UNGULATES MEDIATED EFFECTS ON VEGETATION STRUCTURE AND BIOMASS IN PANNA TIGER RESERVE, CENTRAL INDIA

Thesis submitted for the award of the degree of

DOCTOR OF PHILOSOPHY

in

WILDLIFE SCIENCE

by

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to

Saurashtra University, Rajkot – 360005 (Gujarat)

under the supervision of

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I certify that the research work was appreciated by all who were present, and the comments made by the faculty and researchers have been appropriately included in the thesis.

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DECLARATION

I hereby declare that the work conducted under the thesis entitled "**Ungulates mediated effects on vegetation structure and biomass in Panna Tiger Reserve, central India**", is a record of original work, done by me and subsequently submitted for the degree of Doctor of Philosophy in Wildlife Science to Saurashtra University, Rajkot, Gujarat. This research work has been carried out under the guidance and supervision of Dr. K. Ramesh, Scientist-F and co-supervision of Dr. G. S. Rawat, Former Dean, Wildlife Institute of India, Dehradun. The work has not formed the basis for the award of any other degree, diploma or any other qualification. I also declare that the thesis embodies my own work, analysis, observation and understanding and the particulars given in it are true to the best of my knowledge.

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CERTIFICATE

This is to certify that the thesis by Ms. Deepti Gupta entitled "**Ungulates mediated effects on vegetation structure and biomass in Panna Tiger Reserve, central India**" is an original and independent research work submitted to the **Saurashtra University, Rajkot, Gujarat**, for the award of the degree of **Doctor of Philosophy** in **Wildlife Science**.

Ms. Deepti Gupta has put more than six semester of research work embodied in this thesis under my guidance and supervision. The work presented in this thesis has not been submitted to any other university or institute for the award of any degree, diploma or distinction.

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Gupta, D. & Krishnamurthy, R. (2023). Spatial density patterns of herbivore response to seasonal dynamics in the tropical deciduous forest of central India. *Biotropica*: 1-14.; https://doi.org/10.1111/btp.13197

B) Conferences

1. National conference

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2. International conference

Gupta D., Ramesh K., Rawat, G. S., 2019. Effects of dominance and richness of tree species on biomass in the tropical dry deciduous forests of central India. Presented at Association for Tropical Biology and Conservation, Asia-Pacific conference 2019 held at Srilanka from 10th – 13th September 2019.

Gupta D., Ramesh K., 2020. Seasonal influence on abundance distribution of Ungulates in dry deciduous forest of central India. Presented at Festival of Ecology, British Ecological Society held online from 14th to 18th December 2020.

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EXECUTIVE SUMMARY

Ungulates play an important role in shaping the plant community structure, species richness and distribution through herbivory, seed dispersal, trampling and adding nutrient to the soil. They also act as important component of food chain, and hence their abundance and distribution are directly related to the large carnivore survival. Distribution of ungulates is strongly influenced by plant phenology, spatial heterogeneity of the forage plants and seasonal rhythm. The tropical dry deciduous forest of central India experience a brief period of growth during monsoon after a very long dry season of around six months. The strong seasonality of dry deciduous forests leads to seasonal variation in the phenology of different plant species, and consequently, resources become sparsely distributed in space and time. Seasonal variation in soil moisture, temperature, nutrients and other factors leads to dynamism in vegetation and habitat conditions which drives ungulates to make their preferences across habitats.

Ungulates not only make choices across the habitats, but by feeding selectively on preferred species they also affect the recruitment, regeneration and survival of the floral species. However, the direction of these interactions has been debated over half a century, whether these ecosystem processes are controlled by top-down effect where ungulates abundance and distribution are regulated by intra-species competition and predation or by bottom-up effect where vegetation parameters regulate ungulates abundance through structural and chemical (anti-herbivory) mechanisms.

Ungulates having different body sizes, habitat preferences, and anti-predator strategies might show a range of responses to the vegetation structure and composition (tree density, basal area and species richness), habitat parameters (terrain complexity, water availability and slope) and anthropogenic pressure (cattle abundance and human proximity). Ungulates in tropical dry deciduous forests have been majorly studied as primary prey to large carnivores. Their yearly population status across habitats and their preference for the habitat and forage have been

studied the most in various landscapes. However, there have been only a few studies describing ungulates' response to the vegetation, habitat and anthropogenic pressure driving their distribution in space and time, especially in tropical dry deciduous forests where ungulates are found in high diversity and abundance.

Historically, wild ungulates were widely distributed in India, which are now restricted to the protected areas, facing severe threats due to livestock grazing, habitat fragmentation and other anthropogenic pressure. Livestock abundance, secondary forest formations and variable climatic conditions broadly influence ungulates' interaction with vegetation in dry deciduous forests. Based on the aforementioned information, I chose dry deciduous forest of central India, Panna Tiger Reserve.

Panna Tiger Reserve (PTR), situated in the Vindhyan mountain ranges in Madhya Pradesh, central India, between 24°27′N to 24°46′N latitude and 79°45′E to 80°09′E longitude. PTR is uniquely characterized by its 'terraced topography' and presents two tabletop mountains and a valley formed by the Ken River. The study area can be divided into the upper plateau, middle plateau, and river valley. PTR is primarily dependent on monsoon rainfall from July–September. The average annual rainfall is approximately 1100 mm, but the area is known for its poor water retention capacity. Most monsoonal water percolates down to the valley quickly, leaving plateaus dry. Following the monsoon is the winter season from November-February, when the minimum temperature drops to 5°C, followed by dry summer in April-June when the maximum temperature often exceeds 45°C. Three distinct seasons and topographic features in PTR provide a unique setup to study the ungulate–habitat interaction.

For this study, I chose four ungulates species having different habitat preferences, dietary requirements and body size viz., sambar (primarily a browser), chital (primarily a grazer), Nilgai (mixed feeder) and wild pig (omnivorous).

Sambar is a large-sized ungulate categorized as vulnerable in the IUCN red list. Sambar occurs in small groups. The species prefers hilly terrain and densely forested habitats. Sambar show variation in seasonal ranges in response to forage availability, temperature and breeding opportunity. It is primarily a browser in winter and summer but shifts to green grasses during monsoon. The remaining three study species of ungulates are of the least concern as per IUCN red list. Chital, an endemic cervid of south Asia, is a species of grassland-forest interface and is considered an ecotone species. Chital is a group-living species that use more wooded habitats during winter and early summer and moves in large herds to open grasslands in monsoon in response to forage availability. It is primarily a grazer, but browses are also consumed in summer.

Nilgai, the largest antelope in south Asia, is a mixed feeder primarily found in open habitats with flat and undulating terrains. It prefers grasses during monsoon. Nilgai is a partly social animal and does not often occur in large groups. Its population status is stable in India. Indian wild pig is widely distributed throughout India. Wild pigs are omnivorous, show a seasonal diet shift, and mainly depend on water availability. They are not obligatory group-living species and sometimes congregate in large groups. Their seasonal shifts in the diet are dictated by the forage availability. All four ungulate species are important prey of large carnivores such as tigers and leopards and are directly related to the conservation of large predator populations. Based on the above information, I formulate three research objectives as follows:

1. To determine the vegetation structure and composition and quantify the above-ground biomass
2. To estimate the density of ungulates across space and seasons.
3. To model the ungulates-habitat relationships and related functional responses.

Chapter: Vegetation structure and community composition

In this chapter, I assessed the structure and composition of woody vegetation (tree layer) in PTR. I also evaluated tree community composition and described the dominant, co-dominant and associated tree species of a community. For this, I sampled 10m X 10m quadrates along 66 line transects (minimum one in each beat). A total of 450 vegetation plots were sampled during 2016 – 2017, and trees >10 cm GBH (Girth at Breast Height) were measured for their GBH, tree height, number of species and individuals in a plot with species identification. Tree volume was calculated using species and region-specific allometric equations generated by FSI. Tree biomass was then calculated as a function of tree volume and wood density. To find out the present tree communities and their dominant and associated species, I used the divisive hierarchical technique Two Way INdicator SPecies ANalysis (TWINSPAN) in program R with the help of "TwinspanR" package.

A total of 49 species of adults, 36 species of saplings and 37 species of seedlings were recorded during the sampling. *Tectona grandis* was the most abundant species covering 27% of the total population and 18% of the total tree biomass. Seven key tree associations were assessed:

1. *Tectona grandis* mixed forest (n=174, eigenvalue=0.342)
2. *Acacia catechu* mixed forest (n=62, eigenvalue=0.389)
3. *Anogeissus pendula* forest (n=22, eigenvalue=0.489)
4. *Tectona grandis* forest (n=56, eigenvalue=0.342)
5. *Ziziphus xylopyrus* forest (n=51, eigenvalue=0.389)
6. Acacia donaldii mixed forest (n= 15, eigenvalue = 0.489)
7. Ziziphus mauritiana dominated forest (n=7, eigenvalue = 0.672)

The most dominant tree community was *T. grandis* mixed forest. *T. grandis* mixed forest patches were found densely occupied with the highest recorded tree density (997 individuals/ha), basal area (19 m^2/ha) and AGB (73.94 ton/ha). This community appears as a

heterogenous stand. *A. catechu* mixed forest in association with *A. latifolia*, *T. grandis* and *Z. xylopyrus*. *A. catechu* mixed forest also appeared as a heterogeneous forest patch. *A. pendula* forest and *T. grandis* forest were dominated by the *A. pendula* and *T. grandis,* respectively. They both appeared as a homogenous forest patch. Data was compiled from remaining three communities as open woodland due to their similarity in appearance and associated species. Open woodland is represented by small-sized trees. I found four forest types in this study consistent with the classification provided by Champion & Seth (1968) for this region. Of the six forest types, *Boswellia serrata* forest and dry Bamboo brakes have been described as the dominant forest types in earlier classifications (Champion & Seth, 1968; Meher-Homji, 2001). Both species were not found as the dominant tree species in the study area (PTR core). This chapter describes five dominant plant communities with their attributes (basal area, volume and biomass) to understand the structure and function of a species in a community.

Chapter: Seasonal distribution of ungulates

This chapter hypothesizes that ungulate distribution should vary in response to resource availability across seasons. Therefore, I sought to identify seasonal distribution patterns and establish the relationship with habitat variables of four species of ungulates that could affect the distribution across two seasons. I also calculated and mapped uncertainties in the results to ensure the robustness of spatial maps. For this, I walked 66 line transects in four sampling seasons; two winters and two summers. The total survey effort for all species in summer was 356 km and in winter was 518 km. I used two geographic covariates consisting of the Digital Elevation Model (DEM) and Terrain Ruggedness Index (TRI); two habitat parameters consisting of distance to water source (water) and Normalised Difference Vegetation Index (NDVI), and two parameters for anthropogenic influence consisting of distance from the settlements (settlement) and distance from the agricultural fields (agriculture) to model the distribution of all ungulates. I used count per segment as a response variable in Density Surface

Modelling framework, which was modelled given habitat variables using the Generalized Additive Modelling (GAM) approach. Response distribution obtained from DSM was then used to predict density over the whole study area with 200m X 200m prediction cells.

Sambar showed a relationship with NDVI, elevation and distance from the agricultural fields. Chital distribution was influenced by NDVI, elevation and distance from the settlements, whereas Nilgai showed relationship with elevation, water availability and distance from agriculture and settlements. Wild pig showed relationship with NDVI, water availability and terrain ruggedness. For cattle, two anthropogenic variables (distance from the settlements and agriculture) were compiled into one; distance from the forest edge. Cattle abundance was found to be high in the proximity of the forest edge and flat terrain. I also found that season significantly affected the spatial densities of all ungulates, with sambar, chital and nilgai congregating in summer and wild pig in winter. All ungulates showed a clear seasonal shift to the valley in summer and preferred plateaus in winter. The spatially explicit map outputs draw attention to the seasonal hot spots for ungulates abundance and the species and season-specific roles of environment variables in defining their distribution. These results would improve understanding of the species' response to the environmental variables, direct species conservation efforts to the priority areas and reduce the cost of management actions by allocating them to specific habitats.

Chapter: Ungulate – habitat interaction

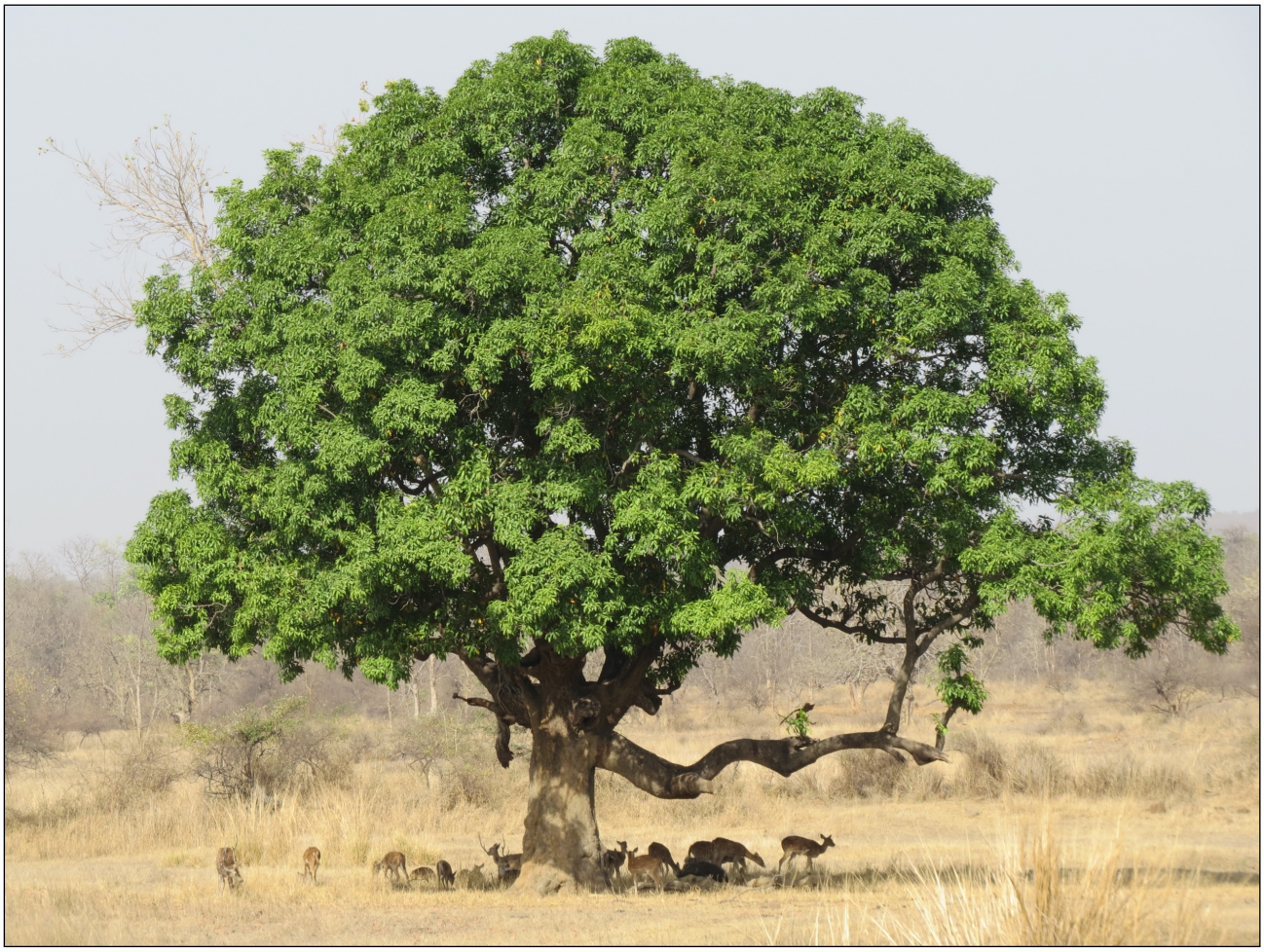
In this chapter, I investigated ungulates' interaction with vegetation parameters such as tree density, basal area, tree species richness, *Lantana* abundance and livestock grazing. For this, I sampled 1m X 1m plots along the line transects to harvest grasses. Seedlings were counted in 5m X 5m plots along the line transect. Grasses were oven dried and weighed for the grass biomass. A palatability list of all the flora was prepared for all four ungulate species based on the observations taken in field, literature and local people's knowledge. Ungulates abundance

for each vegetation plot was extracted from the abundance maps generated in the previous chapter. To understand the ungulates mediated effects on vegetation structure, I used Generalized Linear Modelling (GLM) and developed a response curve between seedling and sambar abundance. For this, I chose sambar as a model species as it is a browser and will show direct effects on the seedling abundance of palatable species. I found sambar to be in the positive relationship with seedling abundance, which suggest sambar's role in seed dispersal of the palatable species.

To investigate ungulates' interaction with vegetation parameters, regression (GLM & GAM) was performed in R program between each species of ungulates and vegetation parameters (tree basal area, tree density, tree species richness, grass biomass and *Lantana* abundance) and cattle abundance. Sambar's positive relation with basal area, species richness and tree density suggested its preference to the old growth, dense and mixed forests. Sambar showed an apparent avoidance of cattle presence. Chital preferred forest with high tree density and basal area. Chital showed significant positive relationship with palatable grass biomass. Chital, Nilgai and Wild pig were found to be in a non-linear relationship with cattle abundance. This suggests ungulates tolerance to a certain limit to cattle due to the habitats of relocated villages. Nilgai and Wild Pig show similar habitat preferences in terms of vegetation parameters however, their preference for terrain features and water dependency is distinct.

Conventionally management actions are implemented based on the species abundance and distribution estimated uniformly across the spatial extent of an area. This study proposes a model-based approach which estimates the precise abundance of terrestrial mammals considering spatial and temporal changes in the environmental conditions. The spatio-temporal model in this study has been used to estimate demographic parameters of four ungulate species having diverse biological traits such as sociality, body size and dietary preferences and hence have broader management implications. As the results describe that species respond spatially

and temporally to changing environmental conditions, I propose using spatio-temporal model-based approach to identify priority areas to most benefit the species from management actions. These techniques can be extended to large scales and help allocate priority areas in species recovery programs, understand the population dynamics, and evaluate the cost-effectiveness of management actions.



Chapter 1 General introduction

1.1 Background

It is a common knowledge that species in an ecosystem have evolved with specific roles and maintain the ecological balance through interdependence and feedback mechanisms. Interactions such as the prey-predator, host-parasite and producer-consumer enable overall stability within an ecosystem (Krebs 2008). The transfer of energy from plants through herbivores to carnivores is regulated by cycling energy and nutrients from one trophic level to another. Ungulates play a functional and structural role in shaping terrestrial ecosystems. They are the principal prey of large carnivores; hence hold a vital position in the trophic level of the ecological pyramid (Schaller 1967, Eisenberg 1980, Johnsingh 1983, Karanth & Sunquist 1992, Chellam 1993) and also affect the growth and survival of floral growth forms by forage selectivity; thereby modifying the pattern of vegetation structure and composition (Côté *et al.* 2004).

Ungulates can act as "biological switches" that pushes forest communities towards alternative successional pathways and distinct stable states (Laycock 1991, Hobbs 1996). They are the important regulator of ecosystem processes and affect competitive interactions among plants, alter successional pathways, soil development and nutrient cycling (Hobbs 1996, Ritchie *et al.* 1998, Paine 2000). Ungulates positively affect net primary productivity in terms of biomass, abundance, survival, and regeneration (McNaughton 1990, Hobbs 1996) and negatively (Ritchie *et al.* 1998, Jia *et al.* 2018, Ramirez *et al.* 2018). Ungulates exert cascading effects on animals by competing directly for resources with other herbivores and indirectly modifying habitats' composition and physical structure (Van Wieren 1998, Fuller 2001, Stewart 2001). Ungulates modify ecosystem patterns and processes by making habitat choices

(Coughenour 1984, Senft *et al.* 1987, Seagle *et al.* 1992). By forage selectivity, they affect the recruitment, regeneration and survival of the floral species and thus can shift the forest understory to an alternative stable state (Stromayer & Warren 1997). Modification of the ecosystem by ungulates is partly dependent on their abundance and distribution across landscapes, forest patches and habitats. These results vary with the different ecosystems with the moisture and nutrient availability, and therefore it becomes crucial to understand the ungulate mediated response in an ecosystem to understand energy flow and nutrient cycling between trophic levels.

1.2 Ungulate – habitat interaction in the Indian context

Historically, wild ungulates were widely distributed in India, which are now restricted to the protected areas, facing severe threats due to livestock grazing, habitat fragmentation and other anthropogenic pressure. Eisenberg & Seidensticker (1976) recommended maintaining vegetation diversity to meet the habitat need of herbivores in addition to maintaining the protected area size large enough to sustain a viable population of herbivores. Unfortunately, with a growing population and developmental activities, protected areas are shrinking at unprecedented rates. For example, there are 41 protected areas in Madhya Pradesh, the number of PAs has doubled in the last one and half decades (20 PAs in 2007) but the area that comes under protection has decreased from 12% in 2007 to 9.3% in 2022 of the total forest area. Shrinking of the habitat, fragmentation, deforestation, and anthropogenic pressure have severely threatened the herbivore population, directly affecting the large carnivore population (Ramakrishnan *et al.* 1999).

Ungulates have been studied as prey to large carnivores in various landscapes. There are many studies reporting the population status of ungulates. The All India Tiger Monitoring project every four years since 2006, reports predator and prey densities in all the protected areas in India. Apart from this, many intensive long-term studies report the habitat preference with the population trend of ungulates. Mathur & Phil (1991) studied sambar, chital and nilgai in the semi-arid landscape of Ranthambhore TR. This study concluded that the three species are ecologically separated and achieve resource partitioning primarily by habitat partitioning. According to them, sambar prefers forest-woodland habitats, chital prefers grassland-woodland habitats, and nilgai prefers miscellaneous-open woodland habitats.

Raman (1997) found that chital group size was positively related to forage availability. They formed large congregations in the dry season, but group size did not vary across the habitat at low densities. Chital was found abundant in scrublands and grasslands. Ramesh *et al.* (2012) studied ungulates as the principal prey of large carnivores in the Western Ghats and reported the group size of sambar and chital across seasons. Awasthi *et al.* (2016) studied ungulate ecology in Kanha TR and reported seasonal preference and density of ungulates in various habitat types. The study found that chital prefers grassland and forms large congregation in both seasons, whereas sambar and wild pig prefers bamboo-mixed forest in both seasons. However, Awasthi *et al.* (2016) report that density estimation through distance sampling needs a large sample size to reach reliable conclusions.

Kumar *et al.* (2021) studied ungulates in Bandipur TR, and found that various combinations of the habitat variable explained the distribution of different ungulate species. They found sambar distributed evenly across the reserve while chital and wild

pig were water-dependent and distributed across the moist-deciduous forest and ecotone areas. They report that ungulates switch to their browsing and grazing habits in response to forage heterogeneity. The distribution of ungulates gets affected in response to terrain complexity, water availability and protection regimes. Bagchi *et al.* (2003) studied niche partitioning of four species in Ranthambhore TR and found that chital and sambar were the forest guild and their habitat requirements are similar. Both the species preferred higher shrub density, grass cover and low livestock grazing pressure. In comparison, nilgai and chinkara (scrub guild) were tolerant to livestock grazing and degraded habitats.

Sharma (1995) studied ungulate-habitat utilization across seasons in Gir national park and found that sambar and nilgai avoid disturbance while there was no effect of disturbance on chital in both the seasons. Karanth & Sunquist (1992) studied the population structure and habitat preferences of ungulates in Nagarhole TR and found that wild pig prefer moist deciduous forests for high food availability. Ungulates biomass is lower in the dry deciduous forest compared to moist deciduous forests and teak plantations. Pokharel & Storch (2016) reported that sambar preferred high shrub cover, whereas chital and wild pig preferred flatter areas. Chital abundance was found to be associated with high grass cover. They suggested that the coexistence of ungulates is facilitated by the habitat mosaics in the study area, and therefore maintaining those habitats in order to facilitate the ungulate population is necessary.

1.3 Ecology of the study species:

Ungulates in the dry deciduous forest have to adapt to seasonal climatic variations. The response of various ungulate species to the various seasonal dynamics of the forests could be different. This study is focused on four species of ungulates viz;

sambar (*Rusa unicolor*), chital (*Axis axis*), nilgai (*Boselaphus tragocamelus*) and wild pig (*Sus scrofa*); a browser, a grazer, a mixed feeder and an omnivore and thus need an understanding of a broad spectrum of foraging, habitat and population ecology. There have been more studies on chital and sambar compared to nilgai and wild Pig. Species ecology has been studied that provides important insight into their biological needs. In the following paragraphs, available information is synthesized from the literature.

1.3.1 Sambar (*Rusa unicolor*)

Sambar is a large-sized ungulate, weighs (male and female) about 125 kg to 320 kg and is distributed throughout India except for arid and desert regions. Sambar is the most preferred prey for large carnivores; thus, its abundance is directly related to the conservation of large carnivores; tiger, leopard and Asiatic lions. Sambar prefers dense vegetation and woody habitats. The sambar prefers areas with moderate to steep slopes (Green 1987) and hilly terrain. It is known to prefer moist deciduous forests over any other habitat, while in Sariska TR, it utilized *Zizyphus* woodland, *Anogeissus* forest and *Boswellia* forest among the other available habitat types. It is mainly a browser, but its diet varies across seasons; browser in winter and summer while it grazes on fresh grasses during monsoon. Sankar (1994) observed sambar utilizing a variety of forage in Sariska TR; 26 species of trees, six of shrubs, five of creepers, 21 of herbs and 14 of grass. Sambar browses on a variety of plants; *Z. xylopyrus*, *Z. mauritiana*, *Bauhinia racemosa*, *H. isora*, *Mitragyna parviflora*, *Wrightia tinctoria*, *Careya arborea*, *Randia dumetorum* etc. being the most preferred. Sambar shows a seasonal shift in response to forage availability and other environmental variables. Home range sizes also change in seasons, largest in winter and smallest in summer. In the dry

season, sambar is confined in smaller groups to cool areas. Group size varies seasonally; larger and unisexual groups in a monsoon while smaller and mixed groups in the breeding season (post-monsoon). Sambar generally avoids high anthropogenic pressure and human presence. It is categorized as Vulnerable species as per the IUCN red data book. It is facing threats because of multiple-fold anthropogenic pressure.

1.3.2 Chital (*Axis axis*)

Chital, also known as spotted deer, is widely distributed in the Indian subcontinent. Once endemic to the Indian subcontinent, now been successfully introduced to other continents. The body weight of males and females ranges from 40 kg to 82 kg. Chital is considered an ecotone species (Krishnan 1972) and frequently prefers grassland-scrubland-forest interface areas. It is found in various forest types, from thorn-scrub forests to coastal dry evergreen forests. Chital is known to become habituated to human presence and found in a large congregation near forest chokies to avoid predators. Chital prefers flat terrain and avoids hills and slopes depending on the forage availability (Schaller 1967, Khan 1994, Bhat & Rawat 1995).

Chital is primarily a grazer (Schaller 1967, Krishnan 1972) and has been reported to shift its dietary preferences according to seasons in response to forage availability. In the dry season, it browses fresh and fallen leaves, fruits and flowers (Johnsingh 1981). The preferred grass species in the literature also relevant to Panna TR for chital are *Heteropogon contortus*, *Dicanthium spp*., *Eragrostis spp*., *Chloris spp*., *Themada quadrivalvis* etc. (Khan 1994, Shukla & Khare 1998). Major browse species consumed by chital are *Acacia catechu*, *Helicteres isora*, *Diospyros melanoxylon*, *Zizyphus mauritiana*, *Z. xylopyrus*, *Z. oenoplia*, *Gardenia latifolia*, *Cassia fistula*, *Terminalia spp*. etc. Apart from this, antler and bone chewing

(osteophagia) are also reported in chital (Barrette 1985), more common in velvet-antlered males due to their increased mineral requirements. Osteophagia was also recorded in chital during fieldwork for this study in Panna TR. Chital also show an association with primates to acquire food dropped by primates (Schaller 1967, Krishnan 1972, Newton 1992, Ramesh, Kalle, *et al.* 2012). This relationship is more common in winter and summer than in monsoon.

Chital shows seasonal variation in group formation, largest in monsoon. This is affected by food availability; in dry seasons, chital forms the smallest groups to reduce competition over food. Group size formation is also affected by habitat types; smaller groups in dense forests while comparatively larger groups in forest-grassland edges. Karanth & Sunquist (1992) reported the smallest herd size in the dry deciduous forest than in moist deciduous forests and teak plantations.

1.3.3 Nilgai (*Boselaphus tragocamelus*)

Nilgai, the largest antelope in Asia, is endemic to the Indian subcontinent. Nilgai males weigh around 240 kg, whereas Nilgai females weigh around 169 kg. They are partly social (Prater 1990) but do not form very large groups. Nilgai utilizes a variety of foods. Their protein requirements are less. Nilgai is considered a coarse feeder (Johnsingh & Sankar 1991) and can survive on the poor-quality of food. In Sariska, nilgai preferred fallen parts of *Z. mauritiana*, *B. monosperma*, *A. catechu* and *A. Leucophloea* among other plants. Nilgai is known to prefer flat or undulating terrain with open woodlands. Being antelope, they are less dependent on water thus less affected by the draughts. Though their native ranges are reduced largely due to hunting, the existing population has no major threat. Nilgai has been considered a serious pest in croplands.

1.3.4 Wild pig (*Sus scrofa*)

Wild pig is most widely distributed among all ungulates in India. They are under least concern category in the IUCN status. They are an important prey for large carnivores. They prefer scrublands, grasslands, mixed deciduous and evergreen forests. Wild pig are not true herbivores but omnivores, though 90 % of their diet contains roots, tubers, seeds and fruits. They also feed on insects, snakes and carcasses. They are non-ruminants with single-chambered stomach unlike other ruminants. Wild Pig are found to be water-dependent species and they form large congregation in water-logged areas. Wild pig are non-territorial social animals that live in groups called sounders, comprising females, their offspring, subadults, related females and sometimes one or two males.

Chapter 2 Study area

2.1 Physical and Geological features:

This study was undertaken in Panna Tiger Reserve (Panna TR) (Figure 2.1) situated in the Vindhyan mountain ranges in Madhya Pradesh, central India, between 24°27′N to 24°46′N latitude and 79°45′E to 80°09′E longitude. It was declared a National park in 1981 and became a tiger reserve in 1994. It is the 22nd tiger reserve in the country and the fifth in Madhya Pradesh. Panna TR occupies 575 km^2 as its core area with a buffer of 1002 km^2 spread over two districts, Panna and Chhatarpur. It comes under the biogeographic Province 6A Deccan Peninsula - Central Highlands (Rodgers & Panwar 1988). Panna TR is divided into six ranges; Panna, Hinota, Madla, Chandranagar, Gahrighat and Kishangarh which comprises 54 beats.

Panna TR is unique in terms of its 'terraced topography' and presents two plateaus and a river valley. The transition from one plateau to another forms rocky and steep escarpments ranging from 10-80 meters in height. The upper and middle plateaus are flatter than the lower river valley, representing the undulating terrain. The Ken River, a tributary of the Yamuna river, cuts through the reserve from south to north and is a lifeline for the reserve's biodiversity. The Ken river shrinks measurably in summer but is not completely dry. Plateau is crisscrossed by many seasonal streams which retain monsoonal water until post-winter.

This area is known for its old geological formation and variable lithology. Geologically, it is composed of Vindhyan sandstone and shales of the Precambrian – Cambrian era. The existence of diamond-bearing conglomerates and Rewa sandstones of the Vindhya system in this area is highly significant. The primary soil type in Panna is Tropical red ferruginous loamy-leached soil and Black soil. The former is subject to

erosion and occurs in red ochre colour. The latter is grey-brown in colour and found in zones between the two higher scarps.

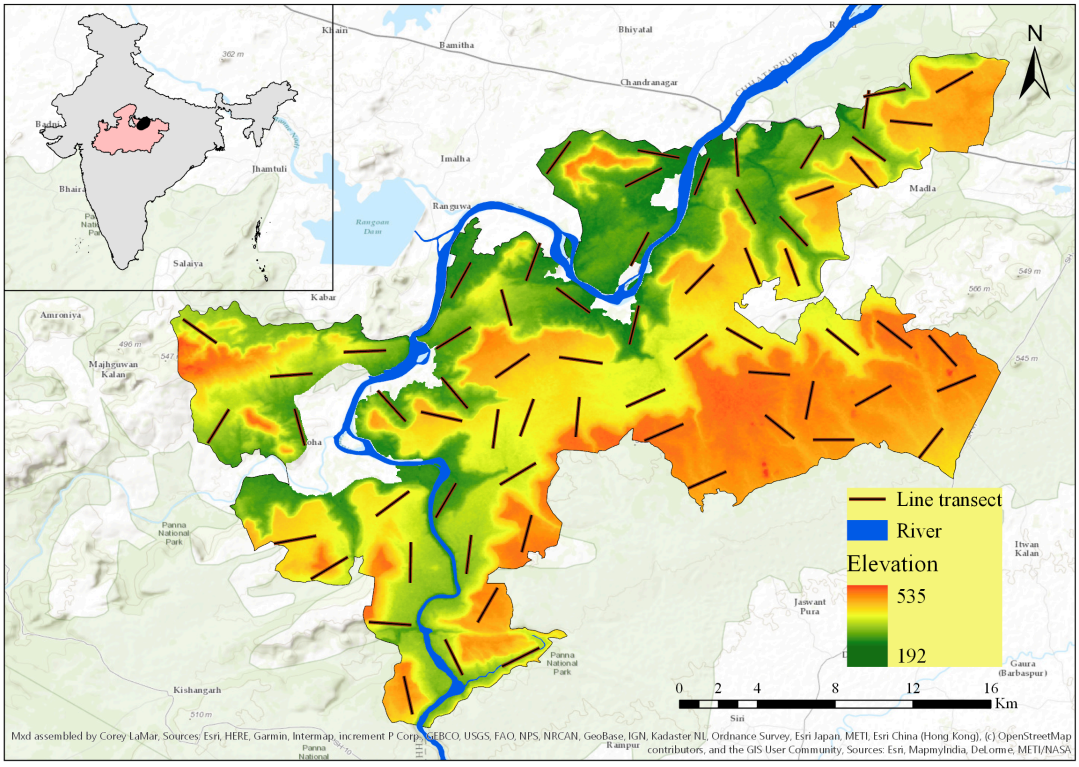


Figure 2.1: Map showing the spatial distribution of line transect survey in the study area, Panna Tiger Reserve overlaid on the digital elevation model data. Elevation divides the whole area into three distinct boundaries viz; upper Panna plateau (south), middle Hinota plateau and lowest Ken river valley (north).

2.2 Climate:

Panna TR is majorly a tropical dry deciduous forest that comes under a warm sub-dry bioclimatic zone (Meher-Homji & Fontanel 1978) represented by mean annual rainfall of 1000 – 1500 mm with seven to eight dry months. Panna TR is primarily dependent on monsoon rainfall from July–September. This area is known for its poor water retention capacity. Most monsoonal water percolates down to the valley very fast, leaving plateaus dry. Following the monsoon, is the winter season from November-

February when the minimum temperature drops to 5°C, followed by dry summer in April-June when the maximum temperature often exceeds 45°C (Karanth *et al.* 2004, Chundawat 2018).

2.3 Fauna:

Panna TR is globally known for its successful tiger relocation history (Krishnamurthy *et al.* 2016, Sarkar *et al.* 2016, 2017). Panna TR now supports a viable population of tigers (*Panthera tigris*) and leopard (*Panthera pardus*). Apart from large predators, striped hyena (*Hyaena hyaena*), dhole (*Cuon alpines*), jackal (*Canis aureus*) and wolf (*Canis lupus*) occur as mesopredators while jungle cat (*Felis chaus*), honey badger (*Mellivora capensis*), rusty-spotted cat (*Prionailurus rubiginosus*), Indian fox (*Vulpes bengalensis*), small Indian civet (*Viverricula indica*) common palm civet (*Paradoxurus hermaphroditus*), ruddy mongoose (*Herpestes smithii*) and grey mongoose (*Herpestes edwardsi*) and Indian pangolin (*Manis crassicaudata*) are among the small carnivores. PTR has a good population of sloth bears (*Melursus ursinus*).

Among the herbivore guild, sambar (*Rusa unicolor*), chital (*Axis axis*), nilgai (*Bocephalus tragocamelus*) and wild pig *(Sus scrofa)* are found in the good number. Besides, four-horned antelope known as chausingha (*Tetracerus quadricornis*), chinkara (*Gazella bennettii*) and blackbuck (*Antilope cervicapra*) are also found in reserve. Blackbuck has only been reported from the fringe area of core and buffer. Among the primates, the Hanuman langur (*Semnopithecus*) is widespread, while rhesus macaque (*Macaca mullata*) is found only along the forest peripheries closer to human habitations.

Panna TR holds approximately 260 sp. of birds, including summer and winter migrants. It is breeding ground for three species of vultures out of seven species found here. The area also supports 55 species of herpetofauna (Das *et al.* 2019) belonging to 21 families and 41 genera, out of which 13 species are Amphibians and 42 are Reptiles. PTR harbours two species of crocodiles and four species of turtles. There are over 50 species of fish including two globally threatened masheer species (*Tor tor*, *Tor putitora*), popularly known as 'King of Freshwater Fishes of India'. Several other biodiversity elements remain unexplored.

2.4 Natural vegetation:

The major forest type is tropical dry deciduous (Meher-Homji & Fontanel 1978) which shows unique seasonality with the scarcity of resources during summer (Chundawat 2018, Singh & Chaturvedi 2018). Panna TR represents the northern most boundary of the natural teak forest and the eastern limit of the *Anogeissus pendula* forest. As per the Champion & Seth (1968) classification Forest has been classified into six following categories;

1. Southern tropical dry deciduous dry teak mix forest 5A/C3
2. Northern tropical dry deciduous mixed forest – 5B/C2
3. Dry deciduous scrub forest.
4. *Boswellia* forest 5/E2
5. Dry bamboo brakes 5/E9
6. *Anogeissus pendula* forest 5/E1

There were 14 villages inside the core area relocated in the last three decades granting an undisturbed habitat for wildlife. Villagers of relocated villages depended on forest resources, with cattle rearing being the predominant occupation. After village

relocation, cattle rearing being the cost-ineffective occupation, villagers left many cattle behind. These cattle became feral, preyed upon by large carnivores and are mainly dependent on the forest for forage. This unregulated grazing has adverse effects on the forest growth and regeneration. Area with high cattle presence shows visible effects such as debarking of trees.

2.5 Study Rationale

Dry deciduous forest in central India withstand anthropogenic pressure since long and most of the vegetation structure that we see today is often degraded or secondary formations. The vegetation communities at most of the places in central India have derived through either natural reformation or plantation after degradation under the given climatic conditions and edaphic factors once given protection. The vegetation maps of French institute of Pondicherry (Meher-Homji & Fontanel 1978) reports that shifting cultivation known as "*hurca*" was predominant in Panna landscape until late seventies which imposed a grim impact on soil fertility, forest growth and regeneration. This landscape has been over exploited for decades for livestock rearing, illicit felling for timber, fuel and fodder requirements. Though above described vegetation classifications has predicted the effect of prevailing degradation to the vegetation communities, however, due to unpredictable increase in anthropogenic influences, anachronism to the standard classification have occurred. This calls a need of constant monitoring of the present dominant vegetation communities in the study area.

Panna landscape is characterized by its unique topography, high seasonality of dry deciduous forest and moisture gradient across the terrain. In addition, it also presents a unique reformation of forest due to its history of relocated villages. There were 14

villages relocated from the core area till 2016 (approximately > 1000 families). People of these relocated villages, before relocation, were majorly dependent on the forest produce for their livelihood. Many villagers left their cattle behind due to their uneconomic and cost-ineffective rearing after relocation. These cattle have now become feral and forage on whatever available in the forest. These anthropogenic factors have shaped the vegetation communities over the years under varying gradient of edaphic and climatic conditions across the landscape. I had observed vegetation communities during field visits before formulating research questions particularly about transition between communities, deciduousness of the forest and tree associations particularly growth reformations in proximity of relocated villages. My observation brought me to the speculation that terrain dynamism, moisture competition and other edaphic factors coupled with anthropogenic pressure have fashioned plant communities in two following ways: 1) open woodlands and savannah forests are found in proximity of the relocated villages. 2) deciduousness of trees enhances as I reach to the plateaux. 3) *Tectona grandis* makes a conspicuous presence irrespective of the community association. This forced me to think that forest structure in Panna landscape has more of local influence than the natural influence and communities are more of secondary formations than the plesioclimax (the potential vegetation communities).

Similarly, distribution of herbivore guild is influenced owing to vegetation dynamisms. Their spatial and temporal distribution varies due to high seasonality of the forest and further resource availability. Resource heterogeneity is distinct in tropical dry deciduous forests due to monsoon and climate (Singh & Chaturvedi 2018). These forest experience a brief growth period during monsoon after a six-seven

months of dry season (Meher-Homji & Fontanel 1978) making herbivores dependent on the monsoonal rainfall directly or indirectly. Strong seasonality of dry deciduous forests leads to seasonal variation in availability of forage, water, shade and shelter. The phenology of floral species across seasons (Singh & Singh 1992) makes forage allocation dynamic in space and time (Singh & Chaturvedi 2018). Further, topography plays a significant role in establishing moisture gradients across regions. Most monsoonal water sink into the river valley, leaving plateaus with drier habitat (Chundawat 2018). Valley, in contrast, retains most of the monsoonal water, provides shady habitats, and is cooler throughout the year. In addition, soil also becomes dry due to wind and insolation (Kapos 1989) and reduces plant productivity in the dry season (Ceballos 1990).

Ungulates in the dry deciduous forest has to adapt to seasonal climatic variations. The response of various ungulate species to the various seasonal dynamics of the forests could be different. Panna TR inhabits four species of ungulates in fairly good number. Sambar is known a species of dense forest and primarily a browser. Chital is a species of grassland-forest interface and primarily a grazer. Nilgai is a mixed feeder and known to prefer open forests whereas Wild pig has omnivorous habits and considered to be a generalist species. The preference of above four species of ungulates to habitats are inherently various and therefore these species are the best possible model species to understand the response to seasonal and resource dynamics.

Ungulates in pilot survey, were sighted evenly throughout the reserve in winter while in large groups and in congregation during summer. It was speculated that dynamism in distribution is result of seasonal allocation of forage, water and shelter. Ungulates are mostly studied as a primary prey of large carnivores in many regions of dry

deciduous forests giving least focus on the fact that they play a very important role in modification of ecosystems by selective foraging and alter successional pathways. A species and season-specific model-based approach focused on ungulate conservation in the tropical forests is gravely lacking, where ungulates achieve the highest diversity. Only a handful of studies in tropical forests describe environmental parameters' role in the ungulate distribution (Sharma 1995, Harihar *et al.* 2014, Awasthi *et al.* 2016, Kumar *et al.* 2021).

Formerly, conservation efforts were constrained to either yearly population trends or conclusions drawn by observing few individuals due to spatial models' absence. There are two limitations to these efforts; first, they do not account for any inherent biases, and second, a large sample size is needed to ensure the precision of the results. With advancements in the methodology, understanding these ecological patterns is now comparatively more straightforward, particularly by building spatial models that allow habitat heterogeneity and identify environmental variables that influence density distribution in space and time. Density Surface Modelling (DSM) (Miller *et al.* 2013) combines spatial modelling techniques with distance sampling (Buckland *et al.* 2001, 2004, Thomas *et al.* 2010), taking into account the probability of detecting an animal at each sampling unit and build maps of the population density distributions. These maps are extremely useful due to their scale flexibility and straightforward interpretation of complex scientific algorithms and, thus, make it easy to communicate results to non-specialists (Miller *et al.* 2013).

2.6 Objectives and Research Questions:

1. **To determine the vegetation structure and composition and quantify the above-ground biomass**
    a. What are the key dominant species and their constituents?
    b. What is the tree community composition in PTR?
    c. What is the status of basal area, volume and above-ground biomass across the different communities and their species-specific contribution?
2. **To quantify the density of ungulates across space and seasons.**
    a. What is the spatial density of ungulates in the study area?
    b. Does the density distribution of ungulates vary across seasons?
3. **To model the ungulates-habitat relationships and related functional responses.**
    a. Does the ungulate density correlate to vegetation parameters like tree density, basal area and above-ground biomass?
    b. Does the availability of palatable species play a role in shaping the animal population dynamics?

Chapter 3: Vegetation structure and community composition

3.1 Background

India is among the most biodiversity-rich countries in the world. The Indian sub-continent encompasses a wide range of ecosystems and diverse forest types spread over nearly one-fourth of its land surface, ranging from alpine forests in the Himalayan region to tropical dry and moist forests in Peninsular India (Champion & Seth 1968). Seventy-three percent of the total forest cover in India is tropical forest, of which 58% is tropical deciduous forest (Forest Survey of India 2019). The tropical forests have great carbon sequestration potential (Dixon *et al.* 1994) and are therefore gaining attention for adaptation and mitigation of climate change (Aalde *et al.* 2006). Although the tropical deciduous forests hold an important place in the forest ecosystem, compared to other tropical forests, they are the most exploited and subject to degradation (Murphy & Lugo 1986). According to the India State of Forest Report (Forest Survey of India 2021), more than 36% of the forest cover has been estimated to be prone to frequent forest fire.

Dry deciduous forests (DDF, hereafter) also known as seasonally dry forests, are characterized by long dry months, brief growth period, low annual rainfall and adaptation to the drought-like conditions (Meher-Homji & Fontanel 1978). Though DDF exhibits comparatively low species richness, their structural and physiological diversity is higher than the rain forests (Singh & Chaturvedi 2018). Their vertical (growth forms) and horizontal structures (associations) vary in the response to severe climatic conditions and are highly dynamic with biotic and abiotic variables. DDF has been reported as one of the most preferred habitats for livelihood because of their climatic suitability for livestock, soil fertility and productivity (Murphy & Lugo 1986) yet they are the most threatened ecosystems. The intensive biotic pressure in DDF

have caused fragmentation and alteration to the natural communities and therefore change in productivity and density. These forests serve crucial ecosystem services, one of the most important of all is carbon sequestration; a mitigation to global warming. Owing to their crucial role and importance, it becomes imperative to devise appropriate conservation strategies. As DDF are dynamic in space and time, it's crucial to assess their conservation status through in-depth knowledge of the structure and function of the forest at the tree community level.

Anthropogenic activities in Panna TR have shaped the plant community structure and composition with its history of relocated villages. Frequent forest fires, unregulated livestock grazing and selective harvesting have led the formation of degraded stages such as; open savanna and shrub savannah (Puri 1989, Meher-Homji 2000, Rawat *et al.* 2001). Many relocated villages inside PTR are such examples of secondary forest formations. Besides, Panna landscape have been reported to exhibit some rare and threatened elements of peninsular plant diversity such as; *Pterocarpus marsupium* (Near threatened as per IUCN red data book) and *Acacia donaldii* (distributed to the small ranges in peninsular India and highly under-reported). Recently CITES has considered *Boswellia* spp. as one of the highly traded species and issued a notification to assess its distribution, population size, status and population trend. *Boswellia serrata* has been reported to as one of the key plant communities of the dry deciduous forest in Panna landscape. However, these forest stands have gone through an intensive impact on structure and composition in the past several decades and might have caused a significant shift to the natural plant communities. As compared to their importance only a handful of in-depth studies on the present community structure, their functioning and dynamics (Sagar & Singh 2005, Balvanera *et al.* 2011, Pulla *et al.*

2017, Joshi & Dhyani 2019) have been conducted in dry deciduous forests reporting parameters of the communities while such studies are scarce in this landscape.

Keeping the aforementioned information, this chapter is designed to answer structural attributes and community composition of the dry deciduous forest of the PTR. In this chapter, I assessed the dominant tree species in PTR in terms of abundance as well as above-ground biomass (AGB). I also assessed tree community composition and described the dominant, co-dominant and associated tree species of a community. This chapter describes five dominant plant communities with attributes to understand the structure and function of a species in a community.

3.2 Methodology

3.2.1 Field survey

To sample vegetation across the reserve, I chose stratified random sampling. One line transect was placed in each beat (54 beats); smallest administrative unit of the reserve. Another line transect was added to the beat if the area of the beat was more than 10 km^2 to get good sampling coverage. Thus, total 66 line transects were used for vegetation sampling. Length of line transects were kept 1.5km to 2km depending upon the habitat complexity. The sampling plot size was kept of standard 10m X 10m for trees considering homogeneity of the study area. Quadrates were sampled on line transects keeping 250m distance between two adjacent plots; therefore, seven plots were sampled over a two kms transect. A total of 420 vegetation plots were sampled during 2016 – 2017 and trees >10 cm gbh (Girth at Breast Height) were measured for their GBH, tree height, number of species and individual in a plot with species ID.

To sample seedlings in a plot 5m X 5m quadrates were placed at the same location where trees were sampled following Saxena & Singh (1982) and species ID, collar

diameter and height were measured. Tree were categorized into adult and sapling. Trees are of >30cm gbh (Mueller-Dombois & Ellenberg 1975) were considered as adults, and are of 10-30 cm gbh were considered as saplings. All the species were identified using local flora (Oommachan 1977, Roy *et al.* 1992, Krishen 2013). The scientific names used are mostly based on the Flora of Madhya Pradesh (Roy *et al.* 1992) and Tree of Central India (Krishen 2013).

3.2.2 Statistical analysis

Tree diameter and basal area, were calculated using gbh. Tree volume of individuals with >30 cm gbh was calculated using species and region-specific allometric equations (Annexure 1) from reports of Forest Survey of India (1996, 2015, 2019, 2021). These equations are checked and edited for all regions every alternative year and hence most reliable to estimate tree volumes. Allometric equation in FSI data is available only for adult trees. Due to unavailability of the allometric equation for trees with <30 cm gbh in FSI data, I used (Chave *et al.* 2005, 2014) regression equation for remaining individuals having 10–30 cm GBH. A total of 420 plots were sampled along the 66 line transects for trees, saplings and seedlings out of which adult individuals were found in 360 plots and the remaining 60 plots had no adult trees. Similarly, saplings were found in 324 plots and seedlings in 361 plots.

Wood density for each species were taken from the Food and Agriculture Organization (FAO) for the United Nations (Brown 1997) and World Agro-Forestry Centre (Kindt *et al.* 2019) database prepared for tree species of tropical Asia. If species-specific wood density was not available in any literature or database, 0.6 was taken as a mean value. Allometric equation and wood density values for each species has been summarized in Annexure 1.

AGB was calculated as a product of wood density and tree volume for each individual of all species. To find out the dominant trees, relative species abundance and relative AGB for each species was calculated. All the equations are given below.

a) Diameter = gbh / π
b) Frequency = Number of plots in which species occurred * 100 / Total number of plots sampled
c) Density = Total number of individuals per unit area
d) Basal area = $(gbh)^2 / 4\pi$
e) Biomass = Wood density * Volume
f) Relative biomass = Total biomass of a species * 100 / Total biomass of all species

To find the present key communities and their dominant and associated species in the study area, ordination was performed. I used divisive hierarchical technique Two Way INdicator SPecies ANalysis (TWINSPAN) (Hill 1979) in program R with the help of "TwinspanR" (Zelený *et al.* 2019) package. Tree basal area, biomass etc described in Section 2.3 were calculated for each species of the community and then for each community as a whole. Shannon diversity (Shannon 1948) and species richness were calculated for each community using "vegan" (Oksanen *et al.* 2019) package in R program.

3.3 Results

A total of 49 species of adult, 36 species of sapling and 37 species of seedling were recorded during the sampling.

3.3.1 Tree species domination of PTR

Tectona grandis was the most abundant species covering 27% of the total population, and it contributed to the highest amount of AGB among PTR tree species, which was 18% (Table 3.1). Relative species abundance was followed by *Diospyros melanoxylon* (7%), *Ziziphus xylopyrus* (7.3%), *Acacia catechu* (7.3%) and *Lagerstroemia parviflora* (5.9%), while the highest AGB contributors were *Terminalia elliptica* (8.6%), *Anogeissus latifolia* (7.7%), *Lannea coromandelica* (7.2%) after *T. grandis.* Five species i.e., *T. elliptica, A. latifolia, L. coromandelica, Butea monosperma* and *Aegle marmelos* contributed a higher proportion of AGB despite their lower abundance. These five species cumulatively contributed 16% of the total population and 32% of the total AGB. *D. melanoxylon, Z. xylopyrus, A. catechu, L. parviflora* and *Anogeissus pendula* despite being abundant seemed to contribute lesser AGB, and 33% of their cumulative abundance had a 23.5% contribution to the AGB. A/F ratio indicates that most species present in the clumped distribution except for *T. grandis*. *T. grandis* shows the random distribution all across the park. *H. isora* and *Carissa spinarum* are highly clumped and found at only a few patches.

Species	Total individuals	Wood density ($g.m^{-3}$)	Total basal area (m^2)	Total volume (m^3)	Total biomass (Mg)	Relative biomass
Tectona grandis	943	0.5	17.20	76.22	42.74	26.86
Diospyros melanoxylon	266	0.68	5.17	17.61	13.48	5.67
Ziziphus xylopyrus	259	0.76	1.99	5.88	6.51	2.73
Acacia catechu	257	0.88	3.62	15.78	14.76	6.21
Lagerstroemia parviflora	210	0.62	3.11	15.67	11.06	4.65
Anogeissus pendula	179	0.86	3.18	10.77	10.13	4.26
Anogeissus latifolia	161	0.78	3.33	22.74	18.37	7.73
Lannea coromandelica	151	0.54	5.77	31.25	17.14	7.21
Aegle marmelos	115	0.75	1.88	9.73	10.11	4.25
Acacia donaldii	97	0.60	0.43	1.94	1.22	0.51
Terminalia elliptica	72	0.76	1.73	26.76	20.52	8.63
Butea monosperma	57	0.48	2.74	22.60	10.92	4.59

Table 3.1 Basal area, volume and above ground biomass of dominant tree species of PTR

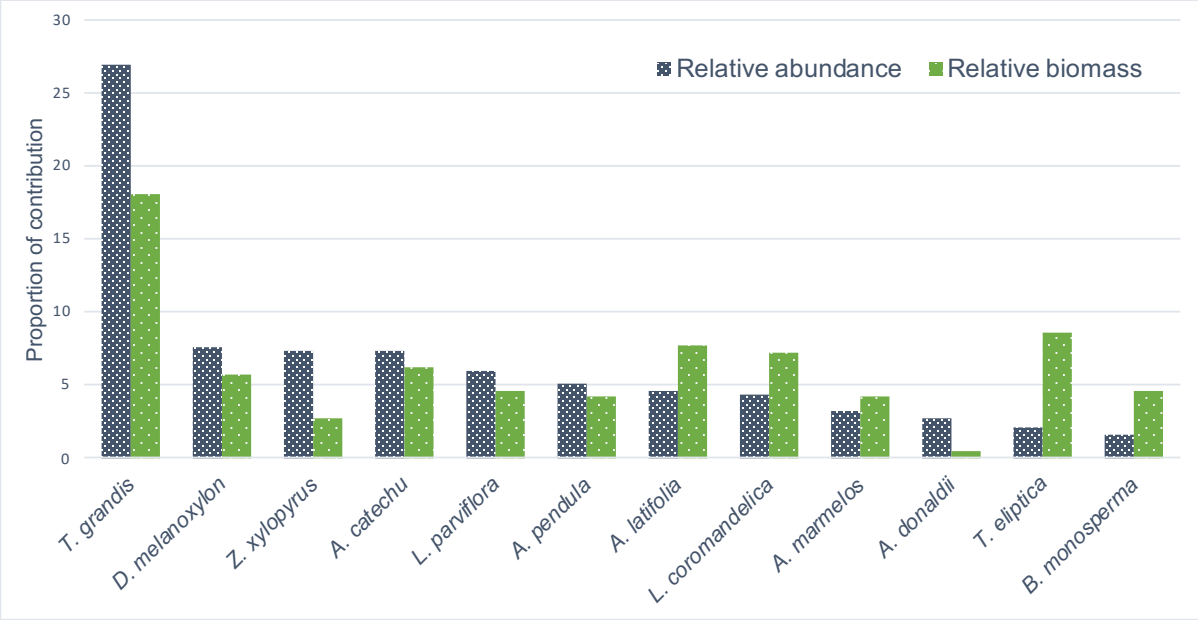


Figure 3.1: Relative Biomass and Relative abundance of dominant tree species of Panna TR

3.3.2 Vegetation community composition in PTR

Seven following key tree associations were assessed in PTR:

1. *Tectona grandis* mixed forest (n=174, eigenvalue=0.342)

2. *Acacia catechu* mixed forest (n=62, eigenvalue=0.389)

3. *Anogeissus pendula* forest (n=22, eigenvalue=0.489)

4. *Tectona grandis* forest (n=56, eigenvalue=0.342)

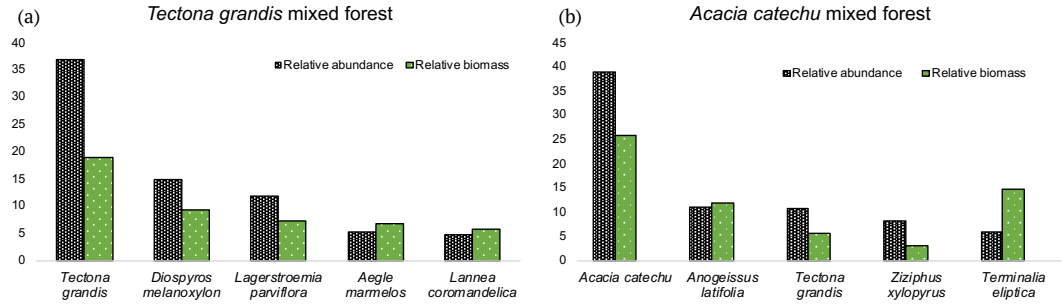
5. *Ziziphus xylopyrus* forest (n=51, eigenvalue=0.389)

6. Acacia donaldii mixed forest (n= 15, eigenvalue = 0.489)

7. Ziziphus mauritiana dominated forest (n=7, eigenvalue = 0.672)

I compiled data from remaining three communities, viz., *Z. xylopyrus*, *A. donaldii* and *Ziziphus* woodland as open woodland (Figure 3.2e), due to the similarity in composition of associated species as well as the appearance of communities in the field. These three communities altogether will be stated as open woodland in further text and figures.

The most dominant tree community was *T. grandis* mixed forest in which the dominant tree species *T. grandis* was found in association with *D. melanoxylon, L. parviflora* and *A. marmelos* (Table 3.2 & Figure 3.2). *T. grandis* mixed forest patches were found densely occupied with the highest recorded tree density (997 individuals/ha), basal area (19 m^2/ha) and AGB (73.94 ton/ha) (Table 3.2). This community appears as a heterogenous stand due to appearance of dominant and associated species in a significant number in a forest patch. This is also represented by the Shannon-diversity index value. It covers contiguous large patches in PTR. It is commonly distributed in the Panna range but found throughout the study area.



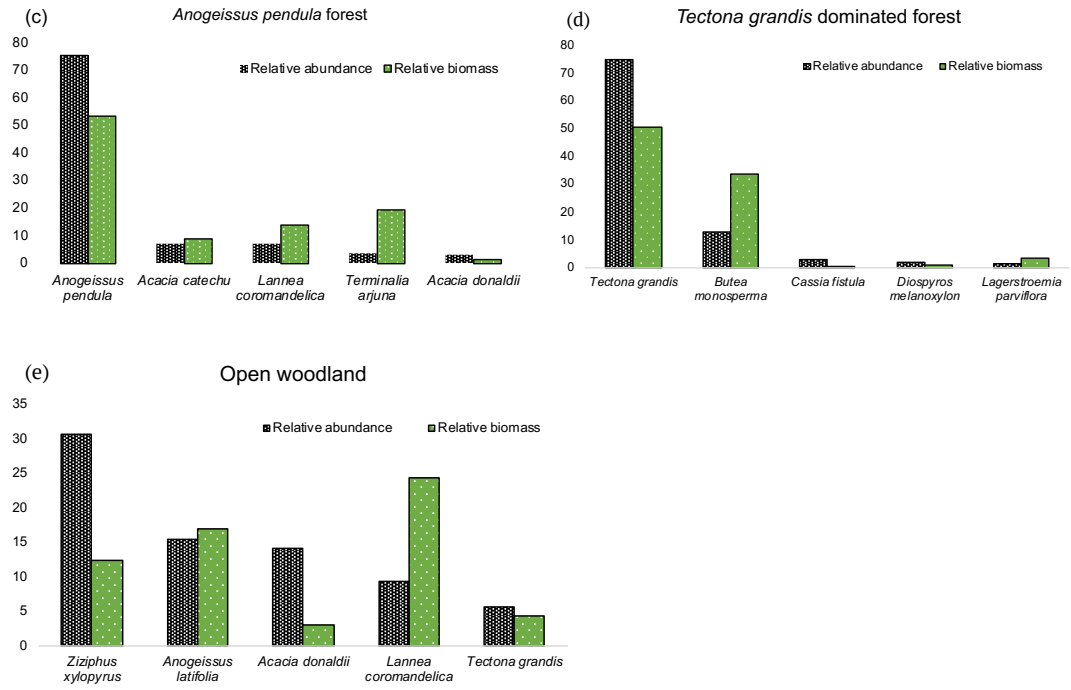


Figure 3.2: Dominant tree communities and their composition in PTR; (a) *Tectona grandis* mixed forest, (b) *Acacia catechu* mixed forest – both communities representing heterogeneous forest patch, (c) *Anogeissus pendula* forest, (d) *Tectona grandis* forest – both communities representing homogeneous forest patch, (e) Open woodland represented by small-sized tree species such as; *Ziziphus xylopyrus*, *Acacia donaldii*.

The second association, *A. catechu* mixed forest (Figure 3.2b) is found as *A. catechu* dominance in association with *A. latifolia*, *T. grandis* and *Z. xylopyrus*. Similar to *T. grandis* mixed forest, this community also appeared as a heterogeneous forest patch as associated species significantly contributes to the population. This community also show higher Shannon diversity index as compared to the other communities. The dominance of *A. catechu* shows linkages to the popular rock paintings of the park. This community can be seen dominant at the beat Bhusor, Kharaiya, Mahadev Ghati, Khamri south and Gangau B.

Tree community	Dominant species	Total individual	Total basal area (m^2)	Total volume (m^3)	Total AGB (Mg)	Relative biomass
Tectona grandis **mixed forest**	*Tectona grandis*	565	9.74	47.96	24.28	18.91
	Diospyros melanoxylon	229	4.51	17.92	11.97	9.33
	Lagerstroemia parviflora	183	2.65	14.92	9.25	7.20
	Aegle marmelos	83	1.61	12.08	8.90	6.93
	Lannea coromandelica	75	2.60	13.51	7.32	5.70
Acacia catechu **mixed forest**	*Acacia catechu*	186	2.50	11.59	9.95	25.83
	Anogeissus latifolia	53	0.93	6.03	4.59	11.91
	Tectona grandis	52	0.95	4.45	2.17	5.64
	Ziziphus xylopyrus	39	0.35	1.49	1.16	3.01
	Terminalia elliptica	29	0.53	7.53	5.69	14.77
Anogeissus pendula **forest**	*Anogeissus pendula*	148	2.14	7.54	6.33	53.32
	Acacia catechu	14	0.24	1.20	1.04	8.79
	Lannea coromandelica	14	0.56	3.07	1.66	13.97

	Terminalia arjuna	7	0.30	3.40	2.31	19.47
	Acacia donaldii	6	0.06	0.26	0.16	1.35
***Tectona grandis* dominated**	*Tectona grandis*	298	6.04	30.29	15.14	50.45
	Butea monosperma	50	2.52	20.93	10.09	33.63
	Cassia fistula	12	0.04	0.13	0.13	0.43
	Diospyros melanoxylon	8	0.14	0.39	0.25	0.84
	Lagerstroemia parviflora	6	0.25	1.74	1.08	3.61
Open woodland	*Ziziphus xylopyrus*	151	1.03	4.26	3.22	12.37
	Anogeissus latifolia	76	0.96	5.93	4.38	16.83
	Acacia donaldii	70	0.27	1.24	0.79	3.04
	Lannea coromandelica	46	1.99	11.62	6.31	24.28
	Tectona grandis	28	0.48	2.27	1.16	4.47

Table 3.2 Species composition and basal area, volume and above ground biomass of dominant communities in PTR

A. pendula forest (Figure 3.2c) is represented by single dominant species *A. pendula* in association with *A. catechu, L. coromandelica* and *Terminalia arjuna*. Due to the high regeneration capability of *A. pendula,* it was also found to be a highly dense forest patch after *T. grandis* mixed forests. This community represent homogeneous forest patches due to the complete dominance of a single tree species. The Association of these species corresponds to good fodder value. Such communities can be seen at beat Nararan, Pipartola, Palkoha and Kharaiya in PTR. In the areas of high disturbance, *A. pendula* are harvested for fencing material, fuel wood and fodder and because of this, this tends to be bushy and forms a thick carpet on the ground in the proximity of villages. Such thick carpets and bushy undergrowth of *A. pendula* can be seen in Palkoha beat of range Chandranagar.

Though *T. grandis* is the most dominant tree species in PTR, pure patches of *T. grandis* were few and scanty; 75% of the abundance and 50% of the relative biomass in *T. grandis* forest (Figure 3.2d) was contributed by a single dominant species *T. grandis.* This association appears homogenous as other species appears occasionally which is also represented by its Shannon-diversity index value (Table 3.3). According to Puri (1960), pure patches of *T. grandis* seem to find in deep alluvial soils, avoiding crystalline rocks and sterile sandstone. These communities are present at the Rajgarh, Raipura, Raja bariya and Jardhoba beats.

Open woodlands dominated by small-sized tree species such as *Z. xylopyrus, Z. mauritiana* and *A. donaldii* in association with *A. latifolia* and *L. coromandelica*. The open woodlands comprise a high Shannon diversity index, which indicates their species-rich community. This community had the lowest tree density as well as the basal area. Open woodlands, despite being species-rich, had the lowest AGB. This

community forms the belt in between *Acacia* dominated forest and Teak mixed forest, thus can be seen in very small patches along both communities. Such communities may not be conspicuous in the field, though they shape animal communities providing benefits of an ecotone region. All of these three communities were mostly found in the relocated villages that represent the forest regrowth at most of the places after prolonged human disturbance such as; Bargadi, Khamariya, Pipartola, Chokan and Gangau which have taken shape of the scrublands due to protection after relocation or fringe areas along the village-park boundary like Kudan, Raja Bariya where woodland species have been harvested a long time ago.

Sl. No.	Key species of the community	Number of individuals	Shannon diversity index	Density (individuals per ha)	Basal area ($m^2.ha^{-1}$)	Volume ($m^3.ha^{-1}$)	AGB ($Mg.ha^{-1}$)
1	*Tectona grandis* mixed forest	1746	2.59	997.71	19.03	117.69	73.94
2	*Acacia catechu* mixed forest	492	2.34	793.55	13.98	90.32	62.42
3	*Anogeissus pendula* dominance	218	1.01	990.91	16.27	74.05	54.77
4	*Tectona grandis* dominance	542	1.47	967.86	17.54	104.52	54.79
5	Open woodland	505	2.49	765.15	10.58	61.91	39.52

Table 3.3 Diversity indices, tree density, basal area, volume and above ground biomass of the present communities in Panna Tiger Reserve.

3.4 Discussion

3.4.1 Tree species domination of PTR

Forest looks homogeneous overall in terms of species composition due to the frequent appearance of *T. grandis*. Manhas et al. (2006) have reported *T. grandis* as one of the major contributors to the AGB and carbon stocks in Madhya Pradesh. The Shannon-diversity values in this study are similar to previous studies done in dry deciduous forests; Krishnamurthy *et al.* (2010) reported 3.30 in Bhadra WLS, Joshi & Dhyani (2019) recorded Shannon diversity index value range from 0.69 to 2.51 while in the dry evergreen forests of South India 1.5 to 2.4 by Parthasarathy & Sethi (1997) and 2.08 to 2.28 by Ramanujam & Kadamban (2001). Though species composition is different in dry deciduous and evergreen forests but a comparative chart shows that tropical dry deciduous forests harbors similar numbers of species while sustaining high anthropogenic disturbance.

Biomass related studies are gaining attention globally due to their importance in measuring carbon sequestration. This study used non-destructive methods to estimate biomass as it cause least damage to the forest and give the reliable estimates of biomass. Allometric equation derived to estimate biomass are a function of tree abundance, species richness and basal area that are subject to differ according to successional stage of the forest, species compositions and disturbance regimes. There have been studies that have derived allometric equations for dry deciduous forest (Roy *et al.* 1995, Kale *et al.* 2004). However, allometric equations varies with region and species and therefore, I used region and species-specific equations published by FSI. Since there have been variation in methodology to estimate biomass in literature

focussed in dry deciduous forests, a comparative chart of biomass statistics across study area would have been created a vague conclusion.

3.4.2 Community structure and composition

In dry deciduous forest, the floral species distribution and community composition are shaped by micro-scale differences in environmental parameters and constant anthropogenic pressure leading to non-contiguous patch formation. The dry deciduous forest in present scenario is more like a mosaic of plant communities representing distinct species composition (Singh & Jha 1990). This therefore makes it difficult to delineate a boundary between two vegetation communities in dry deciduous forest. Table 3.4 compares the communities in this chapter with the communities describes in earlier classifications for a clear picture.

I found four forest types in our study consistent with the classification provided in Champion & Seth (1968) for this region (Table 3.4). Of the six forest types, *Boswellia serrata* forest and dry Bamboo brakes have been described as the dominant forest types in earlier classifications (Champion & Seth, 1968; Meher-Homji, 2001). Both species were not found as the dominant tree species in our study area; however, dry Bamboo brakes were found in very small patches. As sampling units were evenly distributed across the study area, vegetation communities in this chapter do not incorporate the riparian forest found along the river and major stream in the study area. Riparian vegetation community is represented by the dominance of *Syzygium salicifolium* and *T. arjuna*.

This study also brings insights into the community composition of forest regrowth after long human disturbance in the form of open woodland as one of the dominant communities of the PTR core area. All the relocated villages in PTR now represent the

Savannah deciduous scrubland which has been described by Meher-Homji (2000) as a result of prolonged exploitation of dry deciduous forests. Such forest stands show the dominance of *Ziziphus* and *Acacia* species. Such habitats are excellent potential wildlife habitats which need better management interventions to regulate future community composition.

S. No.	Community in current study	Equivalence with forest type given in Champion & Seth (1968)	Equivalence with forest type given in Meher-Homji (2001)	Phytogeographic affinity (Legris & Meher-Homji, 1968)	Remarks
1	Teak-mixed forest	Southern tropical dry or very dry deciduous teak bearing forest	Dry deciduous Teak forest	The dominant elements are Indian (45 – 59 %) and Indo-malayan (21 – 30 %)	
2	Acacia-mixed forest	Shrub – Savanna: Dry savannah forest	Acacia – Anogeissus latifolia Type	---	*Albizia amara* and *Chloroxylon swietenia* which are common in the drier eastern half of South India practically disappear over the basaltic terrain of the Deccan trap country resulting in this association.

3	Anogeissus pendula forest	5/E1 Edaphic climax type of dry tropical forests: "Anogeissus pendula forest"	Dry deciduous open forest (Anogeissus pendula – Acacia catechu association)	This vegetation type is the meeting ground for the western (the Sudano-Rajasthan 10% and the Saharo-Sindian 8% elements) and the eastern (Indo-Malayan – 17%) floristic elements. The western elements represented by the elements. Indian element contribution is 27%.	---
4	Teak-dominated forest	Dry teak forest	Deciduous teak forest types intermediate between dry and moist categories	The dominant element in this vegetation types is Indian (41 – 56 %) and Indi-Malayan (20 – 25%).	These are the intermediate between the dry and the moist teak forest types both in climatic condition and floristic composition.
5	Open woodland	Dry deciduous scrub		---	These forests are the result of long continued overgrazing, lopping and fuel felling.

Table 3.4 A comparative chart of the vegetation communities in the present study and previous classification

Chapter 4 Distribution of ungulates across seasons

4.1 Background

Resource heterogeneity is distinct in tropical dry deciduous forests due to monsoon and climate (Singh & Chaturvedi 2018). These forest experience a brief period of growth during monsoon after a very long dry season of around six months (Meher-Homji & Fontanel 1978) making every taxon utterly dependent on the monsoonal rainfall directly or indirectly. Strong seasonality of dry deciduous forests leads to seasonal variation in phenology of different floral species (Singh & Singh 1992); consequently, food resources become dynamic in space and time (Singh & Chaturvedi 2018). Topography in such a scenario plays a significant role in establishing moisture gradients across regions. Most monsoonal water sink into the river valley, leaving plateaus with drier habitat (Chundawat 2018). Valley, in contrast, retains most of the monsoonal water, provides shady habitats, and is cooler throughout the year. In addition, soil also becomes dry due to wind and insolation (Kapos 1989) and reduces plant productivity in the dry season (Ceballos 1990). Therefore, ungulates in the dry deciduous forest adapt to seasonal climatic variations.

Further, heterogeneity in resource availability in seasonal forests drives ungulates to make their preferences across habitats (Naidoo *et al.* 2012, Schuette *et al.* 2016, Borowik *et al.* 2021). Ungulates preference for different habitats in different seasons (Awasthi *et al.* 2016) is guided by abiotic factors such as topography (Harris *et al.* 2002), water availability (Payne *et al.* 2020) and weather (Borowik *et al.* 2020), and biotic factors such as forage quality and availability (Bailey & Provenza 2008, Boone *et al.* 2008). In the dry deciduous forest, sources of water and shade are often limited, and forage availability becomes scarce during summer in most regions. In such a scenario, dispersal to a suitable habitat allows them to survive the extreme climatic

variations (Boone *et al.* 2008, Singh *et al.* 2012) and help fulfil their nutritional requirements (Senft *et al.* 1985, Scott *et al.* 1995, Coppedge & Shaw 1998).

Ungulates movement patterns in response to seasonal changes and resource availability have been studied in African Savanna (Fryxell & Sinclair 1988b, Yoganand & Owen-Smith 2014, Owen-Smith *et al.* 2020) and temperate forests (Singh *et al.* 2012, Borowik *et al.* 2020, 2021), which forms a strong baseline. As previous studies suggest, ungulates prefer higher elevation and ridges in colder temperatures (Harris *et al.* 2002) and seek shade during hot weather (McIlvain & Shoop 1971). However, a species and season-specific model-based approach focused on ungulate conservation in the tropical forests is gravely lacking, where ungulates attain the highest diversity. Only a handful of studies in tropical forests describe environmental parameters' role in the ungulate distribution (Sharma 1995, Harihar *et al.* 2014, Awasthi *et al.* 2016, Kumar *et al.* 2021). Formerly, conservation efforts were constrained to either yearly population trends or conclusions drawn by observing few individuals due to spatial models' absence. There are two limitations to these efforts; first, they do not account for any inherent biases, and second, a large sample size is needed to ensure the precision of the results. With advancements in the methodology, understanding these ecological patterns is now comparatively more straightforward, particularly by building spatial models that allow habitat heterogeneity and identify environmental variables that influence density distribution in space and time. Density Surface Modelling (DSM) (Miller *et al.* 2013) combines spatial modelling techniques with distance sampling (Buckland *et al.* 2001, 2004, Thomas *et al.* 2010), taking into account the probability of detecting an animal at each sampling unit and build maps of the population density distributions. These maps are extremely useful due to their scale

flexibility and straightforward interpretation of complex scientific algorithms and, thus, make it easy to communicate results to non-specialists (Miller *et al.* 2013).

This chapter hypothesises that ungulate distribution should vary in response to resource availability across seasons. Therefore, I sought to identify seasonal distribution patterns and establish the relationship with habitat variables of four species of ungulates by using DSM that could affect the distribution across two seasons. I also calculated and mapped uncertainties in the results to ensure the robustness of spatial maps. These results would improve our understanding of the species' response to the environmental variables, direct species conservation efforts to the priority areas and reduce the cost of management actions by allocating them to the specific habitats.

4.2 Methodology

4.2.1 Field sampling

I followed the distance sampling protocol (Buckland *et al.* 2004) for data collection. We considered beat, the smallest administrative unit, a sampling unit and walked one line transect in each beat. One line transect was added in each beat if the area of a beat was more than 10 km^2 to get good spatial coverage. Thus, a total of 66 spatially distributed line transects were walked, covering the whole core area of PTR. Sampling was done in both seasons; Summer and Winter. Data was collected for two sampling seasons of winter (late-November to early-February) 2015-2016 and 2016-2017 and two sampling seasons of summer (late-April to mid-June) 2016 and 2017. Line length was kept from 1.5 km to 2.0 km depending upon the habitat and terrain complexity. The transects were walked in the early morning hours at the time of peak activity of the ungulates. All the line transects were subjected to repeated sampling up to thrice in each sampling season.

4.2.2 Statistical analysis

a) Data preparation

Two years of data were compiled for both seasons for each species separately. The total survey effort for all species in summer was 356 km and in winter was 518 km. I divided all transects into 400 meters segments and yielded spatio-temporal replicates of 892 for summer and 1286 for winter. Segment length was taken small enough such that the animal density and covariate values do not vary within a segment and large enough to avoid the false absence of sightings (false zero) in the segment data. I used geographical and local habitat variables to the model spatial density distribution of the ungulate species (Figure S4.1). We derived covariates values directly from remotely sensed data or calculated Euclidean distance (Table 4.1). I used two geographic covariates consisting of the Digital Elevation Model (dem) and Terrain Ruggedness Index (TRI); two habitat parameters consisting of distance to water source (water) and Normalised Difference Vegetation Index (NDVI), and two parameters for anthropogenic influence consisting of distance from the settlements (settlement) and distance from the agricultural fields (agriculture). I also incorporated bivariate smooth of spatial coordinates to address the spatial variations. Due to the dynamic seasonality of the dry deciduous forest, we calculated NDVI and distance from the water source for summer and winter separately. Prediction grids were formed by dividing the whole study area into 200m^2 grids using ArcMap, and mean covariates values were extracted for the centroid of the grid for both seasons. I chose a square grid cell size based on the truncation distance ($2w$; where w is truncation distance; 100m in our analysis) as described in (Miller *et al.* 2013) and thus we yielded 12765 grid cells in summer and 13187 grid cells in winter.

b) Density and abundance estimation

The modelling process is implemented using a two-stage approach. As the first step, we used conventional distance sampling (CDS) to model the density and abundance of all species. CDS models detection probability as a function of observed perpendicular distances. Three key detection functions, i.e. Uniform, Half-normal and Hazard-rate, were fitted to the distance data along with and without cosine adjustment terms (Figure S4.2). The best-fitted model was selected using Akaike's Information Criteria (AIC) as well as goodness of fit test. Data was truncated for the farthest observations up to 9% within the truncation distance based on visual inspection of the histogram (Buckland *et al.* 2001). This analysis was implemented using the Distance package version 1.0.0 (Miller *et al.* 2019) in R version 3.6.0 (R Core Team 2019).

c) Density surface modelling

After fitting the detection function, we used count per segment as a response variable which was modelled given habitat variables using the Generalized Additive Modelling (GAM) approach. The model for count per segment is:

$$\mathbb{E}(n_j) = \hat{p}_j A_j \exp\left[\beta_0 + \sum_k f_k(z_{jk})\right]$$

The initial part of the equation $\hat{p}_j A_j$ defines the detection probability in each segment multiplied by the area of each segment whereas, the later part defines the intercept and smooth functions of the covariate (Miller *et al.* 2013). Count per segment was modelled as a smooth function of predictor variables. Segment area was used as an offset term from 2*wl,* where *w* is truncation distance, and *l* is the segment length. We used default thin plate regression spline smoother in GAM.

I added season as a binary term to the model to assess season's significance on mean density. This model assumes that the relationship between habitat and response variables remains the same in each season, but the mean density may differ. Further, an interaction was added between a smoother and categorical variable season to check whether the mean density and the relationship vary across seasons. I kept the interaction term in the model only if varying relationships across seasons was found. The term selection was performed by checking smoother p-value significance and zero effect (Wood 2006). An extra shrinkage term was imposed in the model allowing smooth terms to be removed during fitting (Wood 2011). The mean-variance relationship was allowed to vary with response family distribution Poisson, Negative binomial and Tweedie (Candy 2004, Foster & Bravington 2012). Dispersion parameter was investigated for each family distribution, and the model was abandoned if data was highly under-dispersed. The basis dimensions in the model were chosen by a repetitive process, in which analysis was rerun to make the model wiggly enough to capture the relationship in the data and not too wiggly to capture the noise in the data. A decision was made for basis dimensions by comparing the effective degree of freedom and random patterns in residuals for each smoother (Pedersen *et al.* 2019). The best-fit model was selected using AIC as well as goodness of fit values. This analysis was implemented using 'dsm' package version 2.3.0 (Miller *et al.* 2020) in R version 3.6.0 (R Core Team 2019). All the models were checked and selected by the iterative process (Annexure II).

Variables	Data Source and processing details	Spatial resolution and time period	Description
Latitude, Longitude (x, y)	Survey location		
Elevation (dem)	Digital elevation- Shuttle Radar Topography Mission data https://earthexplorer.usgs.gov	30 meters	Elevation divides the study area into three distinct regions; two plateaus and one valley. As plateaus are known for their poor water retention capacity, monsoonal water drops into the valley. Hence, plateaus represent drier habitats as compared to the valley.
Topographic Ruggedness index (TRI)	Calculated from SRTM – digital elevation data (Riley *et al.* 1999)	30 meters	This is a measure of roughness in the terrain. In our study area, plateaus represent flat terrain so TRI values for plateaus are low while escarpments and valley are steep and undulating terrain where TRI value varies.
Distance from the water source (water)	Sentinel-2A https://earthexplorer.usgs.gov First, generated a layer of water bodies for two seasons using normalized	10 meters; Winter data: Dec 2016 – Jan 2017; Summer data:	This provides a measurable distance from the water that may affect distribution. Ken river and the streams are the primary water source in the study

	difference water index (NDWI) (McFEETERS 1996) in ERDAS-Imagine tools. We then calculated as Euclidean distance from the water source.	April 2016 – May 2016	area; however, most of the streams dry out during summer.
Normalized difference vegetation index (NDVI)	Sentinel-2A https://earthexplorer.usgs.gov	10 meter; Winter: Dec 2016 – Jan 2017	This is used as vegetation index as it is positively correlated to the tree basal area (Figure S4.2).. In our study area, the dense forest is represented by comparatively higher NDVI values.
Distance from the settlements (settlement)	Calculated as Euclidean distance from the human settlements		This variable is a calculative measure of anthropogenic pressure in terms of access of local people to the forest and caused disturbance.
Distance from the agriculture (agriculture)	Calculated as Euclidean distance from the agricultural fields		This is also a measure of anthropogenic pressure. Agricultural fields retain crops during winters and may become an attraction to the crop-raider species such as Nilgai.

Table 4.1 Predictor variables used in generalized additive modelling framework for spatial modelling.

c) Abundance prediction and variance estimation

Response distribution obtained from DSM was then used to predict density over the whole study area with 200m X 200m prediction cells. Predictions were made for each cell based on predictor variables used to fit the model. To estimate coefficient of variation, I used delta method which assumes that variance component in detection function and spatial models are independent. The total estimate of variance of abundance over the entire area is sum of square of estimated variance of predicted values and square of variance of detection probability from the detection function model. Similarly, I measured CVs for abundance prediction for each cell. The squared coefficient of variation from GAM and detection function were added on a per-cell basis following the approach described in Miller et al. (2013). The maps were produced for the prediction cells overlaid by the CV values to visualise the CVs. I further tested the coverage of covariates of interest to test the reliability of density prediction maps using 'dsmextra' package (Bouchet *et al.* 2019).

4.3 Results

4.3.1 Population estimates of Ungulates

In summer, animal sightings were frequent due to increased visibility and thinner understorey vegetation. Sambar was the most frequently sighted animal in both seasons, followed by nilgai and chital. We found sambar to be most abundant in the study area with total abundance of ($\widehat{N}$= 7248 ± 673 individuals and density $\widehat{D}$ = 12.5 ± 1.16 individuals/ km^2 followed by chital ($\widehat{N}$= 6861 ± 773; $\widehat{D}$ = 11.9 ± 1.34) and nilgai ($\widehat{N}$ = 6306 ± 815; $\widehat{D}$ = 10.94 ± 1.41). Chital and wild pig formed larger groups (Annexure II) with an average group size of 3.59 ± 0.21 and 3.16 ± 0.31 individuals

per group (Table 4.2). However, the highest cluster density was recorded for sambar 5.59 ± 0.48 groups / km^2.

4.3.2 Spatio-temporal distribution and response to habitat variable:

It was found that season significantly affects all the ungulates' density as well as distribution. However, we found a similar relationship between habitat and response variable across seasons for all ungulates except Wild pig density with water. Poisson family distribution explained the mean-variance relationship for all ungulates. In all the final models, at least one terrain variable (TRI or elevation), one habitat variable (NDVI or water) and one variable describing anthropogenic influence (settlement or agriculture) had a significant effect on species densities. The final GAM accounted for 20% to 30% of the variability in species data.

Sambar (*Rusa unicolor)*: Sambar densities vary seasonally, with higher mean densities in summer. They avoid proximity to the agricultural fields, prefer densely forested habitats (positive relationship with NDVI) and higher elevations in both seasons. Densities decline in the northern part of the reserve in winter (Figure 4.3a). Summer densities in the valley are 2.3 individuals/hectare while it is 2.8 individuals/hectare at the middle and upper plateau. These patterns are reflected in the spatial distribution maps (Figure 4.3a). Model predicted low CVs in most of its distributional ranges in both seasons except the riverine area in winter and near the forest edges in summer. The CV varied spatially with 0.05 to 0.63 per hectare in summer and 0.05 to 2.30 per hectare in winter. A higher CV was recorded majorly in those regions where sightings were negligible (Figure 4.4). However, densities were more precise and reliable in the areas of higher abundance. These patterns are shown in the map of the coefficient of variations.

Species	Individual Density / sq km	CV	Cluster density/ km^2	Group size / km^2	Abundance	Detection probability	Goodness of fit (gof)	Encounter rate (individuals / km)	Total Effort (km)	Total covered area (km^2)	Best fit model
Sambar (n=299)	**12.5 ± 1.16**	0.09	5.59 ± 0.48	2.24 ± 0.08	**7248 ± 673**	0.34 ± 0.02	0.53	0.78 ± 0.05	854	170.8	Half Normal cosine
Chital (n=189)	**11.9 ± 1.34**	0.11	3.31 ± 0.32	3.59 ± 0.21	6861 ± 773	0.33 ± 0.01	0.60	0.79 ± 0.07	854	170.7	Uniform cosine
Nilgai (n=230)	**10.94 ± 1.41**	0.12	4.34 ± 0.49	2.52 ± 0.15	6306 ± 815	0.20 ± 0.01	0.70	0.67 ± 0.06	854	256.8	Hazard rate
Wild Pig (n=111)	**6.97 ± 1.27**	0.18	2.20 ± 0.33	3.16 ± 0.31	4071 ± 731	0.29 ± 0.03	0.76	0.41 ± 0.05	854	170.9	Hazard rate

Table 4.2 Density estimates of four species of ungulates in Panna Tiger Reserve

Chital (*Axis axis*): Chital density is predicted to increase with increasing NDVI and away from the settlements. Chital majorly prefers the lower elevation area, the valley. Chital densities are higher towards the east in summer and lesser in winter, while response with longitude is inverse (Figure 4.1). Chital forms larger groups in winter (range varies from 0-16.5 individuals/hectare) when resources are abundant while more dispersed in summer (range varies 0-3.5 individuals/hectare), when resources are scarce. I observe a seasonal shift in the density distribution towards the valley and middle plateau in summer, reflected in spatial distribution maps (Figure 4.3b). The model predicted low CVs in most of its distributional ranges except in the riverine area in summer and the southern region in winter. CV varies comparatively more in summer ranging from 0.02 to 2.5 per hectare. The pattern of CV is shown in the map (Figure 4.4).

Nilgai (*Boselaphus tragocamelus*): It was found that season significantly affects the mean density of Nilgai. Higher densities are recorded at the north-western side of the reserve. They prefer proximity to water and lower elevation. Nilgai seem to prefer habitats distant from the agricultural fields (Figure 4.1). In summer, species are extensively restricted to the valley in large congregations (ranging from 0-11.5 individuals/hectare) contrary to their distribution to the valley and middle plateau in smaller congregations in winter (ranging from 0-1.46 individuals/hectare) (Figure 4.3c). Nilgai shows a clear seasonal shift in the distribution with habitat preference to middle plateau and valley in the winter and completely shifted to the valley in summer. The model predicted very low CVs in most of the distributional ranges in both seasons (Figure 4.4).

Wild Pig (*Sus scrofa*): Wild Pig is the least sighted ungulate; however, data fulfilled the model assumptions and were sufficient to perform the analysis. Season significantly affected the Wild pig abundance with higher mean density in winter. I found higher density at higher NDVI and in rugged terrain. Water presence has profound effects on density in summer compared to winter. Density decreases drastically with increasing distance to the water source in summer. Abundance maps of both seasons show their complete seasonal shifts to the valley in summer (Figure 4.3d). They make larger groups in summer as fewer niches are available due to resource scarcity. Whereas in winter, animals were primarily distributed to the upper plateau. The model predicted low CVs in most of the distributional range in both seasons except the area where detections were less (Figure 4.4).

Cattle: Cattle summer sightings were not enough to do seasonal analysis (n = 110 (21:summer; 89:winter) therefore data were pooled together for both the seasons and abundance map was generated for compiled data. For cattle, two anthropogenic variables (distance from the settlements and agriculture) were compiled into one; distance from the forest edge. Here, this variable explains their distribution more appropriately as cattle in Panna TR are either feral or free ranging. Cattle densities show negative relationship with TRI and distance from the forest edge (Figure: 5.2). Their density were high in the proximity of the forest edge and in flat terrain. The model explained 34% of the deviance in the data and abundance were calculated to be 5610 ± 1198 inside the core area. Abundance maps shows higher densities in two ranges; Chandranagar and Kishangarh. This model observe low CV in most of the area except toward Panna range (Figure 4.5)

Species (n=2178)	Season	Fitted model parameters (p-value < 0.001)	Response family	Dispersion parameter	Deviance explained
Sambar	Winter (Season 1)	$\log\{E(n_i)\} = -12.8267 + f_1(x_i):(y_i) + f_2(\text{elevation}_i) + f_3(\text{NDVI}_i) + f_4(\text{distagri}_i) + f_5(y_i) + \text{off.set}$	Poisson	1.16	20.1%
	Summer (Season 2)	$log\{E(n_i)\} = -10.6045 + f_1(x_i):(y_i) + f_2(elevation_i) + f_3(NDVI_i) + f_4(distagri_i) + f_6(x_i) + off.set$			
Chital	Winter	$log\{E(n_i)\} = -13.9972 + f_1(elevation_i) + f_2(NDVI_i) + f_3(distsettle_i) + f_4(x_i) + f_6(y_i) + off.set$	Poisson	1.15	30%
	Summer	$log\{E(n_i)\} = -8.8255 + f_1(elevation_i) + f_2(NDVI_i) + f_3(distsettle_i) + f_5(x_i) + f_7(y_i) + off.set$			
Nilgai	Winter	$log\{E(n_i)\} = -12.3044 + f_1(elevation_i) + f_2(water_i) + f_3(distsettle_i) + f_4(distagri_i) + f_5(x_i) + f_7(y_i) + off.set$	Poisson	1.03	21.4%

	Summer	$log\{E(n_i)\} = -12.0513 + f_1(elevation_i) + f_2(water_i) + f_3(distsettle_i) + f_4(distagri_i) + f_6(x_i) + f_8(y_i) + off.set$			
Wild Pig	Winter	$log\{E(n_i)\} = -13.5527 + f_1(x_i): (y_i) + f_2(TRI_i) + f_3(water_i) + f_5(NDVI_i) + off.set$	Poisson	0.70	30.6%
	Summer	$log\{E(n_i)\} = -15.0353 + f_1(x_i): (y_i) + f_2(TRI_i) + f_4(water_i) + f_5(NDVI_i) + off.set$			

Table 4.3: Model parameters for generalized additive modelling of spatial model for each species in each season. Here, n = number of sampled units, ($f_1 - f_8$) are the smooth terms for the environmental parameters with significant relationships with density, dispersion parameter shows the distribution of the data around the mean (values >0.50 shows under dispersed or skewed datasets and represent model misfit), Deviance explained shows the amount of variance explained by the model.

Species	Detection function	Detection probability	Response Family	Terms (p-value < 0.01)	Dispersion parameter	Deviance explained	Abundance	CV
Cattle (n = 110 (21: summer; 89: winter)	Half-Normal	0.29 ± 0.01	Tweedie	s(x,y, 13.0), s(TRI, 1.0), s(distedge, 1.0)	2.7	34.3	5610 ± 1198	0.21

Table 4.4: Model parameter and abundance estimate for cattle. No seasonal analysis was performed for cattle due to limited seasonal sightings.

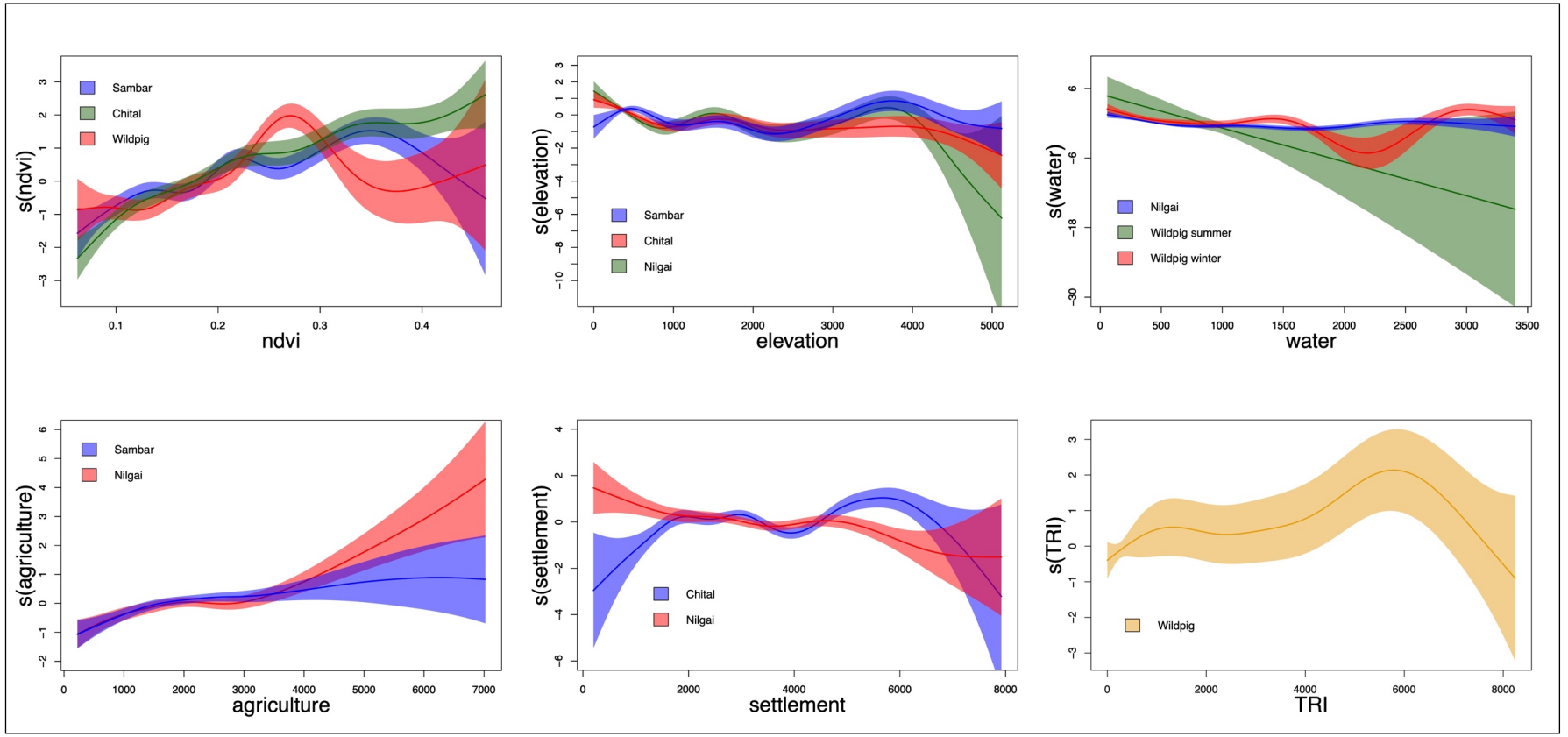


Figure 4.1: Species seasonal response curve with environmental parameters with 95% confidence interval. The response curve was drawn only for those parameters which were significant in the model for each species. Here, y axis is the scale of log link function and x axis shows the range of environmental parameters.

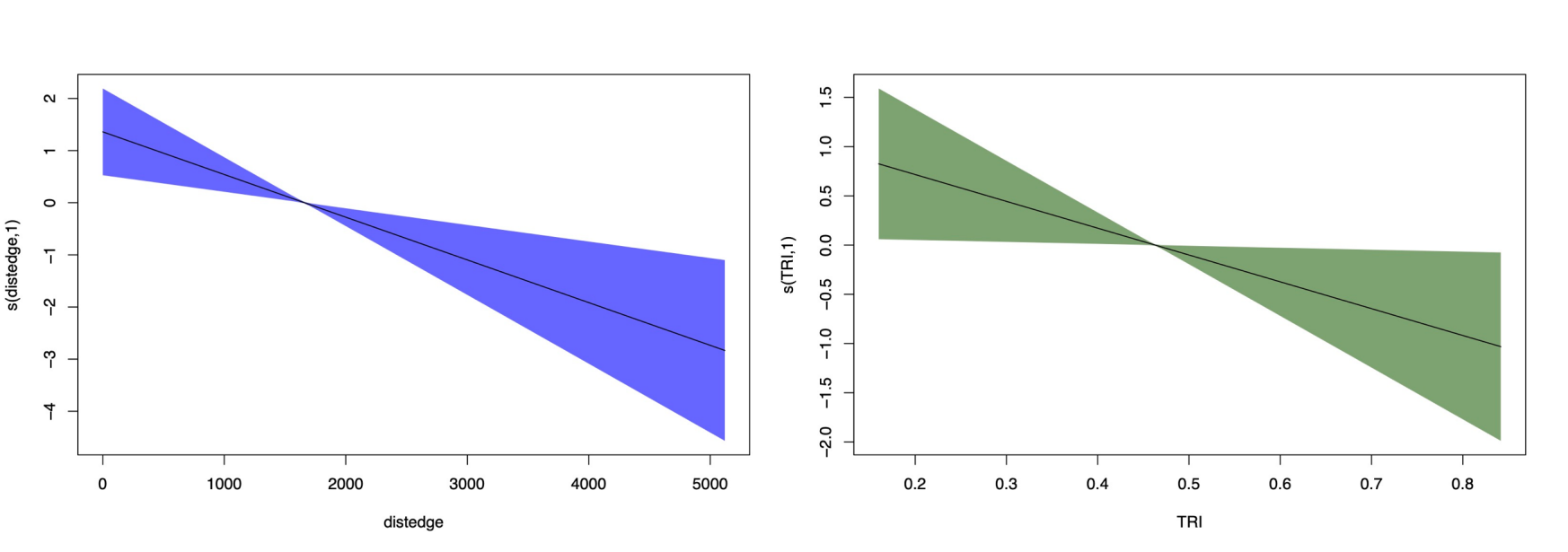
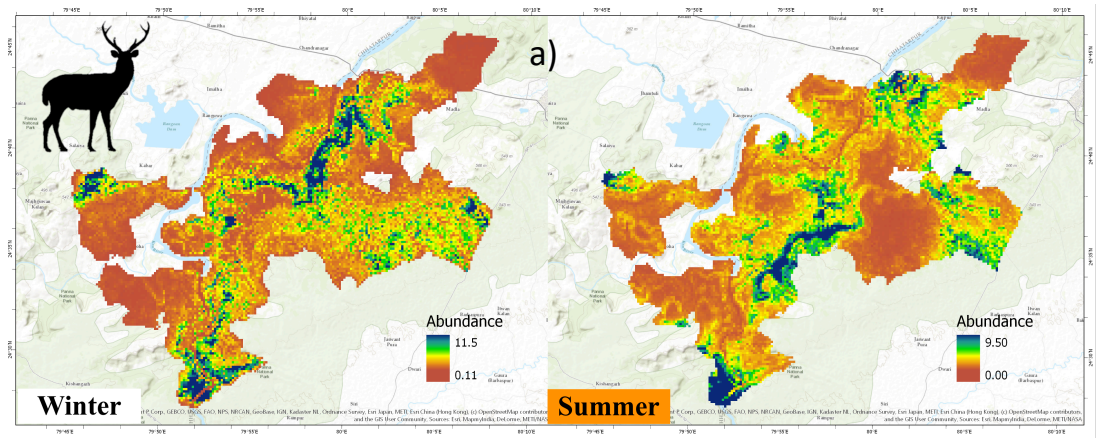
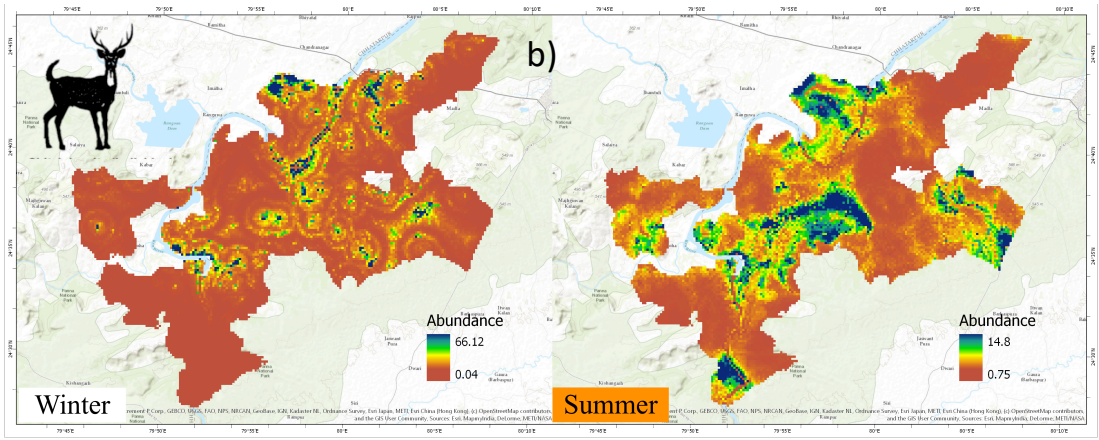
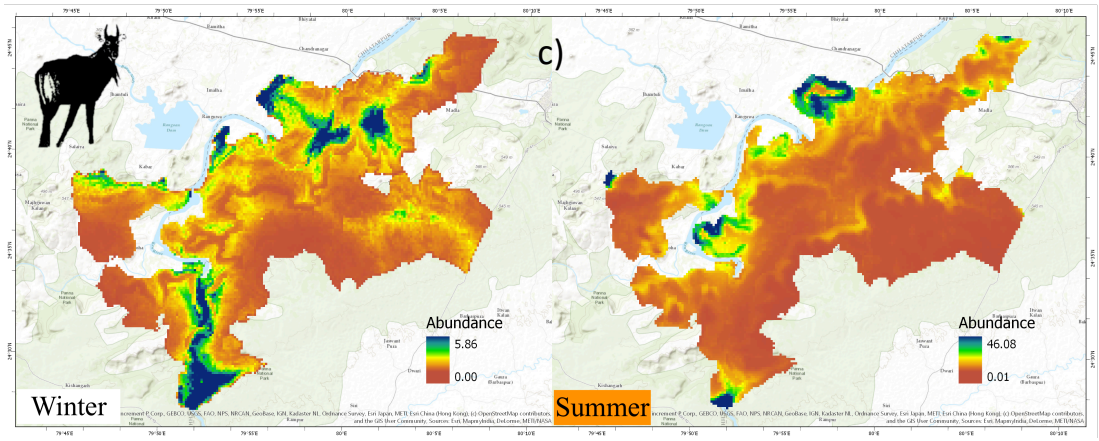


Figure 4.2: Cattle response curve with environmental parameters with 95% confidence interval. Two parameters, distance from the forest edge and terrain ruggedness index showed significant negative response with cattle density.


a)
Abundance
11.5
0.11
Winter
Abundance
9.50
0.00
Summer


b)
Abundance
66.12
0.04
Winter
Abundance
14.8
0.75
Summer


c)
Abundance
5.86
0.00
Winter
Abundance
46.08
0.01
Summer

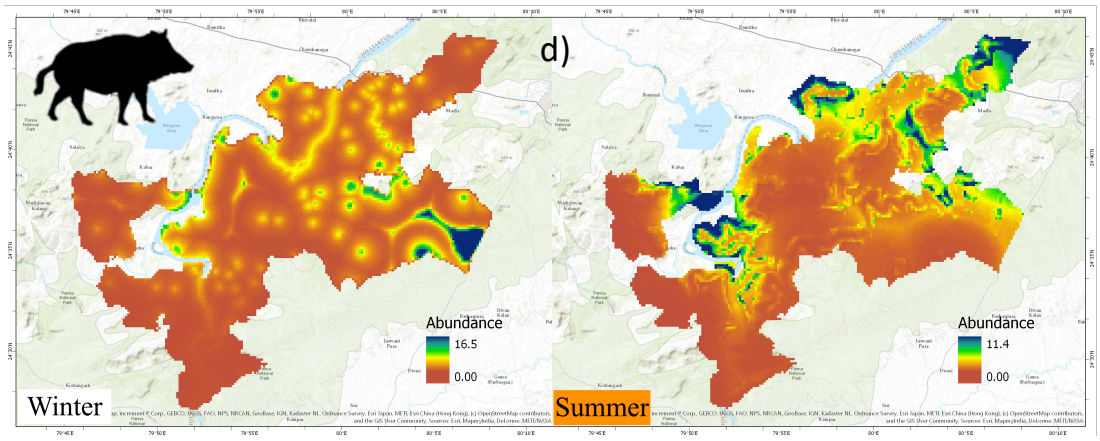
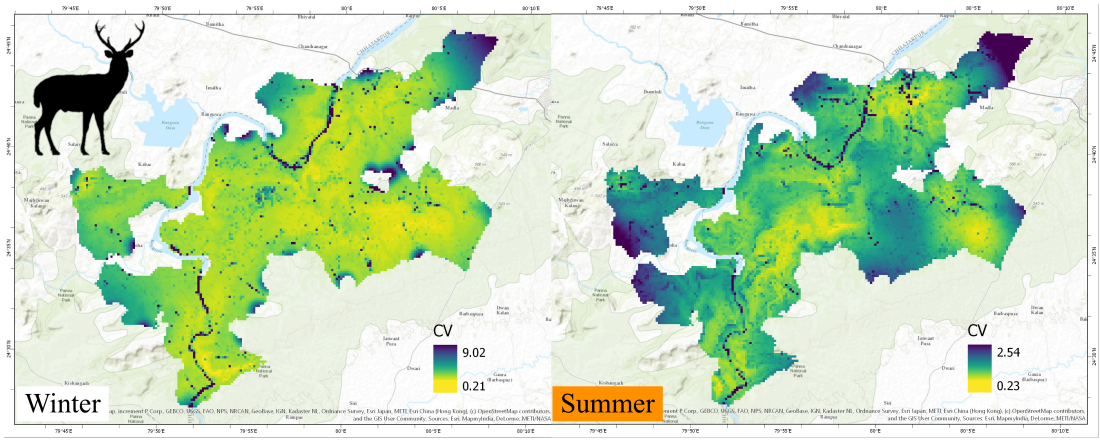


Figure 4.3 Maps of predicted seasonal density (individuals / 4hactares) gradient across the spatial extent of the study area for four ungulate species a) sambar, b) chital c) nilgai, d) wild pig. Here, colour gradient shows a different range of values in each map which was defined at the bottom of the map.



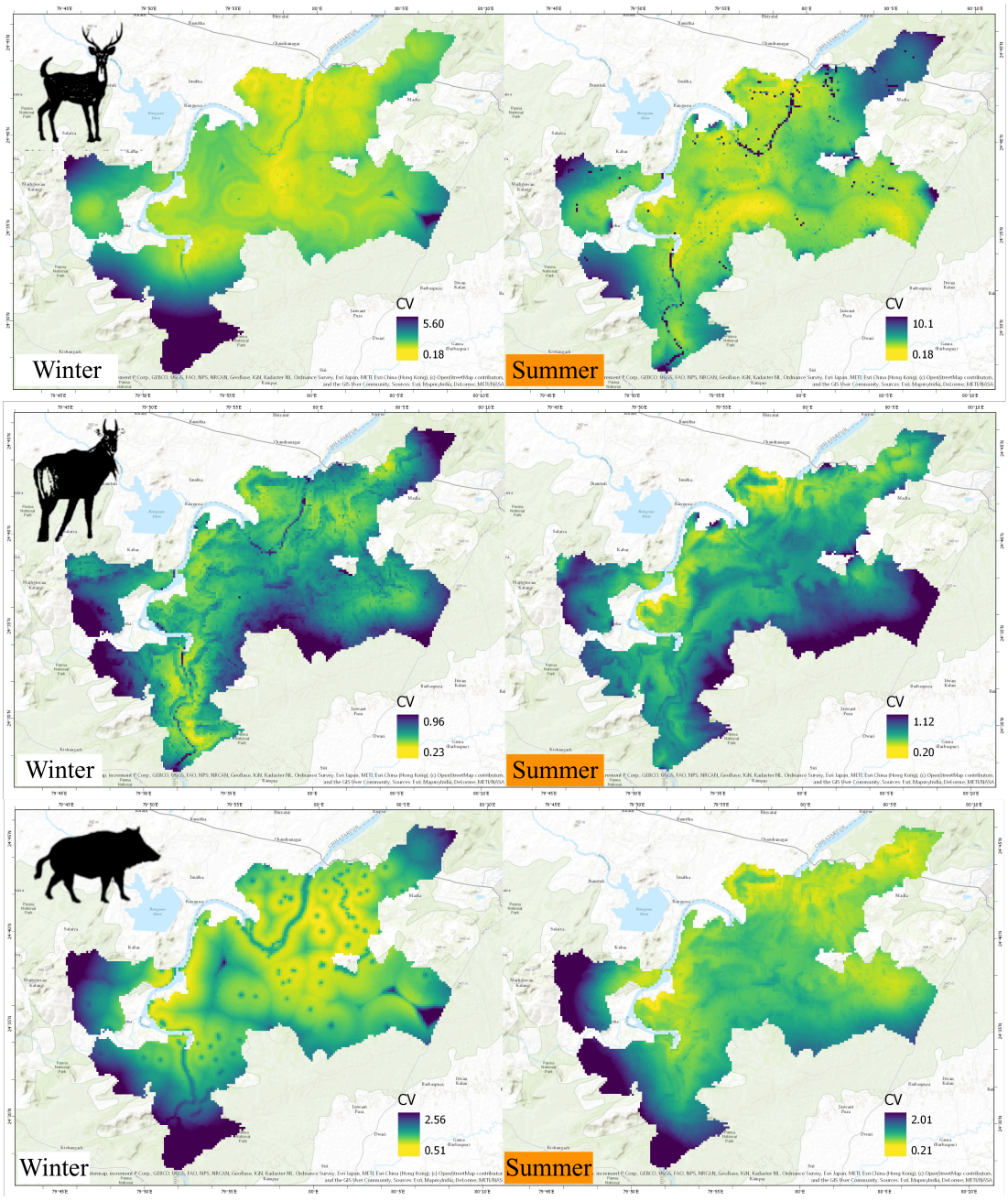


Figure 4.4 Map of the predicted coefficient of variations calculated from both detection function and GAM parameters of the model for four ungulate species (from the top) sambar, chital, nilgai and wild pig in both seasons.

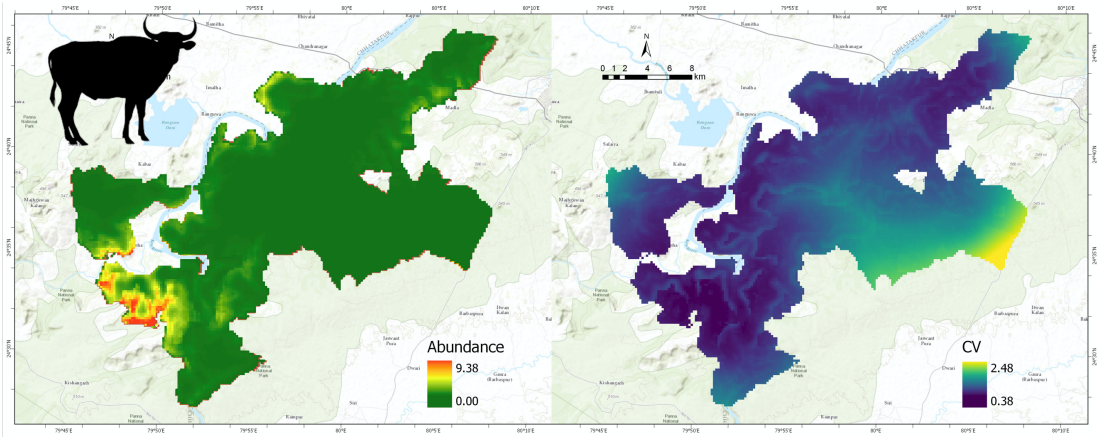


Figure 4.5 Maps of predicted seasonal density (individuals / 4hactares) and coefficient of variation across the spatial extent of the study area for feral cattle.

4.4 Discussion

4.4.1 Population estimates

This chapter found sambar and nilgai at higher densities than other protected areas in the central Indian landscape, such as; Kanha Tiger Reserve (TR), Bandhavgarh TR, Pench TR and Satpura TR (Jhala *et al.* 2018). They both are large-bodied prey of tiger and have helped in population recovery and maintaining a viable population of tigers in our study area. High densities of nilgai in our study area are directly related to the mosaic habitat of PTR, which provides suitable habitat to the species.

4.4.2 Spatio-temporal distribution and response to habitat variable

This study describes seasonal resource heterogeneity that drives density distribution of ungulates to the more suitable habitats and brings attention of the managers to allocated areas for planning effective conservation strategies. Tropical dry deciduous forests show strong seasonality, which in turn cause a difference in resource distribution across habitats (Singh & Chaturvedi 2018). Seasonal dynamics are so

evident that they cause animals to shift their habitat according to resource availability. Our results show a clear seasonal shift in the density distribution of four major ungulate species, more abundant in the valley habitat during summer.

The topography of dry deciduous forests plays a significant role in driving the density distribution of ungulates. Topography defines the ascending moisture gradient from the plateau to the valley, further related to the forage availability (Moura 2007, Singh & Chaturvedi 2018). Thus, when resources become scarce in summer, the valley fulfils all the habitat requirements such as shade to escape the heat, water and green foliage as forage (Schaller 1967, McKay & Eisenberg 1974, Johnsingh & Manjrekar 2015). Whereas in winters, when moisture is not a limiting factor for resource distribution across habitats, animals are distributed more evenly. Density distribution in various topographic regions is also associated with resource availability in different seasons. The plateaus are comparatively drier habitats, harbouring majorly deciduous trees that shed early winters, allowing more sunlight and therefore warmer. Animals move to plateaus to escape cold forest nights in winter. The valley on contrast, provide more shades with thick canopy and hence relatively colder. Consequently, all four species were distributed on the plateaus during winter.

Ungulates seasonal distribution is primarily influenced by the availability of suitable habitat, vegetation cover, water and lack of disturbance (Johnsingh & Manjrekar 2015, Neumann *et al.* 2015). Nilgai in central India is considered a crop-raider. (Sankar 1994), Awasthi *et al.* (2016) and Harihar *et al.* (2014) found Nilgai to be abundant in human-dominated landscapes. In our study, nilgai's positive relationship with distance from agriculture is explained by its habitat suitability to the relocated villages in PTR. There are 14 relocated villages in PTR that inhabit many fruiting trees and ample

grasses in winters provide excellent habitats for such mixed feeders (Sankar 1994). However, higher densities of chital and sambar away from anthropogenic variables explain their habitat preferences to the undisturbed forest.

Plateaus are the preferable habitats in winter as they provide ample resources due to the availability of water post-monsoon. In winter, streams and waterholes retain monsoonal water and thus support higher abundance than the valley. As summer approaches, water shrinks measurably in waterholes and streams. Wild Pig, a water-dependent species, prefers to stay near permanent water sources (Roberts 1997, Johnsingh & Manjrekar 2015, Kumar *et al.* 2021) and moves to areas where river water is easily accessible (Figure 4.3). Local movements and migration activities in response to water limitations in the dry season have been recorded in White-eared kob (Fryxell & Sinclair 1988a), khulan (Payne *et al.* 2020), African elephants (Purdon *et al.* 2018) and different ungulate species in Serengeti. However, browsers and grazers have similar water requirements (Kihwele *et al.* 2020), while few other mammals, such as bats (Heithaus *et al.* 1975) and primates (Brown & Zunino 1990), shift their diet to increase water intake through forage (Galetti & Pedroni 1994). Although the diet preferences have not been included in this study, we suspect that chital and sambar rely more on dietary flexibility for water requirements in the dry season as there was no significant relationship between water and population density for both species (Figure 4.3). Furthermore, water presence does not affect nilgai distributions and are more considerable with water sources (Prater 1990).

These results also show that sambar resource requirements match the chital in both seasons (Figure 4.3). Chital and sambar are both forest species which prefer dense vegetations in winter. This study highlights that group-living animals such as chital

formed larger groups in winter when resources were abundant. This might act as their anti-predatory behaviour, which helps them stay more vigilant when visibility is less, and the cost of resource sharing could be minimised (Johnsingh & Manjrekar 2015).

This chapter brings about the abundance of cattle inside the core area. After almost a decade of successful village relocation, Panna TR is still providing habitat to high number of free ranging cattle that are left behind. They compete with native wild ungulates for resources such as; forage, shelters etc and cause degradation to the habitat. They are the easy prey for large carnivores and contributes a significant proportion to the predator diet. Though their abundance are higher in the proximity of the reserve, they are congregated in large groups in relocated villages which further makes the habitat restoration difficult.

Chapter 5: Ungulate – habitat interaction

5.1 Background

Ungulates play an important role in shaping plant community structure, species richness and distribution directly by herbivory or indirectly by seed dispersal or soil development. They also act as major prey of large carnivores and their abundance and distribution is directly related to the large carnivore survival. The direction of these interactions has been debated over half a century (Cyr and Face 1993; Hairston, Smith, and Slobodkin 1960; Murdoch 1966) whether these ecosystem processes is controlled by top-down effect where ungulates abundance and distribution are regulated by intra-species competition and predation or by bottom-up effect where vegetation parameters regulate ungulates abundance through structural and chemical anti-herbivory mechanisms (Jia et al. 2018; Ramirez, Jansen, and Poorter 2018; Riginos and Grace 2008). In a tropical dry deciduous forest, a complex predator-prey-producer ecosystem, ungulates choose their habitat as to minimize predation risks and to maximize foraging opportunities. Ungulates such as primary browser (sambar), primary grazer (chital) and mixed feeder (nilgai) having different body size, habitat preferences and anti-predator strategies, might show a range of response to the vegetation parameters (tree density, basal area and species richness) and disturbance regimes.

Variation in tree density, cover and species diversity result in variation of forage availability and visibility. For instance, a forest stand with high tree species richness will probably have more palatable species, a choice of habitat for browser. Whereas higher understory cover might result into reduced grass growth and grazers will have to search for grasses in other patches. Ungulates impact on ecosystem have been studied and described unidirectional to multidirectional. It is subject to their

abundance, browsing intensity, biotic pressure, local abiotic factors and management practices whether ungulates have a negative, neutral or positive effect on plant regeneration, existence and survival (Boulanger et al. 2018; Hoven et al. 2022; Jia et al. 2018; Pinchot et al. 2022). Studies have reported unimodal response curve (Rooney and Waller 2003) with ungulates abundance and forest attributes where ungulates at optimum densities enhance forest growth and survival but affect forest negatively if overabundant (Côté et al. 2004; Hobbs 1996). Ungulates interactions in tropical dry deciduous forest are poorly studied. Understanding these interactions is crucial for better management practices. Ungulates response to terrain features and human presence has been described in previous chapter.

The previous chapter describes ungulates interactions with abiotic parameters such as terrain, slope, water availability etc. In this chapter I investigate ungulates interaction with vegetation parameters such as tree density, basal area, tree species richness and livestock grazing.

5.2 Methodology

5.2.1 Field survey

To quantify grass biomass across the reserve, I chose stratified random sampling. One line transect was placed in each beat; smallest administrative unit of the reserve. Another line transect was added to the beat if the area of the beat was more than 10 km^2 to get good sampling coverage. Thus, total 66 line transects were used for vegetation sampling. Length of line transects were kept 1.5km to 2km depending upon the habitat complexity.

i) Grass Biomass: One plot of 1m X 1m was sampled for the forest undergrowth keeping the interval of 250 meters between two plots on a line transect. Therefore, approximately seven plots were sampled on a line transect for grass biomass. All the undergrowth inside the plot were harvested using sharp cutting equipment and immediately weighed for the fresh weight. Unique species were segregated from the harvested vegetation in a plot and then packed in paper bags and oven dried. Dry weight was measured to estimate the biomass for each species. For analysis, grass biomass was separated and quantified from other growth forms. A total of 441 plots were sampled across the reserve post-monsoon in 2017 – 2018.

ii) Species palatability: To understand the palatability status of a plant species for a specific ungulate species, observations were taken in the field. An individual or a group of individuals were followed keeping a safe distance and observed through binoculars in the field. The plant species and the part of the plant that were being eaten were recorded to understand whether a species is palatable for specific ungulate species. Observations were taken for four ungulate species. These observations were matched with previous literature and local people's knowledge for each plant and ungulate species and a final list of palatable species were prepared (Annexure III).

5.2.2 Data procurement

Vegetation parameters such as tree basal area, tree density and biomass were calculated for each plot. Based on the palatability of each plant species for each ungulate, number of palatable species and number of non-palatable species were segregated for each plot. For each sampling point, abundance values of each ungulate species were extracted from the abundance maps given in previous chapter (Figure 4.3).

5.2.3 Statistical analysis:

i) Ungulate – habitat interactions: Regression was performed in R program to find out the interaction between each species of ungulates and vegetation parameters. Data exploration was done before regression for multicollinearity, extreme outliers and linearity and non-linearity between variables. Variance Inflation Factor (VIF) was used to check multicollinearity. Covariate was dropped from the analysis if VIF value was found higher than three. Relationship was checked between predictor and response variable and if found linear, GLM was performed. I found linear relationship between all the variables except livestock interaction with chital, nilgai and wild Pig and thus GAM was performed for these three interactions. Palatable species were not concluded for wild pig due to its omnivorous habits. Because of the strictly positive nature of the abundance data of ungulates (response variable), Gamma family distribution with log identity link was chosen for each analysis. The vegetation variables chosen for analysis are described in the table 5.1.

S. No	Variable	Measures	Explanation
1	Tree Basal Area (BA)	Basal area of trees having >10cm gbh	BA is the area covered with trees that represents ungulates need for cover, shade and shelter.
2	Tree density (Number)	Number of trees in a plot with gbh>10cm	This represents dense or open forest. Low tree density values show open forest.
3	Tree species richness (richness)	Number of tree species in a plot	PTR appears homogenous due to the presence of Teak. Teak is present conspicuously with all the

			communities. High species richness shows the presence of the mixed forest while less values shows the presence of homogenous patches such as; *A. pendula* and *T. grandis* pure patches.
4	Grass Biomass (G_bio)	Dry weight of all the grasses in a plot (1 X 1m)	Grass biomass represents grass height and the area covered with grasses in a plot. Degraded areas in PTR shows very poor grass growth. This variable includes both palatable and non-palatable grass biomass.
5	Lantana abundance (Lantana)	Number of *Lantana spp.* in a plot	Represents area covered with lantana
6	Livestock abundance (cattle)	Values extracted from spatial abundance maps (Chapter 4)	Represents the competition for resources with livestock

Table 5.1 A list of Vegetation parameters incorporated in analysis to find out interaction they have with wild ungulates.

ii) Ungulates – mediated effects: To understand ungulates mediated effects on vegetation, I chose sambar, a primary browser as a model species. The remaining three species, chital, nilgai and wild pig are primarily grazer, mixed feeder and omnivorous and therefore would show effects of other intrinsic and hidden factors. From the palatability list prepared earlier, I chose 5 the most preferred species for sambar based

on the observations taken in field. A 5-meter X 5-meter square plot was sampled to count the number of seedlings of these 5 preferred species in each plot. Seven plots were sampled on a transect line (previously placed in a beat) and therefore a total of 361 plots were sampled. Sambar' point density was extracted for each vegetation plot from the abundance maps generated in chapter 2. A GLM with Poisson family distribution was run to find out the sambar's effect on the seedling abundance in PTR.

5.3 Results

5.3.1 Ungulate – habitat interactions

Sambar shows significant positive relationship with basal area, species richness, tree density and grass biomass and negative relationship with *Lantana* and livestock abundance. However, relationship with *Lantana* and grass biomass were not found to be significant.

Chital shows significant positive relationship with basal area and tree density while negative relationship with *Lantana* abundance. Chital, nilgai and wild Pig show the similar non-linear response curve with livestock abundance. Their abundance increases with livestock abundance to a certain limit and then declines sharply with increasing livestock abundance. Chital did not show any significant relationship with species richness and grass biomass.

Nilgai, similarly as chital and sambar shows significant positive relationship with basal area and tree density and significant negative relationship with lantana abundance. The relationship with grass biomass and species richness were not significant for nilgai.

Wild pig did not show any significant relationships with any variable except *Lantana* abundance and livestock abundance. They are negatively related with *Lantana* abundance.

5.3.2 Ungulates mediated effects on vegetation structure and biomass

Sambar showed preference to the *Z. xylopyrus*, *Helictres isora*, *Aegle marmelos*, *Bamboo* spp. and *Acacia catechu* in PTR. It was found to be in positive interaction with seedlings of palatable species (Figure 5.1). Seedlings of palatable species were abundant where sambar was also abundant.

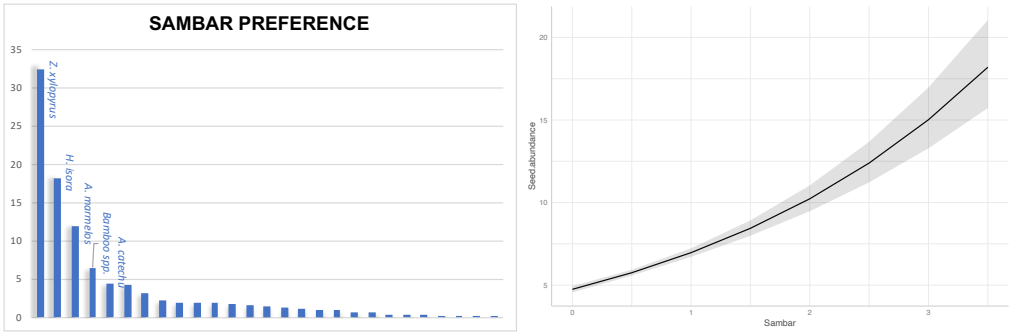
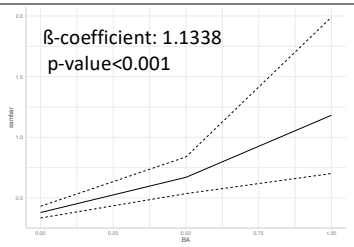
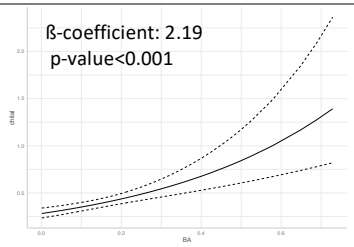
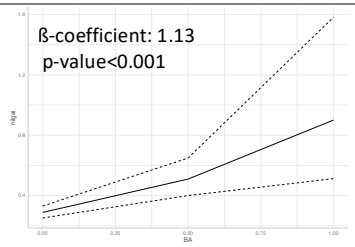
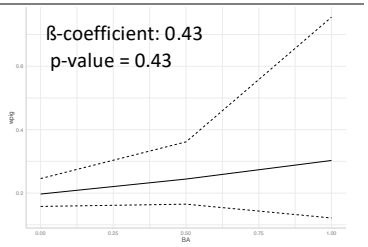
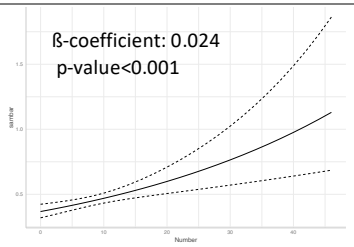
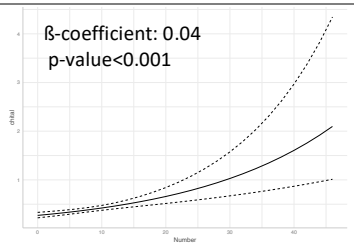
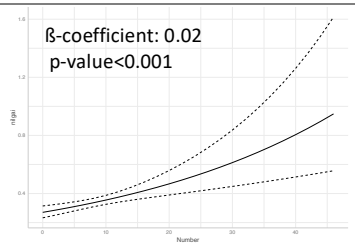
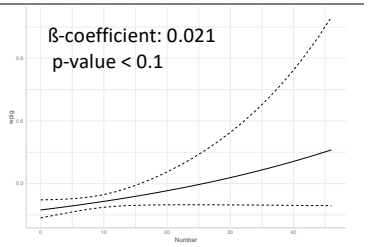
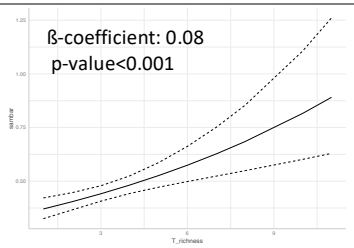
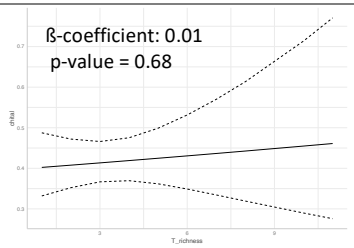
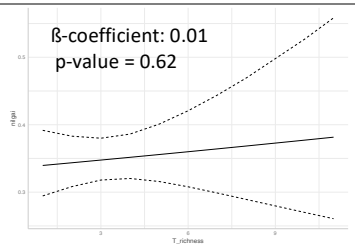
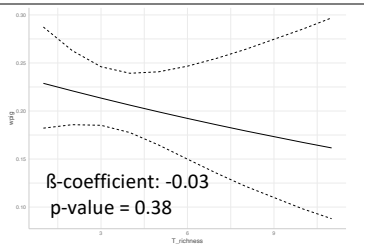


Figure 5.1 Ungulates-mediated effects: a) Sambar's preferred floral species b) Sambar's interaction with seedlings of preferred palatable species.

	Sambar	Chital	Nilgai	Wild Pig
Tree Basal Area				
Tree density				
Tree species richness				

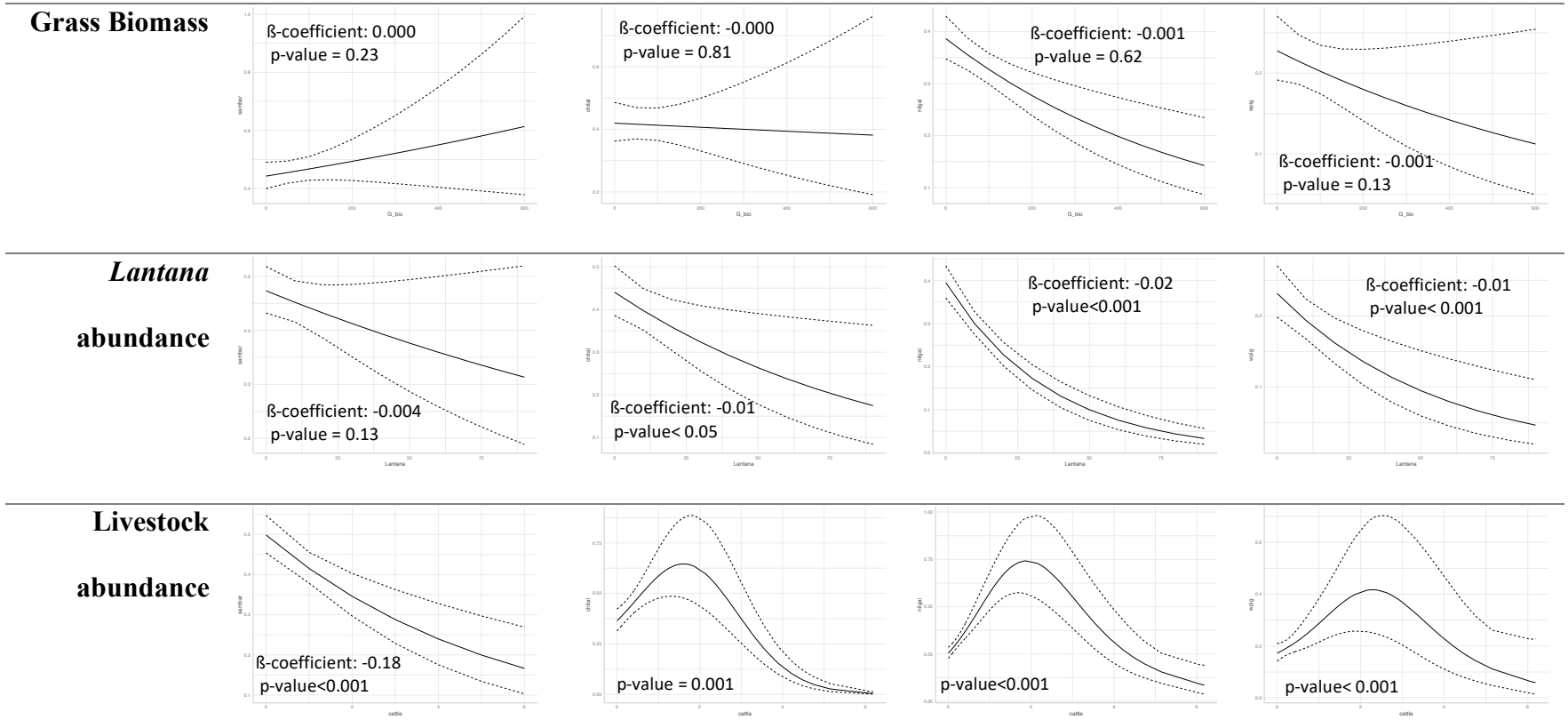


Figure 5.2 Ungulates interaction with vegetation parameters for four ungulate species; sambar, chital, nilgai, wild pig. Here, p-value shows the significance of the interaction.

5.4 Discussion

5.4.1 Ungulate – habitat interaction

Sambar's positive relationship with tree basal area suggests its preference to the forest that is densely occupied with trees. Whereas its preference to the mixed forest (positive relationship with tree species richness) is attributed to the possibility of high browse availability when species richness is high (Loreau and Hector 2001) (A forest stand with higher number of tree species have higher chances of encountering a palatable species in the forest stand). There are three tree communities in Panna TR with high species richness; open woodland, *T. grandis* mixed forest and *A. catechu* mixed forest. These communities are dominated by highly palatable species such as; *Z. mauritiana*, *Z. xylopyrus*, *A. catechu* and *A. donaldii* (Chapter 1). These three communities also show higher AGB than the other communities. Sambar's preference to the densely occupied mixed forest can be related to its preference to these communities.

Sambar's negative relationship with livestock abundance clearly shows its competition with livestock and avoidance to the degraded habitats. Sambar's habitat preferences to the undisturbed habitats makes its conservation a challenging task for conservationists and give a justification to its declining population. Most of the habitat in tropical dry deciduous forests are in degraded forms due to high anthropogenic pressure which makes its distribution restricted to protected areas only. Nevertheless, protected areas are also shrinking and facing fragmentation due to upcoming and unregulated developmental activities, making its conservation more challenging.

Chital preferred forest with high tree density and basal area. Chital's non-significant relationship with tree species richness shows that it probably prefers both homogenous and mixed forest patches. Chital is primarily a grazer and did not show significant

relationship with grass biomass. But while segregating grass biomass into palatable and non-palatable categories, Chital showed significant positive relationship with palatable grass biomass (Figure 5.3). This also signifies its non-significant relationship with tree species richness that Chital abundance do not depend on browse availability. If I compare Chital's relationship with grass biomass to palatable grass biomass, it clearly indicates that Chital do not use grass cover as hide, shelter or anti-predation strategies. Rather it stays in large groups to be more vigilant. Chital's negative relationship with Lantana abundance can be explained by two reasons first, overabundance of Lantana makes the area inaccessible for large group to freely move around and second, Lantana suppresses the grass growth (Figure 5.3) and thus those areas will be devoid of forage for Chital.

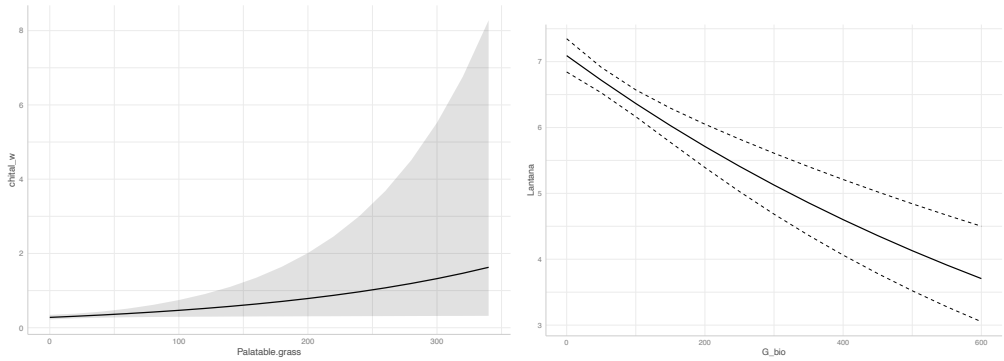


Figure 5.3 a) Chital's significant positive interaction with available palatable grass biomass b) Lantana spp. interaction with grass biomass.

Chital, nilgai and wild Pig's non-linear relationship with livestock is because of the habitats relocated villages provides in Panna TR. Relocated villages are the primary habitat for livestock, also harbor many fruiting trees which attracts wild herbivores in appropriate season. All three ungulates show some tolerance with livestock in these

habitats. But they show sharp decline in abundance with increasing livestock abundance in other habitats.

Nilgai and wild Pig show similar habitat preferences in terms of vegetation parameters however, their preference to terrain features and water dependency is distinct (chapter 2). This is probably the reason that they show spatial overlap in winter but distinct abundance gradient in summer (Figure 4.3). Both ungulates show positive significant relationship with tree basal area and tree density that show their preference to dense and old growth trees. As both ungulate species have varying diet preference, nilgai being mixed feeder and wild Pig being an omnivore, their abundance do not get affected by grass biomass and tree species richness. Both species seem to avoid high *Lantana* abundance.

Schaller (1967) describes four broad habitat requirements which can limit ungulates distribution in their native range; a) terrain b) forage c) water d) disturbance regime. This chapter in combination of the previous chapter represent a clear picture of interactions four species of ungulates may have with their habitat.

5.4.2 Ungulate mediated effects

Sambar's response curve with seedling abundance shows sambar's role in seedling recruitment of the palatable species. Sambar play an important role in seed dispersal through regurgitation and are known to disperse seeds in large quantity over large distances (Brodie 2007; McConkey et al. 2018). In PTR, sambar was also observed feeding on *A. marmelos*, A. catechu and *Zizyphus* spp. fruit on many occasions and might be responsible for recruitment of these species.

Chapter 6 General discussion

6.1 Synthesis

In this study, I assessed the dominant tree species in PTR in combination of tree community composition. This study describes five dominant tree community composition including Ziziphus woodlands as forest regrowth in PTR describing their current status of abundance and richness. This is the first time that tree community composition has been studied in PTR. *Z. xylopyrus*, *A. catechu*, *A. pendula* and *A. donaldii* are among the ten dominant tree species and are also the most palatable species for browsing for sambar, chital and nilgai in PTR. Sambar also play a role in seed recruitment of these palatable species. Three communities viz., *T. grandis* mixed forest, *A. catechu* mixed forest and open woodlands show the highest species diversity and are the most abundant in PTR. The former two communities also record the highest biomass among other communities. High abundance of sambar to tree basal area, tree density and species richness might attribute to its presence to these communities. PTR's rugged terrain and availability of the preferred habitat for sambar is probably the reason that sambar is found in high densities in PTR as compared to other protected areas in central Indian landscape. Sambar's avoidance to livestock and human proximity seem to be the only reason that might limit the species distribution in PTR. The Non-significant response of chital abundance to grass biomass and significant response to palatable grasses signifies that chital do not use grasses as cover, hide or shelter. However, group-living chital forms large groups in winter to remain vigilant when resource sharing is cost effective. Chital and sambar showed similar response to vegetation parameters and habitat conditions and thus their spatial abundance range overlapped across seasons.

Nilgai is considered as a crop-raider and many states like Rajasthan, Bihar, Uttar Pradesh, Haryana and Madhya Pradesh has notified this species as vermin. This study emphasizes positive relation of nilgai abundance to distance from agricultural fields and livestock tolerance. That is why nilgai was found to show preference to relocated villages inside park. Relocated villages (not all the villages) in PTR, which are now abandoned sites, has grown into a variety of habitats with plentiful forage in terms of fruiting trees and grasses providing the best suitable habitats for mixed feeder species such as nilgai. This signifies that if habitat management in protected area is done with mindfulness of ungulates preferences, ungulate conflict in fringe area can be reduced enormously.

Three distinct seasons and distinctive topography in PTR provided a matchless setup to study distribution of ungulates across season. Seasonal shift of all ungulates from plateau to valley in summer directly indicates that there are only a few locations which fulfils the ungulates habitat requirements in summer. Ungulates face inter-species competitions for those locations in summer. This study discusses species and season specific conservation priority areas are for ungulate species inclusive of driving environmental parameters. This will help habitat managers to allocate conservation efforts to those areas. Conservation efforts focussing ungulates will directly benefit the large carnivore and habitat quality.

This study uses Density Surface Modelling (DSM) to map the ungulates abundance which combines spatial modelling techniques with Conventional Distance Sampling (CDS) considering the detection probability at each sampling unit and build robust abundance maps. The abundance maps generated in this study are extremely flexible and can be used to extend the results to large spatial scales with reliability. These maps

also provide straightforward interpretation of complex scientific algorithms and are useful to communicate results to non-specialists. This is a new, robust and cost-effective methodology to study seasonal distribution of ungulates across various topographic regions.

6.2 Future recommendations

1. Relocated villages in PTR has potential to grow into a suitable ungulate habitat but in absence of appropriate habitat management they are becoming full of non-palatable grasses. At many villages, species such as *Ziziphus nummularia* are encroaching the habitat massively and making the complete habitat inaccessible for ungulates. A grassland management plan has to be prepared soon after the village relocation to avoid habitat encroachment by non-native species (trees and grasses) and most benefit the animal species inside the park.

2. As result stated, PTR is facing severe habitat degradation due to large number of cattle. These cattle include feral and free-ranging animals, forage inside the park and cause forest degradation. Debarking of trees is prominent in the areas with high cattle density. The huge damage is caused by the herds of goat and sheep that graze in the fringe areas of the tiger reserve core habitat. These goats are followed by shepherds who lop many palatable trees in order to provide forage. These activities need to be monitored and regulated for further habitat damage.

3. PTR has high abundance of *Lantana* and makes habitat unsuitable for chital, nilgai and wild pig, as they show a clear avoidance with *Lantana*. There was no activity regarding the control of Lantana during field work in PTR. Though Lantana eradication is easier said than done, but its propagation to the new locations should be controlled by active monitoring and appropriate strategies.

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Annexure I

Supplementary material

Chapter 3 Vegetation structure and community composition

Table S3.1 List of floral species in Panna Tiger Reserve

1. Trees

S. No.	Family	Vernacular name	Botanical name
1	Anacardiaceae	Aam	*Mangifera indica*
2	Anacardiaceae	Achar	*Buchanania cochinchinensis*
3	Anacardiaceae	Goonja	*Lannea coromandelica*
4	Anacardiaceae	Khatua	*Toxicodendron parviflorum*
5	Anacardiaceae	Ameda	*Spondias pinnata*
6	Annonaceae	Kari	*Miliusa tomentosa*
7	Annonaceae	Sitafal	*Annona reticulata*
8	Apocynaceae	Doodhi	*Wrightia tinctoria*
9	Apocynaceae	Kurro	*Holarrhena pubescens*
10	Apocynaceae	Doodhi	*Wrightia arborea*
11	Arecaceae	Khajoori	*naringi crenulata*
12	Bignoniaceae	Jaichar	*Dolichandrone falcata*
13	Bignoniaceae	Padar/ Aandhi	*Sterreospermum chelonoides*
14	Boraginaceae	Labedo	*Cordia myxa*
15	Burseraceae	Salai	*Boswellia serrata*
16	Caesalpinioideae	Amaltash	*Cassia fistula*
17	Caesalpinioideae	Kachnar	*Bauhinia variegata*
18	Caesalpinioideae	Mohli	*Bauhinia racemosa*
19	Caesalpinioideae		*Bauhinia purpuria*
20	Caesalpinioideae	Aamti	*Bauhinia malabarica*
21	Caesalpinioideae	Vayni	*Delonix elata*

22	Celastraceae	Jamrassi	*Cassine glauca*
23	Celastraceae	Vyakul	*Gymnosporia senegalensis*
24	Cochlospermaceae	Gabdu	*Cochlospermum religiosum*
25	Combretaceae	Baheda	*Terminalia bellirica*
26	Combretaceae	Dhawa	*Anogeissus latifolia*
27	Combretaceae	Harra	*Terminalia chebula*
28	Combretaceae	Kardhai	*Anogeissus pendula*
29	Combretaceae	Koha	*Terminalia arjuna*
30	Combretaceae	Sajh	*Terminalia eliptica*
31	Combretaceae	Oolta saaj	*Terminalia crenulata*
32	Ebenaceae	Tendu	*Diospyros melanoxylon*
33	Euphorbiaceae	Kapasua	*Mallotus nudiflorus*
34	Euphorbiaceae	Rori	*Mallotus philippensis*
35	Euphorbiaceae	Thuar	*Euphorbia nivulia*
36	Fabaceae	Imli	*Tamarindus indica*
37	Faboideae	Beeja	*Pterocarpus marsupium*
38	Faboideae	Hadua	*Erythrina suberosa*
39	Faboideae	Palash	*Butea monosperma*
40	faboideae	Sandhan	*Desmodium oojeinense*
41	Faboideae	Sison	*Dalbergia latifolia*
42	Faboideae	Dhamasi	*Dalbergia lanceolaria*
43	Faboideae	Dhobin	*Dalbergia lanceolaria subspecies paniculata*
44	Faboideae	Gadha palash	*Erythrina stricta*
45	Faboideae	Kanji	*Pongamia pinnata*
46	Lamiaceae	Khamer	*Gmelina arborea*
47	Lamiaceae	Teak	*Tectona grandis*
48	Lecythidaceae	Khumai	*Careya arborea*
49	Lythraceae	Sijwa	*Lagerstroemia parviflora*
50	Malvaceae	Banga	*Kydia calycina*
51	Malvaceae	Bhoti	*Eriolaena hookeriana*

52	Malvaceae	Dhaman	*Grewia tiliifolia*
53	Malvaceae	Kulu	*Sterculia urens*
54	Malvaceae	Semal	*bombax ceiba*
55	Malvaceae	Udar	*Sterculia villosa*
56	Malvaceae	Dhamna	*Grewia orbiculata*
57	Malvaceae	Kasul	*Grewia eriocarpa*
58	Meliaceae	Neem	*Azadirachta indica*
59	Meliaceae	Rohan	*Soymida febrifuga*
60	Mimosoideae	Babool	*Acacia nilotica*
61	Mimosoideae	Khair	*Acacia catechu*
62	Mimosoideae	Gurar	*Acacia donaldii*
63	Mimosoideae	Reonja	*Acacia leucophloea*
64	Mimosoideae	Sirsa	*Albizia procera*
65	Mimosoideae	Goya khair	*Dichrostachys cinerea*
66	Mimosoideae	Yerma	*Albizia odoratissima*
67	Moraceae	Bargad	*Ficus benghalensis*
68	Moraceae	Gadasi	*Ficus microcarpa*
69	Moraceae	Katbar	*Ficus mollis*
70	Moraceae	Katpeepli	*Ficus arnottiana*
71	Moraceae	Pipal	*Ficus religiosa*
72	Moraceae	Umar	*Ficus racemosa*
73	Moraceae	Pakhad	*Ficus virens*
74	Moraceae	Piprani	*Ficus lambertiana*
75	Myrtaceae	Jamun	*Syzygium cumini*
76	Myrtaceae	Katjamun	*Syzygium salicifolium*
77	Myrtaceae	Amrood	*Psidium guajava*
78	Oleaceae	Mokha	*Schrebera swietenioides*
79	Phyllanthaceae	Aamla	*Phyllanthus emblica*
80	Phyllanthaceae	Kasai	*Bridelia retusa*
81	Phyllanthaceae	Khatua	*Antidesma ghaesembilla*
82	Rubiaceae	Bhadare	*Tamilnadia uliginosa*

83	Rubiaceae	Haldu	*Haldina cordifolia*
84	Rubiaceae	Kaima	*Mitragyna parvifolia*
85	Rubiaceae	Karar	*Ceriscoides turgida*
86	Rubiaceae	Mainhar	*Catunaregam spinosa*
87	Rubiaceae	Papda	*Gardenia latifolia*
88	Rubiaceae	Bhormal	*Hymenodictyon orixense*
89	Rutaceae	Bel	*Aegle marmelos*
90	Rutaceae	Bilsena	*Naringi crenulata*
91	Rutaceae	Kaitha	*Limonia acidissima*
92	Rutaceae	Karineem	*Bargera koenigii*
93	Rutaceae	Rakatbera	*Muraya paniculata*
94	Rutaceae	Bhirra	*Chloroxylon swietenia*
95	Salicaceae	Binjari	*Salix tetrasperma*
96	Salicaceae	Katai	*Flacourtia indica*
97	Salicaceae	Ban Beri	*Casearia elliptica*
98	Salicaceae	Gilchi	*Casearia graveolens*
99	Salvadoraceae	Jaal	*Salvadora persica*
100	Sapindaceae	Kosum	*Schleichera oleosa*
101	Sapotaceae	Khoojai	*Manilkara hexandra*
102	Sapotaceae	Mahua	*Madhuca longifolia*
103	Simaroubaceae	Mahaneem	*Ailanthus excelsa*
104	Rubiaceae	--	*Hymenodictyon excelsum*
105	Mimosaceae	--	*Pithecellobium dulce*
106	Rubiaceae	--	*Morinda tinctoria*
107	Bignoniaceae	--	*Stereospermum chelonoides*

2. Shrubs

S. No.	Family	Botanical name	Growth form	Collection number
108	Malvaceae	*Abutilon incanum*	Shrub	PNTR 84
109	Malvaceae	*Abutilon indicum*	Shrub	PNTR 109
110	Asparagaceae	*Asparagus adscendens*	Shrub	PNTR 50
111	Acanthaceae	*Barleria prionitis*	Shrub	PNTR 95
112	Capparaceae	*Capparis zeylanica*	Shrub	PNTR 123
113	Apocynaceae	*Carissa carandas*	Shrub	Digital
114	Phyllanthaceae	*Flueggea sp*	Shrub	PNTR 126
115	Tiliaceae	*Grewia damine*	Shrub	PNTR 87
116	Rubiaceae	*Hedyotis fruticosa*	Shrub	PNTR 88
117	Mimosaceae	*Mimosa rubicaulis*	Shrub	
118	Rubiaceae	*Randia dumetorum*	Shrub	PNTR 110
119	Tiliaceae	*Triumfetta rhomboidea*	Shrub	PNTR 145
120	Lythraceae	*Woodfordia fruticosa*	Shrub	PNTR 146
121	Rhamnaceae	*Ziziphus oenoplia*	Shrub	Digital
122	Malvaceae	*Sida rumboidia*	Shrub	PNTR 20751
123	Rubiaceae	*Randia tetrasperma*	Shrub	PNTR 20744
124	Salicaceae	*Caseria tomentosa*	Shrub/small tree	Digital
125	Euphorbiaceae	*Securinega virosa*	Shrub/small tree	PNTR 20747
126	Capparaceae	*Crateva religiosa*	Small tree	PNTR 57
127	Verbenaceae	*Lantana americana*	Shrub	
128	Verbenaceae	*Lantana camara*	Shrub	
129	Malvaceae	*Helicteres isora*	Shrub	(Enthi)
130	Apocynaceae	*Carissa spinarum*	Shrub	(Karonda)
131	Oleaceae	*Nyctanthes arbor-tristis*	Small tree	(Siharu)

132	Rhamnaceae	*Ziziphus mauritiana*	Small tree	
133	Rhamnaceae	*Ziziphus xylopyrus*	Small tree	
134	Verbenaceae	*Vitex negundo*	Shrub	PNTR 157
135	Solanaceae	*Datura innoxia*	Shrub	Digital
136	Rubiaceae	*Morinda spp.*	Shrub	NIL
137	Loranthaceae	*Dendrophthoe falcata var. coccinea*	Parasitic shrub	PNTR 58
138	Rhamnaceae	*Ziziphus nummularia*	Shrub	

3. Climbers

S. No.	**Family**	**Botanical name**	**Growth form**	**Collection number**
139	Vitaceae	*Ampelocissus latifolia*	Climber	PNTR 65
140	Leguminosae	*Atylosia scarabaeoides*	Climber	PNTR 117
141	Vitaceae	*Cayratia trifolia*	Climber	PNTR 156
142	Celastraceae	*Celastrus paniculata*	Climber	PNTR 148
143	Menispermaceae	*Cissampelos pareira*	Climber	PNTR 114
144	Vitaceae	*Cissus repanda*	Climber	PNTR 139
145	Menispermaceae	*Cocculus hirsutus*	Climber	PNTR 152
146	Convolvulaceae	*Convolvulus arvensis*	Climber	PNTR 75
147	Apocynaceae	*Cryptolepis buchananii*	Climber	PNTR 153
148	Dioscoreaceae	*Dioscorea bulbifera*	Climber	PNTR 100
149	Liliaceae	*Gloriosa superba*	Climber	PNTR 86
150	Asclepiadaceae	*Gymnema sylvestre*	Climber	PNTR 118
151	Malpighiaceae	*Hiptage benghalensis*	Climber	PNTR 68

152	Apocynaceae	*Ichnocarpus frutescens*	Climber	PNTR 108
153	Convolvulaceae	*Ipomea pes-tigridis*	Climber	PNTR 102
154	Cucurbitaceae	*Mukia maderaspatana*	Climber	PNTR 116
155	Convolvulaceae	*Porana paniculata*	Climber	PNTR 99
156	Fabaceae	*Rhynchosia minima*	Climber	PNTR 155
157	Apocynaceae	*Telosma pallida*	Climber	PNTR 94
158	Cucurbitaceae	*Trichosanthes cucumerina*	Climber	PNTR 26
159	Apocynaceae	*Tylophora hirsuta*	Climber	PNTR 151
160	Cucurbitaceae	*Zehneria scabra*	Climber	PNTR 147
161	Rhamnaceae	*Ventilago calyculata Tul.*	Climber	PNTR 20745
162	Solanaceae	*Ziziphus oenoplia*	Climber	(Makoi; Digital herbarium)
163	Vitaceae	*Tetrastigma sp*	Climber	PNTR 143, PNTR 62
164	Convolvulaceae	*Ipomea sp.*	Climber	PNTR 56
165	Fabaceae	*Rhynchosia sp.*	Climber	PNTR 29
166	Fabaceae	*Butea superba*	Climber	Digital
167	Caesalpinioideae	*Bauhinia vahlii*	Climber	(Mohlan; Digital herbarium)

4. Grasses and Sedge

S. No.	Family	Botanical name	Growth form	Collection number
167	Poaceae	*Bamboo spp*	Grass	
168	Poaceae	*Alloteropsis cimicina*	Grass	PNTR 4
169	Poaceae	*Aristida adscendens*	Grass	PNTR 26, PNTR 27, PNTR 195
170	Poaceae	*Arundinella pumila*	Grass	PNTR 106
171	Poaceae	*Bothriochloa ischaemum*	Grass	PNTR 35, PNTR 39
172	Poaceae	*Brachiaria ramosa*	Grass	PNTR 32
173	Poaceae	*Brachiaria villosa*	Grass	PNTR 31
174	Poaceae	*Cenchrus setigerus*	Grass	PNTR 41
175	Poaceae	*Chloris incompleta*	Grass	PNTR 74
176	Poaceae	*Chloris pallid*	Grass	PNTR 23
177	Poaceae	*Chloris virgata*	Grass	PNTR 22
178	Poaceae	*Chrysopogon fulvus*	Grass	PNTR 172
179	Poaceae	*Chrysopogon serrulatus*	Grass	PNTR 37
180	Poaceae	*Cynodon dactylon*	Grass	PNTR 44
181	Poaceae	*Desmostachya bipinnata*	Grass	PNTR 1
182	Poaceae	*Dicanthium annulatum*	Grass	PNTR 135
183	Poaceae	*Digitaria adscendens*	Grass	PNTR 19, PNTR 21
184	Poaceae	*Digitaria stricta*	Grass	PNTR 20
185	Poaceae	*Echinochloa colona*	Grass	PNTR 80

186	Poaceae	*Elytrophorus spicatus*	Grass	PNTR 2
187	Poaceae	*Eragrostiella nardoides*	Grass	PNTR 134
188	Poaceae	*Eragrostis bifaria*	Grass	PNTR 6
189	Poaceae	*Eragrostis stenophylla*	Grass	PNTR 30
190	Poaceae	*Eragrostis tenella*	Grass	PNTR 5
191	Poaceae	*Eragrostis unioloides*	Grass	PNTR 7, PNTR 29
192	Poaceae	*Eragrostis viscosa*	Grass	PNTR 189
193	Poaceae	*Eremopogon foveolatus*	Grass	PNTR 43
194	Eriocaulaceae	*Eriocaulon sp*	Grass	PNTR 127
195	Poaceae	*Hackelochloa granularis*	Grass	PNTR 36
196	Poaceae	*Heteropogon contortus*	Grass	PNTR 38
197	Poaceae	*Imperata cylindrica*	Grass	DIgital
198	Poaceae	*Iseilema laxum*	Grass	
199	Poaceae	*Oplismenus burmanni*	Grass	PNTR 34
200	Poaceae	*Oplismenus composites*	Grass	PNTR 33
201	Poaceae	*Panicum miliaceum*	Grass	PNTR 25
202	Poaceae	*Panicum sumatrense*	Grass	PNTR 25
203	Poaceae	*Panicum virgatum*	Grass	PNTR 24
204	Poaceae	*Paspalum scrobiculatum*	Grass	PNTR 137
205	Poaceae	*Setaria glauca*	Grass	PNTR 42
206	Poaceae	*Sorghum halepense*	Grass	PNTR 128

207	Poaceae	*Spodiopogon rhizophorus*	Grass	PNTR 45
208	Poaceae	*Sporobolus diander*	Grass	PNTR 136
209	Poaceae	*Themeda anathera*	Grass	
210	Poaceae	*Themeda quadrivalvis*	Grass	Digital
211	Poaceae	*Themeda triandra*	Grass	PNTR 46
212	Poaceae	*Vetiveria zizanioides*	Grass	PNTR 28
213	Poaceae	*Agrostis stenophylla*	Grass	Digital
214	Poaceae	*Chloris dolichostachya*	Grass	Digital
215	Poaceae	*Cymbopogon martinii*	Grass	Digital
216	Poaceae	*Eragrostis intreputa*	Grass	Digital
217	Poaceae	*Ischamum indicum*	Grass	Digital
218	Poaceae	*Ischamum aristatum*	Grass	Digital
219	Poaceae	*Sporobolus pallidus*	Grass	Digital
220	Poaceae	*Cyperus bervifolious*	Grass	Digital
221	Poaceae	*Arthraxon hispidus*	Grass	NIL
222	Poaceae	*Brachiaria eruciformis*	Grass	NIL
223	Poaceae	*Digitaria sanguinalis*	Grass	NIL
224	Cyperaceae	*Cyperus iria*	Sedge	PNTR 134, PNTR 14
225	Cyperaceae	*Cyperus kyllingia*	Sedge	PNTR 10
226	Cyperaceae	*Cyperus metzii*	Sedge	PNTR 17
227	Cyperaceae	*Cyperus nutans*	Sedge	PNTR 23
228	Cyperaceae	*Cyperus pumilus*	Sedge	PNTR 9
229	Cyperaceae	*Cyperus rotundus*	Sedge	PNTR 8
230	Cyperaceae	*Cyperus sp.*	Sedge	PNTR 12

231	Cyperaceae	*Fimbristylis dichotoma*	Sedge	PNTR 16, PNTR 13, PNTR 18
232	Cyperaceae	*Fimbristylis miliacea*	Sedge	PNTR 85
233	Cyperaceae	*Scirpus articulates*	Sedge	PNTR 11

5. Herbs

S. No.	**Family**	**Botanical name**	**Growth form**	**Collection number**
234	Adiantaceae	*Adiantum incisum*	Fern	PNTR 47
235	Adiantaceae	*Adiantum lunulatum*	Fern	PNTR 48
236	Adiantaceae	*Adiantum cuneatum*	Fern creeper	PNTR 50
237	Amaranthaceae	*Achyranthes aspera*	Herb	PNTR 93
238	Amaranthaceae	*Aerva lanata*	Herb	PNTR 192
239	Amaranthaceae	*Aerva scandens*	Herb	PNTR 149
240	Fabaceae	*Aeschynomene indica*	Herb	PNTR 64
241	Acanthaceae	*Ageratum conyzoides*	Herb	PNTR 183, PNTR 198
242	Fabaceae	*Alysicarpus bupleurifolius*	Herb	PNTR 66
243	Fabaceae	*Alysicarpus vaginalis*	Herb	PNTR 66
244	acanthaceae	*Andrographis echioides*	Herb	PNTR 184
245	Convolvulaceae	*Argyreia nervosa*	Herb	PNTR 141
246	Asteraceae	*Bidens biternata*	Herb	PNTR 101
247	Asteraceae	*Bidens pilosa*	Herb	PNTR 150

248	Acanthaceae	*Blepharis maderaspatensis*	Herb	PNTR 71
249	Rubiaceae	*Borreria stricta*	Herb	PNTR 72
250	Asteraceae	*Caesulia axillaris*	Herb	PNTR 138
251	Gentianaceae	*Canscora decussata*	Herb	PNTR 61
252	Caesalpiniaceae	*Cassia mimosoides*	Herb	PNTR 119
253	Adiantaceae	*Cheilanthes farinosa*	Herb	PNTR 49
254	Liliaceae	*Chlorophytum tuberosum*	Herb	PNTR 133
255	Cleomaceae	*Cleome viscosa*	Herb	PNTR 103
256	Commeliniaceae	*Commelina erecta*	herb	PNTR 120
257	Commeliniaceae	*Commelina obliqua*	herb	PNTR 53
258	Tiliaceae	*Corchorus aestuans*	Herb	PNTR 111
259	Leguminosae	*Crotalaria albida*	Herb	
260	Fabaceae	*Crotalaria prostrata*	Herb	PNTR 177
261	Malvaceae	*Croton sp*	Herb	PNTR 76
262	Hypoxidaceae	*Curculigo orchioides*	Herb	PNTR 112
263	Commeliniaceae	*Cyanotis sp.*	Herb	PNTR 52
264	Fabaceae	*Desmodium gangeticum*	Herb	PNTR 158
265	Fabaceae	*Desmodium heterocarpon*	Herb	PNTR 77
266	Fabaceae	*Desmodium laxiflorum*	Herb	PNTR 78
267	Fabaceae	*Desmodium pulchellum*	Herb	PNTR 79
268	Acanthaceae	*Dicliptera bupleuroides*	Herb	PNTR 199, PNTR 196

269	Acanthaceae	*Dicliptera roxburghii*	Herb	PNTR 63
270	Fabaceae	*Dolichos sp*	Herb	PNTR 132
271	Asteraceae	*Elephantopus scaber*	Herb	PNTR 98
272	Poaceae	*Eleusine indica*	Herb	PNTR 113, PNTR 105
273	Acanthaceae	*Elytraria acaulis*	Herb	PNTR 21
274	Euphorbiaceae	*Euphorbia hirta*	Herb	PNTR 82
275	Euphorbiaceae	*Euphorbia niruri*	Herb	
276	Convolvulaceae	*Evolvulus alsinoides*	Herb	PNTR 83
277	Convolvulaceae	*Evolvulus arvensis*	Herb	PNTR 67
278	Convolvulaceae	*Evolvulus nummularius*	Herb	PNTR 60
279	Amaranthaceae	*Gomphrena celosioides*	Herb	PNTR 104
280	Celastraceae	*Gymnosporia sp.*	Herb	PNTR 125
281	Lamiaceae	*Hyptis suaveolens*	Herb	PNTR 89
282	Balsaminaceae	*Impatiens balsamina*	Herb	PNTR 92
283	Fabaceae	*Indigofera linifolia*	Herb	PNTR 105
284	Colchicaceae	*Iphigenia indica*	Herb	PNTR 27
285	Acanthaceae	*Justicia pectinata*	Herb	
286	Acanthaceae	*Justicia simplex*	Herb	PNTR 191
287	Boraginaceae	*Lappula semiglabra*	Herb	
288	Acanthaceae	*Lepidagathis incurva*	Herb	PNTR 113
289	Lamiaceae	*Leucas cephalotes*	Herb	PNTR 183
290	Scrophulariaceae	*Lindernia antipoda*	Herb	PNTR 129

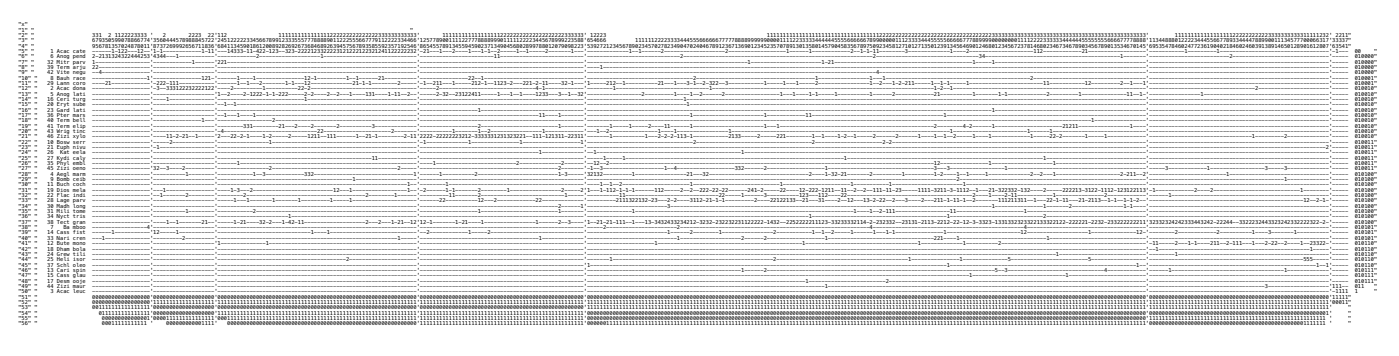
291	Linaceae	*Linum usitatissimum*	Herb	
292	Onagraceae	*Ludwigia octovalvis*	Herb	PNTR 54
293	Malvaceae	*Malvastrum coromandelianum*	Herb	PNTR 121
294	Acanthaceae	*Nelsonia canescens*	Herb	
295	Rubiaceae	*Oldenlandia affinis*	Herb	PNTR 91
296	Lamiaceae	*Oscimum basallicum*	Herb	PNTR 131
297	Poaceae	*Paspalidium flavidum*	Herb	PNTR 40
298	Acanthaceae	*Peristrophe bicalyculata*	Herb	PNTR 140
299	Acanthaceae	*Peristrophe paniculata*	Herb	PNTR 115
300	Euphorbiaceae	*Phyllanthus simplex*	Herb	PNTR 51
301	Euphorbiaceae	*Phyllanthus virgatus*	Herb	PNTR 96
302	Polygalaceae	*Polygala abyssinica*	Herb	PNTR 39
303	Polygalaceae	*Polygala arvensis*	Herb	PNTR 22
304	Polygalaceae	*Polygala persicariifolia*	Herb	PNTR 38
305	Acanthaceae	*Rungia pectinata*	Herb	PNTR 143
306	Cyperaceae	*Scirpus barbatus*	Herb	PNTR 15
307	Malvaceae	*Sida acuta*	Herb	PNTR 69
308	Malvaceae	*Sida humilis*	Herb	PNTR 178
309	Fabaceae	*Smithia ciliata*	Herb	PNTR 122
310	Boraginaceae	*Trichodesma zeylanicum*	Herb	PNTR 144
311	Asteraceae	*Tridax procumbens*	Herb	PNTR 107
312	Fabaceae	*Uraria picta*	Herb	PNTR 97

313	Fabaceae	*Vigna trilobata*	Herb	PNTR 90
314	Solanaceae	*Solanum surattense*	Herb	Digital
315	Caesalpiniaceae	*Cassia occidentalis*	Herb	PNTR 20751
316	Gentianaceae	*Enicostema axillare*	Herb	PNTR 81
317	Euphorbiaceae	*Euphorbia prostrata*	Herb	PNTR 83
318	Acanthaceae	*Justicia procumbens*	Herb	PNTR 59
319	Acanthaceae	*Barleria cristata*	Herb	NIL
320	Nyctaginaceae	*Boerhavia diffusa*	Herb	NIL
321	Acanthaceae	*Hygrophila polysperma*	Herb	NIL
322	Acanthaceae	*Justicia quinquangularis*	Herb	NIL
323	Acanthaceae	*Lepidagathis cristata*	Herb	NIL
324	Orchidaceae	*Vanda tessellata*	Herb	Digital
325	Lythraceae	*Rotala sp.*	Herb	PNTR 55
326	Rubiaceae	*Hedyotis sp.*	Herb	PNTR 70
327	Amaranthaceae	*Pupalia lappacea*	Herb	NIL

Table S3.2 Volume equation and wood density value of tree species

S. No.	Species	Wood density	Volume equation
1	*Acacia catechu*	0.88	−0.048108+5.873169*(D)*(D)
2	*Acacia donaldii*	0.60	$0.17553-0.71434*(D)^2+7.94663*D*D$
3	*Acacia leucophloea*	0.76	$-0.00142+2.61911*D-0.54703*(D)^2$
4	*Aegle marmelos*	0.75	$0.17553-0.71434*(D)^2+7.94663*D*D$
5	*Albizia procera*	0.52	−0.034+0.291*D*D*H
6	*Anogeissus latifolia*	0.78	0.145667−2.704089*D+17.4656*D*D−10.4903*D*D*D
7	*Anogeissus pendula*	0.86	0.00085−0.35165*D+4.77386*D*D−0.90585* D*D*D
8	*Bauhinia racemosa*	0.67	$0.17553-0.71434*(D)^2+7.94663*D*D$
9	*Bombax ceiba*	0.33	0.076+0.228*D*D*H
10	*Boswellia serrata*	0.50	−0.1503+2.79425*D
11	*Buchanania cochinchinensis*	0.45	0.017+0.381*D*D*H
12	*Butea monosperma*	0.48	−0.032−0.0619*D+7.208*D*D
13	*Cassia fistula*	0.71	$0.17553-0.71434*(D)^2+7.94663*D*D$
14	*Cassine glauca*	0.74	$0.17553-0.71434*(D)^2+7.94663*D*D$
15	*Ceriscoides turgida*	0.64	$0.17553-0.71434*(D)^2+7.94663*D*D$
16	*Desmodium oojeinense*	0.60	$0.17553-0.71434*(D)^2+7.94663*D*D$
17	*Diospyros melanoxylon*	0.68	0.15581−2.2075*D+9.17559*D*D
18	*Dolichandrone falcata*	0.44	$0.17553-0.71434*(D)^2+7.94663*D*D$
19	*Eriolaena hookeriana*	0.70	$0.17553-0.71434*(D)^2+7.94663*D*D$
20	*Erythrina suberosa*	0.32	$0.17553-0.71434*(D)^2+7.94663*D*D$
21	*Euphorbia nivulia*	0.47	$0.17553-0.71434*(D)^2+7.94663*D*D$
22	*Ficus mollis*	0.39	$0.17553-0.71434*(D)^2+7.94663*D*D$
23	*Flacourtia indica*	0.77	$0.17553-0.71434*(D)^2+7.94663*D*D$
24	*Gardenia latifolia*	0.64	$0.17553-0.71434*(D)^2+7.94663*D*D$

25	*Grewia tiliifolia*	0.68	0.775−7.787*D+22.748*D*D
S. No.	**Species**	**Wood density**	**Volume equation**
26	*Holoptelea integrifolia*	0.60	$0.17553-0.71434*(D)^2+7.94663*D*D$
27	*Kydia calycina*	0.48	$0.17553-0.71434*(D)^2+7.94663*D*D$
28	*Lagerstroemia parviflora*	0.62	0.10529−1.68829*D+10.29573*D*D
29	*Lannea coromandelica*	0.54	0.046731−0.962906*D+7.301883*D*D
30	*Madhuca longifolia*	0.74	0.046883−0.894379*D+7.220441*D*D
31	*Miliusa tomentosa*	0.62	$0.17553-0.71434*(D)^2+7.94663*D*D$
32	*Mitragyna parvifolia*	0.56	(0.04778/D*D−1.17815/D+10.68031)*D*D
33	*Moringa concanensis*	0.26	$0.17553-0.71434*(D)^2+7.94663*D*D$
34	*Nyctanthes arbor-tristis*	0.88	$0.17553-0.71434*(D)^2+7.94663*D*D$
35	*Phyllanthus emblica*	0.80	−0.038+0.344*D*D*H
36	*Pterocarpus marsupium*	0.67	$0.17553-0.71434*(D)^2+7.94663*D*D$
37	*Salix tetrasperma*	0.38	$0.17553-0.71434*(D)^2+7.94663*D*D$
38	*Schleichera oleosa*	0.96	$0.17553-0.71434*(D)^2+7.94663*D*D$
39	*Soymida febrifuga*	0.97	$0.17553-0.71434*(D)^2+7.94663*D*D$
40	*Sterculia urens*	0.67	$0.17553-0.71434*(D)^2+7.94663*D*D$
41	*Stereospermum chelonoides*	0.62	$0.17553-0.71434*(D)^2+7.94663*D*D$
42	*Tectona grandis*	0.50	0.062108−0.927983*D+6.613031*D*D
43	*Terminalia arjuna*	0.68	−0.042473+6.996762*D*D+0.137468* D*D*H
44	*Terminalia bellirica*	0.72	−0.042473+6.996762*D*D+0.137468* D*D*H
45	*Terminalia elliptica*	0.76	$(0.203947+3.159215*D)^2$
46	*Wrightia tinctoria*	0.75	$(0.050294+3.115497*D-0.687813*(D)^2)^2$
47	*Ziziphus mauritiana*	0.76	$0.17553-0.71434*(D)^2+7.94663*D*D$
48	*Ziziphus xylopyrus*	0.76	$0.17553-0.71434*(D)^2+7.94663*D*D$



Annexure II

Supplementary Information

Chapter 4 Seasonal distribution of ungulates

Figure S4.1: Predictor variables

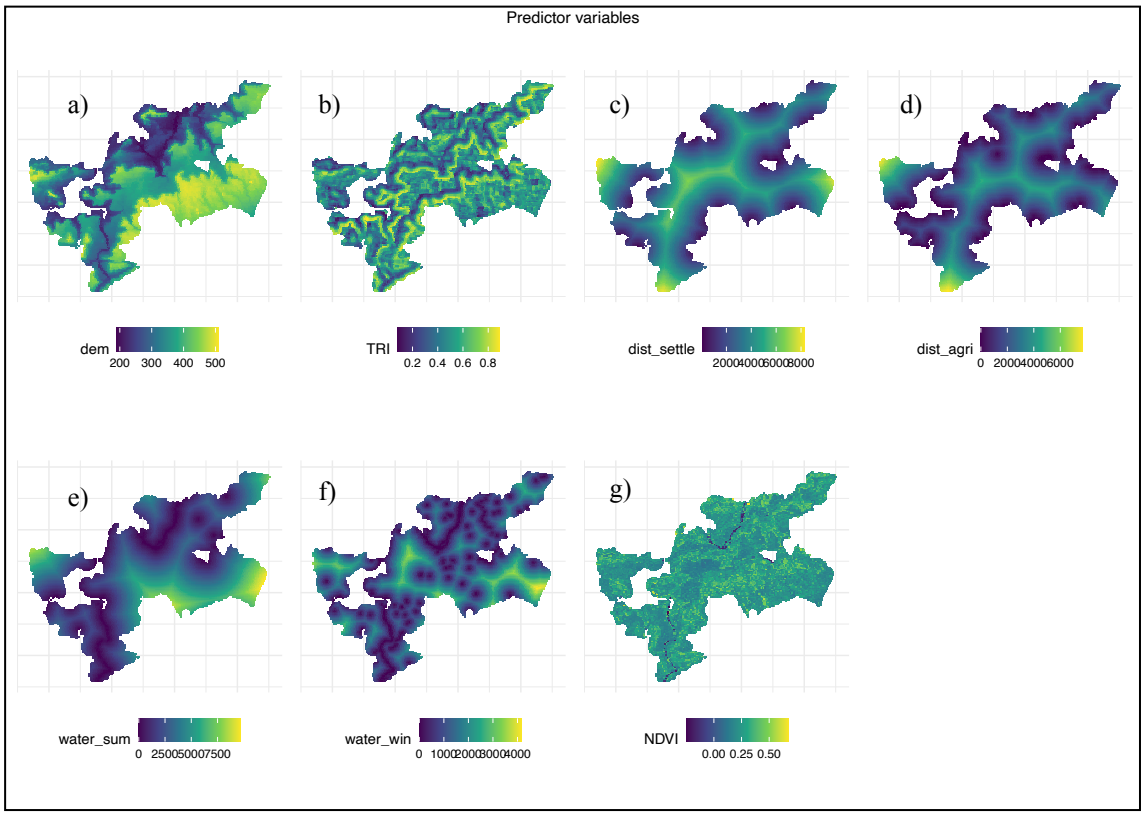


Figure S4.1: Spatial distribution of all the predictor variable in the study area from left above: a) Digital elevational model, b) Topographic Ruggedness Index, c) Distance from the settlements, d) Distance from the agriculture, e) Distance from the water source in summer season, f) Distance from the water source in winter season, g) NDVI

Figure S4.2: GLM response curve of NDVI with tree Basal Area in study area

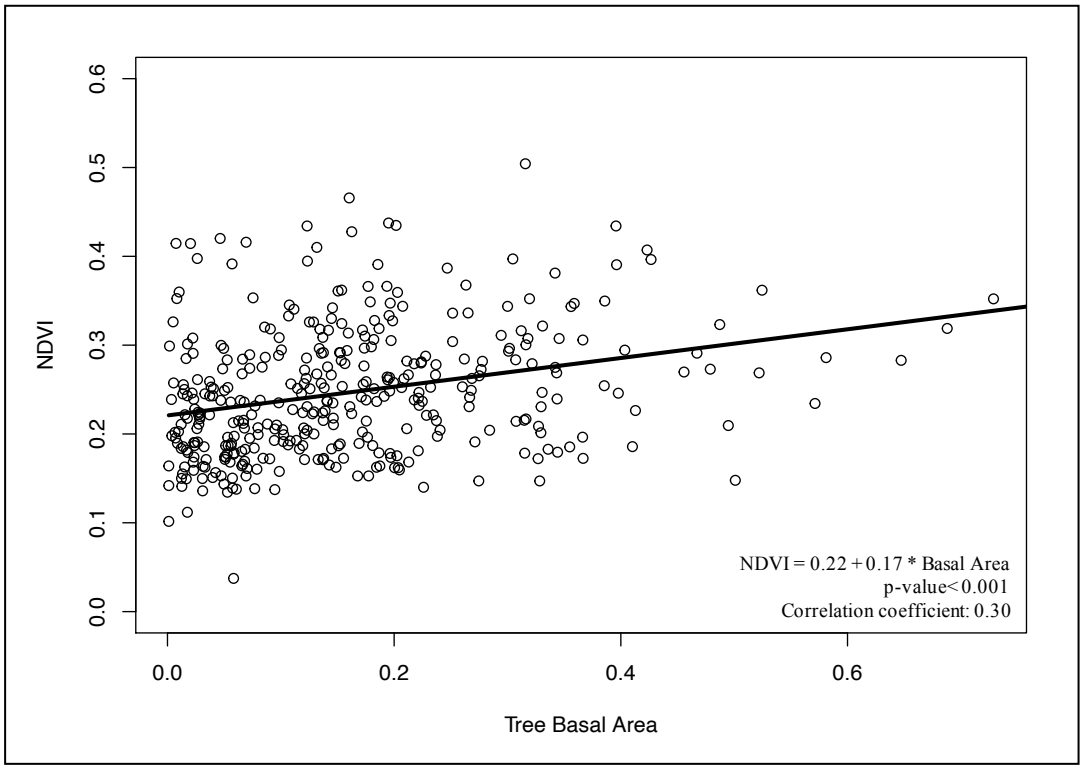


Figure S4.2: GLM response curve shows significant positive relationship of Basal Area with NDVI. In addition, both variable show positive correlation (0.30) with each other in our study area. Here, tree basal area defines the area covered with all woody vegetation >10cm gbh and >3 meters height. This relationship clearly tells the presence of dense forests when NDVI value is high.

Figure S4.3: Histograms of fitted detection function using Distance sampling methods

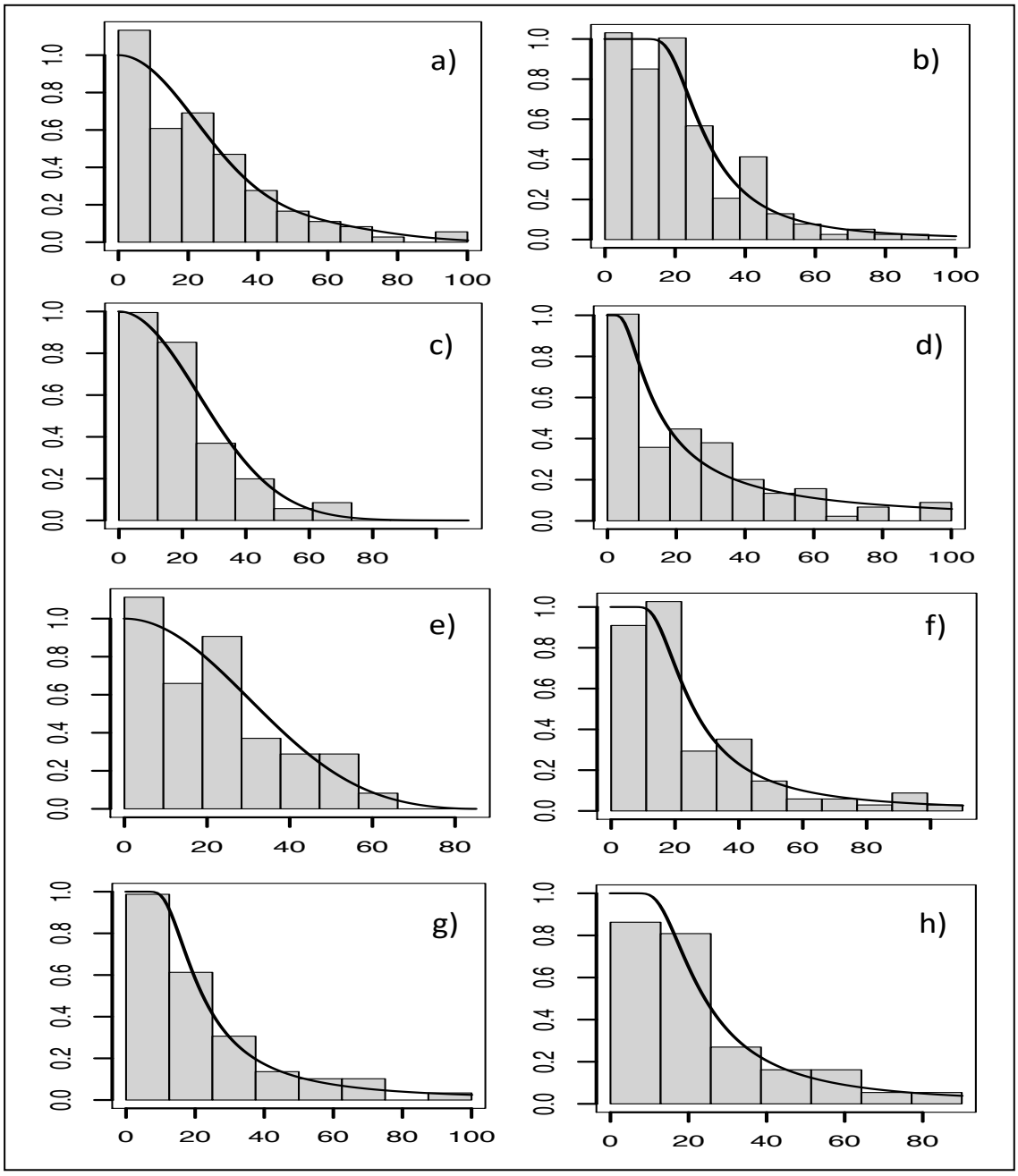


Figure S4.3: Fitted detection function using Distance sampling method for all four species in both seasons; Sambar a) Summer, b) Winter; Nilgai c) Summer, d) Winter; Chital e) Summer, f) Winter; Wild pig g) Summer, h) Winter. x-axis shows detection probability and y-axis shows observed perpendicular distances.

Figure S4.4: CI plot depicting group size of different species

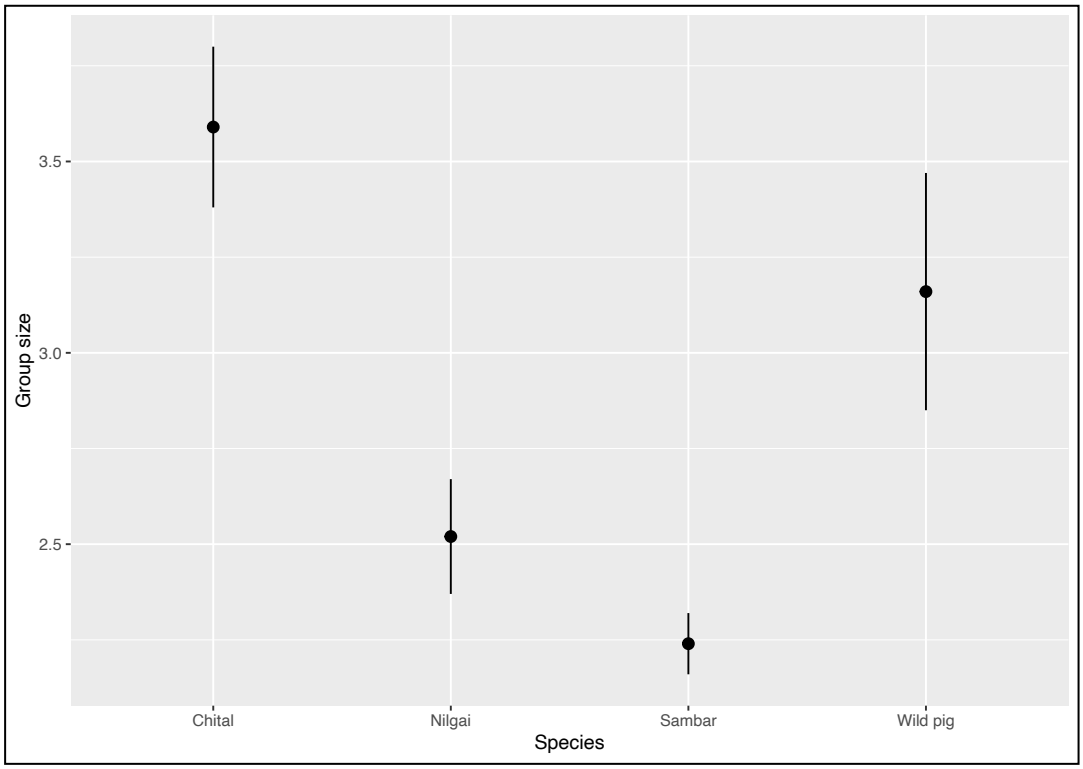


Figure S4.4: Group size plot of four species, Sambar makes the smallest groups all across the year where Chital has the largest group size which varies across the year. Wild pig also has a large confidence interval that shows their varying habits of living in a group across the year.

Appendix A

Density Surface Modelling: Data exploration and Model selection procedure

A. Data exploration:

Data exploration was performed in R program using package 'lattice' (Sarkar 2008) and 'latticeExtra' (Sarkar & Andrews 2019) packages following (Zuur & Ieno 2016). Cleveland dot plots were used to inspect predictor variables for extreme observations. Pair plot and VIF values were used to assess collinearity. Multi-panel scatterplots with LOESS smoother were used to visualize relationships between predictor and response variables. Data were checked for zero-inflation and correlation structures. We found non-linear relationships between predictor and response variables with no correlation structure. Hence, we used Generalized Additive Modelling (GAM) (Wood 2006, 2017) approach in Density Surface Modelling (DSM) (Miller *et al.* 2013) framework. The cluster size for each species in both seasons along with the transect lines were overlaid on the predictor variables to visualize the spatial distribution of observations.

B. Model checking and selection:

Models were selected based on restricted maximum likelihood (REML) scores, deviance explained. We chose REML score over generalised cross-validation and unbiased risk estimators because REML provides fitting criteria with a more pronounced optima that avoid some problems with parameter estimation (Miller *et al.* 2013). However, we did not rely solely on REML score and deviance explained due to their sensitivity, though both values played an important role in our model selection process. We calculated the dispersion parameter to understand the mean-variance relationship explained by the model. We checked the models with standard GAM diagnostic plots and smoothing parameter estimation convergence information (Wood

2017). The standard GAM diagnostic plots corresponded to the various residual plots visualising if residual patterns remained in the model. A slight departure from the assumed distributions was not considered problematic if the dispersion parameter was accurate (Heyde 1997, Augustin *et al.* 2012).

We further investigated our model for data independence due to model misfit by plotting residuals versus each covariate in the model and also versus each covariate not in the model. Any patterns in these plots were considered dependency due to model misfit caused by covariate and the model was corrected for the variation.

When models were fitted with multiple smooth we checked our model for concurvity. Concurvity measures how well one smooth term can be explained by some combination of the other smooth terms in the model (Pedersen *et al.* 2019). We removed one of the two variables if the two have concurvity values>0.8. We checked our model for influential observations by plotting the cook's distance and influential observations were removed. Spatial auto-correlation was checked by using a semi-variogram and residual box plot for each sampling site. Our data did not show any correlation structure therefore, we stick to generalised additive modelling and did not incorporate generalised additive mixed modelling. We again performed GAM with model residuals and covariates to check if there is any residual structure left in the model. Patterns were considered systematic if we got a smoothers p-value significant and in such a scenario, the main model was rerun with adjusted parameters.

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Annexure III

Supplementary material: Chapter 5: Ungulate – habitat relationship

Table S5.1 A list of palatable species for four species of ungulates in Panna Tiger Reserve

S. No.	Family	Vernacular name	Growth form	Botanical name	Sambar	Nilgai	Chital	Wild pig
1	Anacardiaceae	Achar	Tree	*Buchanania cochinchinensis*	-	-	P	P
2	Annonaceae	Kari	Tree	*Miliusa tomentosa*	-	-	P	-
3	Apocynaceae	Doodhi	Tree	*Wrightia tinctoria*	P	P	P	-
4	Apocynaceae	Kurro	Tree	*Holarrhena pubescens*	P	-	-	-
5	Arecaceae	Khajoori	Tree	*Phoenix sylvestris*	P	P	P	-
6	Bignoniaceae	Jaichar	Tree	*Dolichandrone falcata*	-	-	P	-
7	Caesalpinioideae	Amaltash	Tree	*Cassia fistula*	P	P	P	-
8	Caesalpinioideae	Mohli	Tree	*Bauhinia racemosa*	P	P	P	-
9	Combretaceae	Baheda	Tree	*Terminalia bellirica*	-	-	P	-
10	Combretaceae	Dhawa	Tree	*Anogeissus latifolia*	P	P	-	-
11	Combretaceae	Kardhai	Tree	*Anogeissus pendula*	P	P	P	-
12	Combretaceae	Koha	Tree	*Terminalia arjuna*	P	-	P	-

13	Combretaceae	Sajh	Tree	*Terminalia eliptica*	P	P	P	-
14	Ebenaceae	Tendu	Tree	*Diospyros melanoxylon*	P	P	P	-
15	Euphorbiaceae	Thuar	Tree	*Euphorbia nivulia*	-	-	P	-
16	Fabaceae	Imli	Tree	*Tamarindus indica*	-	-	P	-
17	Faboideae	Beeja	Tree	*Pterocarpus marsupium*	P	P	P	-
18	Faboideae	Palash	Tree	*Butea monosperma*	-	P	P	-
19	Lamiaceae	Teak	Tree	*Tectona grandis*	P	P	P	-
20	Malvaceae	Dhaman	Tree	*Grewia tiliifolia*	P	P	-	-
21	Malvaceae	Semal	Tree	*bombax ceiba*	P	-	-	-
22	Meliaceae	Rohan	Tree	*Soymida febrifuga*	-	P	-	-
23	Mimosoideae	Babool	Tree	*Acacia nilotica*	P	P	P	-
24	Mimosoideae	Khair	Tree	*Acacia catechu*	P	P	P	-
25	Mimosoideae	Gurar	Tree	*Acacia donaldii*	P	P	P	-
26	Mimosoideae	Reonja	Tree	*Acacia leucophloea*	P	P	P	-
27	Mimosoideae	Sirsa	Tree	*Albizia procera*	-	-	P	-
28	Moraceae	Bargad	Tree	*Ficus benghalensis*	P	-	-	-
29	Moraceae	Pipal	Tree	*Ficus religiosa*	-	-	P	-
30	Myrtaceae	Jamun	Tree	*Syzygium cumini*	-	-	P	-

31	Myrtaceae	Katjamun	Tree	*Syzygium salicifolium*	-	-	P	-
32	Phyllanthaceae	Aamla	Tree	*Phyllanthus emblica*	P	P	P	-
33	Rubiaceae	Haldu	Tree	*Haldina cordifolia*	P	-	-	-
34	Rubiaceae	Kaima	Tree	*Mitragyna parvifolia*	P	P	P	-
35	Rubiaceae	Karar	Tree	*Ceriscoides turgida*	-	-	P	-
36	Rubiaceae	Papda	Tree	*Gardenia latifolia*	-	-	P	-
37	Rutaceae	Bel	Tree	*Aegle marmelos*	P	P	P	-
38	Rutaceae	Bilsena	Tree	*Naringi crenulata*	P	-	-	-
39	Rutaceae	Kaitha	Tree	*Limonia acidissima*	-	-	P	-
40	Salicaceae	Katai	Tree	*Flacourtia indica*	P	P	P	-
41	Sapotaceae	Mahua	Tree	*Madhuca longifolia*	-	-	P	-
42	Malvaceae	NA	Shrub	*Abutilon incanum*	P	-	-	-
43	Asparagaceae	NA	Shrub	*Asparagus adscendens*	-	-	P	-
44	Apocynaceae	NA	Shrub	*Carissa carandas*	P	P	P	-
45	Rubiaceae	NA	Shrub	*Randia dumetorum*	-	-	P	-
46	Rhamnaceae	NA	Shrub	*Ziziphus oenoplia*	P	P	P	P
47	Verbenaceae	NA	Shrub	*Lantana camara*	-	-	P	-
48	Malvaceae	NA	Shrub	*Helicteres isora*	P	P	P	-
49	Rhamnaceae	NA	Small tree	*Ziziphus mauritiana*	P	P	P	P

50	Rhamnaceae	NA	Small tree	*Ziziphus xylopyrus*	P	P	P	-
51	Rhamnaceae	NA	Shrub	*Ziziphus nummularia*	-	-	P	-
52	Dioscoreaceae	NA	Climber	*Dioscorea bulbifera*	-	-	P	-
53	Solanaceae	NA	Climber	*Ziziphus oenoplia*	P	P	P	-
54	Poaceae	NA	Grass	*Bamboo spp*	P	-	P	-
55	Poaceae	NA	Grass	*Aristida adscendens*	-	-	P	-
56	Poaceae	NA	Grass	*Bothriochloa ischaemum*	-	-	P	-
57	Poaceae	NA	Grass	*Brachiaria ramosa*	-	-	P	-
58	Poaceae	NA	Grass	*Chloris incompleta*	-	-	P	-
59	Poaceae	NA	Grass	*Chloris virgata*	-	-	P	-
60	Poaceae	NA	Grass	*Dicanthium annulatum*	-	-	P	-
61	Poaceae	NA	Grass	*Digitaria adscendens*	-	-	P	-
62	Poaceae	NA	Grass	*Echinochloa colona*	-	-	P	-
63	Poaceae	NA	Grass	*Eragrostiella nardoides*	-	-	P	-
64	Poaceae	NA	Grass	*Eragrostis bifaria*	-	-	P	-
65	Poaceae	NA	Grass	*Eragrostis stenophylla*	P	P	P	-
66	Poaceae	NA	Grass	*Eragrostis tenella*	-	-	P	-
67	Poaceae	NA	Grass	*Eragrostis unioloides*	-	-	P	-

68	Poaceae	NA	Grass	*Eragrostis viscosa*	-	-	P	-
69	Poaceae	NA	Grass	*Heteropogon contortus*	P	P	P	-
70	Poaceae	NA	Grass	*Oplismenus burmanni*	-	-	P	-
71	Poaceae	NA	Grass	*Panicum sumatrense*	-	-	P	-
72	Poaceae	NA	Grass	*Setaria glauca*	-	-	P	-
73	Poaceae	NA	Grass	*Themeda quadrivalvis*	-	-	P	-
74	Poaceae	NA	Grass	*Themeda triandra*	P	-	P	-
75	Poaceae	NA	Grass	*Vetiveria zizanioides*	-	-	P	-
76	Cyperaceae	NA	Sedge	*Cyperus iria*	-	-	P	-
77	Cyperaceae	NA	Sedge	*Cyperus sp.*	-	-	P	-
78	Cyperaceae	NA	Sedge	*Fimbristylis dichotoma*	-	-	P	-
79	Poaceae	NA	Grass	*Apluda mutica*	-	-	P	-
80	Fabaceae	NA	Herb	*Cassia tora*	P	P	P	-

CERTIFICATES

AMITY INSTITUTE OF FORESTRY AND WILDLIFE & Society for Conservation Biology Asia Section

Organise

SOCIETY FOR CONSERVATION BIOLOGY ASIA SECTION CONFERENCE

19th-20th March, 2018

CERTIFICATE OF PARTICIPATION

This is to certify that Prof./ Dr. /Mr. /Ms. Deepti Gupta

from Wildlife Institute of India has participated/presented scientific paper(s) titled Assessment of population status of Chital and its winter habitat correlates in Panna Tiger Reserve, Madhya Pradesh

during the Conference held on 19th-20th March, 2018 at Amity University Uttar Pradesh.

Dr. N. P. S.Chauhan
Director
Amity Institute of Forestry & Wildlife

Dr. Ghazala Shahabuddin
Membership Liaison Officer
SCB-Asia Section

Prof. (Dr.) Balvinder Shukla
Vice Chancellor
Amity University Uttar Pradesh


CERTIFICATE OF RECOGNITION
This certificate is presented to
DEEPTI GUPTA
For having presented an abstract
(Oral Presentation / Speed-Talk / Poster)
at the
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BRITISH ECOLOGICAL SOCIETY

BES Annual Meeting: Festival of Ecology
14 - 18 December 2020, Online

This certificate confirms that

Deepti Gupta

Attended the above online Annual Meeting and delivered an online **POSTER** presentation in the session **COMMUNITY ECOLOGY** titled:

Seasonal influence on abundance distribution of ungulates in the dry deciduous forest of central India.

Georgina Glaser

Events Officer
British Ecological Society

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Society for Conservation Biology
A global community of professionals dedicated to science and the conservation of biodiversity

September 4, 2020

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The Society for Conservation Biology is the world's largest scientific society dedicated to advancing the science and practice of conserving Earth's biological diversity. SCB Graduate Student Research Fellowship Awards support the development and training of the next generation of conservation scientists.

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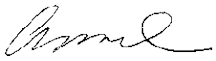
Once again – congratulations on being a **winner** of the 2020 SCB Graduate Student Research Fellowship Awards!

We hope that you will remain an SCB member throughout your career and reap the many rewards this scientific community has to offer.

Best regards,



Adina Merenlender, President of the Society for Conservation Biology

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FIELD PHOTOS

1. Study Species:




a) Sambar (*Rusa unicolor*) b) Chital (*Axis axis*) c) Nilgai (*Boselaphus tragocamelus*)

d) Wild pig (*Sus scrofa)*

2. Ungulates foraging on plant species:





a) Sambar feeding on A. donaldii sapling b) Lantana c) A. marmelos fruit; d) Chital feeding on Ziziphus fallen leaves, e) Chital in relocated village f) Nilgai feeding on *Mitragyna parvifolia* fallen leaves

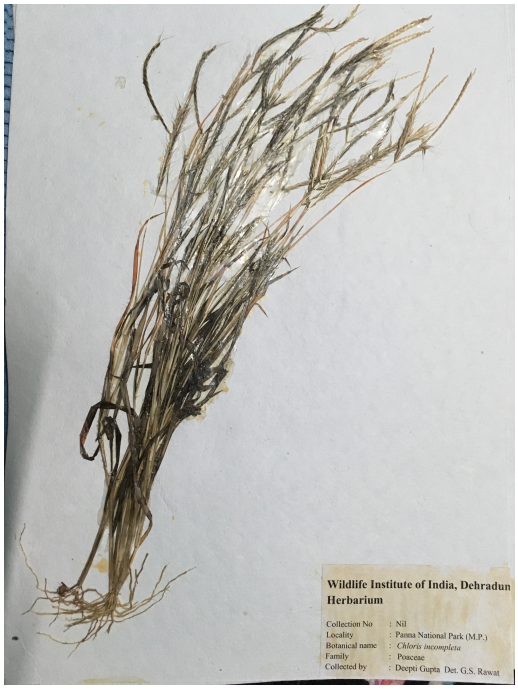
3. Osteophagia in ungulates:


a) Sambar b) Chital chewing on fallen antlers

4. Livestock in relocated villages:

a) & b) Livestock grazing in relocated villages c) Vultures gathered for feast on cattle carcass inside park d) Cattle using riverine area intensively post-monsoon

5. Field sampling:



a) Field observation for palatable plant species b) sample plot for grass biomass c) &

d) Scanned sheet of herbarium for this study

6. Other ungulates in Panna Tiger Reserve:

a) Chinkara b) Chousingha

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bioTROPICA ASSOCIATION FOR TROPICAL BIOLOGY AND CONSERVATION WILEY

ORIGINAL ARTICLE

Spatial density patterns of herbivore response to seasonal dynamics in the tropical deciduous forest of central India

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Abstract

Resource dynamism in seasonal forests leads ungulates to differential habitat preference; hence, their distribution aligns with environmental covariates across spatial and temporal scales. Seasonal patterns of four species of ungulates, namely sambar, chital, nilgai, and wild pig, were investigated and identified as the environmental variables driving the density gradient across two seasons, summer and winter, in the tropical dry deciduous forest of Panna Tiger Reserve, central India. Distance sampling data were analyzed using density surface modeling for ungulates with a survey effort of 518 km in winter and 356 km in summer in a generalized additive modeling framework. We found that season significantly affected the spatial densities of all ungulates, with sambar, chital, and nilgai congregating in summer and wild pig in winter. All ungulates showed a clear seasonal shift to the valley in summer and preferred plateaus in winter. The spatially explicit map outputs draw attention to the seasonal hot spots for ungulates abundance and the species and season-specific roles of environment variables in defining their distribution. These results provide a scientific basis for direct conservation efforts to the spatially prioritized habitats for cost-effective management interventions.

KEYWORDS
density surface modeling, distance sampling, resource selection, ungulate-habitat interactions

1 | INTRODUCTION

Resource heterogeneity is distinct in tropical dry deciduous forests due to seasonal patterns of rainfall and temperature. These forests experience a brief period of growth during rainy season after a very long dry season of around 6 months (Meher-Homji et al., 1978), making every taxon utterly dependent on the seasonal rainfall directly or indirectly. The strong seasonality of dry deciduous forests leads to seasonal variation in the phenology of different floral species (Singh & Singh, 1992); consequently, food resources become dynamic in space and time. Topography in such a scenario plays a significant role in establishing moisture gradients across regions. Most monsoonal waters sink into the river valley, leaving plateaus with drier habitats (Chundawat, 2018). Valley, in contrast, retains most of the monsoonal water, provides shady habitats, and is cooler throughout the year. In addition, soil also becomes dry due to wind and insolation (Kapos, 1989) and reduces plant productivity in the dry season (Ceballos, 1990). Therefore, ungulates in the dry deciduous forest adapt to seasonal climatic variations.

Further, heterogeneity in resource availability in seasonal forests drives ungulates to make their preferences across habitats (Borowik et al., 2021; Naidoo et al., 2012; Schuette et al., 2016).

Ungulates' preference for different habitats in different seasons (Awasthi et al., 2016) is guided by abiotic factors such as topography (Harris et al., 2002), water availability (Payne et al., 2020), and weather (Borowik et al., 2020), biotic factors such as forage quality and availability (Bailey & Provenza, 2008; Boone et al., 2008). In the dry deciduous forest, sources of water and shade are often limited, and forage availability becomes scarce during summer in most regions. In such a scenario, dispersal to a suitable habitat allows them to survive the extreme climatic variations (Boone et al., 2008; Singh et al., 2012) and help fulfill their nutritional requirements (Coppedge & Shaw, 1998; Scott et al., 1995; Senft et al., 1985).

Ungulates' movement patterns in response to seasonal changes and resource availability have been studied in African Savannas (Fryxell & Sinclair, 1988b; Owen-Smith et al., 2020; Yoganand & Owen-Smith, 2014) and temperate forests (Borowik et al., 2020, 2021; Singh et al., 2012), which forms a strong baseline. Previous studies suggest that ungulates prefer higher elevations and ridges in colder temperatures (Harris et al., 2002) and seek shade during hot weather (McIlvain & Shoop, 1971). However, a species and season-specific model-based approach focused on ungulate conservation in tropical forests is gravely lacking, where ungulates attain the highest diversity. Only a handful of studies in tropical forests describe environmental parameters' role in ungulate distribution (Awasthi et al., 2016; Harihar et al., 2014; Kumar et al., 2021). Formerly, conservation efforts were constrained to either yearly population trends or conclusions drawn by observing few individuals due to the absence of spatial models. There are two limitations to these efforts: First, they do not account for any inherent biases, and second, large sample size is needed to ensure the precision of the results. With methodological advancements, understanding these ecological patterns is comparatively more straightforward, particularly by building spatial models that allow habitat heterogeneity and identify environmental variables that influence density distribution in space and time. Density surface modeling (DSM; Miller et al., 2013) combines spatial modeling techniques with distance sampling (Buckland et al., 2001, 2004; Thomas et al., 2010), taking into account the probability of detecting an animal at each sampling unit and building maps of the population density distributions. These maps are useful due to their scale flexibility and straightforward interpretation of complex algorithms and, thus, make it easy to communicate results to non-specialists (Miller et al., 2013).

Here we hypothesize that ungulate distribution should vary in response to resource availability across seasons. Therefore, we sought to identify seasonal distribution patterns and establish the relationship with habitat variables of four species of ungulates by using DSM, which could affect the distribution across two seasons. We also calculated and mapped uncertainties in our results to ensure the robustness of our spatial maps. These results improve our understanding of the species response to the environmental variables, direct species conservation efforts to the priority areas, and reduce the cost of management actions by allocating them to specific habitats.

2 | METHODOLOGY

2.1 | Study area

This study was undertaken in Panna Tiger Reserve (PTR; Figure 1), situated in the Vindhyan mountain ranges in Madhya Pradesh, central India, between 24°27′N to 24°46′N latitude and 79°45′E to 80°09′E longitude. PTR is uniquely characterized by its "terraced topography" and presents two tabletop mountains and a valley formed by the Ken River. The study area can be divided into the upper plateau, middle plateau, and river valley. There is not much variation in elevation at a specific plateau region, but escarpments that delineate three topographic regions are 10–80 m steep in height. The river valley represents an undulating region with an elevation range of up to 40 m. The Ken River cuts through the reserve from southwest to northeast and is a significant water source.

Panna Tiger Reserve is primarily dependent on monsoon rainfall from July to September. The average annual rainfall is approximately 1100 mm, but the area is known for its poor water retention capacity. Most monsoonal water percolates down to the valley quickly, leaving plateaus dry. Following the monsoon is the winter season from November to February, when the minimum temperature drops to 5°C, followed by dry summer in April–June, when the maximum temperature often exceeds 45°C (Chundawat, 2018; Karanth et al., 2004).

Panna Tiger Reserve is globally known for its successful tiger relocation history (Krishnamurthy et al., 2016; Sarkar et al., 2016, 2017). PTR now supports a viable population of tigers (*Panthera tigris*) and leopards (*Panthera pardus*). Apart from large predators, striped hyena (*Hyaena hyaena*), dhole (*Cuon alpines*), jackal (*Canis aureus*), and wolf (*Canis lupus*) occur as mesopredators. The major forest type is tropical dry deciduous (Meher-Homji et al., 1978), which shows strong seasonality with the scarcity of resources during summer (Chundawat, 2018). Five prominent vegetation types dominate this landscape: *Tectona grandis* dominated forest, *T. grandis* mixed forest, *Acacia catechu* mixed forest, *Anogeissus pendula* forests, and scrublands dominated by *Ziziphus* spp. and *Acacia* spp. (D. Gupta, G. S. Rawat & R. Krishnamurthy, Unpublished data).

2.2 | Study species

Herein, we focused on four species of ungulates sambar (*Rusa unicolor*), chital (*Axis axis*), nilgai (*Bocephalus tragocamelus*), and wild pig (*Sus scrofa*). Sambar is a large-sized ungulate (males weighing around 225–320 kg) categorized as vulnerable in the IUCN red list. Its population trend is decreasing. It is mostly found in tropical forests of Southeast Asia. Sambar occurs in small groups; however, it may form larger groups in response to resource requirements and to avoid predators (Schaller, 1967). The species prefers hilly terrain and densely forested habitats (Johnsingh & Manjrekar, 2015). The mean annual and seasonal home range for males (4.06 km^2) is larger than for females (2.01 km^2). Home range varies across seasons with males

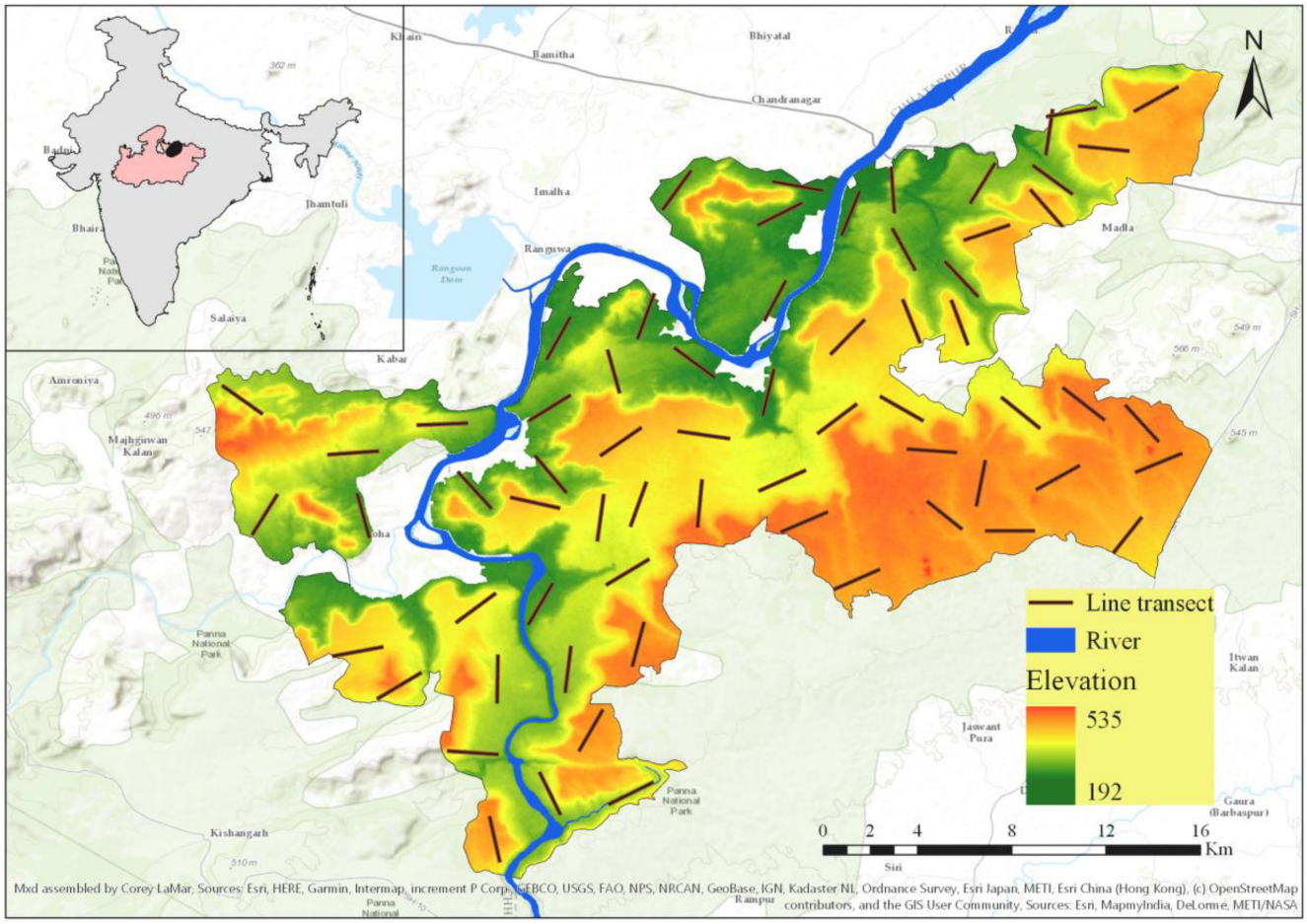


FIGURE 1 Map showing the spatial distribution of line transect survey in the study area, Panna Tiger Reserve overlaid on the elevation data. Elevation divides the whole area into three distinct boundaries viz; upper Panna plateau (south), middle Hinota plateau and lowest Ken river valley (north).

being largest in winter and smallest in summer. Sambar exhibits seasonal deviation related to forage availability, the number of females, and extremely hot conditions. It is primarily a browser in winter and summer but shifts to green grasses during monsoon.

The remaining three study species of ungulates are of the least concern as per IUCN red list. Chital, an endemic cervid of south Asia, is a species of grassland-forest interface and is considered an ecotone species (Krishnan, 1972). Chital is a group-living species and makes large varying herds according to habitat quality (Schaller, 1967). Chital uses more wooded habitats during winter and early summer and moves in large herds to open grasslands in monsoon in response to forage availability. It is primarily a grazer and eats a variety of grasses. In the unavailability of green grass in summer, browse is also consumed.

Nilgai, the largest antelope in south Asia, is distributed in the Indian subcontinent. Nilgai is a mixed feeder (Sankar, 1994) primarily found in open habitats with flat and undulating terrains (Berwick, 1974). It prefers grasses during monsoon. Nilgai is a partly social animal and does not often occur in large groups. Its population status is stable in India. Indian wild pig is widely distributed throughout India. Wild pigs are omnivorous, show a seasonal diet shift, and mainly depend on water availability (Roberts, 1997). They are not obligatory group-living species and sometimes congregate in large groups. Their seasonal shifts in the diet are dictated by the seasonal abundance of fruits, roots, and fungi. All four ungulate species are important prey of large carnivores such as tigers and leopards and are directly related to the conservation of large predator populations.

2.3 | Field sampling

We followed the distance sampling protocol (Buckland et al., 2004) for data collection. We considered beat, the smallest administrative unit, a sampling unit and walked one line transect in each beat. We added a line transect in each beat if the area of a beat was more than 10 km^2 to get good spatial coverage. Thus, 66 spatially distributed line transects were walked, covering the entire core area of PTR. Sampling was done in both seasons, summer and winter. We collected data for two sampling seasons of winter (late November to early February), 2015–2016 and 2016–2017, and two sampling seasons of summer (late April to mid-June), 2016 and 2017. Line length

was kept from 1.5 to 2.0 km depending upon the habitat and terrain complexity. We walked transects in the early morning hours at the time of peak activity of the ungulates. On each sighting of ungulate, group size of each species, sighting angle, radial distance of the animal/group, and distance from the line transect start point were collected. All the line transects were repeated thrice within a sampling season.

2.4 | Statistical analysis

2.4.1 | Data preparation

Two years of data were compiled for both seasons for each species separately. The total survey effort for all species in summer was 356 km and in winter was 518 km. We divided all transects into 400 m segments and yielded spatio-temporal replicates of 892 for summer and 1286 for winter. Segment length was sufficiently small such that the animal density and covariate values did not vary within a segment and large enough to avoid the false absence of sightings (false zero) in the segment data. We used geographical and local habitat variables to model the spatial density distribution of the ungulate species (Figure S1). We derived covariates values directly from remotely sensed data or calculated Euclidean distance (Table 1). We used two geographic covariates consisting of elevation (calculated using Digital Elevation Model data; Table 1) and Terrain Ruggedness Index (TRI; Riley et al., 1999); two habitat parameters consisting of distance to water source (water) and Normalized Difference Vegetation Index (NDVI; Pettorelli, 2013), and two parameters for anthropogenic influence consisting of distance from the settlements (settlement) and distance from the agricultural fields (agriculture). We validated NDVI values based on the field data and found that NDVI shows a significant positive relationship with tree basal area in our study area (Figure S2), based on which we used NDVI values as a proxy of dense vegetation in our analysis. We also incorporated a two-way interaction term of spatial coordinates (s(*x*,*y*)) to address spatially the underlying patterns of abundance variations. Due to the dynamic seasonality of the dry deciduous forest, we calculated distance from the water source for summer and winter separately. Prediction grids were formed by dividing the whole study area into 200 m^2 grids using ArcMap, and mean covariates values were extracted for the centroid of the grid for both seasons. We chose a square grid cell size based on the truncation distance (2*w*, where *w* is truncation distance; 100 m in our analysis) as described in Miller et al. (2013), and thus, we yielded 12,765 grid cells in summer and 13,187 grid cells in winter.

2.4.2 | Density and Abundance estimation

The modeling process was implemented using a two-stage approach. As the first step, we used conventional distance sampling (CDS) to model the density and abundance of all species. CDS models detection probability as a function of observed perpendicular distances. Three key detection functions, that is, uniform, half-normal, and hazard-rate, were fitted to the distance data along with and without cosine adjustment terms (Figure S3). The best-fitted model was selected using Akaike's information criteria (AIC) and the goodness-of-fit test. Data were truncated for the farthest observations up to 9% within the truncation distance based on visual inspection of the histogram (Buckland et al., 2001). This analysis was implemented using the Distance package version 1.0.0 (Miller et al., 2019) in R version 3.6.0 (R Core Team, 2019).

2.4.3 | Density surface modeling

After fitting the detection function, we used count per segment as a response variable which was modeled given habitat variables using the generalized additive modeling (GAM) approach. The model for count per segment is as follows:

$$\mathbb{E}(n_j) = \hat{p}_j A_j \exp\left[\beta_0 + \sum_k f_k(z_{jk})\right]$$

The initial part of the equation $\hat{p}_j A_j$ defines the detection probability in each segment multiplied by the area of each segment whereas, the later part defines the intercept and smooth functions of the covariate (Miller et al., 2013). Count per segment was modeled as a smooth function of predictor variables. Segment area was used as an offset term from 2*wl*, where *w* is truncation distance, and *l* is the segment length. We used default thin plate regression spline smoother in GAM.

We added season as a binary term to the model to assess season's significance on mean density. This model assumes that the relationship between habitat and response variables remains the same each season, but the mean density may differ. Further, we added interaction between a smoother and categorical variable season to check whether the mean density and the relationship vary across seasons. We kept the interaction term in the model only if we found varying relationships across seasons. The term selection was performed by checking smoother *p*-value significance and zero effect (Wood, 2006). An extra shrinkage term was imposed in the model allowing smooth terms to be removed during fitting (Wood, 2011). The mean–variance relationship was allowed to vary with response family distribution Poisson, Negative binomial and Tweedie (Candy, 2004; Foster & Bravington, 2012). A dispersion parameter was investigated for each family distribution, and the model was abandoned if data were highly under-dispersed. The basis dimensions in the model were chosen by a repetitive process, in which the analysis was rerun to make the model wiggly enough to capture the relationship in the data and not too wiggly to capture the noise in the data. A decision was made for basis dimensions by comparing the effective degree of freedom and random patterns in residuals for each smoother (Pedersen et al., 2019). The best-fit model was selected using AIC and goodness-of-fit values. This analysis was implemented

TABLE 1 Predictor variables used in generalized additive modeling framework for spatial modeling.

Variables	Data source and processing details	Spatial resolution and time period	Description
Latitude, Longitude (*x*, *y*)	Survey location		
Elevation (DEM)	Extracted elevation data from Digital elevation-Shuttle Radar Topography Mission data https://earthexplorer.usgs.gov	30 m	Elevation divides the study area into three distinct regions: two plateaus and one valley. As plateaus are known for their poor water retention capacity, monsoonal water drops into the valley. Hence, plateaus represent drier habitats as compared to the valley
Topographic Ruggedness index (TRI)	Calculated from SRTM—digital elevation data (Riley et al., 1999)	30 m	This is a measure of roughness in the terrain. In our study area, plateaus represent flat terrain so TRI values for plateaus are low while escarpments and valley are steep and undulating terrain where TRI value varies
Distance from the water source (water)	Sentinel-2A https://earthexplorer.usgs.gov First, generated a layer of water bodies for two seasons using normalized difference water index (NDWI) (McFeeters, 1996) in ERDAS-Imagine tools. We then calculated as Euclidean distance from the water source	10 m; Winter data: December 2016 to January 2017; Summer data: April 2016 to May 2016	This provides a measurable distance from the water that may affect distribution. Ken river and the streams are the primary water source in the study area; however, most of the streams dry out during summer
Normalized difference vegetation index (NDVI; Pettorelli, 2013)	Sentinel-2A https://earthexplorer.usgs.gov	10 m; December 2016 to January 2017	This is used as a vegetation index as it positively correlates to the tree basal area (Figure S2). In our study area, the dense forest is represented by comparatively higher NDVI values
Distance from the settlements (settlement)	Calculated as Euclidean distance from the human settlements		This variable is a measure of anthropogenic pressure in terms of access of local people to the forest and caused disturbance
Distance from the agriculture (agriculture)	Calculated as Euclidean distance from the agricultural fields		This is also a measure of anthropogenic pressure. Agricultural fields retain crops during winters and may become an attraction to the crop-raider species such as nilgai

TABLE 2 Table quantifies the proportion of extrapolation outside the coverage of covariate values.

		Summer				Winter			
		Univariate	Combinatorial	Analogue	Total grid cells	Univariate	Combinatorial	Analogue	Total grid cells
Sambar	Count	580	7	**12,178**	12,765	592	31	**12,564**	13,187
	Percentage	4.54	0.05	**95.4**		4.49	0.24	**95.28**	
Chital	Count	764	4	**11,997**		576	17	**12,594**	
	Percentage	5.99	0.03	**93.98**		4.37	0.13	**95.5**	
Nilgai	Count	434	11	**12,320**		1111	29	**12,047**	
	Percentage	3.4	0.09	**96.51**		8.42	0.22	**91.36**	
Wild pig	Count	743	7	**12,015**		383	—	**12,804**	
	Percentage	5.82	0.05	**94.12**		2.9	—	**97.1**	

Note: Here, Univariate: Mathematical extrapolation occurs. It represents conditions outside the range of individual covariates in the reference sample; Combinatorial: multivariate extrapolation occurs based on the combination values encountered within the range of reference covariates and Analogue: is an interpolation within the range of covariates. Most of our distribution maps have excellent coverage of covariates and are hence reliable.

TABLE 3 Results of the distance sampling analysis for all ungulates.

Species	Individual density/km^2	CV	Cluster density/km^2	Group size/ km^2	Abundance	Detection probability	Goodness-of-fit (gof)	Encounter rate (individuals/ km)	Total effort (km)	Total covered area (km^2)	Best-fit model	AIC
Sambar (n = 299)	12.5 ±1.16	0.09	5.59 ±0.48	2.24 ±0.08	7248 ±673	0.34 ±0.02	0.53	0.78 ±0.05	854	170.8	Half Normal cosine	2400.7
Chital (n = 189)	11.9 ±1.34	0.11	3.31 ±0.32	3.59 ±0.21	6861 ±773	0.33 ±0.01	0.60	0.79 ±0.07	854	170.7	Uniform cosine	1550.0
Nilgai (n = 230)	10.94 ±1.41	0.12	4.34 ±0.49	2.52 ±0.15	6306 ±815	0.20 ±0.01	0.70	0.67 ±0.06	854	256.8	Hazard rate	1970.7
Wild Pig (n = 111)	6.97 ±1.27	0.18	2.20 ±0.33	3.16 ±0.31	4071 ±731	0.29 ±0.03	0.76	0.41 ±0.05	854	170.9	Hazard rate	898.08

using "dsm" package version 2.3.0 (Miller et al., 2020) in R version 3.6.0 (R Core Team, 2019). All the models were checked and selected by the iterative process (Appendix S1A).

2.4.4 | Abundance prediction and variance estimation

The response distribution obtained from DSM was then used to predict density over the whole study area with 200×200 m prediction cells. Predictions were made for each cell based on predictor variables that fit the model. To estimate coefficient of variation, we used delta method, which assumes that variance component in detection function and spatial models are independent. The total variance estimate over the entire area is sum of square of estimated variance of predicted values and square of variance of detection probability from the detection function model. Similarly, we measured CVs for abundance prediction for each cell. The squared coefficient of variation from GAM and detection function was added on a per-cell basis following the approach described by Miller et al. (2013). We produced maps for the prediction cells overlaid with the CV values to visualize the CVs. We further tested the coverage of covariates of interest to test the reliability of density prediction maps using "dsmextra" package (Bouchet et al., 2019; Table 2).

3 | RESULTS

3.1 | Population estimates of ungulates

In summer, animal sightings were frequent due to increased visibility and thinner understory vegetation. Sambar was the most frequently sighted animal in both seasons, followed by nilgai and chital. We found sambar to be most abundant in the study area with total abundance of ($\hat{N} = 7248 \pm 673$ individuals and density $\hat{D} = 12.5 \pm 1.16$ individuals/km^2) followed by chital ($\hat{N} = 6861 \pm 773$; $\hat{D} = 11.9 \pm 1.34$) and nilgai ($\hat{N} = 6306 \pm 815$; $\hat{D} = 10.94 \pm 1.41$). Chital and wild pig formed larger groups (Figure S4) with an average group size of 3.59 ± 0.21 and 3.16 ± 0.31 individuals per group (Table 3). However, the highest cluster density was recorded for sambar 5.59 ± 0.48 groups/km^2.

3.2 | Spatio-temporal distribution and response to habitat variable

We found that season significantly affects all the ungulates' density and distribution. However, we found a similar relationship between habitat and response variables across seasons for all ungulates except wild pig density with water. Poisson family distribution explained the mean–variance relationship for all ungulates. In all the final models, at least one terrain variable (TRI or elevation), one habitat variable (NDVI or water) and one variable describing anthropogenic influence (settlement or agriculture) had a significant effect

TABLE 4 Model parameters for generalized additive modeling of spatial model for each species in each season.

Species (n = 2178)	Season	Fitted model parameters (p-value <.001)	Response family	Dispersion parameter	Deviance explained
Sambar	Winter (Season 1)	$\log\{E(n_i)\} = -12.8267 + f_1(x_i):(y_i) + f_2(\text{elevation}_i) + f_3(\text{NDVI}_i) + f_4(\text{distagri}_i) + f_5(y_i) + \text{off.set}$	Poisson	1.16	20.1%
	Summer (Season 2)	$\log\{E(n_i)\} = -10.6045 + f_1(x_i):(y_i) + f_2(\text{elevation}_i) + f_3(\text{NDVI}_i) + f_4(\text{distagri}_i) + f_6(x_i) + \text{off.set}$			
Chital	Winter	$\log\{E(n_i)\} = -13.9972 + f_1(\text{elevation}_i) + f_2(\text{NDVI}_i) + f_3(\text{distsettle}_i) + f_4(x_i) + f_6(y_i) + \text{off.set}$	Poisson	1.15	30%
	Summer	$\log\{E(n_i)\} = -8.8255 + f_1(\text{elevation}_i) + f_2(\text{NDVI}_i) + f_3(\text{distsettle}_i) + f_5(x_i) + f_7(y_i) + \text{off.set}$			
Nilgai	Winter	$\log\{E(n_i)\} = -12.3044 + f_1(\text{elevation}_i) + f_2(\text{water}_i) + f_3(\text{distsettle}_i) + f_4(\text{distagri}_i) + f_5(x_i) + f_7(y_i) + \text{off.set}$	Poisson	1.03	21.4%
	Summer	$\log\{E(n_i)\} = -12.0513 + f_1(\text{elevation}_i) + f_2(\text{water}_i) + f_3(\text{distsettle}_i) + f_4(\text{distagri}_i) + f_6(x_i) + f_8(y_i) + \text{off.set}$			
Wild Pig	Winter	$\log\{E(n_i)\} = -13.5527 + f_1(x_i):(y_i) + f_2(TRI_i) + f_3(\text{water}_i) + f_5(\text{NDVI}_i) + \text{off.set}$	Poisson	0.70	30.6%
	Summer	$\log\{E(n_i)\} = -15.0353 + f_1(x_i):(y_i) + f_2(TRI_i) + f_4(\text{water}_i) + f_5(\text{NDVI}_i) + \text{off.set}$			

Note: Here, n = number of sampled units, ($f_1 - f_8 f_1 - f_8$) are the smooth terms for the environmental parameters with significant relationships with abundance, dispersion parameter shows the distribution of the data around the mean (values > 0.50 shows under dispersed or skewed datasets and represent model misfit), deviance explained shows the amount of variance explained by the model.

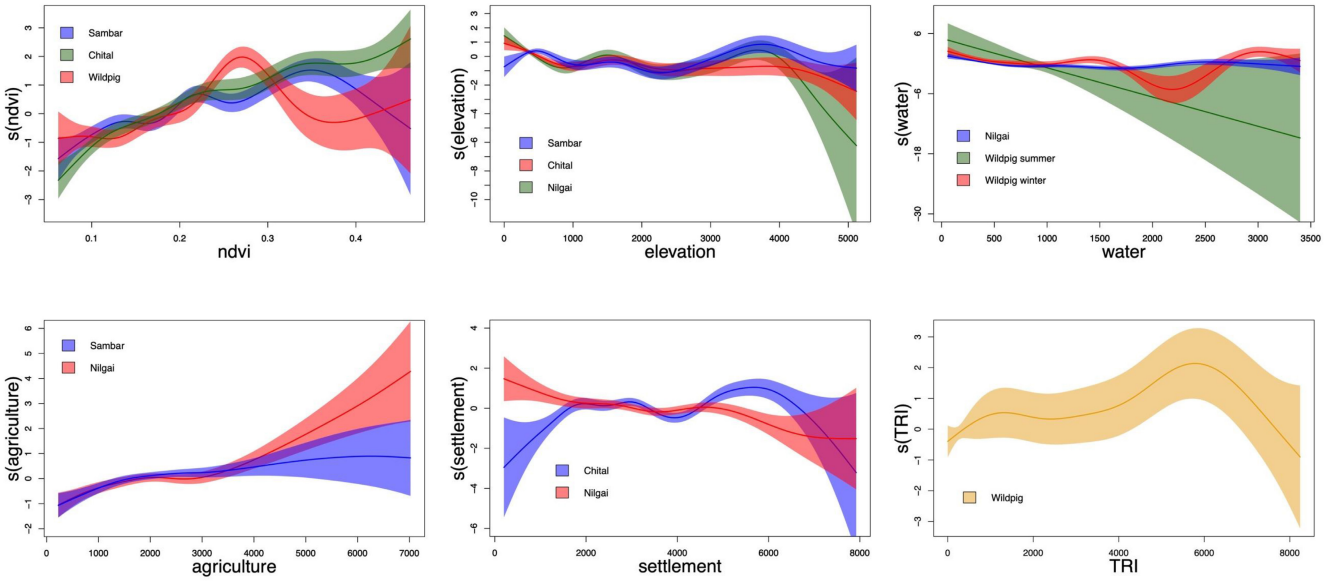


FIGURE 2 Species seasonal response curve with environmental parameters with 95% confidence interval. The response curve was drawn only for those parameters which were significant in the model for each species. Here, *y*-axis is the scale of log link function and *x*-axis shows the range of environmental parameters.

on species densities. The final GAM accounted for 20%–30% of the variability in species data (Table 4).

3.2.1 | Sambar (*Rusa unicolor*)

Sambar densities vary seasonally, with higher mean densities in summer. They avoid the agricultural fields, prefer densely forested habitats (positive relationship with NDVI) and higher elevations in both seasons. Densities decline in the northern part of the reserve in winter (Figure 2). Summer densities in the valley are 2.3 individuals/ha while it is 2.8 individuals/ha at the middle and upper plateau. These patterns are reflected in the spatial distribution maps (Figure 3a).

We recorded low CVs in most of its distributional ranges in both seasons except the riverine area in winter and near the forest edges in summer. The CV varied spatially with 0.05–0.63/ha in summer and 0.05–2.30/ha in winter. We recorded higher CVs in those regions where sightings were negligible (Figure 4). However, densities were more precise and reliable in the areas of higher abundance.

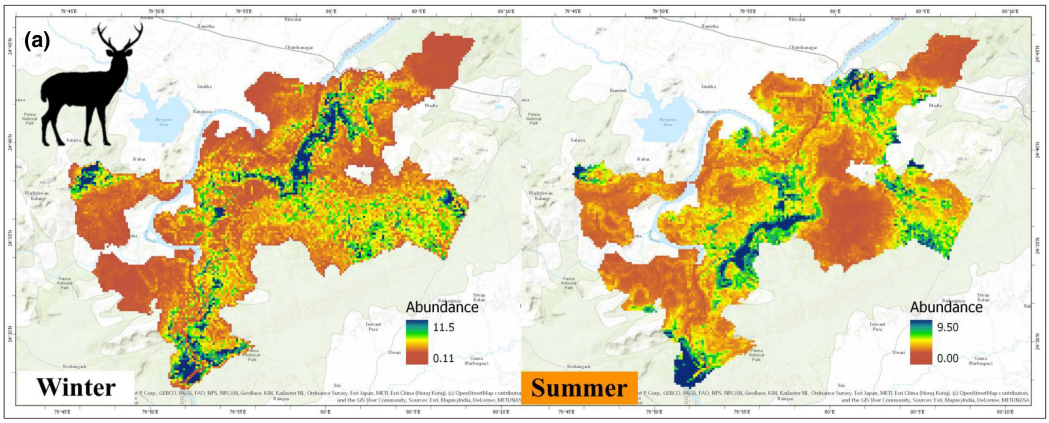
3.2.2 | Chital (*Axis axis*)

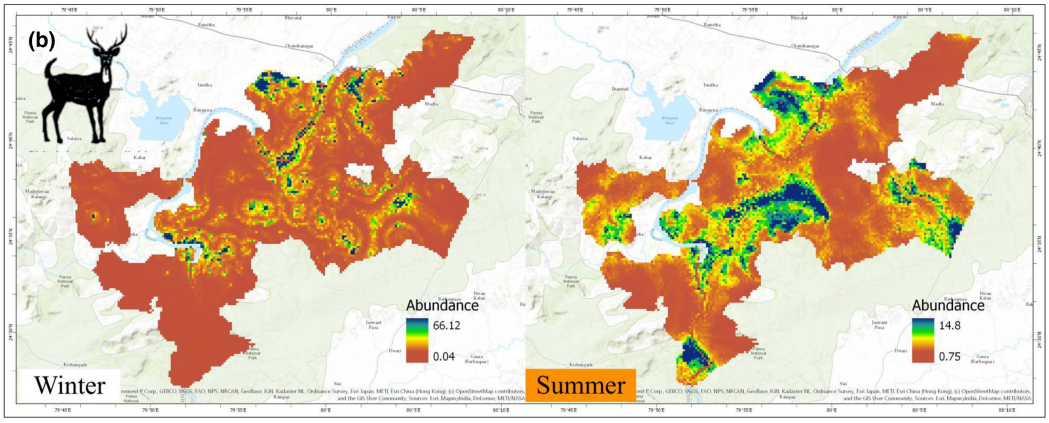
Chital abundances are predicted to increase with increasing NDVI and away from the settlements. Chital prefers the lower elevation area, the valley. Chital abundances are higher towards the east in summer and lesser in winter, while response with longitude is inverse (Figure 2). Chital forms larger groups in winter (range varies from 0 to 16.5 individuals/ha) when resources are abundant, while more dispersed in summer (range varies from 0 to 3.5 individuals/ha) when resources are scarce. We observed a seasonal shift in the abundance distribution towards the valley and middle plateau in summer, reflected in spatial distribution maps (Figures 3b). We observed low CVs in most of its distributional ranges except in the riverine area in summer and the southern region in winter. CV varies comparatively more in summer ranging from 0.02 to 2.5/ha.

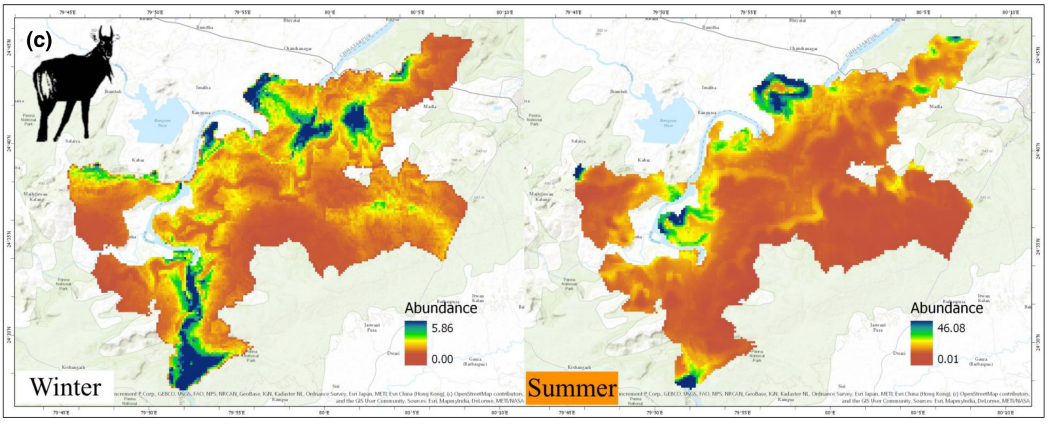
3.2.3 | Nilgai (*Bocephalus tragocamelus*)

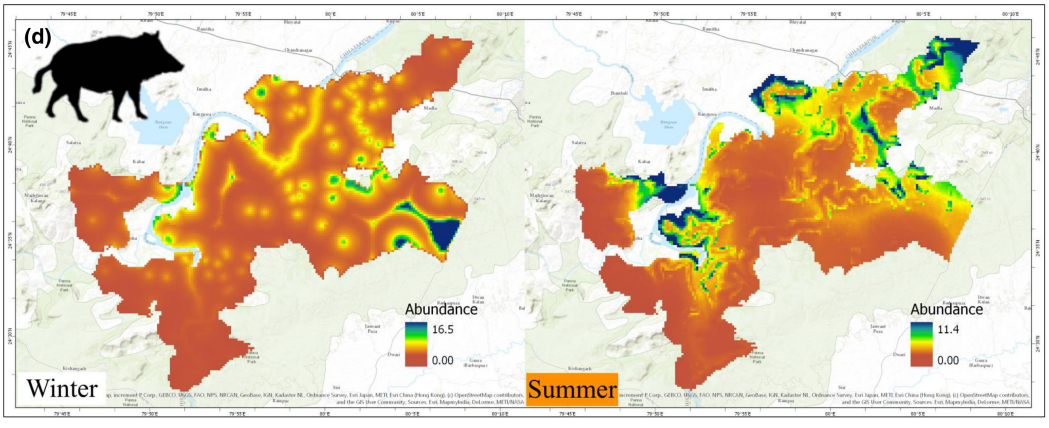
We found that season significantly affects the mean density of nilgai. Higher densities were recorded at the north-western side of the reserve. They prefer proximity to water and lower elevation. Nilgai seems to prefer habitats distant from the agricultural fields (Figure 2). In summer, species are extensively restricted to the valley in large congregations (ranging from 0 to 11.5 individuals/ha), contrary to their distribution to the valley and middle plateau in smaller congregations in winter (ranging from 0 to 1.46 individuals/ha; Figure 3c). Nilgai shows a clear seasonal shift in the distribution with habitat preference to the middle plateau and valley in the winter and completely shifted to the valley in summer. We recorded very low CVs in most of the distributional ranges in both seasons (Figure 4).

FIGURE 3 Map of predicted seasonal density (individuals/4 ha) gradient across the spatial extent of the study area for four ungulate species (a) sambar, (b) chital, (c) nilgai, and (d) wild pig. Here, abundance color gradient shows a different range of values in each map which was defined at the bottom of the map.


(a)
Abundance
11.5
0.11
Winter
Abundance
9.50
0.00
Summer


(b)
Abundance
66.12
0.04
Winter
Abundance
14.8
0.75
Summer


(c)
Abundance
5.86
0.00
Winter
Abundance
46.08
0.01
Summer


(d)
Abundance
16.5
0.00
Winter
Abundance
11.4
0.00
Summer

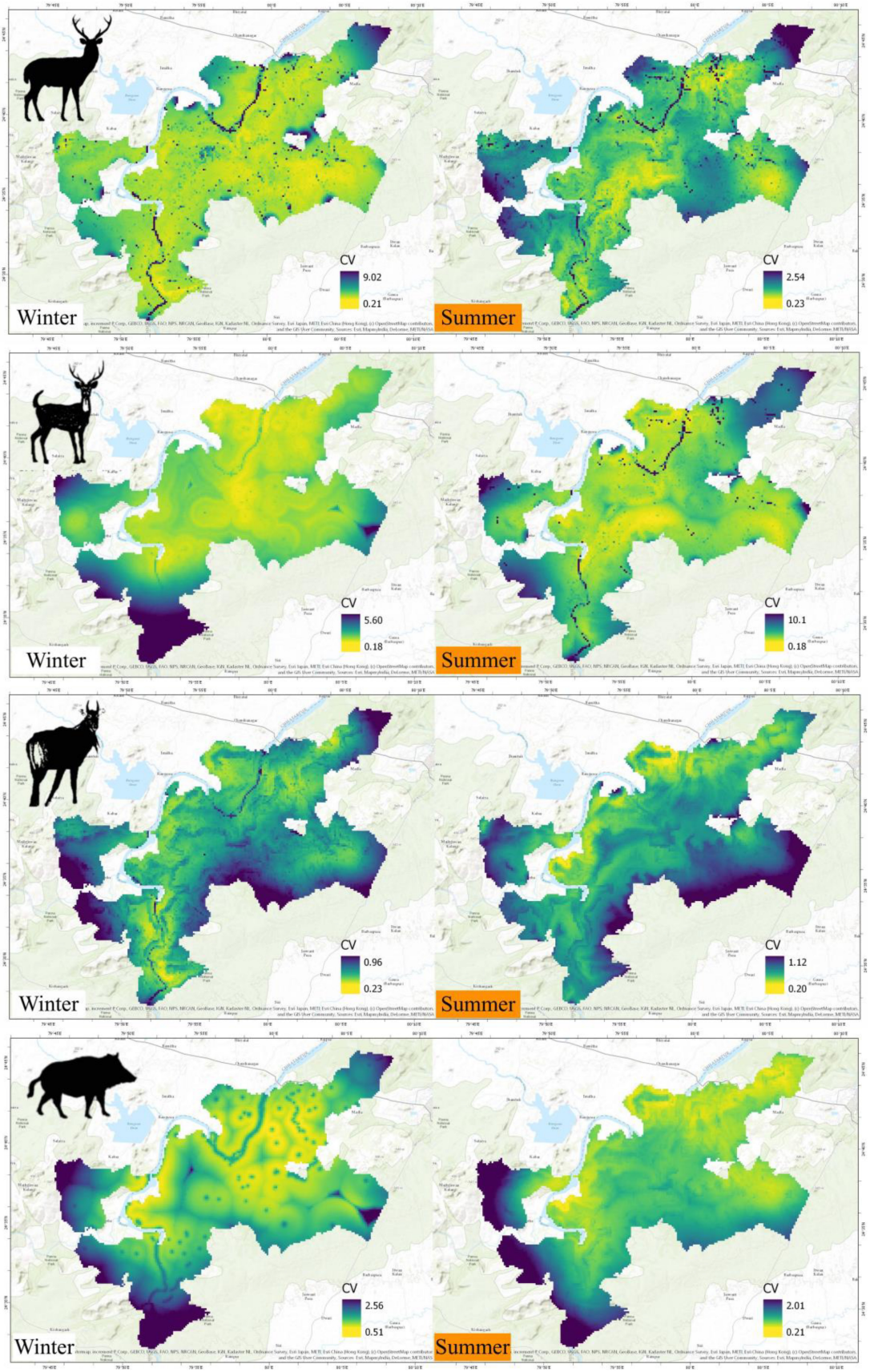


FIGURE 4 Map of the predicted coefficient of variations calculated from both detection function and GAM parameters of the model for four ungulate species (from the top) sambar, chital, nilgai, and wild pig in both seasons.

3.2.4 | Wild pig (*Sus scrofa*)

Wild pig is the least sighted ungulate; however, data fulfilled the model assumptions and were sufficient to perform the analysis. Season significantly affected the wild pig abundance with higher mean density in winter. We found higher density at higher NDVI and in rugged terrain. Water presence has profound effects on density in summer compared to winter. Density decreases drastically with increasing distance to the water source in summer. Abundance maps of both seasons show their complete seasonal shifts to the valley in summer (Figure 3d). They make larger groups in summer as fewer niches are available due to resource scarcity. Whereas in winter, animals were primarily distributed to the upper plateau. We observe low CVs in most of the distributional range in both seasons except in the area where detections were less (Figure 4).

4 | DISCUSSION

4.1 | Population estimates

Our study found sambar and nilgai at higher densities than other protected areas in the central Indian landscape, such as Kanha Tiger Reserve (TR), Bandhavgarh TR, Pench TR, and Satpura TR (Jhala et al., 2018). They both are large-bodied prey of tiger and have helped in population recovery and maintaining a viable population of tigers in our study area. High densities of nilgai in our study area are directly related to the mosaic habitat of PTR, which provides suitable habitat for the species.

4.2 | Spatio-temporal distribution and response to habitat variable

This study describes seasonal resource heterogeneity that drives the abundance of ungulates to the more suitable habitats and may help managers to plan effective conservation strategies. Tropical dry deciduous forests show strong seasonality, which in turn causes a difference in resource distribution across habitats. Seasonal dynamics cause animals to shift their habitat according to resource availability. Our results show a clear seasonal shift in the abundance distribution of four major ungulate species, more abundant in the valley habitat during summer.

The topography of dry deciduous forests plays a significant role in driving the abundance distribution of ungulates. Topography defines the ascending moisture gradient from the plateau to the valley, further related to the forage availability (Moura, 2007). Thus, when resources become scarce in summer, the valley fulfills all the habitat requirements such as shade to escape the heat, water and green foliage as forage (Johnsingh & Manjrekar, 2015; McKay & Eisenberg, 1974; Schaller, 1967). Whereas in winter, when moisture is not a limiting factor for resource distribution across habitats, animals are distributed more evenly. Density distribution in various topographic regions is also associated with resource availability in different seasons. The plateaus are comparatively drier habitats, harboring majorly deciduous trees that shed early winters, allowing more sunlight and therefore warmer. Animals move to plateaus to escape cold forest nights in winter. The valley, in contrast, provides more shades with a thick canopy and hence relatively colder. Consequently, all four species were distributed on the plateaus during winter.

Ungulates' seasonal distribution is primarily influenced by the availability of suitable habitat, vegetation cover, water, and lack of disturbance (Johnsingh & Manjrekar, 2015; Neumann et al., 2015). Nilgai in central India is considered a crop-raider. Sankar (1994), Awasthi et al. (2016) and Harihar et al. (2014) found nilgai to be abundant in human-dominated landscapes. In our study, nilgai's positive relationship with distance from agriculture was explained by its habitat suitability to the relocated villages in PTR. There are 14 relocated villages in PTR that provide many fruiting trees and ample grasses in winter, providing excellent habitats for such mixed feeders (Sankar, 1994). However, higher densities of chital and sambar away from anthropogenic variables explain their habitat preferences in the undisturbed forest.

Plateaus are the preferable habitats in winter as they provide ample resources due to the availability of water post-monsoon. In winter, streams and waterholes retain monsoonal water and thus support a higher abundance than the valley. As summer approaches, water shrinks measurably in waterholes and streams. Wild pig, a water-dependent species, prefers to stay near permanent water sources (Johnsingh & Manjrekar, 2015; Kumar et al., 2021; Roberts, 1997) and move to areas where river water is easily accessible (Figure 2). Local movements and migration activities in response to water limitations in the dry season have been recorded in white-eared kob (Fryxell & Sinclair, 1988a), khulan (Payne et al., 2020), African elephants (Purdon et al., 2018), and different ungulate species in Serengeti. However, browsers and grazers have similar water requirements (Kihwele et al., 2020), while few other mammals, such as bats (Heithaus et al., 1975) and primates (Brown & Zunino, 1990), shift their diet to increase water intake through forage (Galetti & Pedroni, 1994). Although the diet preferences have not been included in this study, we suspect that chital and sambar rely more on dietary flexibility for water requirements in the dry season as there was no significant relationship between water and population density for both species (Figure 2).

Furthermore, water presence did not affect nilgai distributions. Ungulates' need for cover is partly explained by their relationship with NDVI. Because NDVI captures the tree canopy cover and is positively related to the tree basal area (Figure S2), it refers potentially to shade and escape cover, specifically in the dry deciduous forest where the light porosity is higher. Chital and sambar are forest species and prefer dense vegetation to fulfill their need for shade and shelter in both seasons. Nilgai and wild pig distribution remain

independent of NDVI, which further explains their preference to open habitats. However, due to the dry deciduous nature of the forest, NDVI does not grant a large range of variation across the study area. Therefore, the results from NDVI may be taken as indicative and detailed research involving empirical field data and remote sensing data would add further clarification to the interpretation of these relationships.

Our results also show that sambar resource requirements match the chital in both seasons (Figure 2). Chital and sambar are both forest species which prefer dense vegetation in winter. This study highlights that group-living animals such as chital formed larger groups in winter when resources were abundant. This might act as their anti-predatory behavior, which helps them stay more vigilant when visibility is less, and the cost of resource sharing could be minimized (Johnsingh & Manjrekar, 2015).

Conventionally management actions are implemented based on the species abundance and distribution estimated uniformly across the spatial extent of an area. This study proposes a model-based approach which estimates the precise abundance of terrestrial mammals taking into account spatial and temporal changes in the environmental conditions. The spatio-temporal model in this study has been used to estimate demographic parameters of four ungulate species having diverse biological traits such as sociality, body size, and dietary preferences and hence have broader management implications. As our results describe that species respond spatially and temporally to changing environmental conditions, we propose using spatio-temporal model-based approach to identify priority areas to most benefit the species from management actions. These techniques can be extended to large scales and help allocate priority areas in species recovery programs, understand the population dynamics, and evaluate the cost-effectiveness of management actions.

AUTHOR CONTRIBUTIONS

RK developed the larger project and facilitated field data collection; DG and RK designed the experiment and data collection protocols. DG conceived the idea, collected data, performed statistical analyses, and wrote the article; both authors discussed the results and reviewed the manuscript.

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CONFLICT OF INTEREST STATEMENT

We have no competing interest to disclose.

DATA AVAILABILITY STATEMENT

The data were collected as a part of a large conservation project involving Tiger Reintroduction in Panna Tiger Reserve and most are confidential due to the location of endangered species, but the data may be shared by the Principal Investigator of the project (RK) upon reasonable request for any important purpose.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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