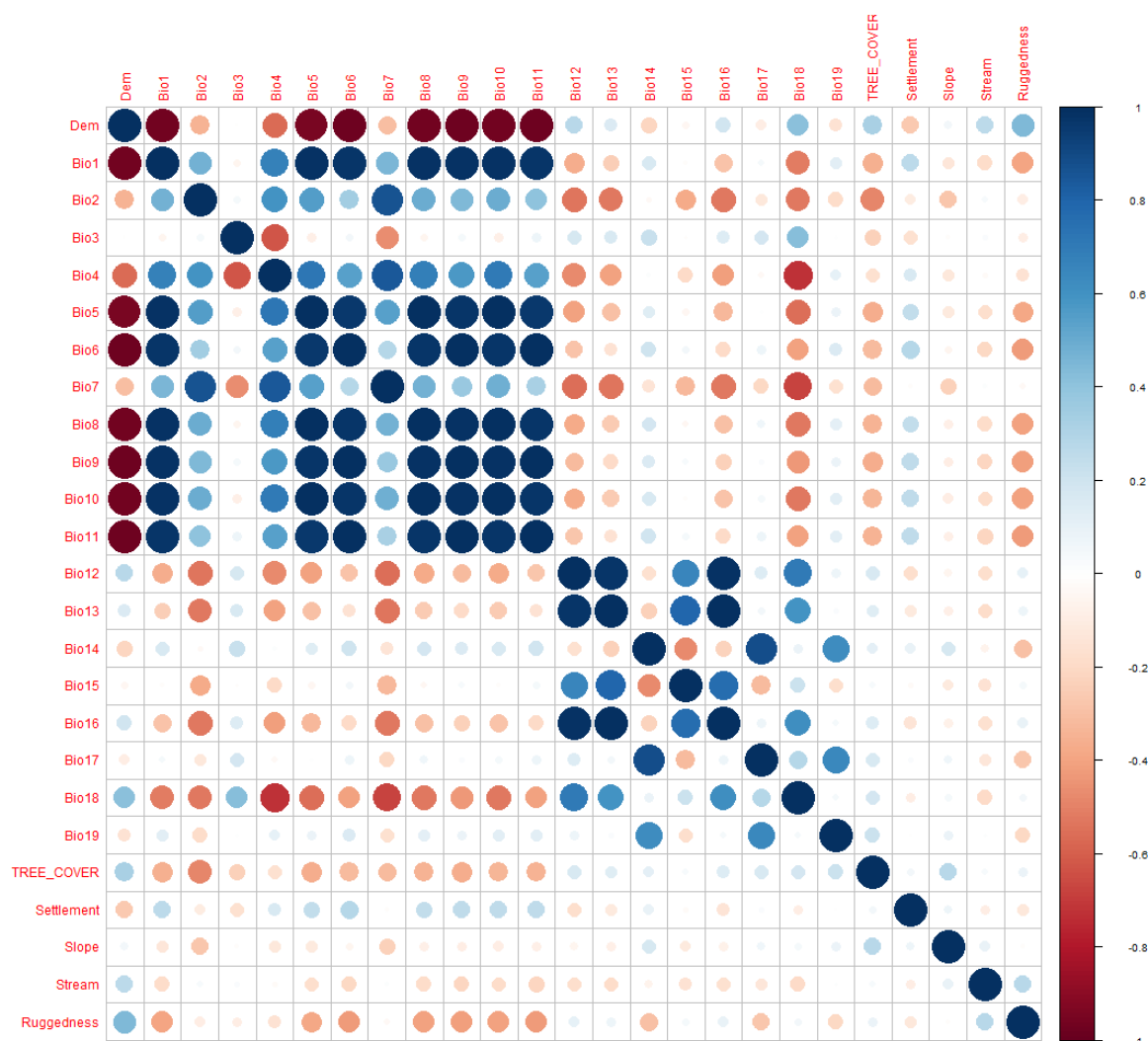


Figure 5.4 Correlation matrix of all potential variables primarily selected for analysis.

5.3 Results

Only 18 communal striped hyaena dens were located on two mountain slopes across the study area. Of these, 16 were “clumped” relatively close along one mountain slope, whereas the other two occurred on the second slope. Due to this unexpectedly low sample size, more complex analyses of den site characteristics were unfortunately not possible. In addition, 74 distinct hyaena presence points were recorded out of which 18% (n=14) were photographic evidence from 194 camera-trap stations (Figure 5.5), and 82% (n=60) were indirect evidence of hyaena presence (e.g., scats, tracks, etc.) collected from 248 sign survey trails. Tiger presence at 68 camera-trap locations (35.1%) and from 60 (29%) trail surveys were recorded, whereas

leopards were recorded from 61 camera-traps (31.4%) and through indirect evidence collected from 104 survey trails (41.9%). Like hyaenas, dholes were rare, being recorded at only 58 camera-trap stations (29.9%) and 43 survey trails (17.3%). Among the potential prey species, chital and sambar were frequently recorded. For example, the presence of the former was recorded from 91 camera-trap stations (46.9%) and 212 sign trails (85.5%), whereas the latter were recorded from 113 camera-traps (58.2%) and 160 trails (64.5%).

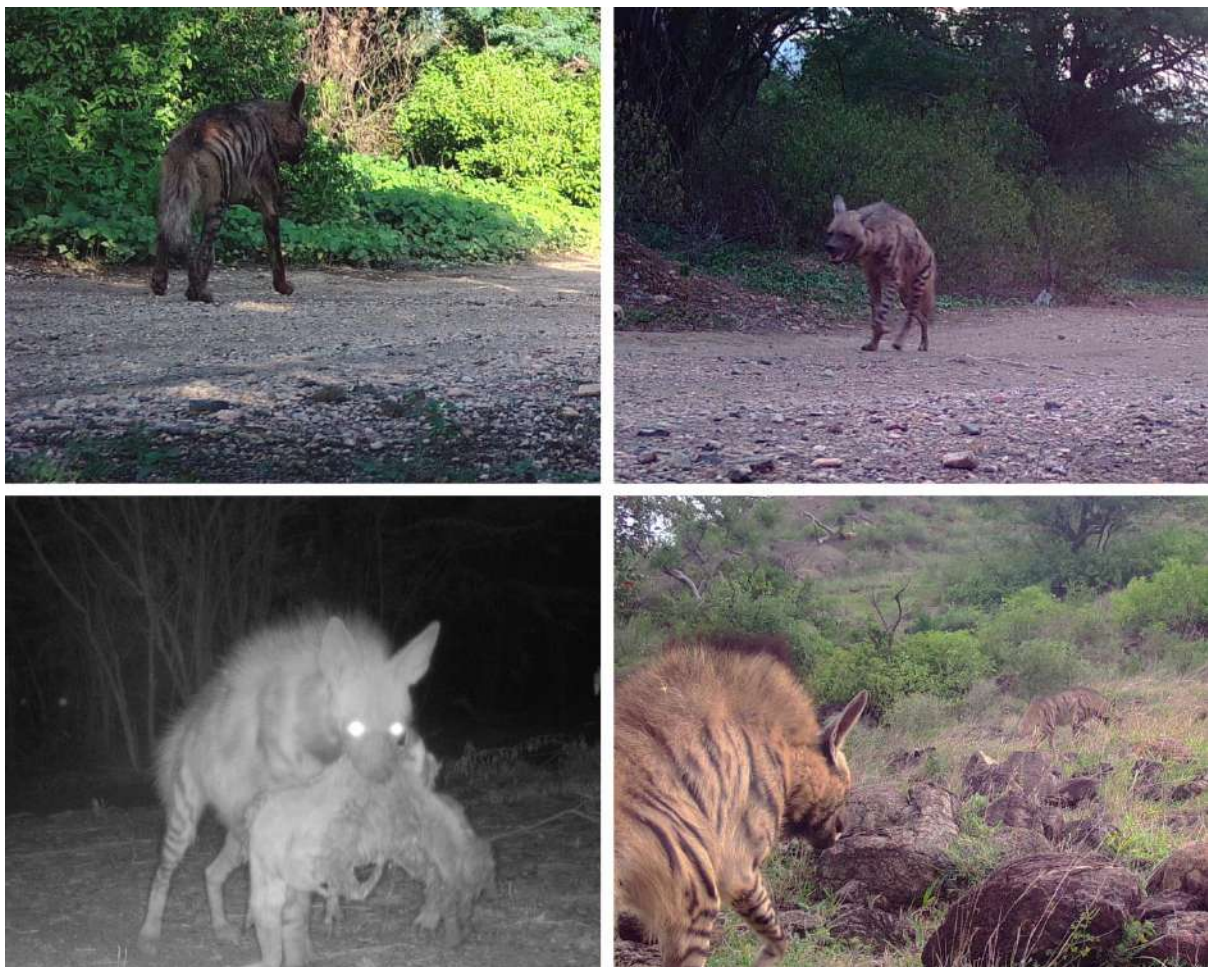


Figure 5.5 Camera trap pictures of hyaenas captured from animal paths.

Based on the sign and camera-trap surveys, the study found that the striped hyaena population was mostly confined to the Bhavanisagar and Nilgiri eastern slope ranges of both the STR and MTR respectively, with unconfirmed reports of hyaenas originating from other adjoining forest ranges (Figure 5.6). In contrast, many of the other carnivore species were found to be well distributed across the entire study area, and relatively abundant across the otherwise

heterogeneous landscape. For example, chital, dhole, and leopard were recorded from most of the surveyed areas (Figure S5.2, S5.10, S5.14). In contrast, sambar and tiger were recorded largely from relatively less disturbed habitats (Figure S5.6, S5.18), although their sporadic presence was also recorded from Coimbatore, Dharmapuri, and Hosur Forest Divisions, as well as from the CNWLS, which are areas with larger anthropogenic footprints.

The best-calibrated random forest model indicated that only approximately 21% of the entire study area is suitable for striped hyaenas (Figure 5.6). The model was found to have an overall error rate of 12.41% based on data that were not used for model construction (i.e., data that were not used in model construction, but rather kept aside for model validation); the false positivity rate (i.e., the % of “absence” data misclassified as “presence”) was approximately 14%, and the false negative rate (i.e., the % of “presence” data misclassified as “absence”) was 11.11% (Figure 4.7). Based on low error, false positive, and false negative rates, overall model accuracy was high. Both mean decrease in accuracy (mean minimum depth of tree nodes), and the Gini index, were congruent in their indications that elevation, Bio3 (WorldClim), chital, cattle density, and dhole presence, appeared to be the most important variables, among those that were included and influenced the distribution of hyaenas in the study area (Figure 5.8).

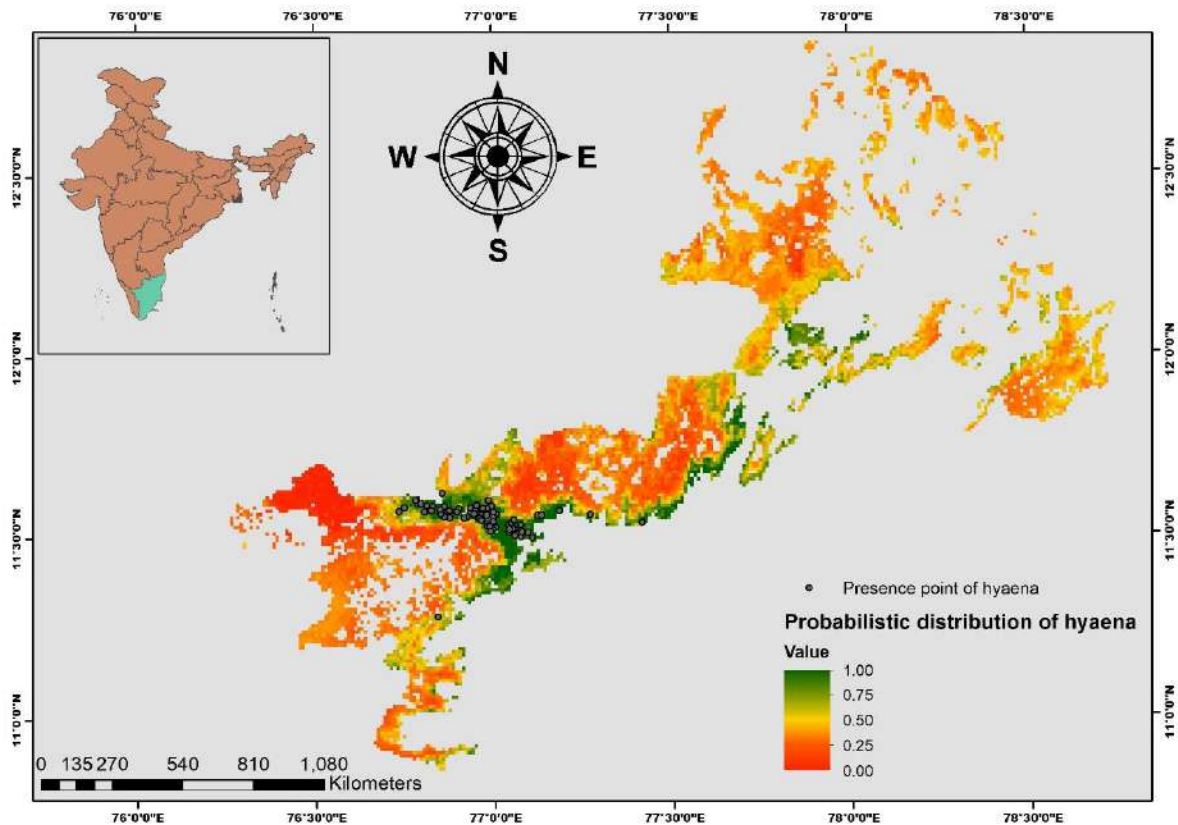


Figure 5.6 Predicted probability of hyaena distribution in the Western and Eastern Ghats part of Tamil Nadu.

Though annual mean temperature was not included in the model because of its strong negative relationship with elevation ($r = -0.96$; Figure 5.4), its overall importance to hyaena occurrence cannot be ignored. In the study, elevation appeared to be the most important variable overall and negatively impacted striped hyaena occurrence, i.e., as elevation increased, the probability of hyaena occurrence decreased (Figure 5.8 & 5.9). In contrast to elevation, therefore, annual mean temperature was positively related to striped hyaena occurrence. Bio3 was found a climatic variable indicative of the range of temperature fluctuations within a calendar month and its relationship to annual mean temperature, was also important; specifically, the habitat model suggested that areas subjected to fewer temperature fluctuations were more suitable for striped hyaenas. The occurrence probability of chital and precipitation of the driest month (Bio14) showed a strong positive impact on the species distribution while Bio16 showed a strong negative relation. Hyaenas showed a weak positive relation with proximity to settlements as the occurrence probability of hyaena was observed to decrease with an increase in distance beyond 10 km from settlements. The partial dependency graph shows that sambar occurrence probability has a very weak and positive effect on the hyaena occurrence. In LULC,

only thorn forest was observed to have a strong and positive effect on the distribution of the species. While dry deciduous forests showed a weak positive relation, the rest of the classes had a negative relation with hyaena occurrence probability. Finally, hyaenas were more likely to occur in areas with a lower to medium occurrence probability of leopards and tigers, whereas they exhibited a strong negative relationship with the probability of dhole occurrence. Likewise, annual precipitation (Bio12) also showed a strong negative relation with hyaena occurrence probability.

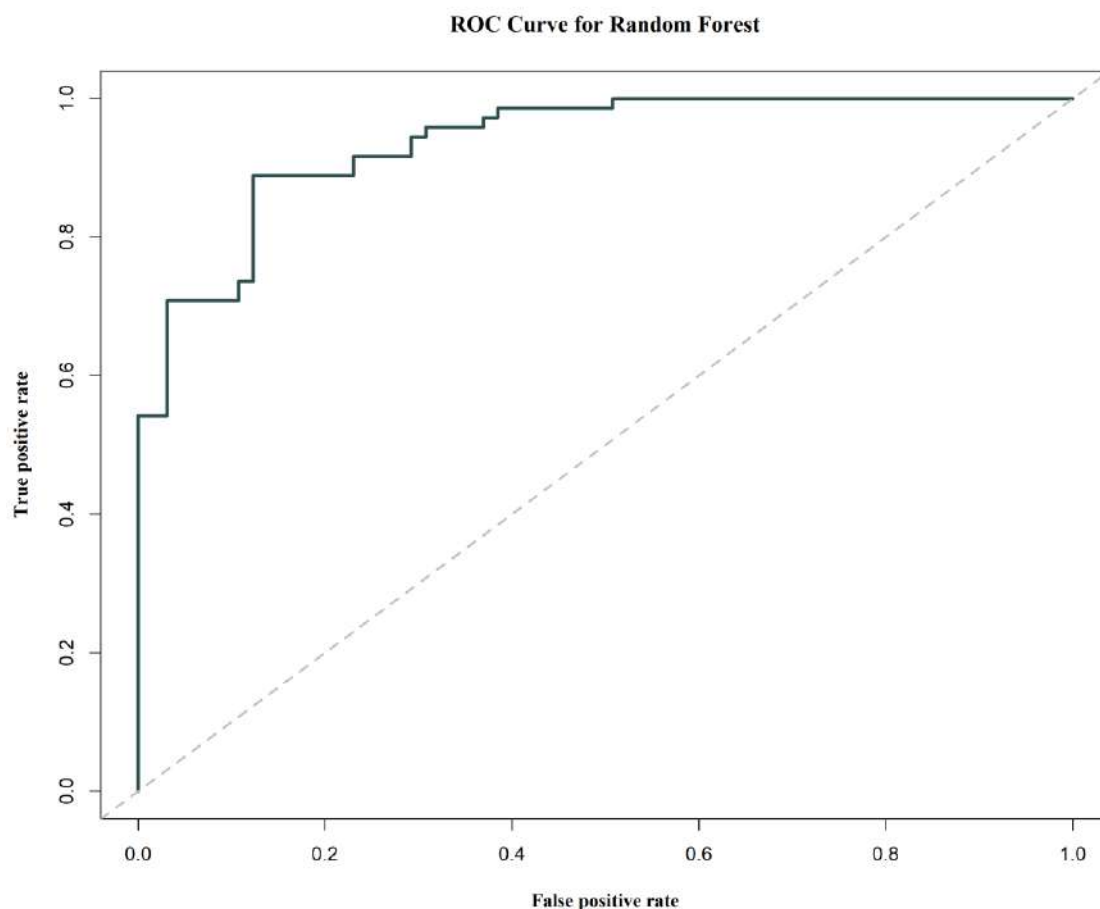


Figure 5.7 The accuracy of the calibrated model was determined by plotting the Receiver Operating Characteristics (ROC) curve which is a trade-off between the proportion of correctly identified (True positive rate) and wrongly identified (False Positive rate) occurrence of hyaena from the dataset.

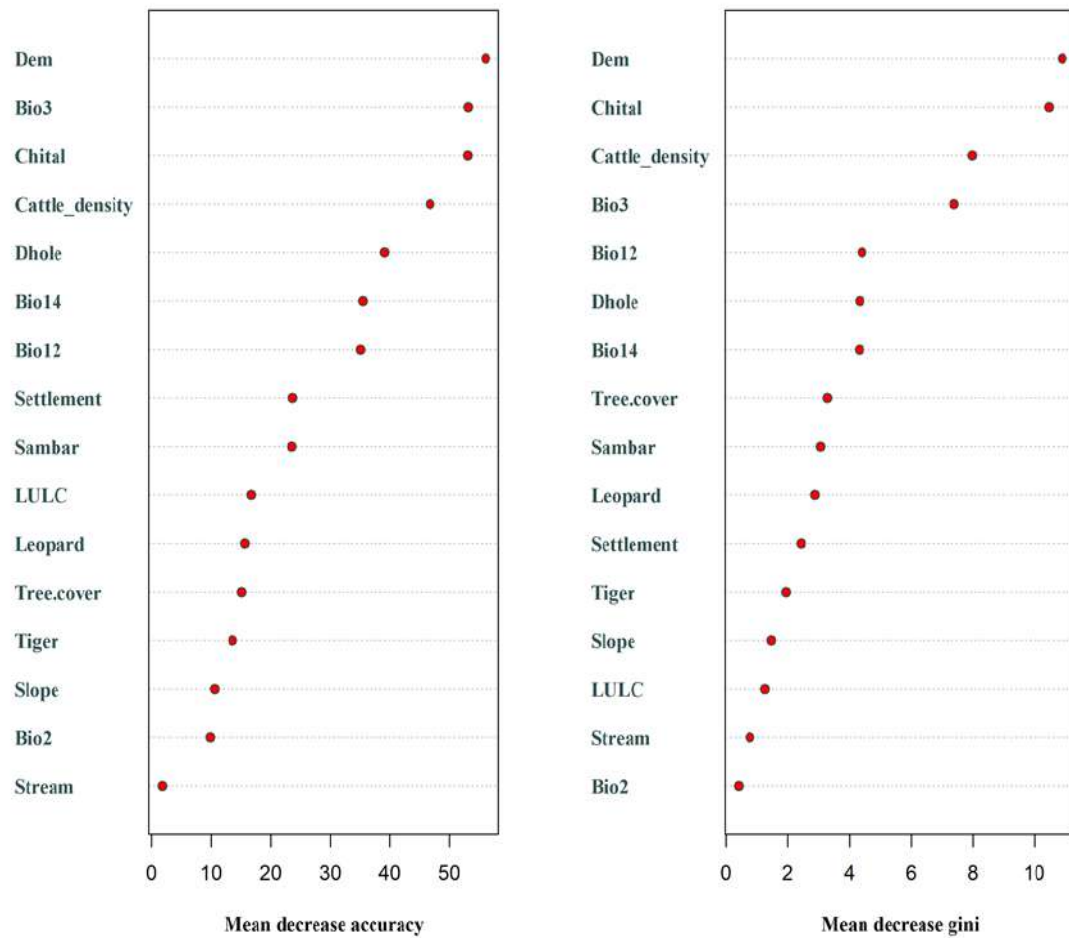


Figure 5.8 Variable importance graph shows the relative importance of all explanatory variables in determining the occurrence probability of hyaena. Mean decrease in accuracy (depth of forest node) and mean decrease in the Gini index are two different measures of random forest used in assessing the importance of a variable in explaining the current distribution of the species. In both measures, variables Dem (elevation), Bio3, chital, cattle density, and dhole appeared to be important variables determining the distribution of hyaena in the landscape. (Dem: Elevation, Bio3: Isothermality, Chital: Occurrence probability of chital, Dhole: Occurrence probability of dhole, Bio14: Precipitation of Driest Month, Bio12: Annual Precipitation, Settlement: distance from settlement, Sambar: Occurrence probability of sambar, Leopard: Occurrence probability of leopard, Tiger: Occurrence probability of tiger, Bio2: Mean Diurnal Range).

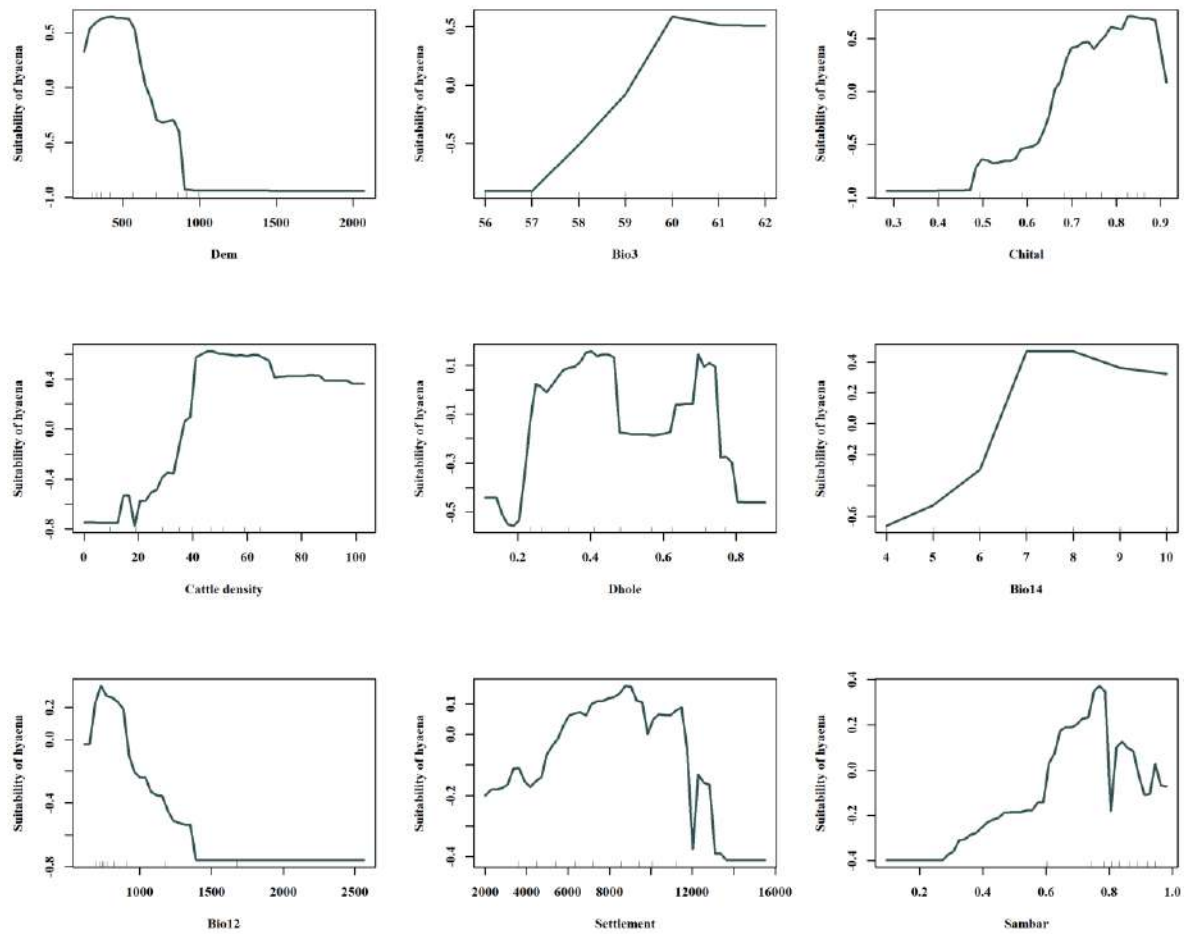


Figure 5.9 Partial dependency graphs of nine most important variables show their marginal effect on hyaena occurrence. Here the marginal effect refers to how changes in the value of a variable keeping others at a constant value affects the likelihood for occurrence of hyaena. These graphs cogently show changes in the likelihood of hyaena occurrence with values of important variables (Dem: Elevation, Bio3: Isothermality, Chital: Occurrence probability of chital, Dhole: Occurrence probability of dhole, Bio14: Precipitation of Driest Month, Bio12: Annual Precipitation, Settlement: distance from settlement, Sambar: Occurrence probability of sambar).

5.4 Discussion

The persistence of mammals, particularly carnivores, across landscapes and their “spatial incumbency” are likely the result of many complex factors, including both bottom-up and top-down ecological mechanisms and processes (Wallach *et al.* 2015). For striped hyaenas in the WEGPTN, the calibrated model was consistent with our field observations in that ‘suitable’ habitat for hyaenas across the study area was sparse, constituting $< \frac{1}{4}^{\text{th}}$ of the entire area. The

population was found to be majorly confined to the Moyar valley of WEGPTN which is spread in the Bhavanisagar and Nilgiri eastern slope range of STR and MTR respectively. Field data also showed the intermittent distribution of the species from the Masinagudi and Sigur forest ranges of MTR. In consensus with the field data, the habitat model also predicted that the Moyar Valley and Sigur plateau are highly suitable for the species in WEGPTN along with some other parts of STR and Erode Forest Divisions. These areas have dry and arid climatic conditions as well as mostly characterized by dry thorn forests which provide optimal habitat for the species. In contrast to hyaena distribution, other predators living in this landscape, were more widespread. Both hyaenas and the other carnivores relied extensively on lowland habitat, which was critically important in determining their spatial distribution across the landscape.

Findings from this chapter are also consistent with prior findings on the species (Singh *et al.* 2010; Sharma *et al.* 2011; Singh *et al.* 2014), which have underscored the importance of rugged terrain in shaping hyaena presence. The Moyar Valley of the Sigur plateau is geographically complex and has substantial rugged terrain bounded by parallel mountain chains and other plateaus in the area, the importance of which has been asserted by several studies (May *et al.* 2008; Ritchie & Johnson 2009; Singh *et al.* 2010). Such rugged terrain adds to landscape heterogeneity and may create “competition refugia”, including greater cover, more ways to avoid line-of-sight interactions, and/or optimal but secretive or cryptic denning habitats. This may effectively mitigate interspecific competition and intraguild predation or other agonistic interactions, and further safeguard a species from worsening or otherwise encroaching anthropogenic threats (Petren & Case 1998; Finke & Denno 2006; Ritchie & Johnson 2009; Wallach *et al.* 2015; Karanth *et al.* 2017). In the case of striped hyaenas, rugged terrain likely provides safer denning refugia, and thus opportunities to coexist with other predators where they overlap. This is at least consistent with our identification of all 18 hyaena den sites amidst the steep slopes of two mountain ranges in Moyar. Furthermore, because steep slopes are an “energy expensive terrain,” mobility through such terrain may burden energetic expenditures relative to more flat/less steep terrain; larger predators therefore may be more inclined to avoid them, or use them less intensively (Langman *et al.* 1995; Shepard *et al.* 2008; Dunford *et al.* 2020). This could give striped hyaenas an advantage, allowing them to persist in the landscape over time. Such rough terrain not only provides competition refugia from larger guild members but may also allow hyaenas to establish a foothold among humans and guard dogs (Singh *et al.* 2010)

That striped hyaenas across the study area were consistently found in topographically and altitudinally diverse terrain is consistent with the findings of other studies for other carnivores. For example, leopards exploit structural complexity in the vertical strata of forests to coexist with larger predators (Ritchie & Johnson 2009; Karanth *et al.* 2017). The persistence of more than one predator species in a landscape is also driven by other factors, like climatic attributes and prey abundance. Pumas that are sympatric with jaguars are known to utilize more open, drier habitats to avoid fatal interactions with the latter, more powerful felid (Sollmann *et al.* 2012). For this study area, the occurrence probability of striped hyaena was found to be positively related to isothermality, aridity, and annual mean temperature. Potential prey in the form of chital and sambar were also positively associated with hyaena occurrence (Figure 5.9), and the predictive value of increased domestic cattle density was likely reflective of increased scavenging opportunities for the species.

Finally, although striped hyaenas are known to co-occur with other predators across their range, including western India (Arivazhagan *et al.* 2007; Alam *et al.* 2014; Singh *et al.* 2014; Jhala *et al.* 2020), prior to this study, little information existed on the specific mechanisms that facilitate hyaena coexistence with other large predators. Despite small sample sizes, evidence from this chapter is more consistent with hyaenas making fine-scale investments in the use of certain habitats and microhabitat features considered less suitable by other predators, than temporal avoidance. It was also noted that although striped hyaenas have a foothold in the Moyar Valley, this population is very small, and thus potentially vulnerable to inbreeding depression and anthropogenic threats. It is the only major breeding population of hyaenas in all of southern India, which marks this population as important for the conservation of the species in southern India. Apart from the Moyar Valley where the population is currently distributed, more suitable areas were also identified in the Coimbatore Forest division (Figure 5.6). The contiguous forest area from Moyar Valley to Coimbatore Forest division should be prioritized for hyaena conservation because this is the only alternative suitable habitat found in this study through habitat suitability analysis. The findings also call for the implementation of a long-term monitoring program to map the trajectory and status of this hyaena population or meta-population and a critical analysis of what if any management tools or approaches can effectively enhance suitable habitat.

Chapter 6



Chapter 6: Conclusion

Findings of this research work and literature review suggested that the studied population is the only last remaining major breeding population of striped hyaena in entire Southern India. This population holds important conservation values and needs sincere efforts to conserve this critical population. A study by Lande (1988) suggested that the demography of a population is of immediate importance in wildlife conservation. Primarily, there is bare information on the population size and its demographic structure available. Population size is a very important parameter of demography and critical in determining befitting conservation strategies (Harmon & Braude 2010). There is an urgent need to have a holistic understanding of the demography of the population so that the information can aid in its scientific conservation. Furthermore, the population was found to be very small and majorly confined to a small area of approximately 314 sq. km. This small population is highly vulnerable to extinction due to unforeseen catastrophes which can potentially wipe out the entire confined population and also prone to inbreeding dispersion. Inbreeding can adversely affect the overall fitness of the population by deteriorating the sperm quality and also increasing susceptibility to disease (Frankham 2005; Hedrick and Fredrickson 2010; Furlan *et al.* 2012). The status of inbreeding in the population needs to be assessed as soon as possible so that required scientific management intervention can be initiated in the direction of conserving this small hyaena population. Furthermore, the daunting threat of inbreeding can be reduced by establishing a metapopulation of the species in the landscape. There are certain regions in the landscape that are climatically suitable for the species as identified through habitat suitability but need further studies so that translocation of subpopulation can be considered. This study recommends a further detailed study encompassing multiple aspects that can affect the sustainability of hyaena population to ascertain alternative suitable regions for the species.

When the population is critically small even a minute variation in survival rate and reproductive success to any reason can significantly affect the population. In this population, the survival fitness of every individual is critical. Thus, this study recommends close monitoring of every possible individual in the population at regular intervals and initiates appropriate steps to minimize the unnatural or accidental causality of individuals. Highways can have a severe impact on wildlife conservation and road kills have emerged as a major concern among conservation biologists (Samson *et al.* 2016). Roadkill is also reported to be one of the reasons

for the accidental death of the hyaena in this landscape (The Hindu, 2021). For the conservation of hyaena, it is recommended that appropriate management of traffic and speed of vehicles on the highways particularly crossing the Masinagudi range of Mudumalai Tiger Reserve (MTR), Bhavanisagar and Sathyamangalam ranges of Sathyamangalam Tiger Reserve (STR) are required. Road humps can be installed on the roads crossing these regions to regulate vehicle speed.

During the field survey, instances of persecution of hyaenas by villagers were also recorded. Further, the empirical investigation based on questionnaires survey elucidated acute intolerance for hyaena conservation due to over-generalization of fear elicited under high economic stress remarkably articulated with livestock predation, livestock loss to disease, people's livelihood, and importantly perpetual uncertainty on predatory efficiency of species. This intolerance poses an immense threat to hyaena conservation and may nullify all managerial efforts to conserve the population until and unless intolerance among the stockholders is significantly reduced. To reduce intolerance, it is important to reduce the economic stress elicited by livestock predation with prompt compensation programs. Some initiatives like the arrangement of stall feeding for livestock that generally grazes inside forests also help to curb livestock predation by large carnivores and eventually will be conducive to gaining villagers' support to conserve this critical population. Better veterinary facilities will also aid the management in reducing the economic stress of people elicited by cattle mortality due to the dearth of appropriate medical facilities. Furthermore, reducing dependency by providing different alternative opportunities in the form of eco-tourism and small-scale handicraft industry in the area will also be helpful in the long-run conservation of this last remaining major breeding population of hyaena in southern India. This study also suggests awareness programs for the people living in and around the current distributional range of the population about the non-predatory scavenging behavior of hyaena. Spotted hyena are valued in Ethiopia and tolerated by people for ecosystem services provided by the species (Yirga *et al.* 2015). There should be clear cognizance about the role of hyaena in removing carcasses and subsequently controlling associated diseases among local communities. Making people aware of the scavenging behavior of striped hyaenas and their role in the ecosystem would also help in the conservation of the population in the landscape. This will also help people to realize the scavenging behavior of species and will aid in halting the ill-generalization.

Habitat management is also a very important conservation practice. During the study, it was found that hyaenas preferred open and dry habitats of the Sigur plateau, Masinagudi, and Moyar valley. DeVault *et al.* (2011) stress that open habitat facilitates vertebrate scavengers in

finding carcasses in comparison to dense habitats. While, the wide proliferation of exotic species like *Lantana camara*, *Opuntia dillenii*, and *Prosopis juliflora* has been observed in current hyaena distribution ranges turning habitat inconveniently denser for the species (Johnsingh *et al.* 2010). The concern of weed proliferation should be taken up by the forest department to address it with a befitting approach. This region also harbours a large number of cattle herds which are also seen grazing on adjoining mountain slopes and ridges. Such undulating terrains are potential denning sites of hyaenas and should be free of any form of anthropogenic disturbances. Livestock and domestic dogs can potentially spread many contagious diseases to wildlife through multiple ways. Here, this thesis suggested the use of common water sources like the Moyar River should be restricted for cattle and a number of feral dogs in fringe areas should also be controlled through appropriate managerial interventions.

In this large-scale investigation of top-down effects, no significant impact of large predators on hyaena distribution was observed. Analyzing hyaena presence-absence in response to the presence-absence of large predators, the results suggest no absolute avoidance of large predators by hyaenas. Hyaenas are known to coexist with sympatric large carnivores such as tigers and leopards across their distribution range. This research suggests that such coexistence may be achieved by exhibiting different spatial behaviors, like selecting den sites or suboptimal habitats of large predators, which act as competition refugia for the species. This suggests that top-down control effects may be density-dependent and could impact hyaena populations if large predator numbers surpass a certain threshold. The inferences drawn from this research on top-down control are based on presence-absence data, and therefore, further investigation with abundance data is needed for deeper insights into these intricate dynamics.

This hyaena population is critical and needs synergetic efforts to conserve this species at the landscape level as the distribution of the species highly overlaps with endangered vulture breeding sites in the same landscape. Below are some recapitulated important points that would be conducive to better scientific management of this important population.

- 1) There is an immediate need for constituting a hyaena advisory committee encompassing experts from different areas like ecology, conservation biology, sociology, data science, and conservation psychology as well as people well acquainted with hyaena ecology in this landscape and respective Park Managers.

- 2) A synergetic effort should be made by the committee to conceive a comprehensive study to understand the biology and ecology of the population. The intended study should initially aim to understand the demography of the population, stress physiology, and habitat use in detail and also to identify alternative suitable habitats for the population through a long-term study.
- 3) Personnel of forest departments should be trained properly so that the required data or samples can be gathered during their regular visit for population monitoring.
- 4) Data collected by field staff including camera trap data should be made available to competent members of the constituted committee so that data can be leveraged by experts to make better inferences conducive to conservation of the population.
- 5) The reduction of economic loss by identifying and controlling more prevalent epidemics will increase the tolerance level of people towards carnivores and will also increase the sustainability of both humans and wildlife together.
- 6) Appropriate steps like prompt compensation programs, better veterinary facilities, and community awareness should be taken to reduce the ill-generalization towards the species. Community support for the conservation of the population is very important and can't be ignored. This community support improves coexistence between the hyaena population and local communities and maintains appropriate habitat conditions to have a viable hyaena population in the landscape.
- 7) Arrangement of stall feeding for the livestock grazing in and around the current distribution range might be helpful. This will minimize the instances of livestock predation by other sympatric carnivores and eventually will aid in reducing ill-generalization by people.
- 8) Cattle grazing on hills or mountains adjacent to settlements that support denning sites and use of common water sources like Moyar River by cattle need to be regulated.
- 9) Poisoning of domestic cattle carcasses in retaliation by herders targeting large carnivores such as tiger, leopard, and dhole can play a major role in the population decline of hyaena. Necessary steps should be taken to bury the cattle carcasses where species are more vulnerable to poisoning.
- 10) Hyaena tend to avoid the high occurrence probability area of their co-predators but arid climatic conditions, and prey abundance primarily determined spatial incumbency in the landscape. Furthermore, hyaena chose to co-exist in an area with low to medium relative abundance of co-predators. This finding indicates that the conservation of threatened species should be of multispecies approach oriented rather than tiger

conservation centric. Secondary habitats such as scrubland and savanna grasslands should be given equal conservation importance for maintaining the vital population of side-lined species such as hyaenas, Jackals and Foxes etc.

- 11) This study identified highly suitable zones of hyaena which comprise only 21% of the total study area. The current hyaena population which is mainly confined to the Nilgiri Eastern Slope and Bhavanisagar ranges of MTR and STR is the only major population of the landscape and is highly subjected to inbreeding syndrome, subsequently to reduction in overall biological fitness and eventually to downfall of the population. The predictive model also identified other potential areas that are part of the Coimbatore, Masinagudi range, Sigur, Erode and Dharmapuri Forest Divisions. The improved prediction would be very helpful to overcome such potential problems by mapping the current distribution and predicting other potential habitats to increase the mobility of the population by improving connectivity between all possible patches.
- 12) Management should also take appropriate steps to control the population of feral dogs and wild pigs as well as the proliferation of invasive species in and around the current hyaena distribution range. These two species are increasingly becoming competitors of hyaena at dump yards and may affect the foraging opportunities for scavengers like hyaenas.
- 13) Though drugs like diclofenac are banned, there are alternative equally dangerous drugs available, Flunixin, aceclofenac, nimesulide, and ketoprofen which can potentially affect the scavenger community such as hyaena and vulture. The effect of these Non-Steroidal Anti-Inflammatory Drugs (NSAIDs) needs to be investigated which is imperative to assure the toxic free scavenging opportunities in the landscape.
- 14) Toxic-free livestock carcasses should also be made available for these scavengers assuring enough scavenging opportunities. These can be facilitated by providing necessary financial aid to the local communities.
- 15) From a large perspective, outside PAs also harbour a good population of the species throughout India. Those population also needs immediate conservation attention so that genetic diversity in hyaena population throughout its distribution ranges can be restored through establishing meta-population.

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Appendices

Appendix I

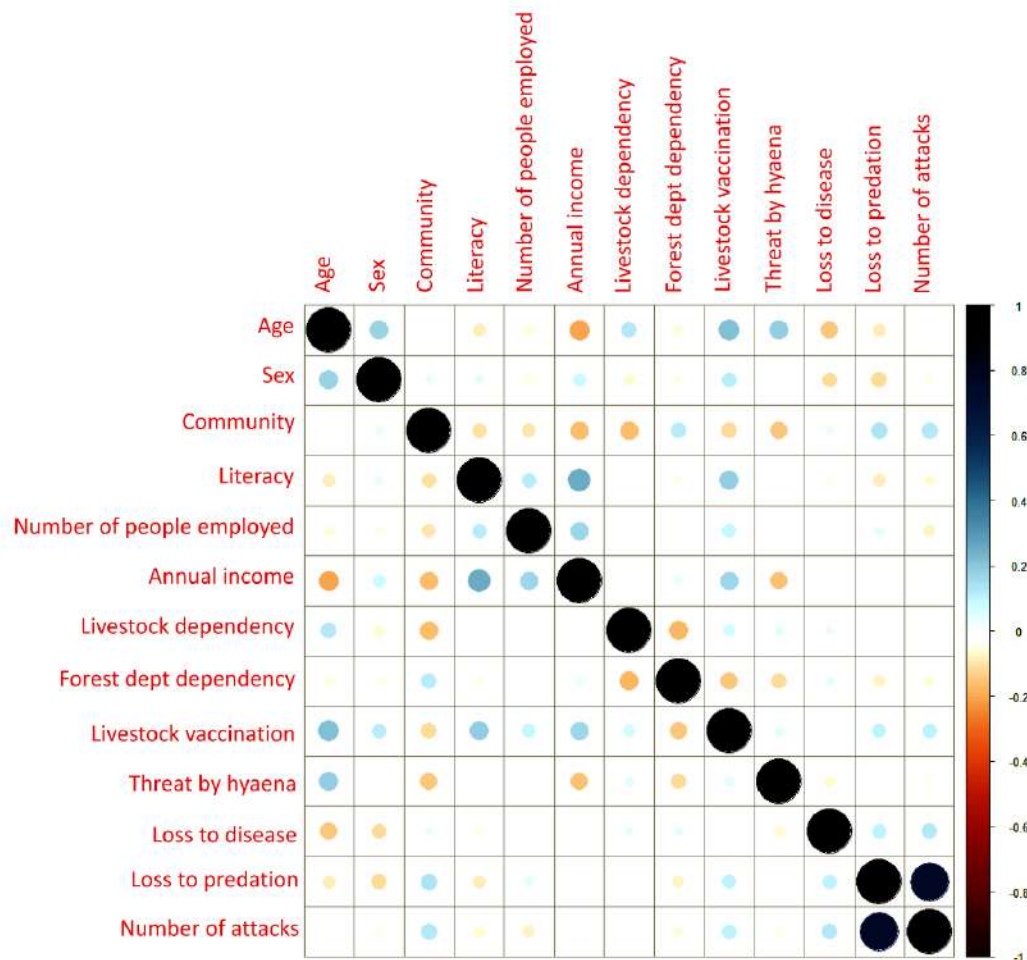


Figure S3. 1 Correlation graph. Pearson correlation test was performed between 13 identified variables to check collinearity between the variables. Number of attacks by predators and economic loss to predation found to be highly correlated. Therefore, economic loss to predation was retained for the modelling and number of attacks was discarded.

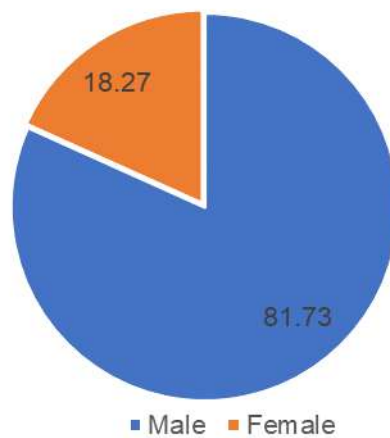


Figure S3.2 The percentage of male and female interviewed. During questionnaire survey, percentage of respondent was appeared to be male 81.73% (n=161) and female 18.27% (n= 36) respectively.

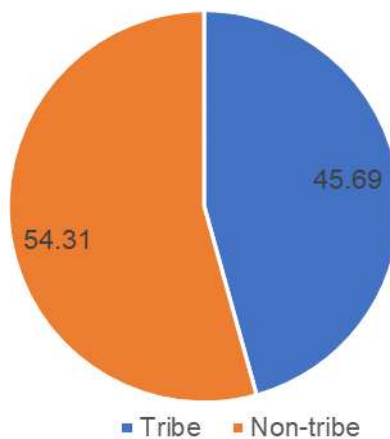


Figure S3.3 The percentage of tribe and non-tribe interviewed. During questionnaire survey, percentage of respondent was appeared to be non-tribe 54.31% (n=107) and tribe 45.69% (n= 90) respectively.

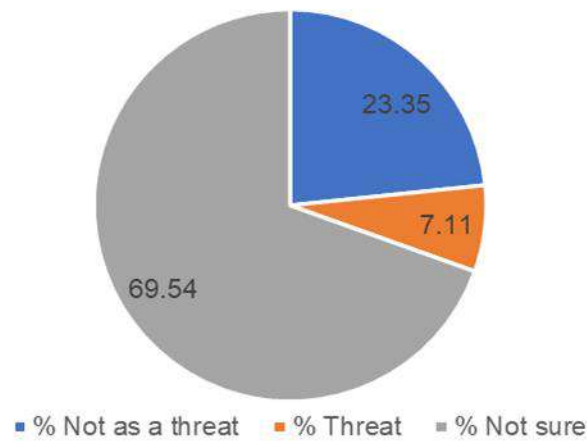


Figure S3.4 People's perception on predatory behaviour of hyaena in percentage. Multitude of respondent 69.54% (n=137) were ambiguous about predatory behaviour or efficiency of hyaena on livestock, 23.35% (n=46) perceived hyaena not as a threat and only 7.11% (n=14) considered hyaena as a threat for their livestock.

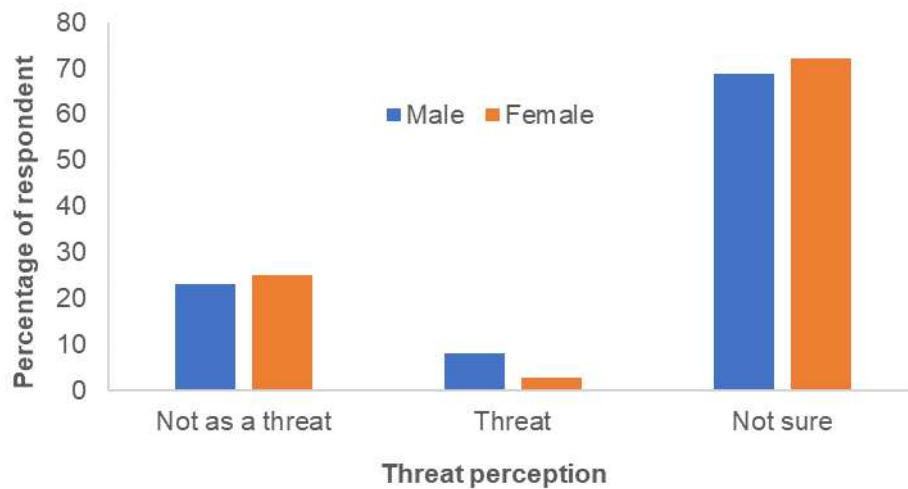


Figure S3.5 Frequency distribution graph of sex corresponding to predatory perception for hyaena. Most of the people from both classes (male 68.94% & female 72.22%) were not sure about predatory efficiency/behaviour of hyaena on livestock while only 8.07% of males and 2.78% of females reported hyaena as problematic or threat.

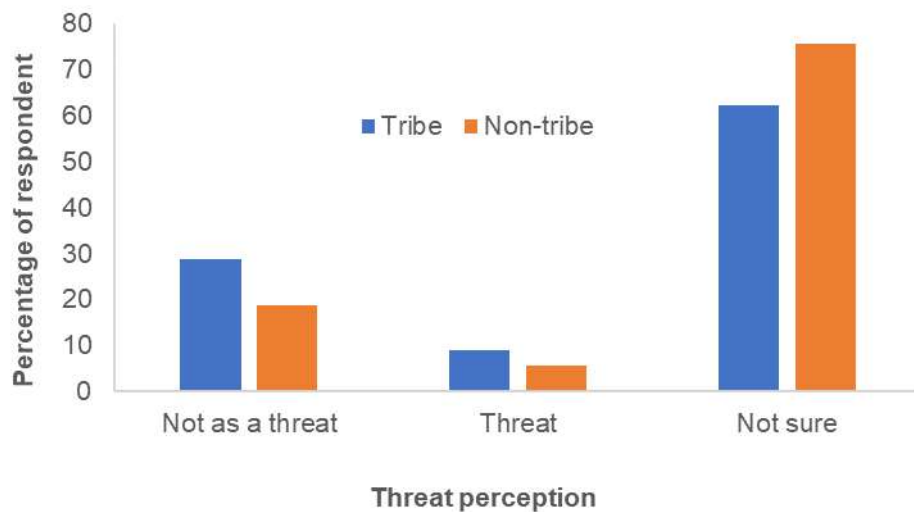


Figure S3.6 Frequency distribution graph of ethnicity (community) corresponding to predatory perception for hyaena. Most of the people from both of the classes (tribal 62.22% & non-tribal 75.70%) were not sure about the predatory efficiency/behaviour of hyaena on livestock while 8.89% of tribal and 5.61% of non-tribal respondents perceived hyaena as threat.

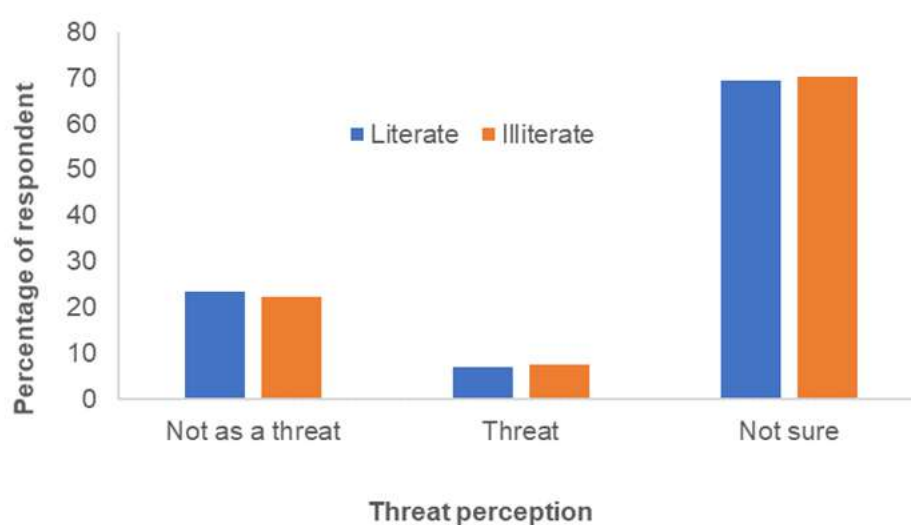


Figure S3.7 Frequency distribution graph of literacy corresponding to predatory perception for hyaena. Most of people from both the classes (literate 69.4% & illiterate 70.37%) were not sure about predatory efficiency/behaviour of hyaena on livestock while only 7.06% of literate and 7.41% of illiterate reported hyaena as problematic or threat.

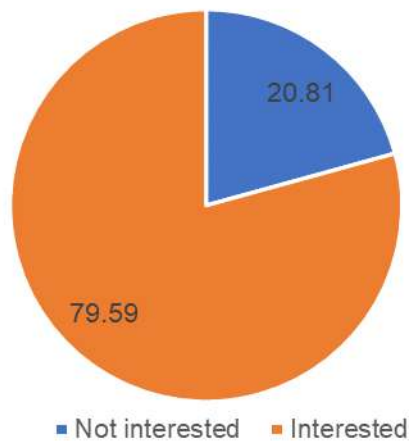


Figure S3.8 Percent conservation attitude of people. During the questionnaire survey, 79.59% (n= 156) of respondents were found to be interested in conserving the species and 20.81% (n=41) were found to be not interested.

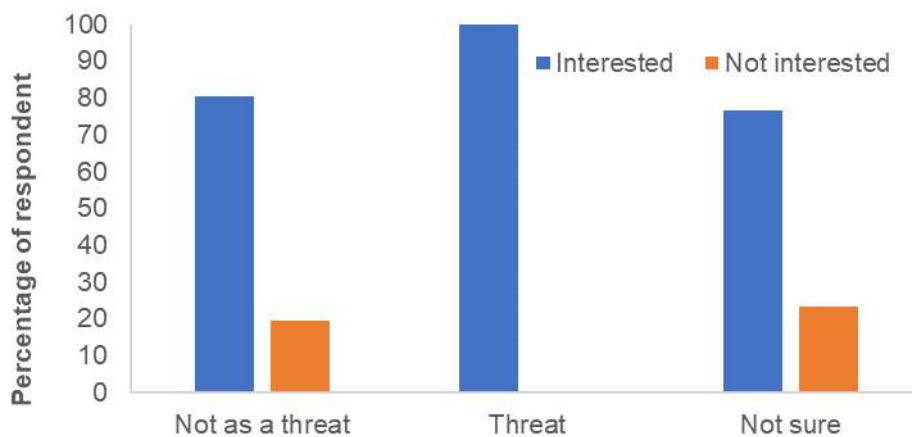


Figure S3.9 The graph representing percentage of interest for conserving the species corresponding to perceived threat for livestock. Across the perception, people who were uncertain about predatory behaviour of hyaena represented highest percentage of intolerance (23.36%) towards the species while all respondent who reported hyaena as a threat supported hyaena conservation.

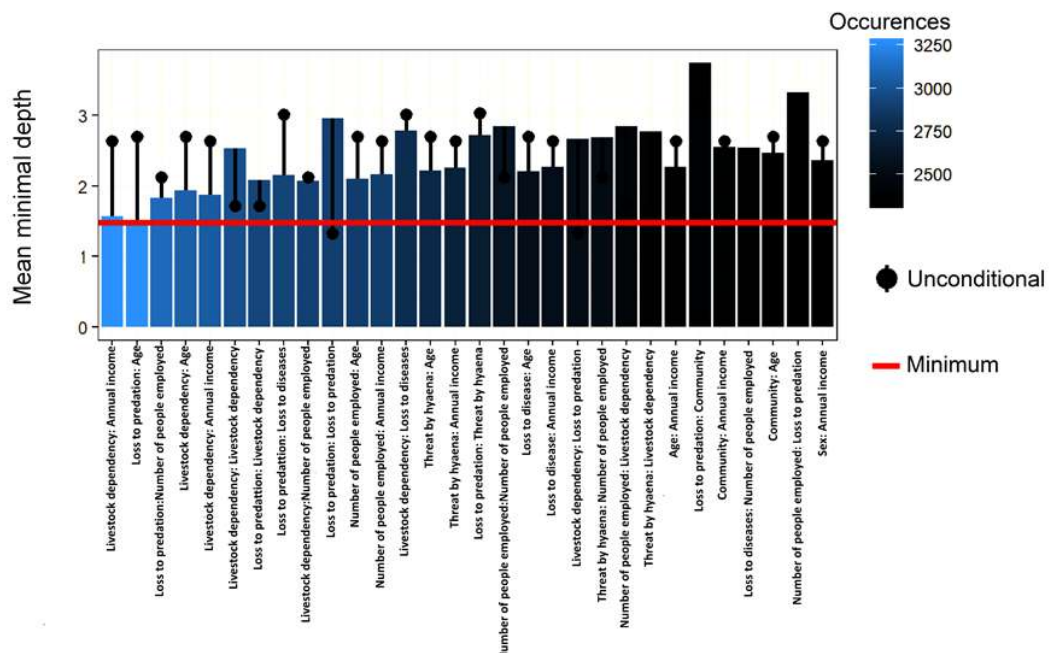


Figure S3.10 Best 30 interactions of variables according to mean of conditional minimal depth. Here occurrence correspond to the number of times the interaction appeared in the model.

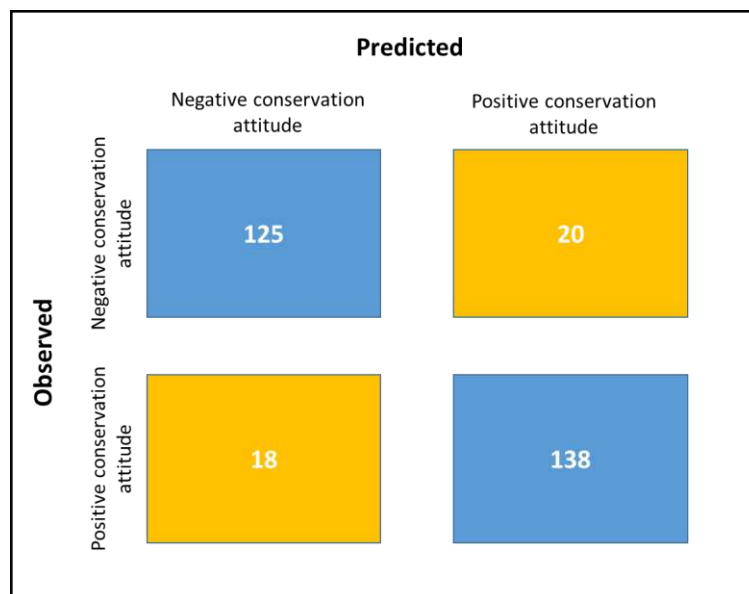


Figure S3.11 Error rate of the model

Table S3.1 Values of two measures of variable importance Mean minimal depth and Gini index for the variables used for modeling. In the case of mean minimal depth, the lower the value higher the importance in model but in the case of Gini index higher the value higher the importance.

Variables used in the model	Minimal mean depth	Gini index
Age	2.67	16.77
Annual income	2.65	16.81
Community	3.22	7.51
Forest department dependency	6.74	0.35
Literacy	4.18	4.79
Livestock dependency	1.75	23.73
Livestock vaccination	5.03	2.73
Loss to disease	2.96	12.98
Loss to predation	1.31	30.87
Number of people employed	2.13	18.65
Sex	3.82	5.13
Threat by hyaena	2.99	8.38

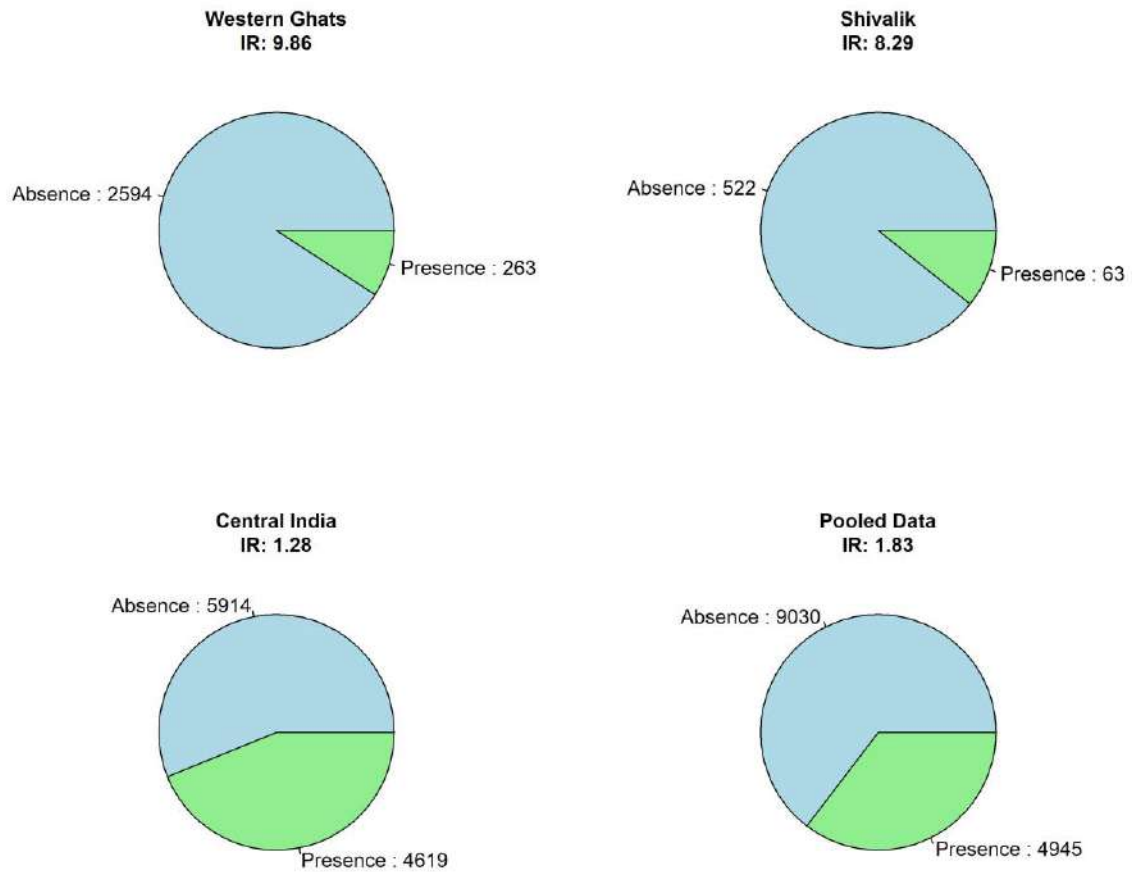


Figure S4.1 The pie chart illustrates the presence-absence distribution and class imbalance ratios (IR: the Imbalance ratio of the sample size of the majority class, Absence, to the minority class, Presence) for hyaenas across different regions and pooled data. We observed a smaller sample size and higher imbalance ratios in the relatively smaller regions, such as Shivalik and the Western Ghats, compared to Central India and the pooled data.

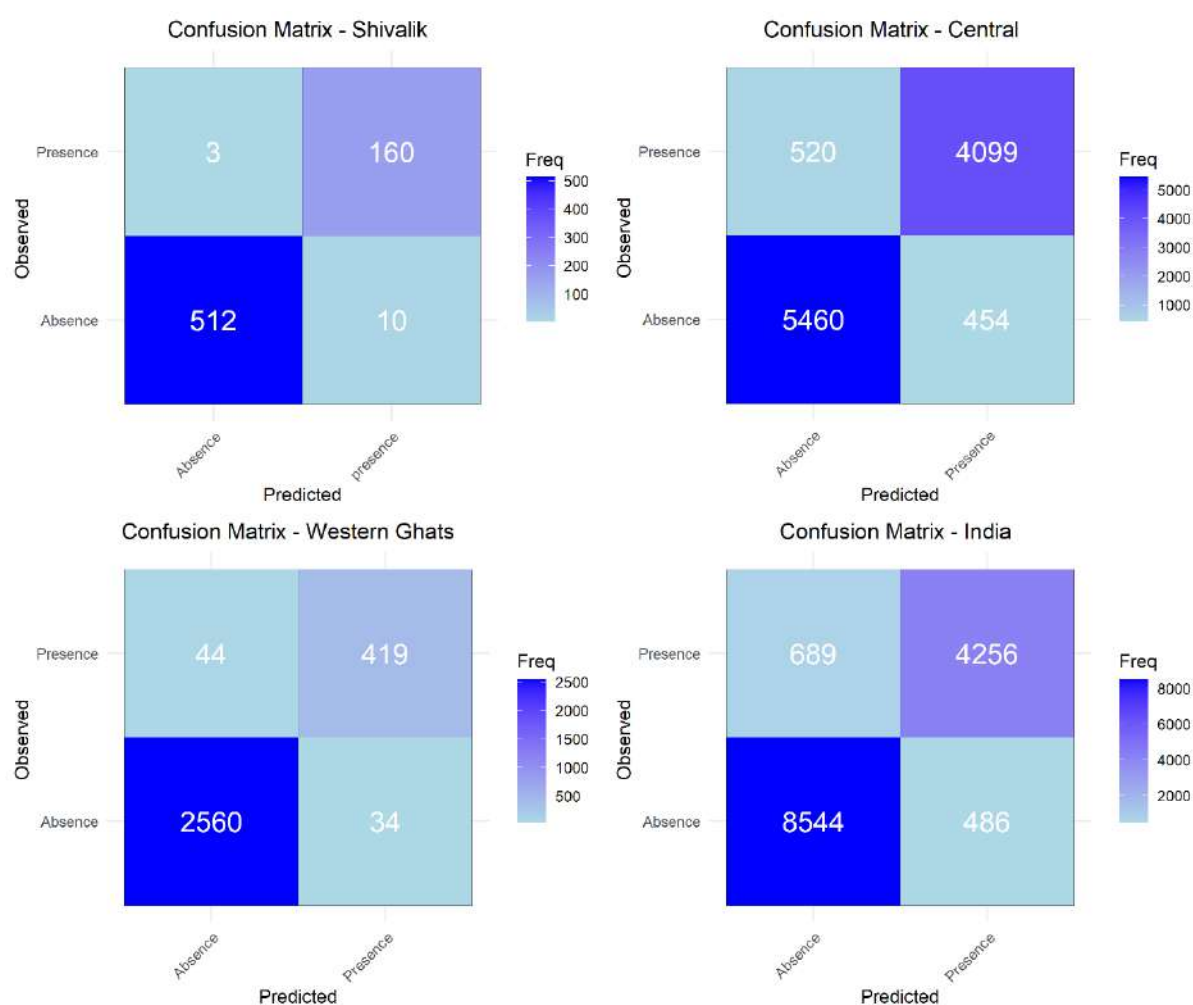


Figure S4.2 The confusion matrix graphs depict the class error on Out-of-Bag (OOB) data for regional models of the hyaena, including Shivalik (after upsampling), Western Ghats (after upsampling), Central India, and the global model.

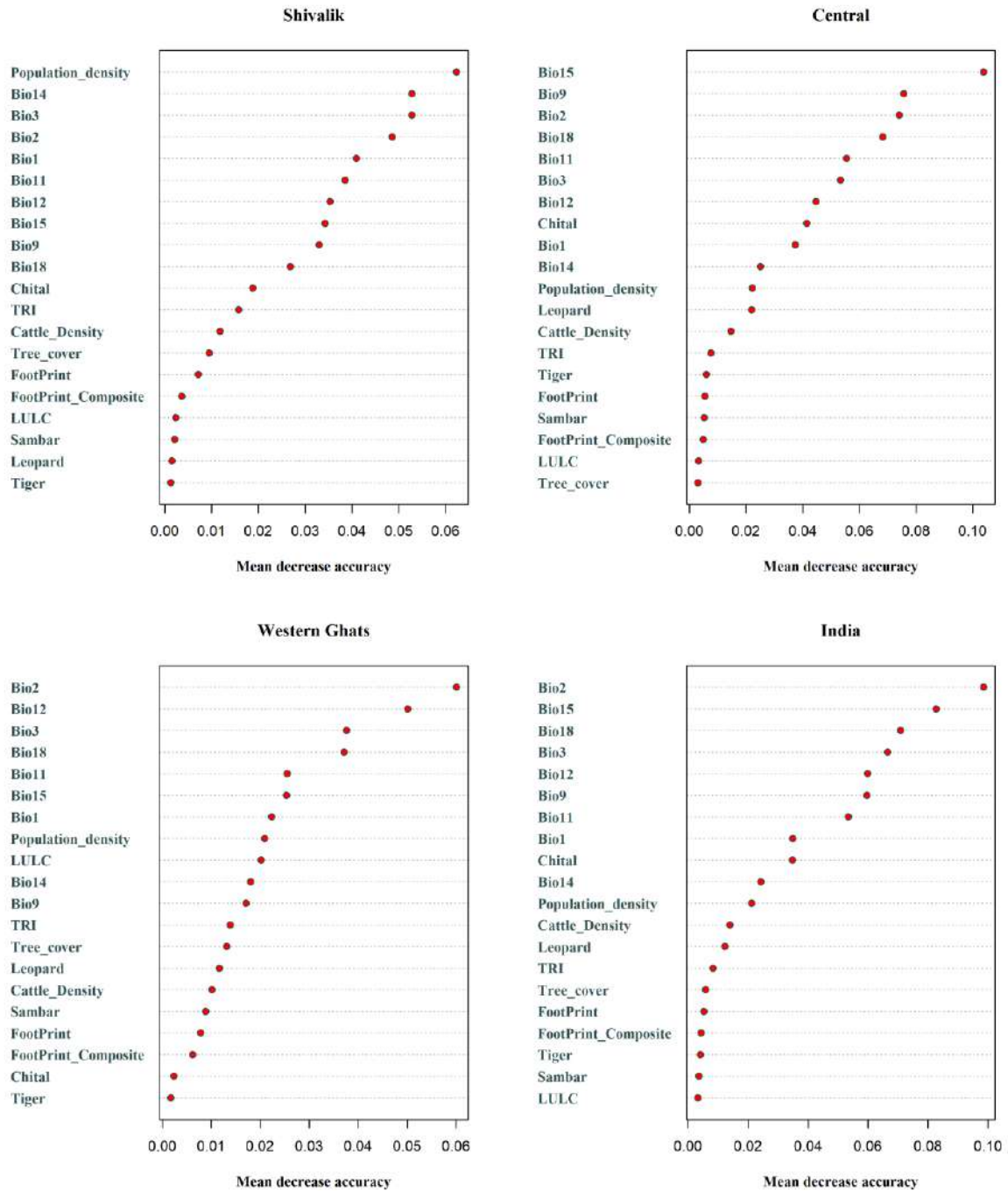


Figure S4.3 This variable importance graphs show the relative importance of all explanatory variables in determining the occurrence probability of hyaena in three tiger conservation landscapes and of Global model on pooled data.

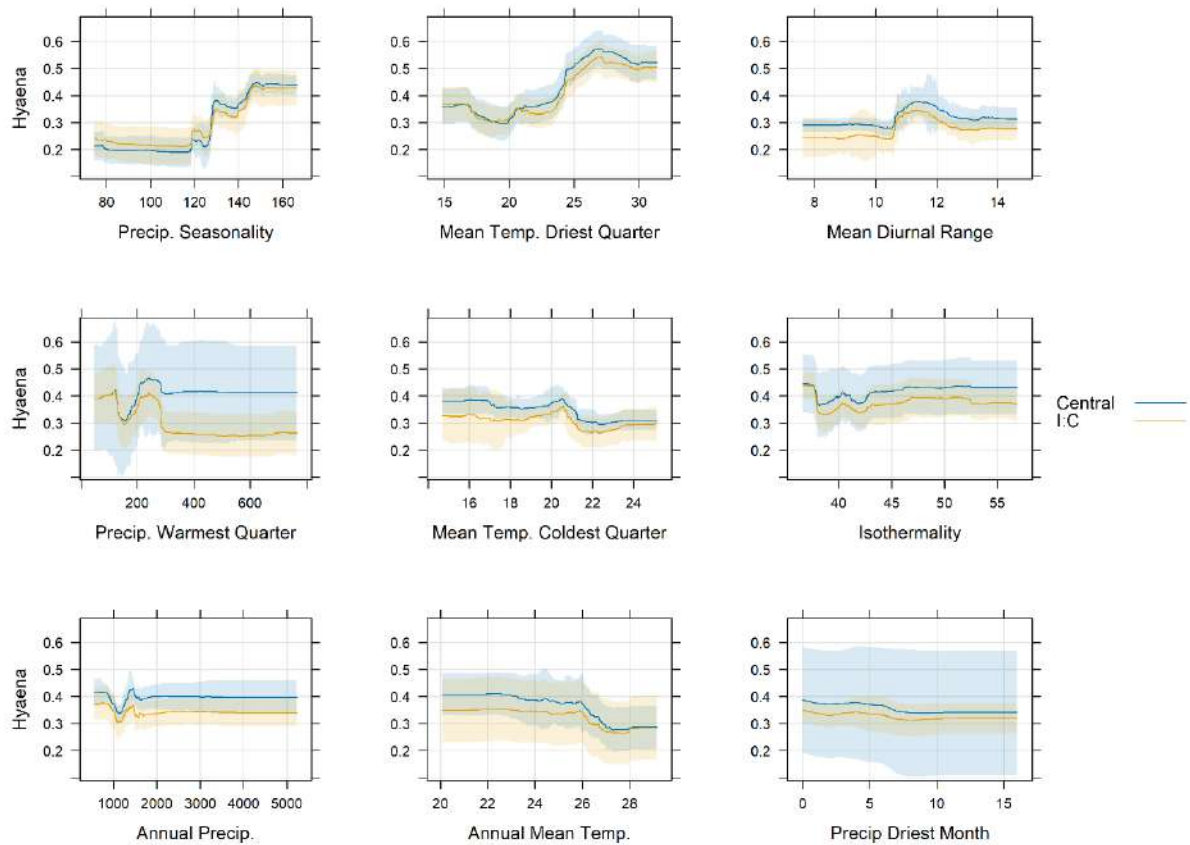


Figure S4.4 The graph compares the Region-Specific Global Responses (RSGRs = I:C) of hyaenas in Central India with the corresponding regional model responses for the nine most important limiting factors. The RSGRs showed no deviation from the trends predicted by the regional model, demonstrating high consistency, which suggests a stronger influence of Central India in the global model. The efficiency of I:C in reducing uncertainty was notable for variables where the local Central India model performed poorly, such as Precipitation of the Driest Month and Precipitation of the Warmest Quarter.

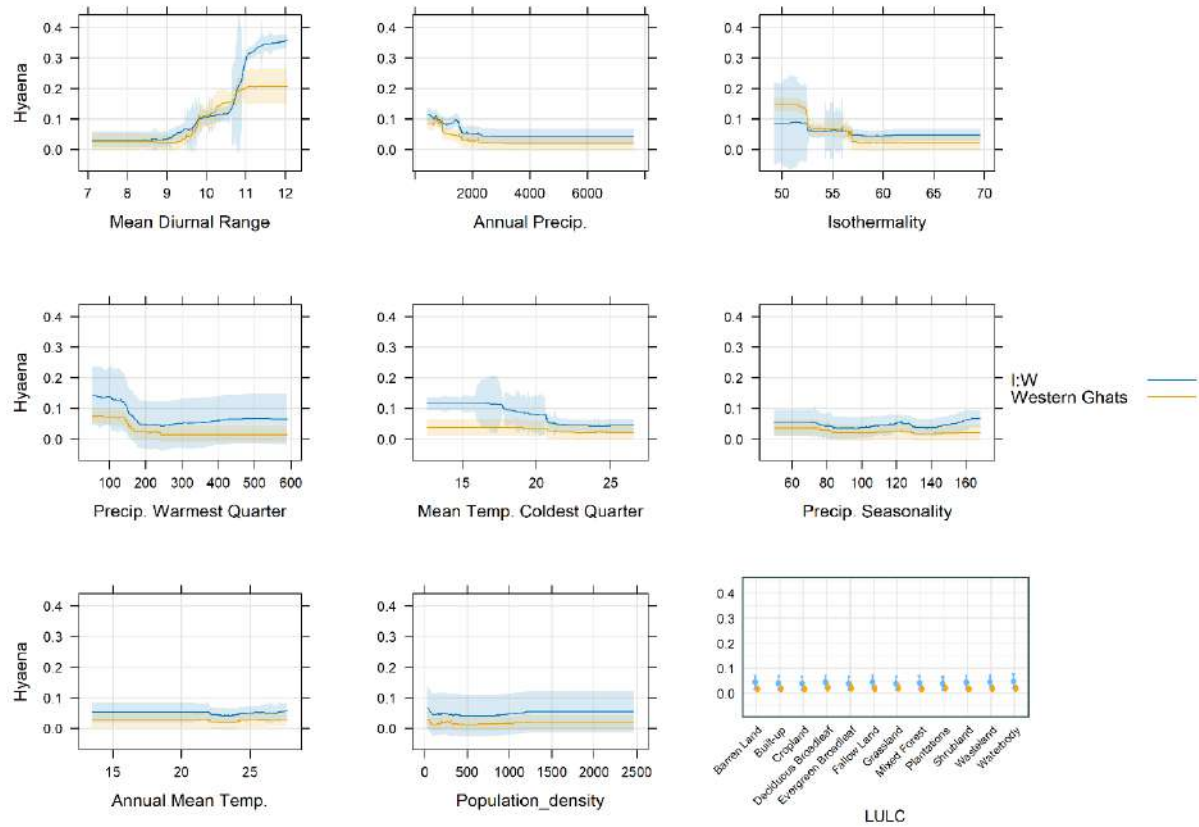


Figure S4.5 The graph compares the Region-Specific Global Responses (RSGRs = I:W) of hyaenas in the Western Ghats with the corresponding regional model responses for the nine most important limiting factors affecting the species. Uncertainty of RSGRs was found to vary with variables and did not show any significant deviations from trends in the Western Ghats - specific local model, except for a tolerable deviation in mean diurnal range over a short gradient.

Table S5.1 Land-use and land cover (LULC) classes, and associated abbreviations.

Sl No.	Name of landuse landcover class	Abbreviation used	Data type assigned
1	Evergreen	1	Nominal
2	Semi evergreen	2	Nominal
3	Moist deciduous	3	Nominal
4	Dry deciduous	4	Nominal
5	Thorn forest	5	Nominal
6	Bamboo	6	Nominal
7	Sholas	9	Nominal
8	Riverine	10	Nominal
9	Plantation	11	Nominal
10	Degraded forest	14	Nominal
11	Savana	16	Nominal
12	Grassland	23	Nominal
13	Agriculture	24	Nominal
14.	Barren land	26	Nominal
15.	Water bodies	27	Nominal
16.	Settlement	29	Nominal

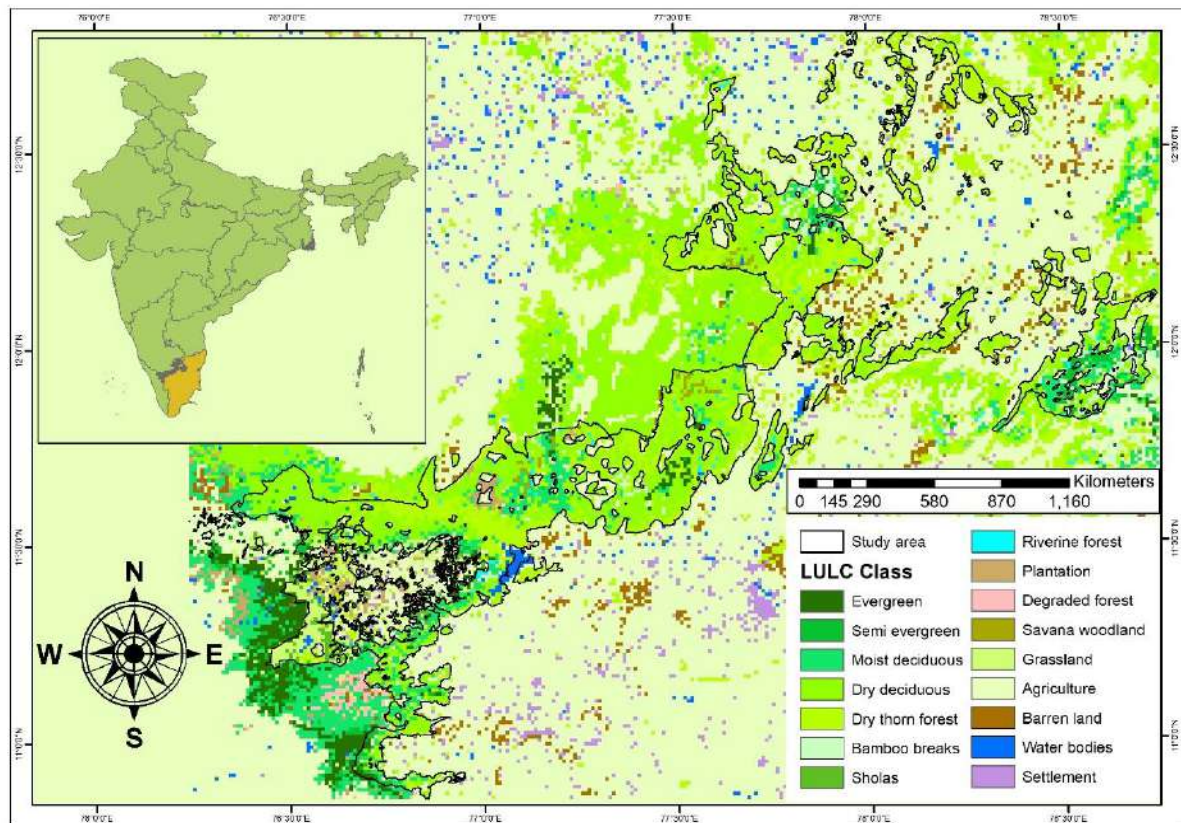


Figure S5.1 Broad classes of land use and land cover (general habitat) from the study area.

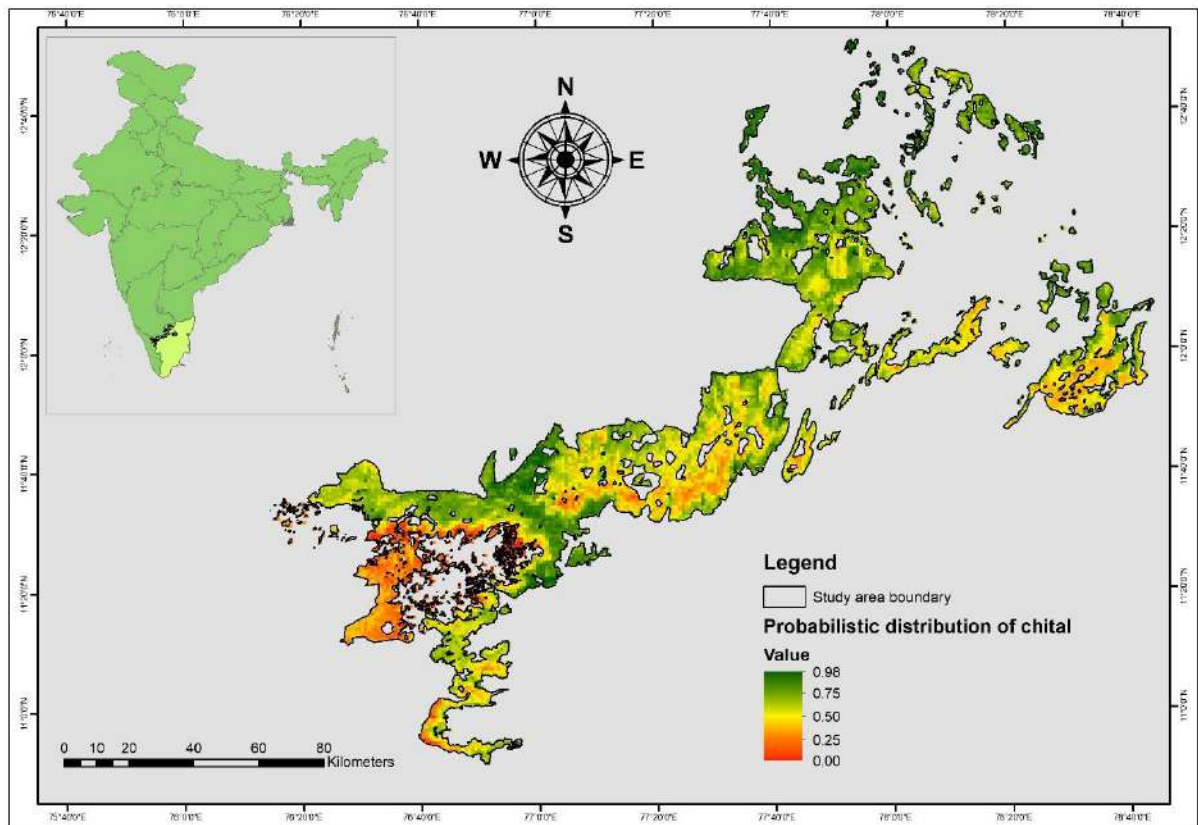


Figure S5.2 Predicted (probabilistic) distribution of chital in the Western and Eastern Ghats part of Tamil Nadu.

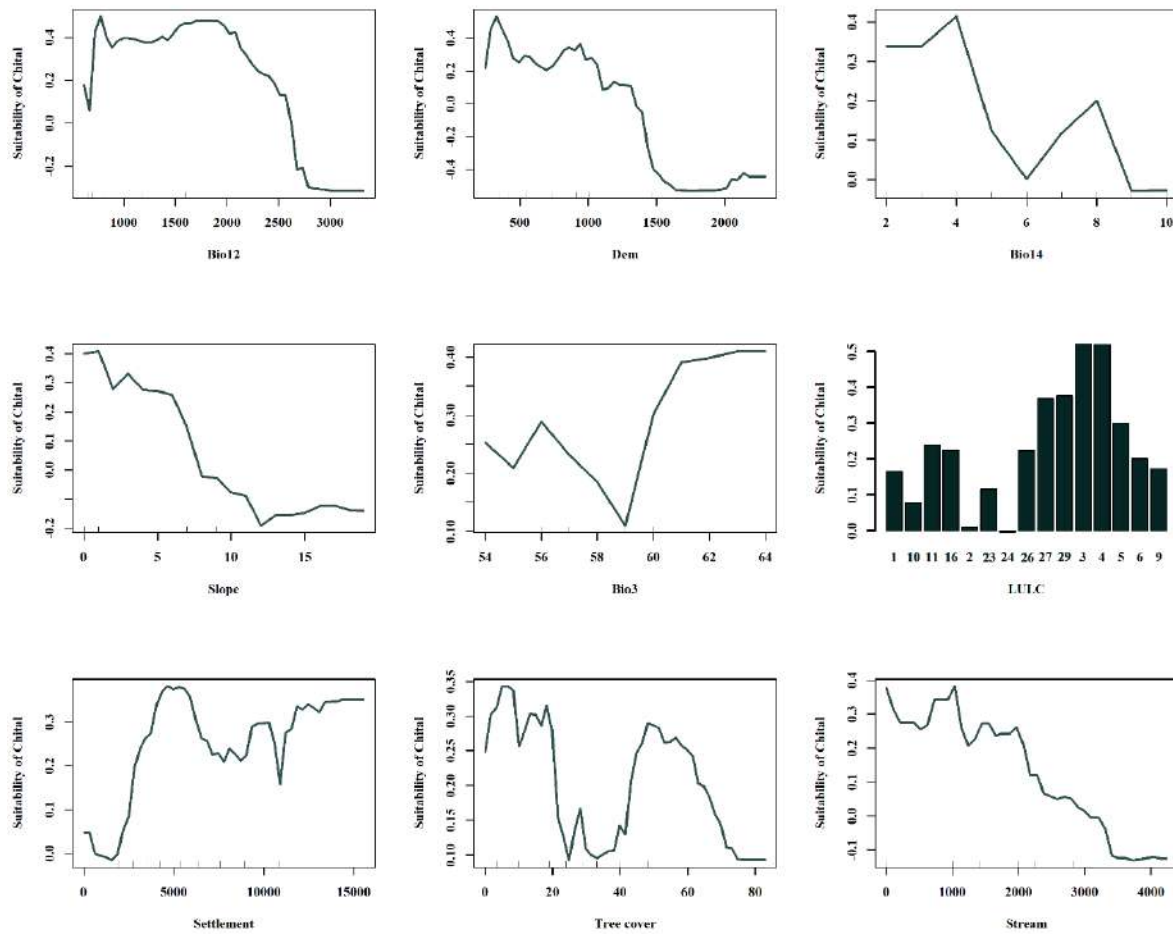


Figure S5.3 Partial dependency graphs of the nine most important variables show their effect on chital occurrence. Here, the marginal effect refers to how changes in the value of a variable while keeping others constant affect chital occurrence likelihood. These graphs depict changes in the likelihood of chital occurrence as influenced by the most important variables, including: Dem = Elevation; Bio3 = Isothermality; Bio14 = Precipitation of the Driest Month; Bio12 = Annual Precipitation; Settlement = distance from settlements; Stream = distance from streams; and LULC = land use/land cover.

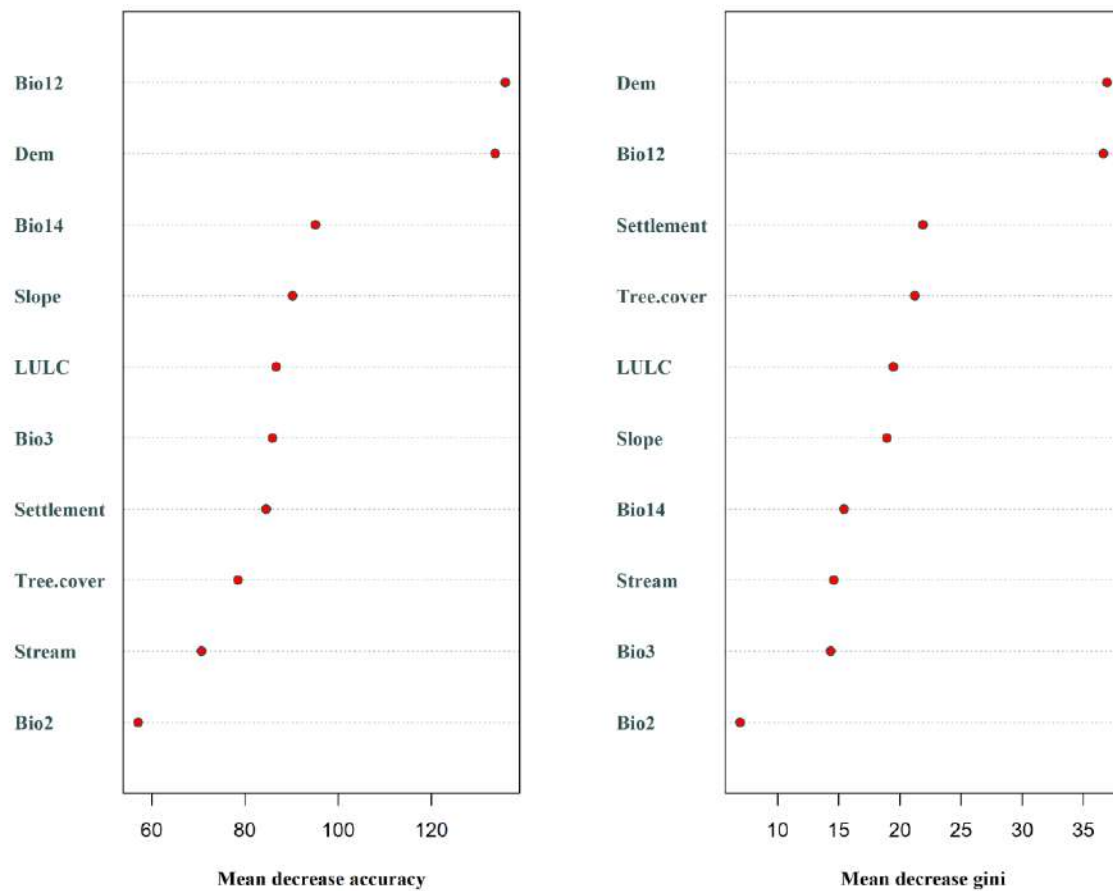


Figure S5.4 Variable relative importance graphs depict relevance of all explanatory variables influencing the occurrence probability of chital. Mean decrease in accuracy (forest depth from node) and mean decrease in Gini Index are two different measures of random forest used to assess the importance of variable explaining the current distribution of the species; higher values for each indicates high relative importance for the model. (Dem = Elevation; Bio3 = Isothermality; Bio14 = Precipitation of Driest Month; Bio12 = Annual Precipitation; Settlement = distance from settlement; Stream = distance from stream; LULC = land use/ land cover).

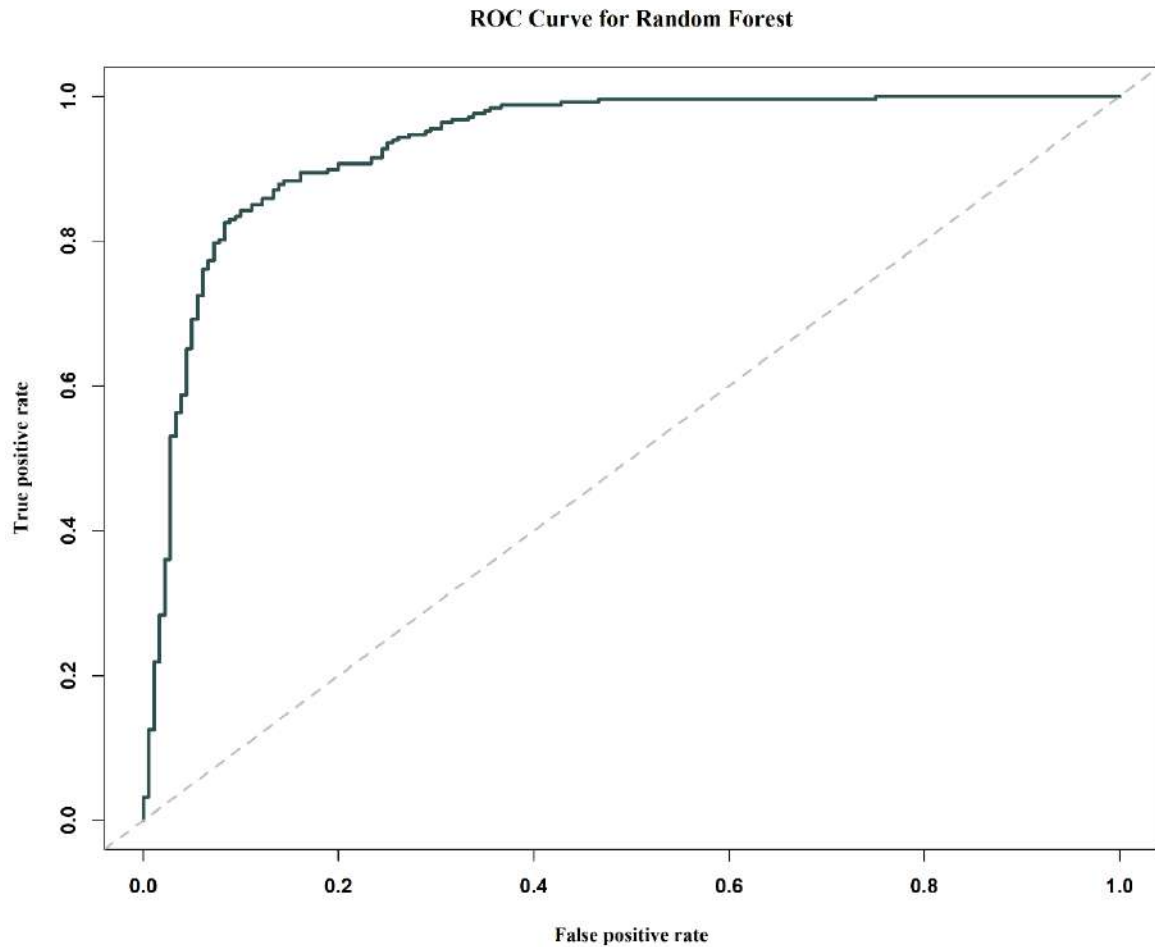


Figure S5.5 The accuracy of the calibrated model for chital was checked by plotting the Receiver Operating Characteristics (ROC) curve, which is a trade-off between the proportion of correctly identified points (True positive rate) and incorrectly assigned points (False positive rate) regarding hyaena occurrence, as determined from the dataset.

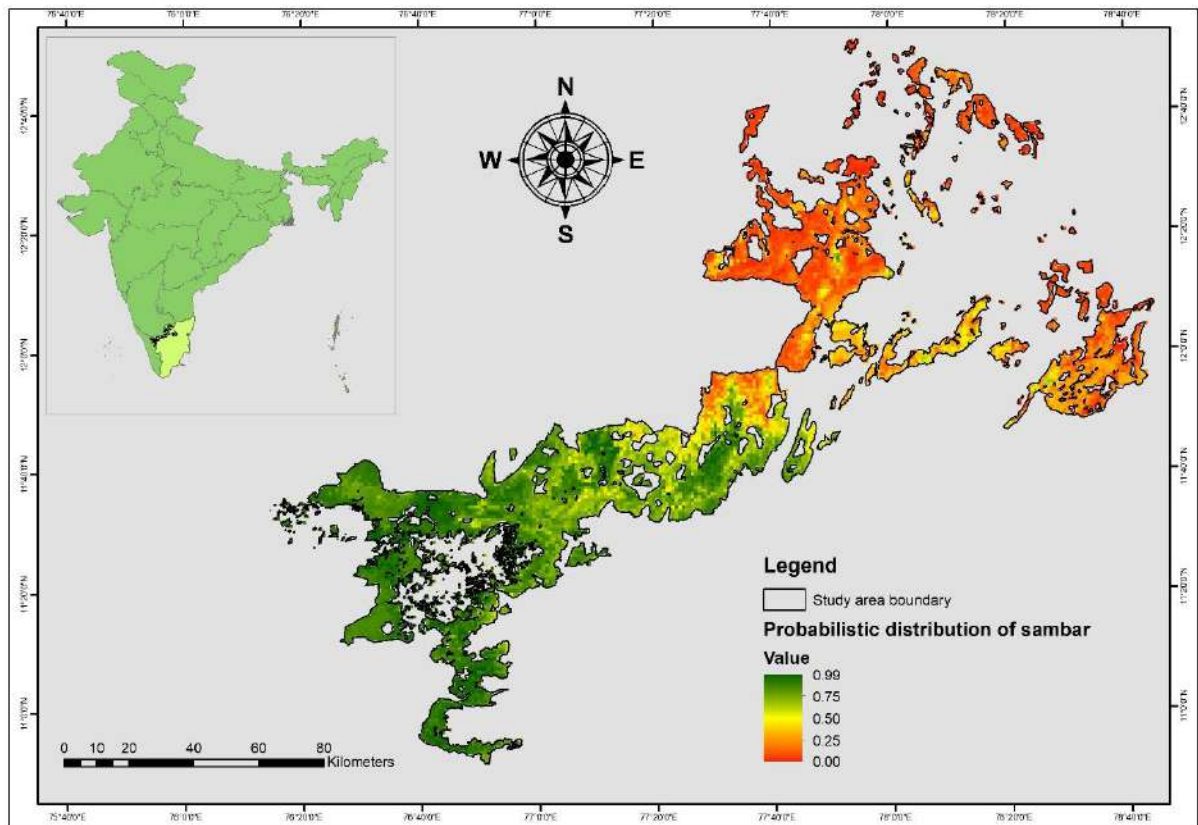


Figure S5.6 Predicted (probabilistic) distribution of sambar in the Western and Eastern Ghats part of Tamil Nadu.

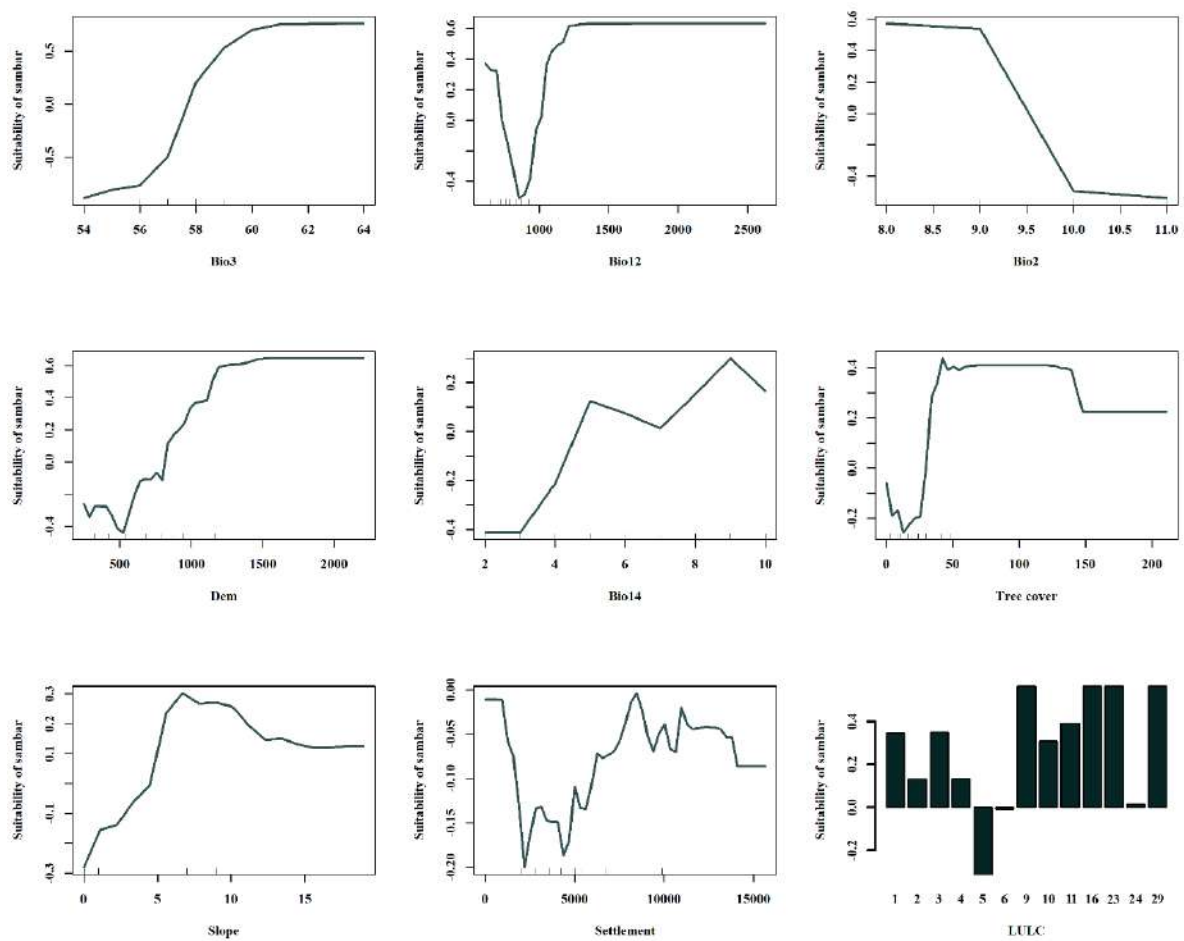


Figure S5.7 Partial dependency graphs of the nine most important variables show their effect on sambar occurrence. Here, the marginal effect refers to how changes in the value of a variable while keeping others constant affect sambar occurrence likelihood. These graphs depict changes in the likelihood of sambar occurrence as influenced by the most important variables, including: Dem = Elevation; Bio3 = Isothermality; Bio14 = Precipitation of the Driest Month; Bio12 = Annual Precipitation; Settlement = distance from settlements; and, Stream = distance from streams; LULC = land use/land cover.

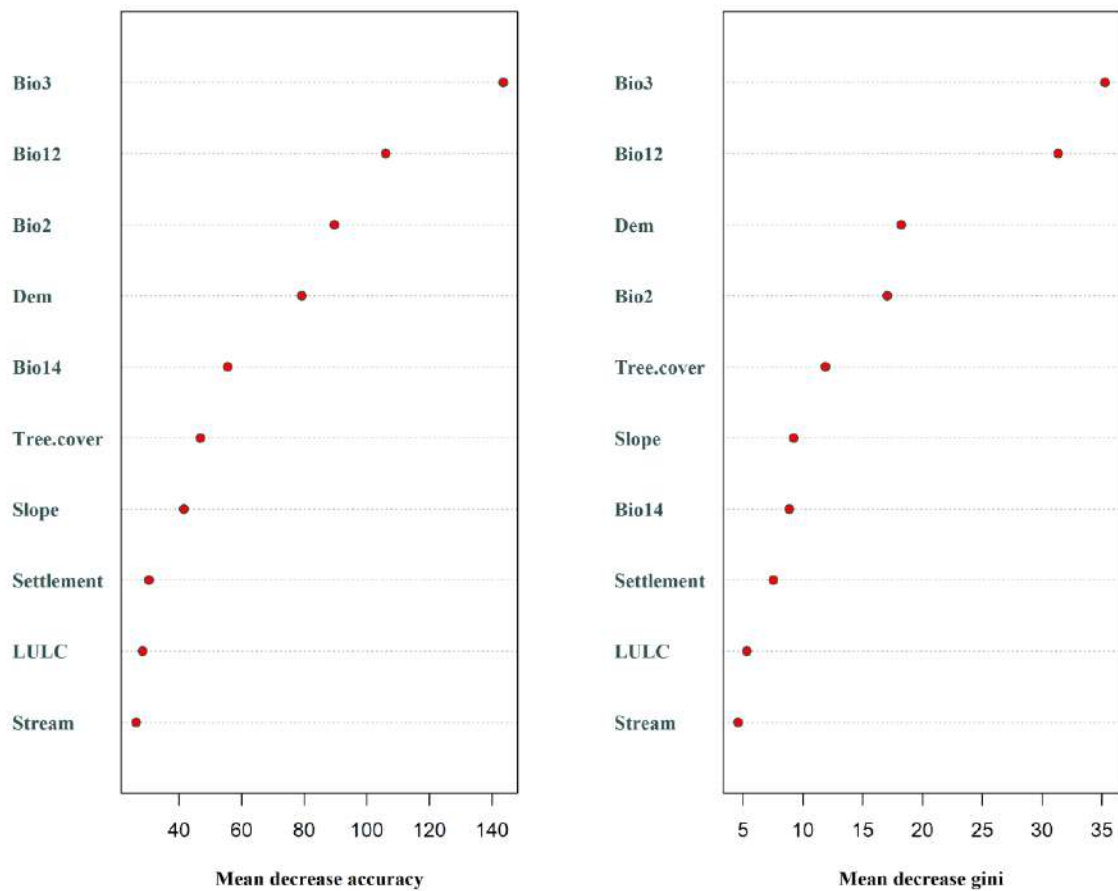


Figure S5.8 Variable relative importance graphs depict relevance of all explanatory variables influencing the occurrence probability of sambar. Mean decrease in accuracy (forest depth from node) and mean decrease in Gini Index are two different measures of random forest used to assess the importance of variable explaining the current distribution of the species; higher values for each indicates high relative importance for the model. (Dem = Elevation; Bio3 = Isothermality; Bio14 = Precipitation of Driest Month; Bio12 = Annual Precipitation; Settlement = distance from settlements; Stream = distance from streams; LULC = land use/land cover).

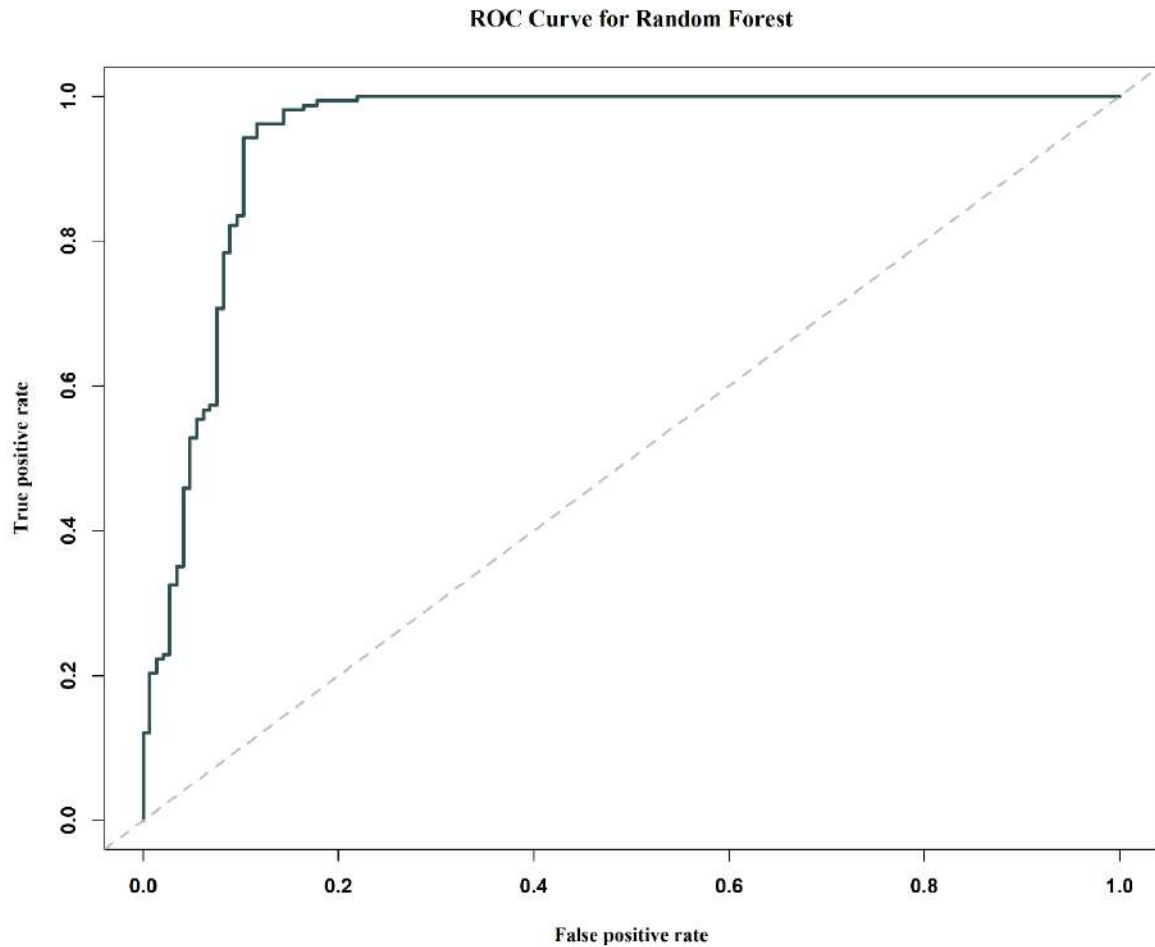


Figure S5.9 The accuracy of the calibrated model for sambar was checked by plotting the Receiver Operating Characteristics (ROC) curve, which is a trade-off between the proportion of correctly identified points (True positive rate) and incorrectly assigned points (False positive rate) regarding hyaena occurrence, as determined from the dataset.

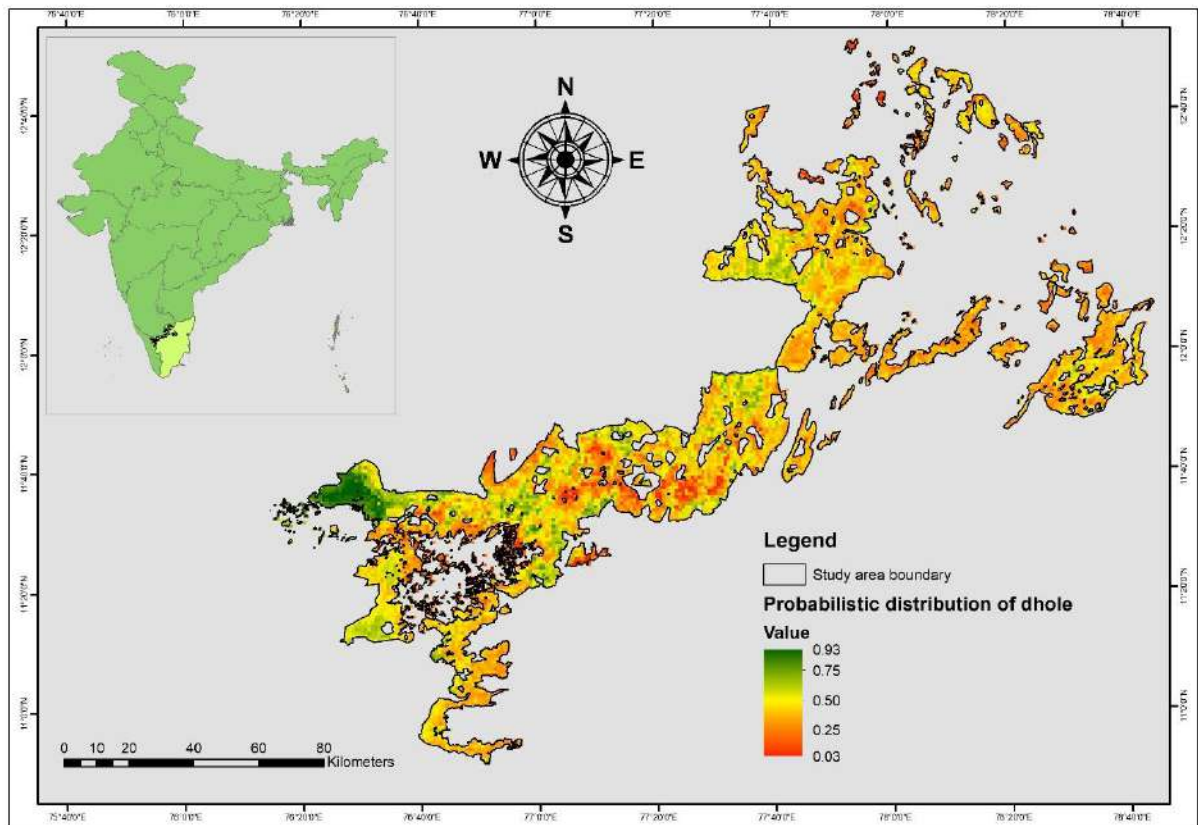


Figure S5.10 Predicted (probabilistic) distribution of dhole in the Western and Eastern Ghats part of Tamil Nadu.

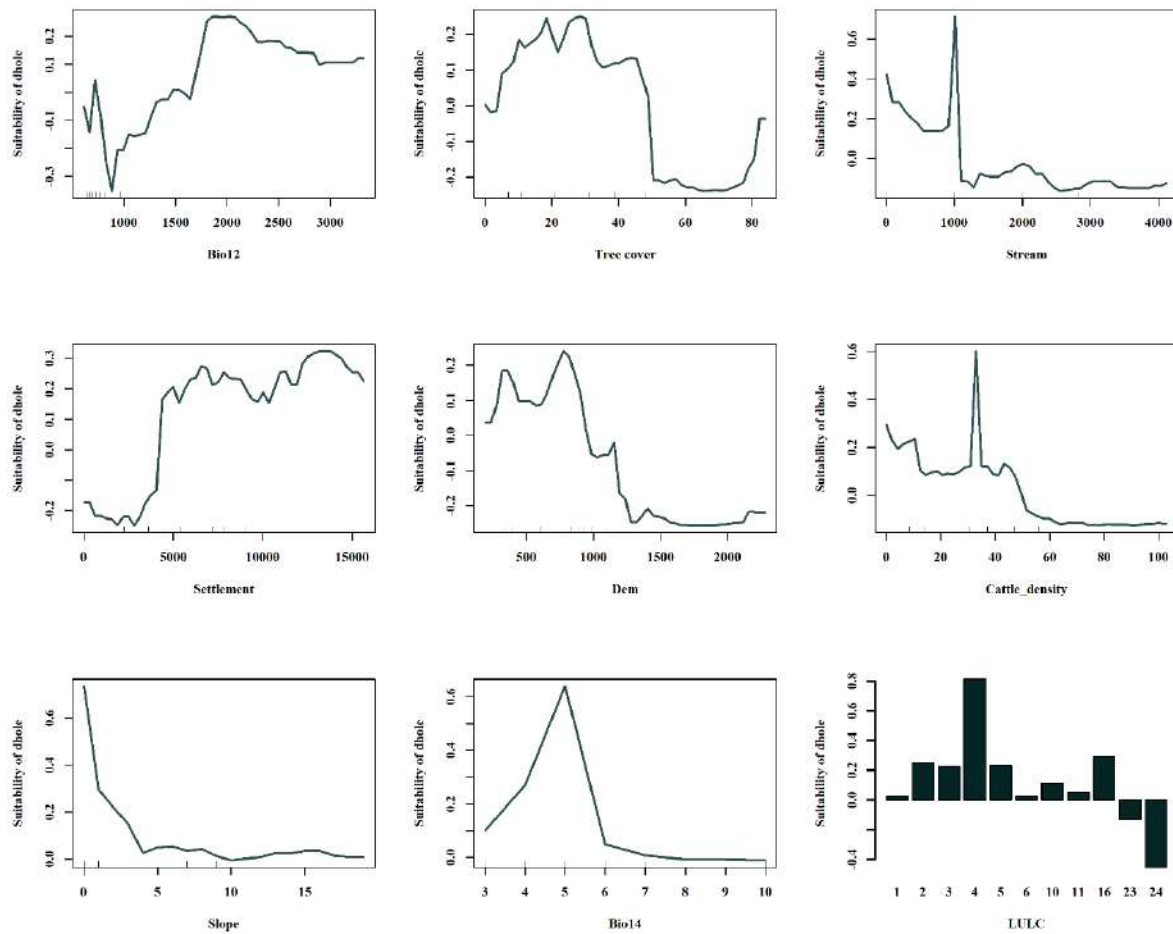


Figure S5.11 Partial dependency graphs of the nine most important variables show their effect on dhole occurrence. Here, the marginal effect refers to how changes in the value of a variable while keeping others constant affect dhole occurrence likelihood. These graphs depict changes in the likelihood of dhole occurrence as influenced by the most important variables, including: Dem = Elevation; Bio3 = Isothermality; Bio14 = Precipitation of the Driest Month; Bio12 = Annual Precipitation; Settlement = distance from settlements; and, Stream = distance from streams; LULC = land use/land cover.

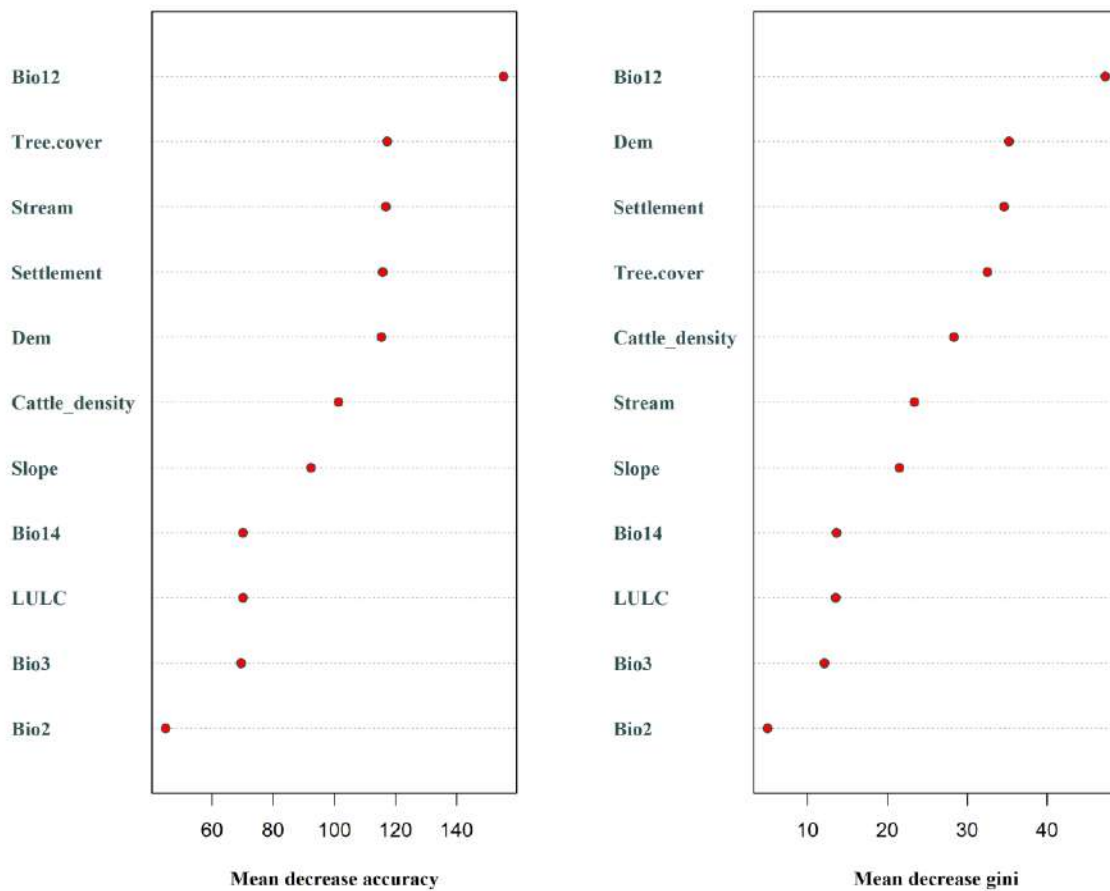


Figure S5.12 Variable relative importance graphs depict relevance of all explanatory variables influencing the occurrence probability of dhole. Mean decrease in accuracy (forest depth from node) and mean decrease in Gini Index are two different measures of random forest used to assess the importance of variable explaining the current distribution of the species; higher values for each indicates high relative importance for the model. (Dem = Elevation; Bio3 = Isothermality; Bio14 = Precipitation of Driest Month; Bio12 = Annual Precipitation; Settlement = distance from settlements; Stream = distance from streams; LULC = land use/land cover).

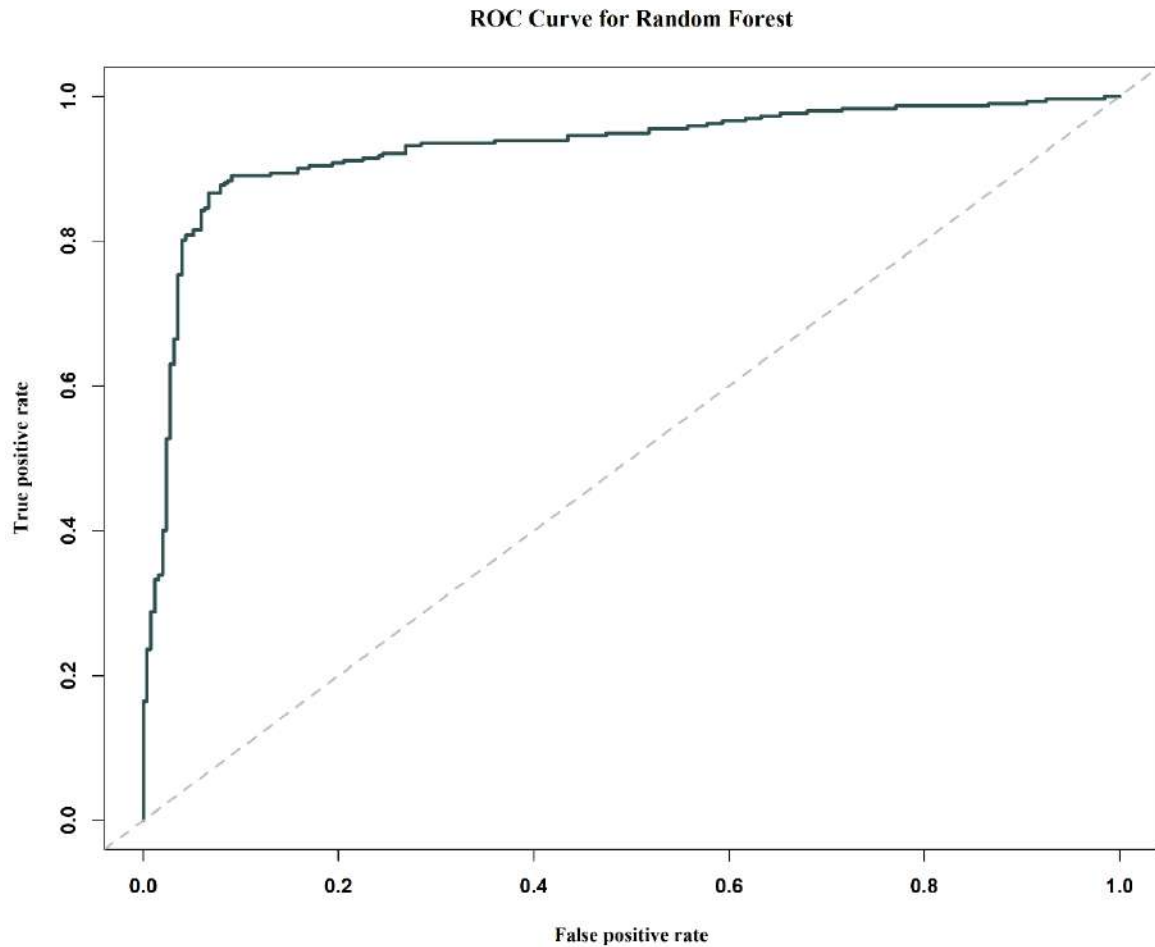


Figure S5.13 The accuracy of the calibrated model for dhole was checked by plotting the Receiver Operating Characteristics (ROC) curve, which is a trade-off between the proportion of correctly identified points (True positive rate) and incorrectly assigned points (False positive rate) regarding hyaena occurrence, as determined from the dataset.

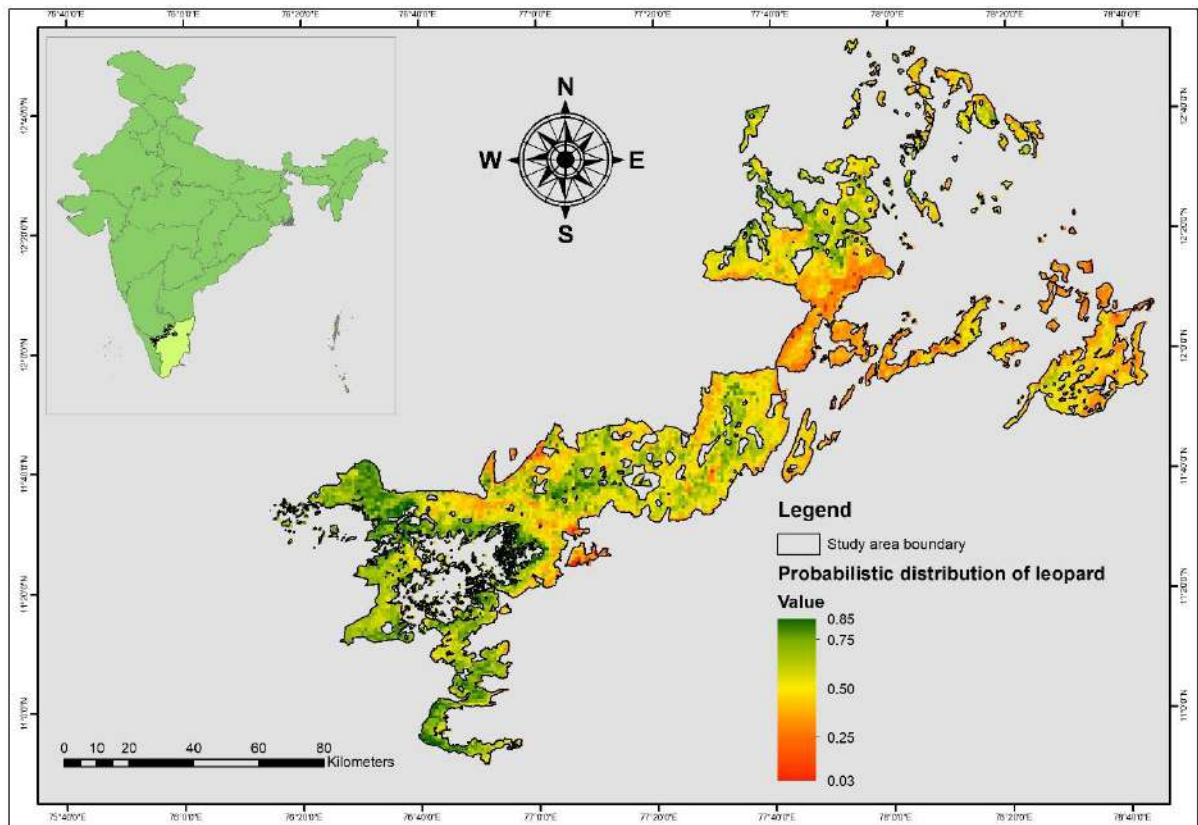


Figure S5.14 Predicted (probabilistic) distribution of leopard in the Western and Eastern Ghats part of Tamil Nadu.

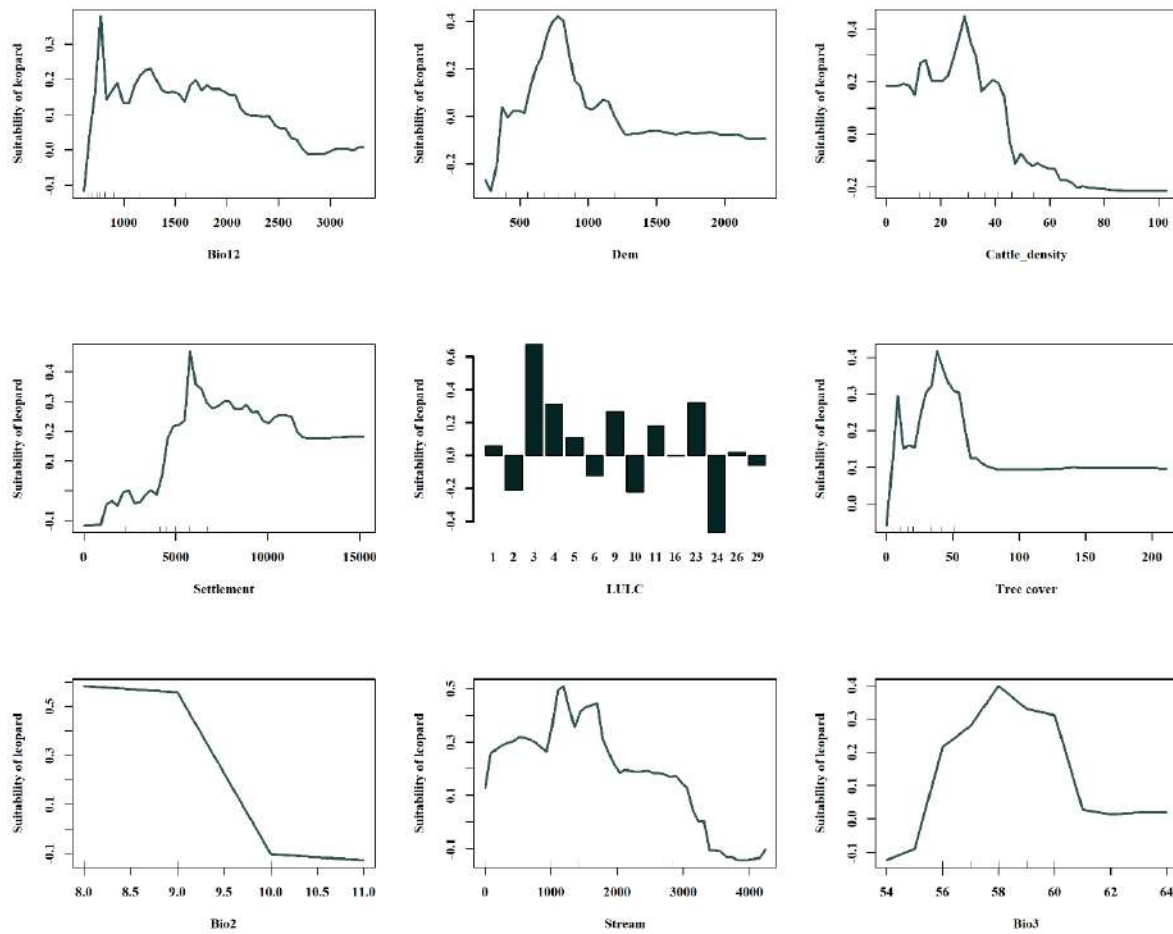


Figure S5.15 Partial dependency graphs of the nine most important variables show their effect on leopard occurrence. Here, the marginal effect refers to how changes in the value of a variable while keeping others constant affect leopard occurrence likelihood. These graphs depict changes in the likelihood of leopard occurrence as influenced by the most important variables, including: Dem = Elevation; Bio3 = Isothermality; Bio14 = Precipitation of the Driest Month; Bio12 = Annual Precipitation; Settlement = distance from settlements; and, Stream = distance from streams; LULC = land use/land cover.

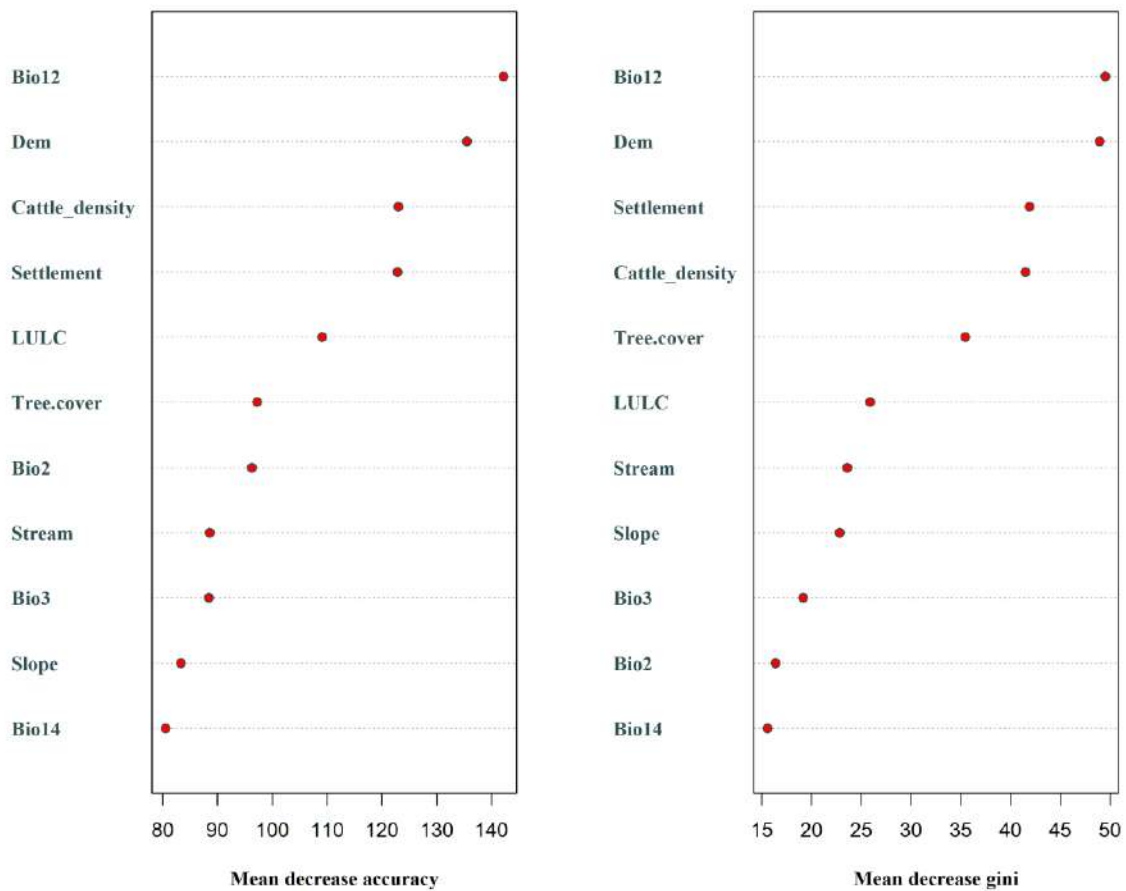


Figure S5.16 Variable relative importance graphs depict relevance of all explanatory variables influencing the occurrence probability of leopard. Mean decrease in accuracy (forest depth from node) and mean decrease in Gini Index are two different measures of random forest used to assess the importance of variable explaining the current distribution of the species; higher values for each indicates high relative importance for the model. (Dem = Elevation; Bio3 = Isothermality; Bio14 = Precipitation of Driest Month; Bio12 = Annual Precipitation; Settlement = distance from settlement; Stream = distance from stream; LULC = land use/ land cover).

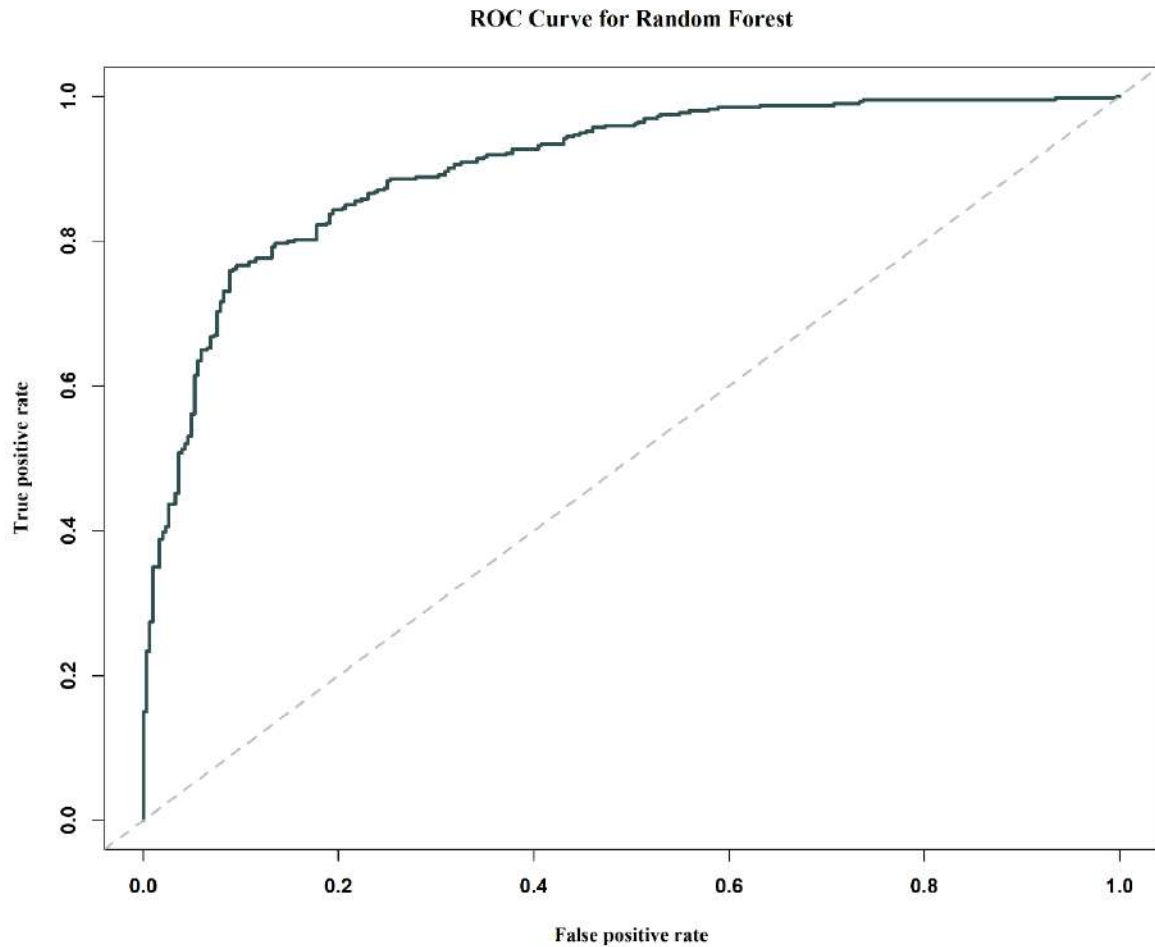


Figure S5.17 The accuracy of the calibrated model for leopard was checked by plotting the Receiver Operating Characteristics (ROC) curve, which is a trade-off between the proportion of correctly identified points (True positive rate) and incorrectly assigned points (False positive rate) regarding hyaena occurrence, as determined from the dataset.

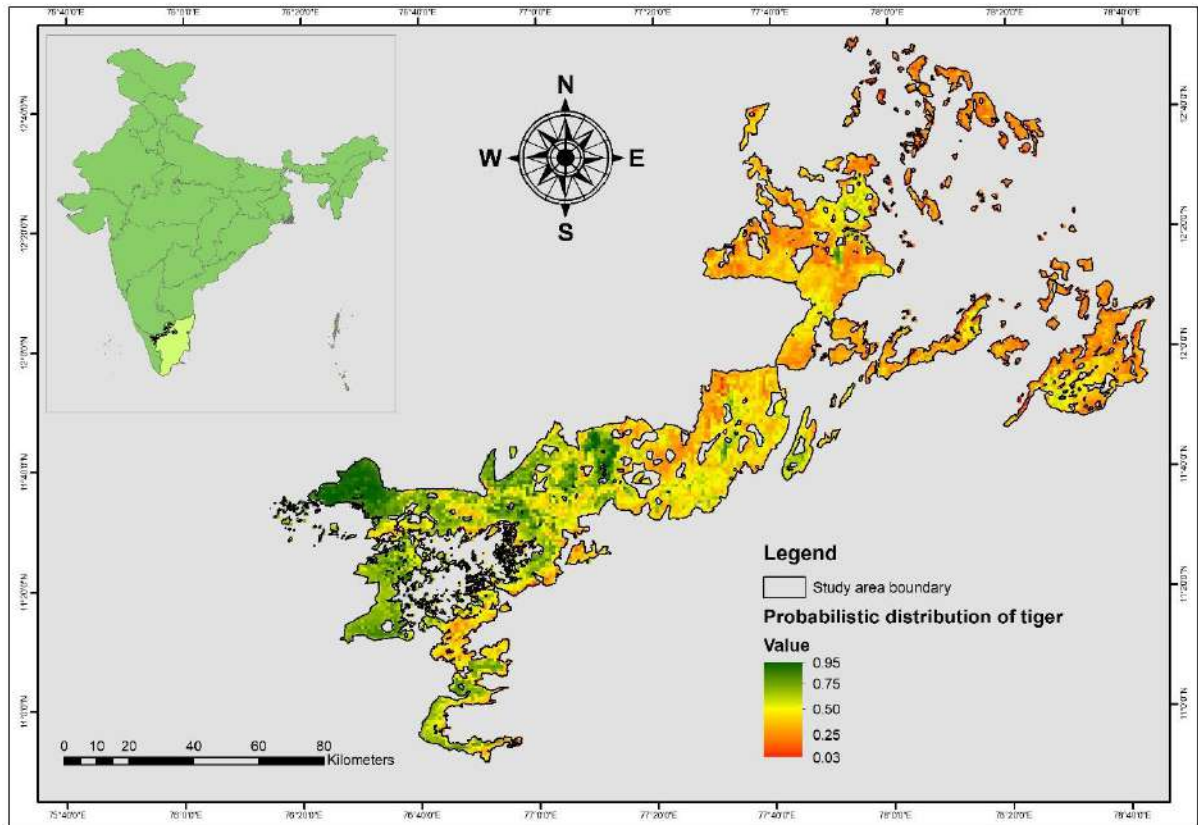


Figure S5.18 Predicted (probabilistic) distribution of tigers in the Western and Eastern Ghats part of Tamil Nadu.

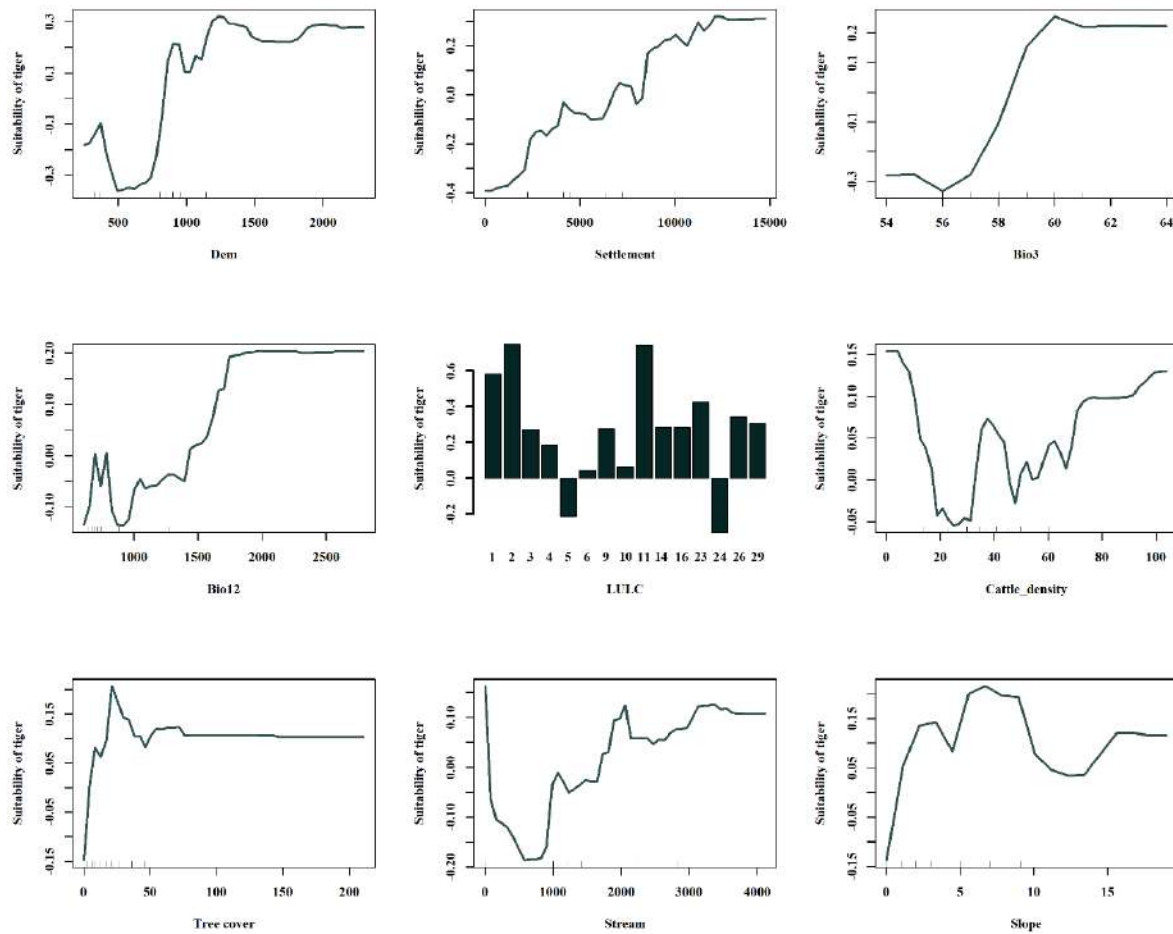


Figure S5.19 Partial dependency graphs of the nine most important variables show their effect on tiger occurrence. Here, the marginal effect refers to how changes in the value of a variable while keeping others constant affect tiger occurrence likelihood. These graphs depict changes in the likelihood of tiger occurrence as influenced by the most important variables, including: Dem = Elevation; Bio3 = Isothermality; Bio14 = Precipitation of the Driest Month; Bio12 = Annual Precipitation; Settlement = distance from settlements; and, Stream = distance from streams; LULC = land use/land cover.

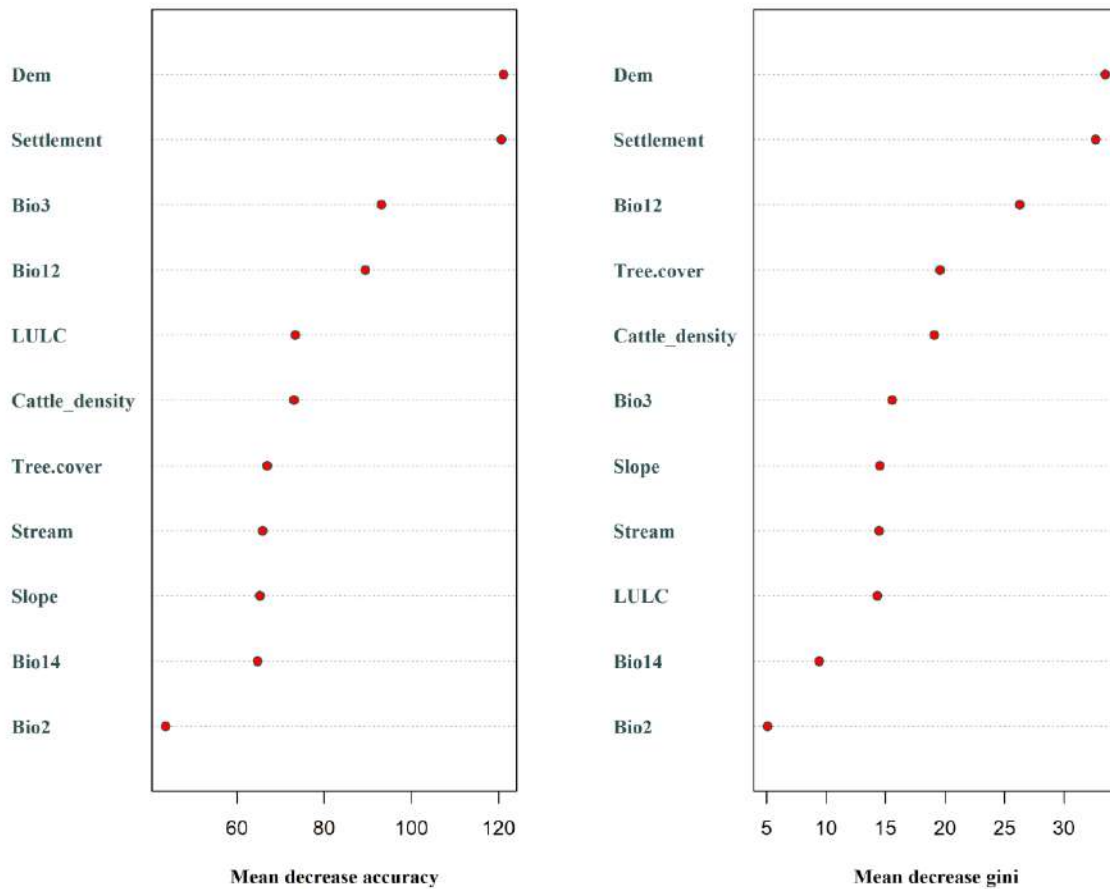


Figure S5.20 Variable relative importance graphs depict relevance of all explanatory variables influencing the occurrence probability of tiger. Mean decrease in accuracy (forest depth from node) and mean decrease in Gini Index are two different measures of random forest used to assess the importance of variable explaining the current distribution of the species; higher values for each indicates high relative importance for the model. (Dem = Elevation; Bio3 = Isothermality; Bio14 = Precipitation of Driest Month; Bio12 = Annual Precipitation; Settlement = distance from settlements; Stream = distance from streams; LULC = land use/land cover).

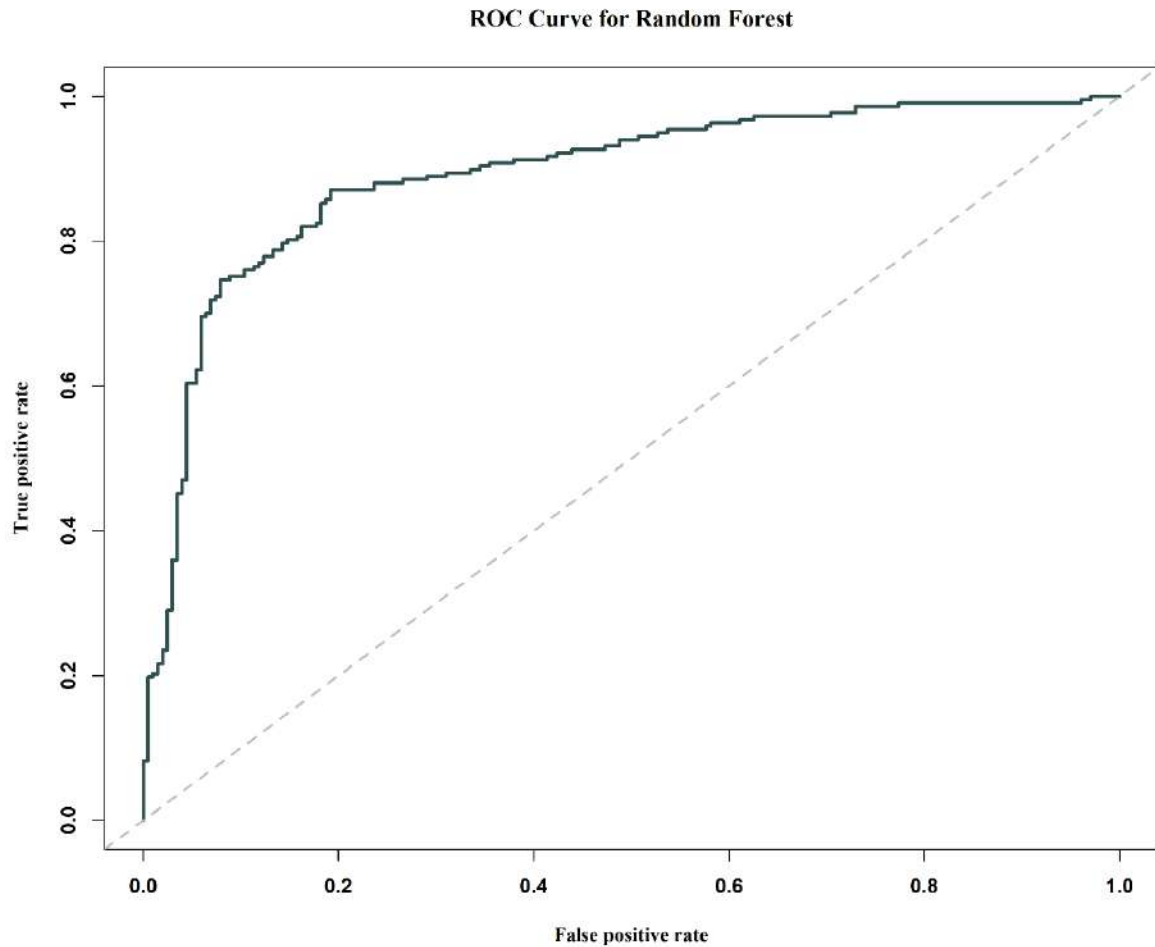


Figure S5.21 The accuracy of the calibrated model for tiger was checked by plotting the Receiver Operating Characteristics (ROC) curve, which is a trade-off between the proportion of correctly identified points (True positive rate) and incorrectly assigned points (False positive rate) regarding hyaena occurrence, as determined from the dataset.



Photo plate 1. Potential scrub habitat (a), exploring potential hyaena den sites like river bed (b) and hill slope (c), rocky habitat (d), researcher placing camera trap (e) and rockiness of mountain slope from where the cluster of 16 den located in the study area (f).



Photo plate 2. Mound occupied hyaena to raise their cubs (a), outcropped rock used as a den by hyaena (b), hyaena scat and hoarded bone at hyaena den site (c), accumulation of bones (d) and scats (e) at den site and researcher surveying stream habitat (f) in the study area.



Photo plate 3. Hyaena with pups at den site (a), a hyaena resting inside its den during day time (b), hyaena pups are resting outside their den during day time (c), hyaena carrying a carcass of a prey species (d), hyaena photo captured from a hyaena den (e) and Camera trap photo showing three hyaenas in the potential habitat (f) in the study area.

Publications

Publications

- **Ashish, K., Ramesh, T., Kalle, R., & Arumugam, R. (2022).** *Generalization of threats attributed to large carnivores in areas of high human–wildlife conflict.* *Conservation Biology*, 36(5), e13974.
- **Ashish, K., Ramesh, T., & Kalle, R. (2022).** *Striped hyaena den site selection in Nilgiri Biosphere Reserve, India.* *Journal of Tropical Ecology*, 38(6), 472-479.
- **Ashish, K., Ramesh, T., Kalle, R., & Giordano, A. J. (2024).** *Spatial heterogeneity facilitates coexistence between striped hyaenas and sympatric carnivores.* *Journal of Biogeography*, 51(2), 173-184.

Conference Proceedings

- **Ashish, K., Ramesh, T., Kalle, R., and Arumugam, R. (2021).** *High human-carnivore conflict, a precursor to daunting generalization thwarts the hyaena conservation in southern India.* *International Congress for Conservation Biology (ICCB) held Virtually, Rwanda, from 13-17 December 2021 and organised by Society for Conservation Biology's (SCB), Washington DC. USA.*
- **Ashish, K. (2023)** *An integrated modelling framework to guide species reintroductions amidst anthropogenic and climate changes.* *14th International Conference for Prospective Leaders in Climate Protection and climate-related Resource Conservation, Humboldt, Germany.*
- **Ashish, K., Ramesh, T., Kalle, R., Arumugam, R. (2023).** *Decision trees based cognitive models are efficient tools to assess the vulnerability of a non-inimical species prone to the threats of overgeneralization.* *Behaviour 2023, Bielefeld University, Germany (Oral presentation).*
- **Ashish, K., Ramesh, T., Kalle, R., & Giordano, A. J. (2023).** *Judicious space overlap, a co-existing mechanism of striped hyaena in a large carnivore conservation landscape.* *Young Scientist Conference, India International Science Festival 2023, Bhopal, India.*

CONTRIBUTED PAPERS

Generalization of threats attributed to large carnivores in areas of high human–wildlife conflict

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Article impact statement: Economic stress and high levels of human–carnivore conflict jeopardize conservation of lesser-known species

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Abstract

Fear-induced generalization of threats to noninimical stimuli is a behavioral tendency of humans to minimize exposure to potential threats. In human–carnivore conflict zones, people often generalize their fear of predation by obligate carnivores to nonobligate carnivores despite differences in species' predation rates. We investigated the effect of a perceived threat of large obligate carnivores to livestock on tolerance and perception of striped hyena (*Hyaena hyaena*) in an area of high human–carnivore conflict. We surveyed 197 households through a semistructured questionnaire to determine people's perception and tolerance of striped hyenas in Sathyamangalam and Mudumalai Tiger Reserves after identification of the current distribution range of hyena determined through camera trap and sign surveys. Through the random forest algorithm, we modeled the level of tolerance of striped hyena as a function of loss of livestock to predation and from disease, the perceived threat of predation by hyena, and other socioeconomic attributes. Animal husbandry was a major source of income but was severely affected by livestock loss due to predation and disease. Sixty-nine percent of people were uncertain about predatory behavior of hyena; out of that, 23% reported a negative conservation attitude. Only 6 instances of hyena depredation on livestock and 2 on dogs were reported. Our model confirmed that economic instability associated with increased loss to predation and disease, livestock dependency, and a decrease in family annual income negatively affected people's tolerance of hyena. Perceptual uncertainty related to predatory behavior of hyena also negatively affected people's tolerance. In our study area, economic instability and perceptual uncertainty led to generalization of fear of large carnivores to a nonobligate predator. Such generalization may affect the attitude of people toward many other species. Understanding the role of economic instability and perceptual uncertainty should facilitate conservation of species, such as the hyena, that are vulnerable to false generalization.

KEYWORDS

false memory, generalization, human–carnivore conflict, hyena, livestock predation, random forest, tolerance

Generalización de las Amenazas Atribuidas a los Grandes Carnívoros en las Áreas con un Elevado Conflicto Humano-Fauna

Resumen: La generalización de las amenazas inducidas por el miedo a los estímulos no desfavorables es una tendencia del comportamiento humano para minimizar la exposición ante las amenazas potenciales. En las zonas de conflicto humano-carnívoros, las personas transfieren con frecuencia su miedo a los carnívoros obligados hacia los no obligados a pesar de las diferencias en las tasas de depredación de las especies. Investigamos el efecto de la amenaza percibida que representan los grandes carnívoros obligados para el ganado sobre la tolerancia a y la percepción de la hiena rayada (*Hyaena hyaena*) en un área con

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Research Article

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Striped hyaena den site selection in Nilgiri Biosphere Reserve, India

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Abstract

The den is a multi-purpose critical space of carnivores and provides a growth conducive refuge which ensures both substances and protection from interspecific predation and harsh climate. Selection of optimal den sites determined by various site-specific factors potentially reduces aversive interspecific interactions and provides cost-effective access to food sources. In this study, we have assessed the factors determining the den site selection by a small population of striped hyaena, *Hyaena hyaena* in a shared landscape dominated by large carnivores. We assessed den site selection as a function of vegetation patch characteristics, site-specific anthropogenic threats/activities and topographical variables using Bayesian algorithm through field collected binomial data on den use by the species. Our model suggested that hyaenas select rocky refugia surrounded by trees and tall grasses, situated on mountain slopes proximate to a water body. Our study consolidated the importance of undulating terrain in the species ecology and postulated the slope as an 'energy-expensive' terrain that refrains frequent movement of other carnivores, in turn providing more affordable denning space for the striped hyaena. This study provides critical information on denning ecology of last remaining major breeding population striped hyaena of southern India.

Introduction

Altricial species have appropriate different physiological and behavioural mechanisms to offset their early postnatal limitations and to enhance reproductive success (Bosque & Bosque 1995; Gilbert *et al.* 2007; Geiser *et al.* 2019). That include both biological and selection of external habitats that protect fragile young from adverse climate and predation and ensure nutritional requirements for the development of motor coordination (Case 1978; Wolff & Peterson 1998; Kinlaw 1999). Denning is a behavioural mechanism used by most carnivores (Caro 1994), providing safe and 'growth conducive' refugia to relatively undeveloped young ones (Boydston *et al.* 2006; Paul *et al.* 2014). Interspecific competition is reported to cause high mortality of young in some species (Mills 1993; Mills & Mills 2014). Therefore, carnivores select dens in or close to their optimum habitat abundant in food resources, water bodies and relatively free from anthropogenic disturbances (Nurvianto *et al.* 2015; Majumder *et al.* 2016; Moehlman 2019). However, den site selection is predominantly determined by den availability and site-specific attributes like slope and vegetation cover that reduce detection probability of den.

Burrows and rocky refugia are the two major den forms known to be inhabited by carnivores (Caro 1994; Alam 2011). Animals occupy rocky regions of different forms like beneath out-cropped rocks, under a large boulder/mound, in rock crevices, or caves. Though rock dens refugia are reported to be preferred by many animals (Akram & Ilyas 2017), selection may depend on their availability, placement, season, animal ecology and intended use (Endres & Smith 1993; Griesemer *et al.* 1998). Carnivores are either primary excavators or occupy rocky refugia (rock den) or burrows dug by other species. These refugia are not only footholds for young but also resting sites for adults (Prestrud 1992; Chourasia *et al.* 2020). Although significant differences in the micro-habitat conditions between natal and resting sites have been reported in many studies (Pruss 1999; Mukherjee *et al.* 2018; Chourasia *et al.* 2020). Slope and vegetation cover either in the form of shrub, canopy or grass cover are key determinants in the placement of natal dens for most carnivore species. Multiple and narrow den openings are other characteristics observed in natal den to evade intra-guild predation (Frafjord 2003).

The striped hyaena, *Hyaena hyaena*, is a carnivore and predominantly a scavenger by its feeding habit. The species has a wide distributional range which includes the Middle East, Caucasus region, Central Asia and the Indian subcontinent, with their southern and western limits in Africa (Mills & Hofer 1998; AbiSaid & Dloniak 2015; Bhandari & Chalise 2016; Bhandari *et al.* 2021). Historically, the species was widely distributed in India but has experienced a steep population decline probably because of poisoning, competition from co-existing

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Spatial heterogeneity facilitates coexistence between striped hyaenas and sympatric carnivores

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Abstract

Aim: Interspecific competition plays a key role in shaping carnivore communities. Top-down effects can impact the coexistence of superordinate and subordinate competitors and prey across a shared landscape. Limited resources, their abundance and diminishing habitats can all exacerbate interspecific competition. Sometimes, behavioural mechanisms or adaptations are critical for subordinate carnivores to coexist with larger species. Here, we investigated the distribution pattern of the striped hyaena (*Hyaena hyaena*) population with respect to habitat features, sympatric carnivores and their prey species across a large landscape.

Location: Western and Eastern Ghats, India.

Taxon: Striped hyaena.

Methods: We collected presence-absence data for hyaenas, tigers, leopards, dholes and their prey using camera-trapping and indirect sign surveys. Using a random forest algorithm, we modelled the local distribution of hyaenas as a function of important ecological variables, including climate, domestic prey abundance and the predicted probabilities of occurrence of other large carnivores and their prey.

Results: We found that striped hyaenas were confined to relatively small, discrete areas compared to the three other predators, likely a mechanism for achieving coexistence in the landscape. Our empirical results suggested that hyaenas tend to avoid high occurrence probability areas of their co-predators at a landscape level but foothold opportunities such as, arid climatic conditions, and prey abundance primarily determined spatial incumbency. Coexistence in an area with low to medium relative abundance of co-predators offsets the interplay between carcass acquisition and risk associated. The coexistence of species was favoured by altitudinal heterogeneity probably providing denning refugia and also by their preference towards suboptimal thorn forests that sustain a low density of co-predators.

Main Conclusions: Our study showed a desisting impact of large predators on the distribution of the striped hyaena population. Furthermore, we suggest preventing habitat alteration in suboptimal habitats of large carnivores to facilitate coexistence in a shared landscape.



Alexander von
HUMBOLDT
STIFTUNG

CERTIFICATE OF PARTICIPATION

This is to certify that

Ashish Kumar

gave a presentation and played an active role in the:
14th International Conference for Prospective Leaders in Climate Protection and climate-related Resource
Conservation (held as Online conference)

“Global Climate Change – Approaches to International Collaboration”

at the invitation of the Alexander von Humboldt Foundation in Bonn.

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This is to certify that Dr./Mr./Mrs/Ms. **Ashish Kumar** has participated in Young Scientist Conference of IISF 2022 held at Maulana Azad National Institute of Technology (MANIT), Bhopal during January 22-24, 2023 and presented his/her work entitled "*Judicious space overlap, a coexisting mechanism of striped hyaena in a large carnivore conservation land scape*" through poster presentation under the theme **Biodiversity, Environment and Climate Change**.



(Dr. Jajati Kesari Nayak)
Coordinator, Young Scientist Conference

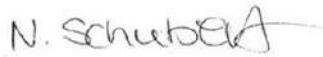
CERTIFICATE OF ATTENDANCE

Ashish Kumar

has attended Behaviour 2023 at Bielefeld University, Germany.

We are grateful for Ashish Kumar's participation in the congress and the oral presentation with the title "Decision trees based cognitive models are efficient tools to assess the vulnerability of a non-inimical species prone to the threats of overgeneralization."

Bielefeld, August 2023



Nadine Schubert,
Conference organisation

