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FACTORS AFFECTING HABITAT OCCUPANCY OF TIGER IN THE TERAI ARC LANDSCAPE, INDIA

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DOCTOR OF PHILOSOPHY
IN
WILDLIFE SCIENCE

BY

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June 2009

DECLARATION

I hereby declare that the thesis entitled “Factors Affecting Habitat Occupancy of Tiger in the Terai Arc Landscape, India” submitted to Saurashtra University, Rajkot for the award of the degree of Doctor of Philosophy in Wildlife Science, is a record of original research work done by me under the supervision of Dr. S. P. Goyal, Wildlife Institute of India, Dehradun, and it has not formed the basis for the award of any other degree or diploma. I also declare that the thesis embodies my own work, observations and analysis and this work contributes towards advancement of knowledge in the subject.

Date: 16th June 2009

(K. Rajapandian)

Place : W.I.I., Dehradun

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CERTIFICATE

This is to certify that the thesis entitled "Factors Affecting Habitat Occupancy of Tiger in the Terai Arc Landscape, India" submitted to Saurashtra University, Rajkot for the award of the degree of Doctor of Philosophy in Wildlife Science, is a record of original research work carried out by K. Rajapandian under my guidance and supervision. No part of this thesis has been submitted for any other degree and it fulfills all the requirements laid down in the ordinance of Saurashtra University, Rajkot for this purpose.

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SUMMARY

Most rare and critically endangered species such as tiger (*Panthera tigris*) exist in human-dominated landscapes as small, fragmented and isolated populations in most part of its range. A prerequisite for conservation efforts and management is to identify the factors which affect the distribution and abundance of the species of interest and connectivity between populations occupying the remaining fragments. Tiger populations have dramatically declined in recent years in the Indian part of Terai Arc Landscape (TAL). This top priority landscape for tiger conservation was once continuous across the Himalayan foothills but is now highly fragmented and most of the remaining large, intact habitats are located within protected areas. As tigers cannot sustain viable populations in small habitat fragments an assessment of potential suitable habitat and connectivity among the remaining habitat patches is required to assess possibilities to ensure the creation of a single functioning metapopulation unit for tiger. The goal of this study, therefore, was to identify the factors affecting the distribution of tiger and assess the distribution of suitable habitat patches and the connectivity between these patches for successful dispersal in the Indian part of TAL.

I developed GIS probability models for tiger and its prey species and a spatially explicit individual-based dispersal model (SEIBM) for tiger in order to identify and assess the factors which are affecting the occupancy of tiger and subsequently predict potential suitable habitats and estimate the connectivity between the fragmented subpopulations in the Indian as well as between Indian and Nepal part of TAL.

Data were collected on presence/absence of four wild ungulates (sambar *Cervus unicolor*, chital *Axis axis*, nilgai *Boselaphus tragocamelus*, and wild pig *Sus scrofa*), which are important prey species of tiger in two phases during the period between 2002 and 2006. Remote sensing and topographic data were used to develop spatial layers of land use, vegetation characteristics and topography. I integrated the presence and absence information with landscape characteristics and indices of human disturbance using generalized linear models (GLM) at different neighbourhood scales.

Model results were agreed well with previous knowledge on species' habitat selection and yielded model accuracy larger than 73%, except for wild pig. Final models indicated that different factors determined habitat suitability for 4 study species and quantifying habitat suitability over the Indian part of TAL showed that they segregate considerably in space. Model predicted most of the terai habitats to be suitable for 3 ungulate species (chital, nilgai and wild pig) and the hilly terrain habitats, bhabar and Shivaliks, suitable for chital and sambar. More quantitatively, about 38% (*c*.16200sq.km) of the study area was suitable for at least one of four prey species, but in 58% (*c*.9400sq.km) of this area only one species would occur, in 29% (*c*.4700sq.km) two species and in 13% (*c*.2100sq.km) three species. Overall, 63% of the TAL was classified as unsuitable and only 16% (*c*.6800sq.km) of the landscape was suitable for more than one species.

For tiger, I used an approach based on presence and pseudo-absence data, combining ecological niche factor analysis (ENFA) and GLM. The tiger presence locations were based on the evidences of tiger's scat and pugmark. Data for two most important prey species, chital and sambar, were taken from plots laid for collection of prey species faecal pellet groups. All these data collected from the Indian part of TAL. An information theoretic approach of model selection was used to confront my data on tiger presence to hypotheses on tiger habitat selection (i.e., protective habitat, prey species, disturbance, and natural habitat) at several spatial neighbourhood scales.

All hypotheses yielded models with high prediction accuracy (> 90%). The most parsimonious model supported the "prey species hypothesis" and contained two variables characterizing the amount of two prey species (chital and sambar) habitat suitability within a 37sq.km neighbourhood scale area. The best model of the human disturbances hypothesis suggested that the presence of agriculture land and human habitation and diversity in landuse types had negative effects and presence of protected area had positive effect on tiger distribution. More detailed assessment of the potentially suitable areas using an extended source-sink approach suggested that most of the habitats outside the protected areas were attractive sink-like habitats, i.e., they showed high "natural" quality but suffered high levels of human

disturbance. Potential corridors had generally a low proportion of suitable habitat and showed high levels of human disturbance.

In the next step, I developed a SEIBM of dispersing tiger behaviour and assessed the connectivity among the major habitat patches and investigated the effect of potential initiatives to restore corridors in the Indian and between India and Nepal part of TAL.

Model clearly showed that connectivity is not solely a function of distance between patches, but an outcome of the interplay between behaviour and landscape configuration, with asymmetric connectivity explained by canalizing or diffusing effects of the landscape, and depending on the landscape context of the starting patch. The most important model parameter determining patch connectivity was the autocorrelation in movement, followed by the daily movement capacity.

The results of this study, in addition to contributing to the knowledge on factors affecting suitable habitat distribution and dispersal of tiger, have many implications for conservation of tiger in the Indian part of TAL. This study has also identified critical areas needed for management initiatives for functional unit of tiger conservation in the TAL. These are discussed in this thesis.

CHAPTER 1

INTRODUCTION

1.1 General introduction

In the present conservation scenario habitat degradation, loss and fragmentation are among the most evident threats to the biological diversity (Wilcox and Murphy 1985; Wilcove *et al.* 1986; Saunders *et al.* 1991; McCullough 1996; Wilcove *et al.* 1998). Habitat loss may also lead to fragmentation of the habitat into small, isolated remnants (Fahrig 1997). Habitat fragmentation often leads to the isolation of small populations that are more vulnerable to local extinction (Pimm *et al.* 1988) because of demographic as well as stochastic events (Gilpin and Soule 1986). Fragmentation results in the subdivision of the natural habitat into smaller, isolated patches, which are surrounded by a more or less hostile matrix, reducing the continuity or connectivity of the landscape (With 1997; Ferreras 2001). Populations in fragmented habitats result in small isolated patches. The connectivity between these patches facilitates the gene flow between subpopulations and is vital for population survival (Fahrig and Merriam 1985; Bennett 1990; Farina 1998; Crooks 2002). Metapopulations are sets of local populations connected by inter-patch dispersal and dispersal is a key process in determining the survival of these populations (Davis and Howe 1992; Fahrig and Merriam 1994; Hanski *et al.* 1994).Connectivity is a key factor in the dynamics and persistence of metapopulations because the probability of long-term viability of populations in smaller and isolated patches is undoubtedly very low (Crooks 2002). The indirect effects of reduced inter-patch dispersal are the major ecological consequences of habitat fragmentation (Schumaker 1996).

Corridors are popular tools for mitigating habitat fragmentation and conservation of biological diversity (Hess and Fischer 2001). Corridors may enhance connectivity by providing safe passage between fragmented habitats (Beier 1993; Noss *et al.* 1996; Beier and Noss 1998). The term corridor has been widely defined in literature mainly focusing on function, the movement of flora and fauna (e.g. Loney and Hobbs 1991; Beier and Loe 1992; Simberloff *et al.* 1992; Rosenberg *et al.* 1995, 1997). However, Hess and Fischer (2001) discussed the confusion over the different definitions, because, corridors serve a variety of functions at many scales and corridor designed for one specific function will also serve other functions hence, the concept and terms associated with this will ignore the simple definition. In the field of landscape ecology, the term corridor has been structurally defined as a linear surface area that differs from the matrix on either side (Hess and Fischer 2001). The utility of corridor as a conservation tool to increase the connectivity of isolated patches is important to protect biological diversity because the process of isolation and population extinction ultimately leads to a reduction in biological diversity (Rosenberg *et al.* 1997). It has been widely accepted that increased interchange of individuals among population will increase local and regional population persistence for smaller and isolated populations (Fahrig and Merriam 1994; Sjogren 1991; Rosenberg *et al.* 1997). In reserve designs, corridors have emerged as an important tool to protect biological diversity (Rosenberg *et al.* 1997). Moreover, protection of naturally existing corridors promotes ecological process and may benefit local and regional biological diversity (*Ibid* 1997). Wikramanayake *et al.* 2004 developed the GIS-based model to identify the suitable corridors for dispersal of tigers from breeding subpopulations for persistence of metapopulation across the Terai Arc Landscape.

To evaluate corridors in a region or landscape, it is important to select “umbrella species” because it is assumed that protection of umbrella species may benefit other species that may have the greatest needs for a corridor (Noss 1991; Beier and Loe 1992). Beier (1993) mentioned the mountain lion can become a valuable focal species in larger, more intact habitat blocks because it requires a large home range and is sensitive to environmental perturbations. In fragmented habitats, individuals might expand their home range including several fragments for additional resources for their survival (Redpath 1995; Collins and Barrett 1997; Little and Crowe 1998; Tigas *et al.* 2002). However, maintaining such a home range requires movement between habitat fragments through urban matrix or corridors (Tigas *et al.* 2002).

Mammalian carnivores are particularly vulnerable to local extinction in fragmented landscapes because of their large home ranges, low numbers and sensitive to changes in habitat conditions (Noss *et al.* 1996; Woodroffe and Ginsberg 1998; Crooks 2002). They require movement corridors for their survival in smaller and isolated habitats. So they can be excellent focal organisms to evaluate the degree of functional landscape level connectivity (Beier 1993; Noss *et al.* 1996; Soule and Terborgh 1999; Crooks 2002).

As the increasing human populations around the forest areas creating enormous human disturbances for carnivore populations, the gap between law and reality needs to be filled with realistic concepts about the co-existence of people and predators (Breitenmoser 1998). Management plans describing how to handle conflicts with large predators are needed (Schröder and Promberger 1993). This challenging task needs a multidisciplinary approach involving scientists (wildlife biologists, conservation biologists, sociologists), policy makers, the local authorities, as well as representatives of the different interest groups (e.g. hunters, sheep breeders, and conservationists). In order to develop efficient conservation and recovery strategies, wildlife and conservation biologists need to understand and evaluate the various threats confronting populations, and to predict the potential distribution and explore ways to reach it. The geographic information system (GIS) combined with habitat modeling has proved to be an important tool to assess the habitat suitability (HS) for a given species. It gives among others information about the spatial extent, arrangement and fragmentation of suitable habitat. This is a necessary prelude to estimate the potential population size (Mladenoff and Sickley 1998). The HS maps can furthermore be used as input maps for other models. Patches of suitable habitat derived from HS maps used as source patches to parameterize the dispersal model and in cost-distance analyses in the GIS to assess the functionality of the existing corridors and estimate connectivity between the fragmented subpopulations.

1.2 Study species: Tiger *Panthera tigris*

Evidence for the evolution of the tiger comes from the fossil remains, as well as from the modern molecular phylogenies. The genus *Panthera* probably evolved within the last five million years or so (Hemmer 1976; Collier and O'Brien 1985; Wayne *et al.* 1989; Kitchener 1999). It is almost certain that the tiger originated in eastern Asia (Hemmer 1981, 1987; Herrington 1987; Mazak 1981, 1996; Kitchener 1999). Tigers had colonized the Indian sub-continent 12000 years ago (Luo *et al*. 2004) either coming through north-east Asia via central Asia (Hemmer 1987; Mazak 1981), or through north-west India (Heptner and Sludskii 1992).

The species *Panthera tigris* has been divided into nine distinctive sub-species (*P. t. tigris, P. t. altaica, P. t. amoyensis P. t. sumatrae, P. t. corbetti*, *P. t. jacksoni, P. t. sondaica, P. t. balica* and *P. t. virgata*, the three are extinct), which apparently vary in body size, characteristics of the skull, and colour and markings of the pelage (Mazak 1981, 1996; Herrington 1987; Nowell and Jackson 1996; http://www.savethetigerfund.org/). The definition of a sub-species is recently given as a label for a local geographical variant to represent a morphologically- and genetically-distinct sub-population, which has evolved in isolation, but which may subsequently hybridise with neighbouring populations to a limited extent (Corbet 1970, 1997; Mayr and Ashlock 1991; O'Brien and Mayr 1991). The advent of molecular techniques has shown that there is often a real discrepancy between traditionally-recognised sub-species and genetically-distinct populations (Kitchener 1999).

At present, the tiger is found only in southern, south-eastern and eastern parts of Asia. The geographic distribution of the tiger once extended across Asia from eastern Turkey to the Sea of Okhotsk, but its range has been greatly reduced in recent times. Now tigers survive only in scattered populations from India to Vietnam, and in Sumatra, China, and the Russian Far East (Nowell and Jackson 1996). Tiger occupied forests in India have been classified into 6 landscape complexes; namely (1) Shivalik-Gangetic Plains, (2) Central Indian Landscape Complex (3) Eastern Ghats, (4) Western

Ghats, (5) North-Eastern Hills and Bhramaputra Plains, and (6) Sunderbans. (Jhala *et al*. 2008). Each landscape complex consists of landscape units that still have contiguous tiger habitat and contain one to many breeding populations of tigers (source populations). Within each landscape unit there exists a potential to manage some of the tiger populations as a meta-populations. This enhances the conservation potential of each of the single populations and probability of their long-term persistence in identified each landscapes. Recent estimate showed that there are 297 (259-335) tigers in the study area, the Indian part of Terai Arc Landscape, and overall 1411 (1165-1657) tigers in India (Jhala *et al*. 2008). Recent assessment by Dinersitein *et al*. (2006) and Sanderson *et al*. (2006) on the conservation status of entire tiger habitats at the landscape level showed the Indian part of Terai Arc Landscape contains a large proportion of Global and Regional Tiger Conservation Landscape Priorities.

The tiger has been used as a charismatic flagship species in the efforts to protect overall biodiversity in several Asian countries (Karanth 1995). Despite this, the threats to its survival appear to have increased in recent years due to widespread over-hunting of its prey (Karanth 1991; Rabinowitz 1991), poaching of tigers for commercial reasons (Jackson 1993; Rabinowitz 1993), and from habitat destruction (Seidensticker 1986), combined with slackening protection efforts for socio-political reasons (Ghosh 1993). Habitat loss, as well as habitat degradation and fragmentation, is the main cause of the decline of the large cats, including the tiger, with illegal killing playing an increasingly damaging role as tigers have become more vulnerable (WWF 1999). Habitat loss remains a grave danger for the tiger, particularly in South and South-east Asia, while illegal killing is considered as the immediate threat, which hastens extinction (WWF 1999). According to Nyhus and Tilson (2004), however, the four main reasons for the tiger’s decline are: 1) reduced, degraded and fragmented habitat, 2) diminished prey populations, 3) killing of animals for the illegal trade in tiger parts (Dinerstein *et al.* 1997; Seidensticker 1997; Hemley and Mills 1999; Karanth and Stith 1999), and 4) persecution by humans in response to real or perceived livestock predation and attacks on people (McDougal 1987; Nowell and Jackson 1996; Tilson *et al.* 2000).

Throughout the global range, tiger population sizes are estimated to vary from less than 20 to less than 200 breeding animals (Jackson 1993), which makes the populations vulnerable to stochastic genetic, demographic, and ecological events (Shaffer 1981; Frankel and Solue 1981). A recent assessment by Jhala *et al*. (2008) mentioned that the tiger has lost much ground in India due to direct poaching, loss of quality habitat, and loss of its prey.

1.3 Research in the Indian part of Terai Arc Landscape

Research in the Indian part of Terai Arc Landscape (TAL) has focused on several aspects scattered across different parts of this Landscape. However, only published literature is cited here. Research on vegetation is largely on grasses and grasslands (Singh 1982; Chaturvedi and Mishra 1985; Rodgers *et al*.1990; Rawat *et al.* 1997) and woody vegetation (Joshi *et al.* 1986; Agni *et al.* 2000). Pant and Chavan (2000) mapped the vegetation types and land use patterns in Corbett National Park (NP) using satellite data. Despite the area being highly rich in avifauna, only Bengal florican, *Hubaropsis bengalensis* (Rahmani *et al.* 1989), swamp francolin, *Francolinus gularis* (Javed *et al.* 1999) and raptors (Naoroji 1997a, b and 1999) have received some research attention. Pandey *et al.* (1994) published a very useful bird list for Rajaji NP, based on combined efforts of biologists from Wildlife Institute of India (WII). Although this tract is home to nine species of ungulates (including rhino), studies are available for only five species. Pendharkar and Goyal (1995), and Johnsingh (2001) described the group size and composition, and its general ecology and behaviour of goral (*Nemorhaedus goral*) respectively. Hog deer (*Axis porcinus*) has been studied briefly (Tak and Lamba 1981; Biswas 2002). Chital (*Axis axis*) was studied in Corbett NP (De and Spillet 1966) and Rajaji NP (Bhat and Rawat 1995 and 1999). All the research on swamp deer, *Cervus duvauceli duvauceli* (Holloway 1973; Schaaf and Singh 1976; Singh 1978; Sankaran 1990) has focused only on its conservation status. Sale (1986), Sale and Singh (1987) and Mishra (1989) have highlighted the reintroduction of rhinos (*Rhinoceros unicornis*) into Dudhwa NP. Sighting of rhino near Kotdwara on 20th April 1789 (Rookmaaker 1999) indicates its much wider range even in the recent past. Research on primates

(Lindburg 1977; Makwana 1979; Pirta *et al.* 1980; Laws and Laws 1984; Gupta and Kumar 1994) is very limited. The most intensive studies are on elephants (*Elephas maximus*). Singh (1969 a, 1978 and 1989) assessed the status of elephants in Uttar Pradesh. Johnsingh *et al.* (1990) and Johnsingh (2002) recommended establishment of Chilla-Motichur corridor favouring elephant conservation. Johnsingh and Joshua (1994) suggested the possibility of conserving Rajaji-Corbett NPs using elephant as a flagship species. Joshua and Johnsingh (1995) have explained the ranging patterns of elephants and highlighted its implications for reserve design. Sunderraj *et al.* (1995) evaluated the use of Rajaji-Corbett corridor by elephants. Javed (1996) has published a note on elephants in Dudhwa NP. Williams *et al.* (2001) made a detailed quantification on human-elephant conflict in Rajaji NP. Singh (1969b) documented the status of tiger in Uttar Pradesh and more recently, Johnsingh and Negi (2003) evaluated the conservation status of tiger in the area between Yamuna and Sharda rivers. Johnsingh *et al.* (2004) evaluated the conservation status of tiger and its associated species in the TAL. Harihar *et al.* (2008) assessed the response of tiger and its prey to the removal of anthropogenic influence in Rajaji NP. Harihar *et al.* (2009) assessed the status of tiger and its prey in the Rajaji NP and adjoining forest areas. Other relevant works on tiger are by Singh (1971, 1973, 1981, 1982, 1984 and 1993), Bhadauria and Singh (1994) and Johnsingh *et al.* (2003). Although this area is riddled with numerous conservation problems, published information on conservation issues is limited to Panwar (1985), and Tilak and Sinha (1987). Even research on people is only scanty (Khati 1993; Sharma 1995; Badola 1998).

1.4 Habitat models

Our ability to understand and predict wildlife-habitat relationships will be very useful in effective management and conservation of wildlife populations (Noon 1986; van Manen and Pelton 1993). Models are any formal representation of the real world and are very helpful in understanding complex systems. Spatially explicit wildlife models can be used to identify potential risks to the species and to understand the implications of different land management on endangered species (Stoms *et al.* 1992). They are useful for predicting areas of suitable habitat that may not be currently used by wildlife species (Lawton and Woodroffe 1991). Powerful statistical techniques and GIS tools have allowed the development of predictive habitat distribution models in ecology in the past years. Such models relate the geographical distribution of species or communities to their present environment and are static and probabilistic in nature. One must always bear in mind that a model is a simplification of the reality, and nature’s complexity and heterogeneity cannot be predicted accurately in every aspect of time and space from a single model. Ideally a model should have three desired proprieties: generality, reality and precision. Levins (1966) formulated the principle that only any two of the three can be improved simultaneously. It is often a trade-off between precision and generality (Guisan and Zimmermann 2000). A wide array of spectrums including biogeography, conservation biology, climate change research, and habitat or species management has been covered by different models. We can roughly distinguish between two categories of predictive habitat distribution models: (i) the empirically based models (see Guisan and Zimmerman 2000 for a review), and (ii) the so called expert-models. Empiric models relay on empiric data and statistical analysis (e.g. generalized linear models (GLM): McCullagh and Nelder 1983; generalized additive models (GAM): Yee and Mitchell 1991; ecological niche factor analysis (ENFA): Hirzel *et al*. 2002) whereas expert information may consist of models based on the opinion of experts (e.g. Pereira and Duckstein 1993; Clevenger *et al*. 2002; Schadt *et al*. 2002; Doswald 2002) or qualitative models based on the best information available from the literature (Boone and Hunter 1996). The later have largely been criticized mainly because of their arbitrary algorithms which makes any interpretation difficult. Among the empiric models, GLM are for example used to select the predictors (e.g. forest, distance to roads, elevation…) that best explained the presence/absence of the species of interest. But often data on species distribution are scarce and/or when time and money do not allow collecting presence and absence data in an efficient way. In this case, one possibility to use GLM with presence data only is to generate “pseudo-absence” data in an educated way that avoids absences in suitable areas. One recent approach for this is using ENFA for generation of a first habitat suitability map that is then used as weight during the selection of random pseudo-absences (Engler *et al.* 2004). Besides we can also find more descriptive models governed by simple ecological rules that describe species habitat relationships in a simple and comprehensive manner. These rules can easily be implemented in the GIS to compute habitat suitability maps (e.g. Schadt *et al*. 2002).

1.5 Spatially explicit simulation models

Spatially explicit simulation models simulate dispersal explicitly using an individual-based approach (Grimm and Railsback 2005) where behavioural movement rules describe how organisms interact with landscape structure and are therefore especially suitable for evaluation of dispersal success and connectivity between specific habitat patches in situations where details of landscape structure matter. Our dispersal model understanding is generally very poor, firstly because population models have been developed for much of the last century while the study of spatial process in spatial ecology is recent (Travis and French 2000) and secondly, studies on dispersal very consuming especially with larger species, as a consequence of tracking costs of individual animals during their dispersal or movement processes. Therefore, I developed a spatially explicit individual-based model to estimate the connectivity between the suitable patches for tiger. This type of model has been successfully used in several studies on animals and birds (e.g., Iberian lynx (*Lynx pardinus*)), Eurasian lynx (*Lynx lynx*), capercaillie (*Tetrao urogallus*)) to explain dispersal behaviour and estimate connectivity between habitat patches (e.g., Revilla *et al*. 2004; Kramer-Schadt *et al.* 2004; Tracey 2006; Graf *et al*. 2007; Revilla and Wiegand *in press*).

1.6 Hypotheses and objectives

The goal of this study was to identify the factors affecting the distribution of tiger and assess the distribution of suitable habitat patches and the connectivity between these patches for successful dispersal in the Indian part of TAL.

The specific objectives are

1. To quantify the habitat suitability and its main environmental determinants for tiger’s important prey species, to examine how habitat requirements of the prey species differed, and to highlight critical areas where conservation measures are needed.

2. To identify the factors, which affect the distribution of tigers, and to map and assess the quality of potential suitable habitats in order to identify critical areas for conservation management.

3. To assess the inter-patch connectivity among the major (protected) habitat patches and investigate the effect of potential initiatives to restore identified potential corridors for dispersal of tiger.

The thesis is organized in three main chapters with Chapters 1-2 dealing with introduction and study area description, Chapters 3-4 dealing with habitat modelling and Chapter 5 with dispersal. GLM and ENFA analyses were performed in Chapters 3 and 4 to determine if easily available spatial data in the GIS can successfully describe tiger and its prey species habitat in the Indian and areas connecting Indian and Nepal part of TAL and contribute to a predictive spatial model. In Chapter 3, I did habitat suitability (HS) analyses using GLM and developed HS maps for four prey species of tiger using the presence and absence data from transects laid for the prey species in the Indian part of TAL. Models were developed (1) to quantify the habitat suitability and its main environmental determinants, (2) to examine how habitat requirements of the four species differed, and (3) to identify the areas of high conservation value and to highlight critical areas where conservation measures are needed. In Chapter 4, I did HS analyses using ENFA-weighted GLM and developed HS maps for tiger. The locations of tiger presence collected based on indirect evidences such as pug marks, scats, etc. from the Indian part of TAL were used to develop the models in order (1) to identify the factors which affect the distribution of tigers in the TAL, (2) to map the remaining potentially suitable habitat and to assess the quality of potential corridors linking suitable habitat, and (3) to identify critical areas for conservation with the ultimate aim to assess landscape management needs for the conservation of tiger in the TAL. I used a hypothesis testing framework and contrast several *a priori* models based on our knowledge about tiger biology to our data. In Chapter 5, I assessed the connectivity between the suitable habitats in the fragmented TAL identified in Chapter 4. I estimated the connectivity in Indian part and between India and Nepal part of TAL. I, therefore, used a simple individual-based and spatially explicit dispersal model to (1) assess the inter-patch connectivity among the major (protected) habitat patches for dispersal of tiger in the complex and heterogeneous TAL and (2) to investigate the effect of potential initiatives to restore identified potential corridors for dispersal.

CHAPTER 2

STUDY AREA

2.1 Location

The study area is the Indian part of the Terai Arc Landscape (TAL) which lies between the Yamuna river in the west (77 30’ E &30 30’ N) and Valmiki Tiger Reserve (Bihar) in the east (84 45’ E & 27 15’ N) (Fig. 2.1).The entire stretch is ca. 900km long and 50-60km wide, covering ca. 42,700sq.km. Administratively, it is spread across five states of India (Himachal Pradesh, Haryana, Uttarakhand, Uttar Pradesh and Bihar), and twenty-one districts (one each in Himachal Pradesh, Haryana and Bihar, seven in Uttarakhand and eleven in Uttar Pradesh). The forests are managed under twenty Forest Divisions (FDs), eight Wildlife Sanctuaries (WLSs) and three National Parks (NPs). Three of India’s twenty-seven Tiger Reserves (TRs) are located in this landscape, namely Corbett TR (Corbett NP and Sonanadi WLS) in Uttarakhand, Dudhwa TR (Dudhwa NP, Kishanpur WLS and Katerniaghat Wildlife Division) in Uttar Pradesh and Valmiki TR (Valmiki NP and Valmiki WLS) in Bihar.

2.2 Physical characteristics

This landscape consists of the Shivalik hills, the adjoining bhabar areas and terai plains. These three strata are in the form of narrow strips running parallel to the main Himalaya and there is a continuum of forests and wildlife populations across these zones. The Shivaliks, which run along the base of the Himalaya, are an uplifted ridge system formed from the debris brought down from the main Himalaya. The coarse material brought down by the Himalayan rivers is deposited immediately along the foothills to form a pebbly-bouldery layer referred to as the bhabar, while the finer sediments or clay is carried further to form the terai. The bhabar is characterized by low water table as the deposits are bouldery and porous and all but the major rivers and streams disappear into the ground on emerging from the hills.

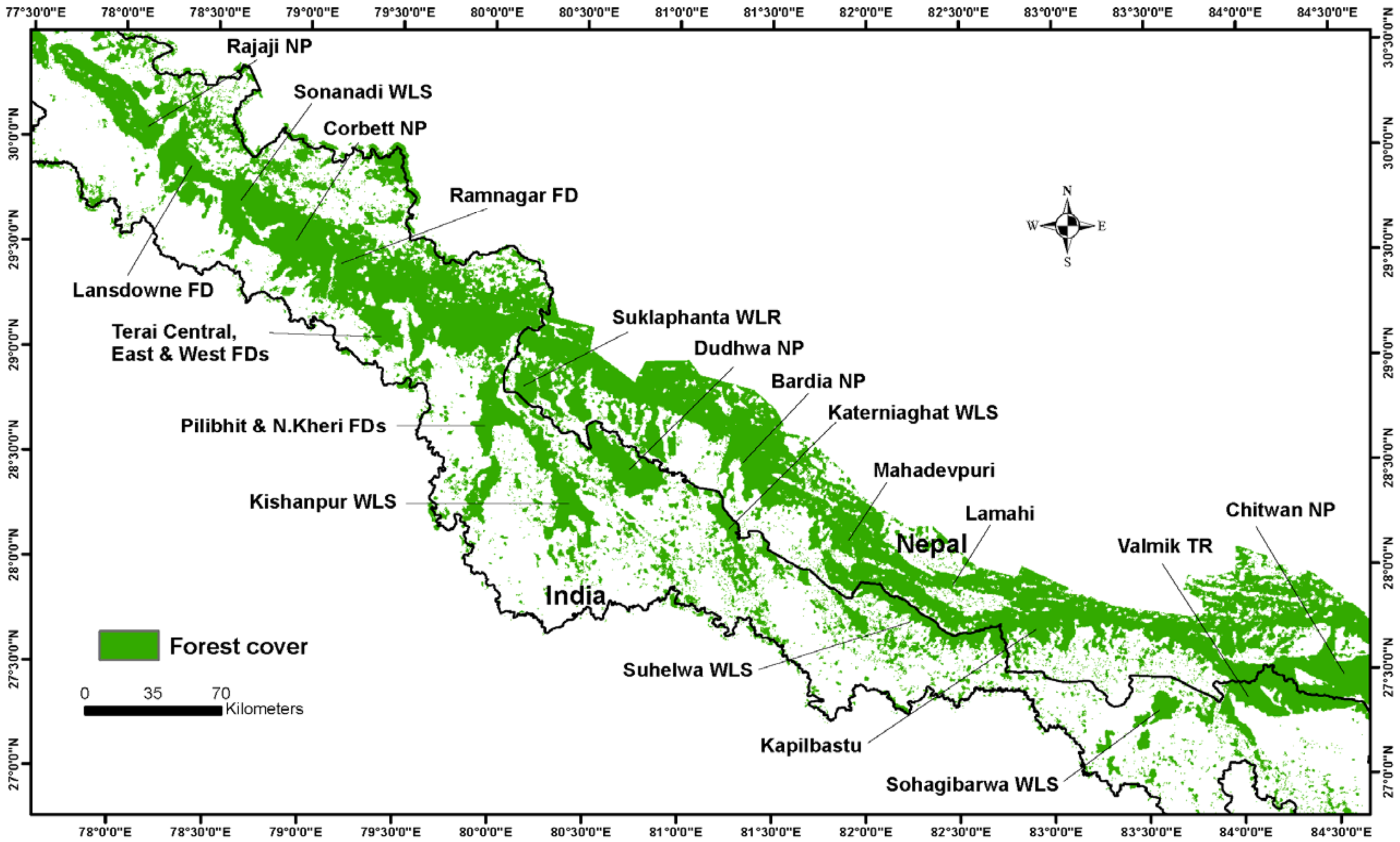


Figure 2.1 The Terai Arc Landscape in India and Nepal with the Indian TAL border (black boundary line), reserve forests (FD, forest division) and protected areas (TR, tiger reserve; NP, national park; WLS, wildlife sanctuary; WLR, wildlife reserve). Forest cover includes all natural forests.

The streams reappear along the terai, which has fine alluvial soil resulting in high water table. Beyond the Teesta River, in north Bengal, these three layers are not continuous and the parallelism disappears. East of Sharda river, the *bhabar* lies in Nepal, while there is an extensive terai tract in India (Atkinson 1882; Tiwari and Joshi 1997). West of Sharda river, habitats in the bhabar tract are in the process of fragmentation and degradation due to emergence of numerous large towns. Altitude within the Shivaliks ranges from 750 to 1400 m. The bhabar zone exhibits an undulating topography with an altitude ranging between 300 and 400 m. Terai is relatively flat with a surface gradient, which is slightly higher near Shivaliks. According to the biogeographic classification by Rodgers and Panwar (1988), the study area represents two distinct zones – Himalayan and Gangetic Plain and includes three provinces: (i) Western Himalaya (areas in Himachal Pradesh, Haryana and Uttarakhand), (ii) Upper Gangetic Plain (southeastern part of Uttarakhand and the entire area in Uttar Pradesh) and (iii) Lower Gangetic Plain (area in Bihar). According to the recent classification proposed by Wikramanayake *et al.* (2001) that takes into consideration both biogeography and conservation values, the study area corresponds to three ecoregions – (i) Upper Gangetic Plains moist deciduous forest, (ii) Terai-Duar savanna and grasslands and (iii) Himalayan sub-tropical broadleaf forest. Of these, the Terai-Duar savanna is listed among the 200 globally important areas, due to its intact large mammal assemblage, even though it scores low on plant species richness and endemism.

2.3 Biological attributes

The vegetation in TAL comprises a mosaic of dry and moist deciduous forests, scrub savannah and productive alluvial grasslands. Even though TAL scores low on plant species richness and endemism, it harbours some of the most productive ecosystems in the world (Wikramanayake *et al*. 2001). On the basis of similarities in the woody vegetation, the Indian side of TAL is classified into three physiographic zones: (i) Western Himalaya, (ii) Northern plains and (iii) Eastern plains (FSI 2001). Champion and Seth (1968) have reported twenty-seven types and sub-types of vegetation from this region based on their associations with soil and rainfall. Vegetation communities have been described in detail for parts of this landscape based on both graminoid and woody vegetation (Singh 1982; Chaturvedi and Mishra 1985; Joshi *et al*. 1986; Rodgers *et al*. 1990; Singh *et al*. 1995; Rawat *et al*. 1997; Agni *et al*. 2000). A study by Johnsingh (*et al.* 2004) yielded five broad vegetation communities viz., (i) Sal forests (dominated by sal *Shorea robusta*), (ii) Sal-mixed forests (*Shorea robusta,* rohini *Mallotus philippinensis,* jamun *Syzygium cumini,* dhaura *Lagerstroemia parviflora,* bhant *Clerodendron viscosum* and kari-patta *Murraya koenigii*), (iii) Riverine forests (khair *Acacia catechu*, shisam or sissoo *Dalbergia sissoo* and *Syzygium cumini*), (iv) Mixed or miscellaneous forests (*Lagerstroemia parviflora*, papri *Holoptelia integrifolia*, chamror *Ehretia laevis*, bel *Aegle marmelos*, haldu *Haldina cordifolia*, bakli *Anogeissus latifolia* and binda *Colebrookia oppositifolia*) and (v) Plantations (teak *Tectona grandis*, *Acacia catechu Dalbergia sissoo*, *Eucalyptus* and lantana *Lantana camara*).

This landscape harbour diverse and rich fauna including several endemic and globally endangered species. Prominent among them are the tiger (*Panthera tigris*), Asian elephant (*Elephas maximus*), one-horned rhinoceros (*Rhinoceros unicornis*) and swamp deer (*Cervus duvauceli duvauceli*). Other endemic and obligate species found in this landscape are hog deer (*Axis porcinus*), hispid hare (*Caprolagus hispidus*), Bengal florican (*Hubaropsis bengalensis*) and swamp francolin (*Francolinus gularis*). Many of these species, surviving in small populations, have their last home in this landscape.

2.4 Socio-economic attributes

This landscape is also among the most populous regions in the country and as per the 2001 census, the total population of the study area is 2, 38, 94,443 persons, which is 2.32% of the country's total population (Johnsingh *et al.* 2004). There has been rapid growth in human population ever since people began to occupy the fertile land after independence, resulting in heavy loss of forest and habitat fragmentation. The landscape is again among the highest human density regions, with an average of 543 individuals/sq.km (range: 137 in Champawat tehsil to 1872 in Haldwani tehsil), much above the national average of 324 individuals/sq.km. The proportion of rural population ranges from 23.5% in Dehradun tehsil to 97.2% in Shrawasti tehsil, with an average of 82%. About 23% of the population belong to Scheduled Castes and Tribes, among the major tribal groups residing within the study area are the *tharus* and *gujjars*; *kanjars* being classified under “Other Backward Classes”. Further, settlers especially refugees from erstwhile East Pakistan, retired soldiers from the hills and other settlers from Punjab comprise part of the population influx observed over the last four decades. Human populations are dependent on several forest-based resources for their subsistence. Firewood and fodder, being the most significant resources extracted out of the forested areas, are regarded as the principle causes of disturbance and degradation within forests, besides forest loss to agricultural expansion. Further, non-timber forest products contribute significantly into the household economy, leading to conflicts with wild animals throughout the area. Crop raiding and injury or loss of livestock leads to added conflict, typical of the forest-human habitation interface.

CHAPTER 3

ASSESSING HABITAT SUITABILITY FOR PREY SPECIES OF TIGER

3.1 Introduction

The identification of factors affecting the distribution and abundance of animals has always been a central issue in ecology. For example, understanding the wildlife-habitat relationships is a prerequisite for effective management and conservation of wildlife populations (Noon 1986; van Manen and Pelton 1993). Predicting the distribution and suitability of habitat is especially critical for management of endangered species (Engler *et al*. 2004) at the landscape level given the threats of habitat loss, degradation, and fragmentation on species persistence (Myers 1997) and the need for effective planning of habitat restoration (MacMahon 1997).

Statistical species distribution models relate species' presence-absence data to the environmental predictors to identify the environmental factors which affect the distribution of animals and for predicting habitat suitability (Buckland and Elsten 1993; Boyce and McDonald 1999). These models can also be used in reserve design to identify high quality habitat for several target species (Cabeza *et al*. 2004). The utility of habitat models has been particularly emphasized for conservation of animals highly sensible to habitat alteration, like large carnivores or herbivores (Mladenoff *et al*. 1995; Didier and Porter 1999; Schadt *et al*. 2002; Boyce *et al*. 2003; Fernandez *et al*. 2003; Naves *et al*. 2003; Linkie *et al*. 2006).

Large herbivores are often used as flagship species for conservation and management planning because of their high public profile (Stanley Price 1989; Bowen-Jones and Entwistle 2002) and because they are keystone species in many ecosystems (Danell *et al*. 2006). Large areas are grazed by communities of wild herbivores that drive the structure, composition and functioning of these ecosystems (Miles 1985; Martin 1993; Thompson *et al*. 1995; Pickup *et al*. 1998; Wallis de Vries *et al*. 1998; Olofsson *et al*. 2004).

High herbivore densities can impact upon the agricultural, conservation and environmental values of the landscape (McShea *et al*. 1997). Moreover, abundance of large predators of conservation concern, such as tiger is largely mediated by densities of different-sized ungulate prey species (Karanth and Stith 1999).

The distribution of herbivores and their impacts on resources depend, at a range of spatial scales, on key resources such as vegetation, water, shelter, but also on the degree of human disturbances and aspects of herbivore sociability (Hunter 1962; Kolasa and Pickett 1991; Bailey *et al*. 1998; Illius and O'Connor 2000; Apps *et al*. 2001; Serneels and Lambin 2001; Boyce *et al*. 2003; Gordon *et al*. 2004). Understanding the species-specific responses of closely related herbivore species to environmental factors, including the effects of human disturbances, is an important precursor for conservation and management of herbivore communities and its predators (Guangshun *et al.* 2006).

The greatest ungulate biomass in southern Asia is found in areas like the TAL (Johnsingh *et al.* 2004). Here grassland and forests form a mosaic and the juxtaposition of diverse vegetation types supports rich ungulate communities (Eisenberg and Seidensticker 1976; Karanth and Sunquist 1992). The heterogeneous TAL in India hosts a co-existing ungulate assemblage including sambar (*Cervus unicolor*), chital (*Axis axis*), nilgai (*Boselaphus tragocamelus*), and wild pig (*Sus scrofa*). These four widely distributed ungulate species also serve, amongst others, as the major prey species of endangered large carnivores such as tiger, Asiatic lion (*Panthera leo persica*), dhole (*Cuon alpinus*), and leopard (*Panthera pardus*). Being the major prey base, these species play a key role in the survival of tiger (Seidensticker 1976; Stoen and Wagge 1996) as well as other carnivore species. The TAL has been classified as one of the world's most important tiger conservation areas (Sanderson *et al.* 2006), but belongs to the most populated areas in the world. This inevitably causes human-wildlife conflicts. In between, the herbivores function as prey basis for large carnivores and are competitors for human resources in this landscape. Therefore, assessing habitat suitability and deriving distribution maps are important for the management of herbivores and tiger and to undertake specific restoration of habitats by field managers.

However, anecdotic information indicates that these species occur in TAL in fragmented populations which are subject to strong anthropogenic pressures due to habitat transformation and poaching (Sankaran 1990; Smith *et al*. 1998; Javed *et al*. 1999; Biswas and Mathur 2000; Johnsingh *et al*. 2004). Moreover, previous studies on these ungulates in India as well as other countries (see section "*Study species*") showed that habitat requirements of these species differed but this available information were not statistically quantified and extrapolated over the entire TAL. Therefore, a combined management strategy for multiple species is needed which involves estimation of the current species ranges and the potentially available habitat, as well as an understanding of the environmental factors which determine habitat suitability for the different species. The specific aims were (1) to quantify the habitat suitability and its main environmental determinants, (2) to examine how habitat requirements of the four species differed, and (3) to identify the areas of high conservation value and to highlight critical areas where conservation measures are needed. I especially target my findings to direct conservation measures in low density areas, un-connected populations, quality areas for the co-existence of ungulates and conservation of tiger.

3.2 Materials and methods

3.2.1 Study species

3.2.1.1 Sambar

The sambar is the largest deer among the seven species of deer found in south Asia that belong to the family *Cervidae* of order *Artiodactyla*. The Indian subspecies *C. u. niger* is considered to be the largest among three subspecies found in south Asia (Lewis *et al*. 1990). The average shoulder height is between 140 and 150cm and the average weight of male sambar ranges between 225 and 320kg and that of female between 135 and 225kg (Crandall 1964; Prater 1971; Downes 1983). The sambar prefers hilly areas with moderate to steep slopes (Green 1987) covered with dense vegetation (Schaller 1967; Johnsingh 1983; Jathanna *et al*. 2003; Kushwaha *et al*. 2004). Sambar subsist on a wide variety of plants and may browse or grass according to season (Schaller 1967; Khan 1994). In India sambar inhibits dry thorn scrub, dry deciduous, moist deciduous, semi evergreen and evergreen forests, and abundances are largely influenced by the availability of suitable habitat with ample cover, water and lack of disturbance (Sankar 1994; Khan 1996). In Sariska TR of dry tropical deciduous habitat, the mean home ranges of sambar male were 4km² and that of females were 1.7km² (Sankar 1994).

3.2.1.2 Chital

The chital is an endemic cervid of south Asia. The average weight of a male chital is approximately 70kg and that of female is approximately 50kg. The species is common and widespread in forest and grassland habitats throughout its range but it avoids habitat extremes like dense moist forest and open semi-desert or desert. Moist and dry deciduous forest areas, especially adjoining dry thorn scrub or grasslands appear to be optimal and the highest densities of chital are reported from these habitats. Chital is a generalist, preferring newly-sprouting grasses (De and Spillett 1966; Schaller 1967; Krishnan 1972; Tak and Lamba 1984; Elliot and Barrett 1985; Henke *et al*. 1988) and numerous plant species (e.g. Schaller 1967; Tak and Lamba 1984; Dinerstein 1987 and 1989). Chital avoids being outside the forest during the heat of the day or when humans are around (Graf and Nichols 1966). Chital avoid high altitude and rugged terrain, generally preferring flat areas (Schaller 1967; Khan 1996), but may use the warmer moderate south and east facing slopes if preferred habitats or forage is available (Bhat and Rawat 1995). A radio-telemetry study carried out in Karnali-Bardia, Nepal, revealed mean male and female annual home ranges of about 2km² and 1.4km², respectively (Moe and Wegge 1994). Chital group size in Karnali-Bardia, Nepal varied from one to 91 individuals (Dinerstein 1980).

3.2.1.3 Nilgai

The nilgai is an endemic antelope in Indian subcontinent and one of the most commonly seen wild animals of northern India. Shoulder height is about 1.2-

1.5 meters, individuals are 1.8-2 meters long, and mature nilgai typically weigh 120-240 kilograms. They are diurnal animals (Schaller 1967) and occur in grass and woodlands and rely their diet on grasses, leaves, buds, and fruits. Nilgai avoid dense forest and prefer the plains and low hills with shrubs (Prater 1971; Khan 1996). In the lower *terai* regions they may be seen together with chital and hog deer. Individual nilgai are encountered also in cultivated or semi-urban areas (Sheffield *et al*. 1983; Wilson and Reeder 1993; Menon 2003).

3.2.1.4 Wild pig

The average shoulder height of the wild pig ranges between 55 and 110 cm, and its body length ranges typically between 90 and 200cm. Wild pigs eat a wide variety of foods (e.g.; seeds, roots, tubers, fruit, nuts, carrion, eggs, and insects) and occur in a variety of habitats; dense forest, grass and scrub lands, and also hills. They are one of the main prey species of tiger, Asiatic lion and leopard (Schmidt 1990; Oliver *et al*. 1993; Wilson and Reeder 1993).

3.2.2 Data collection

Data collection was carried out in two phases. In the first phase (October 2002 - February 2003) data were collected on presence/absence of the four ungulates. Field sampling was restricted to regions left with terai-bhabar vegetation which have the potential to support the target ungulate species. The sampling was done at hierarchical scales, represented by 15x15 minute grids (equivalent to ca.725km^2), forest divisions, and forest ranges. Within the 15-minute grids, forest cover distribution was identified using false colour composite of Indian Remote Sensing satellite IC and 1D - WiFS imageries and forest division maps. The forest ranges were taken as the basic sampling unit in each forest division and protected area. The shape and size of the forest range determined the number of transects or trails (raus (= river beds) in the bhabar region and forest roads in the terai region) to be surveyed. Transects ranged in length from 3 to 9km with an average of 4km, and were spread 3 to 4km apart. Three to four transects were surveyed each day in the morning hours (7.00am – 10.00am) by two well-trained field biologists and two field assistants, accompanied by forest staff. In total, 246 transects adding up to 1001.2km were surveyed in the entire TAL (Fig. 3.1). Presence of ungulate species was also assessed on indirect signs such as tracks and pellet groups and direct observations. In the second phase, 443 10m radius plots laid for ungulate fecal pellet groups were also included in the data base. These plots were also laid at every 250m in 2km transects randomly in the areas between Rajaji NP and Terai west FD during the period between December 2005 and March 2006. Vegetation sampling and ground-truthing for the preparation of land cover maps were carried out during the period between April and June 2003.

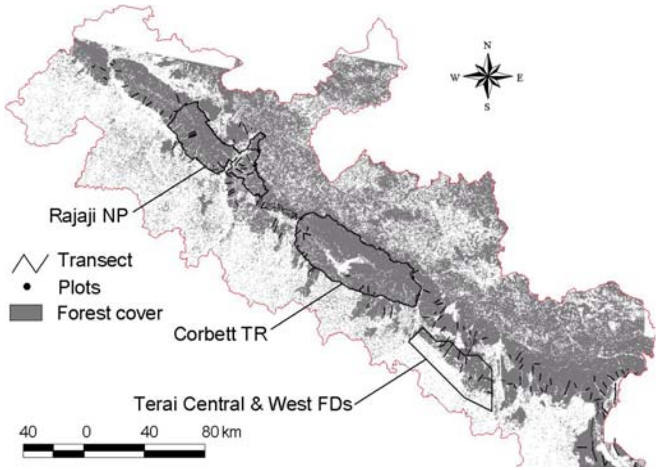
3.2.3 Variable preparation

3.2.3.1 Biology of target species and predictive variables

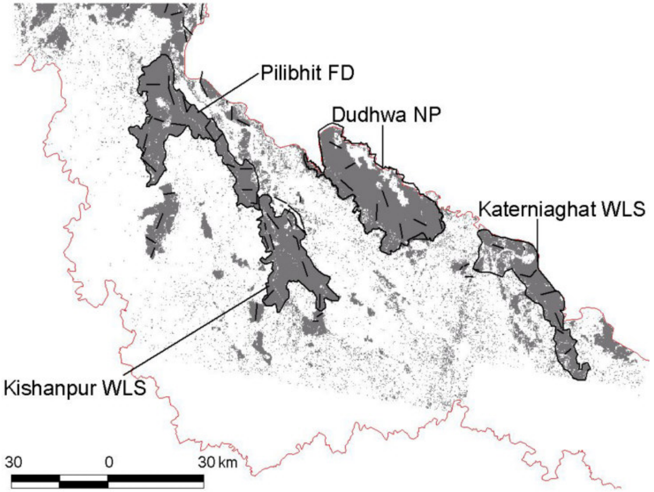
To improve the biological interpretability of the models, the independent variables which were directly linked to the biology of the target species were used (see section "*Study species*"). First, I selected eight land cover classes (Table 3.1) which differentiated among basic vegetation units and their ability to provide cover, their degree of disturbance, as well as water bodies. Second, previous knowledge indicated that the four ungulate species differ in their response to topography. I, therefore, included elevation and several derivate variables describing topography (Table 3.1). Third, the target species (except Nilgai) are highly sensitive to human presence. I therefore included several variables describing human disturbances, including the land cover classes "agricultural and human habitation", "open and disturbed forest", "roads", "villages", and derivate neighbourhood and distance variables (Table 3.1).

Figure 3.1 The Indian part of Terai Arc Landscape and transects for data collection (black lines). Forest cover (grey) includes all natural forests. (A-I) Hilly terrain (bhabar and Sivalik) habitats, western part of the study area from Kalesar Wildlife Sanctuary in Haryana to Haldwani Forest Division in Uttarakhand. (A-II) Low land terai habitats, Pilibhit Forest Division to Katernigaht Wildlife Sanctuary in Uttar Pradesh. (A-III) Hilly terrain (bhabar and Sivalik) habitats, eastern part of study area Suhelwa Wildlife Sanctuary in Uttar Pradesh to Valmik Tiger Reserve in Bihar Protected areas are delineated by black lines.

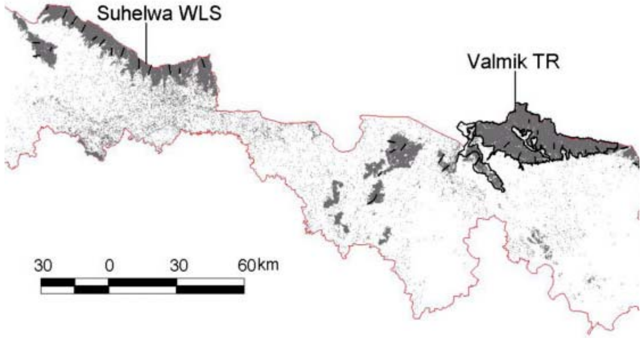
A-I


N
W
E
S
Rajaji NP
Transect
Plots
Forest cover
Corbett TR
Terai Central & West FDs
40
0
40
80 km

A-II


Pilibhit FD
Dudhwa NP
Katerniaghat WLS
Kishanpur WLS
30
0
30 km

A-III


Suhelwa WLS
Valmik TR
30
0
30
60 km

3.2.3.2 Land cover and topographic variables

Remote sensing data and topographic maps were used to develop spatial layers of the land use and vegetation characteristics. For mapping forest cover and landscape pattern, 14 scenes of IRS satellite IC and D – LISS III (23.5 m, 4 bands) with a resolution of 23.5m were used. These imageries dated from October 2001- January 2002. Vegetation was sampling at 1530 ground-truthing points. The classification was done by a hybrid method combining unsupervised isodata cluster analysis and supervised maximum likelihood classification, resulting in eight landcover classes (Table 3.1). Because the presence/absence data were collected at 250m intervals and considering the large size of the study area, I transformed the original land cover data (having a 23.5m resolution) to a resolution of 235m. This was done by calculation the proportion of cells of a given land cover class within 10 × 10 cell blocks which formed one pixel of the final raster map. The 235m resolution is fine enough to allow variation within the typical home range scales of the study species which are in the order of km^2.

Elevation data with a resolution of 3 Arc Second (85m) obtained from the Seamless Data Distribution System (SDDS), U.S. Geological Survey (http://seamless.usgs.gov) were used. These data were converted into a 235m resolution by re-sampling the original data using nearest neighbor method in Arc/View 3.2. The final elevation map was used to derive several additional variables, including slope degree, slope aspects for 8 cardinal directions, surface area, surface ratio, and slope position classification following the Weiss (2001) classification. The slope position classification consists of the six classes (ridge, upper slope, middle slope, flat slope, lower slope, and valley) and was expressed as binary map for each class. Additionally, the classification of slope position was done at two different scales, radii of 5 and 20 grid cells, in order to consider the effect of small and large scales in the model.

Table 3.1 List of predictor variables used for the spatial models.

Abbreviation	**Variable**	**Definition**
Habitat	Category	
C1	% of dense forest	Percentage of 23.5m × 23.5m cells of the given cover class within each 235m × 235m pixel.
C2	% of open and disturbed forest	Percentage of 23.5m × 23.5m cells of the given cover class within each 235m × 235m pixel.
C3	% of tall grass	Percentage of 23.5m × 23.5m cells of the given cover class within each 235m × 235m pixel.
C4	% of short grass	Percentage of 23.5m × 23.5m cells of the given cover class within each 235m × 235m pixel.
C5	% of scrub land	Percentage of 23.5m × 23.5m cells of the given cover class within each 235m × 235m pixel.
C6	% of barren land	Percentage of 23.5m × 23.5m cells of the given cover class within each 235m × 235m pixel.
C7	% of water body	Percentage of 23.5m × 23.5m cells of the given cover class within each 235m × 235m pixel.
C8	% of Agricultural and human habitation at fine scale	Percentage of 23.5m × 23.5m cells of the given cover class within each 235m × 235m pixel.
And 64 additional variables by neighbourhood analysis		
F<scale>C<no>	% of habitat category C<1-8> at scales <3,4,6,7,8,13,21> (dimension in map cells)	% of habitat category C1-8 at radius 0.7km, 0.9km, 1.4km, 1.6km, 1.9km, 2.4km, 3.1km, and 4.9km.
MAE	maximum elevation [m]	Maximum elevation obtained from 235m resolution elevation grid.
And 8 additional variables by neighbourhood analysis		
MAE<scale>	maximum elevation at scales <3,4,6,7,8, 13,21> (dimension in map cells)	Maximum elevation at radius 0.7km, 0.9km, 1.4km, 1.6km, 1.9km, 2.4km, 3.1km, and 4.9km.
MIE	minimum elevation [m]	Minimum elevation obtained from 235m resolution elevation grid.
And 8 additional variables by neighbourhood analysis		
MIE<scale>	minimum elevation at scales <3,4,6,7,8, 13,21> (dimension in map cells)	Minimum elevation at radius 0.7km, 0.9km, 1.4km, 1.6km, 1.9km, 2.4km, 3.1km, and 4.9km.
MEE	mean elevation [m]	Mean elevation obtained from 235m resolution elevation grid.
And 8 additional variables by neighbourhood analysis		
MEE<scale>	mean elevation at scales <3,4,6,7,8, 13,21> (dimension in map cells)	Mean of elevation at radius 0.7km, 0.9km, 1.4km, 1.6km, 1.9km, 2.4km, 3.1km, and 4.9km.
RE	range elevation [m]	Difference between maximum and minimum elevations at scale 235
And 8 additional variables by neighbourhood analysis		
RE<scale>	range elevation at scales <3,4,6,7,8, 13,21> (dimension in map cells)	Difference between maximum and minimum elevations at radius 0.7km, 0.9km, 1.4km, 1.6km, 1.9km, 2.4km, 3.1km, and 4.9km.

Table 3.1, continued.

Abbreviation	**Variable**	**Definition**
SD	slope degree [°]	Slope values calculated in degrees from 235m resolution elevation grid
SE	east aspect [°]	East slope aspect in degrees calculated from 235m elevation grid
SNE	northeast aspect [°]	Northeast slope aspect in degrees calculated from 235m elevation grid
SN	north aspect [°]	North slope aspect in degrees calculated from 235m elevation grid
SNW	northwest aspect [°]	Northwest slope aspect in degrees calculated from 235m elevation grid
SSE	southeast aspect [°]	Southeast slope aspect in degrees calculated from 235m elevation grid
SS	south aspect [°]	South slope aspect in degrees calculated from 235m elevation grid
SSW	southwest aspect [°]	Southwest slope aspect in degrees calculated from 235m elevation grid
SW	west aspect [°]	West slope aspect in degrees calculated from 235m elevation grid
SA	surface area [m]	Surface area, measured in meters, calculated from 235m elevation grid by generating 8 3-dimensional triangles connecting each cell centerpoint with the centerpoints of the 8 surrounding cells, then calculating and summing the area of the portions of each triangle that lay within the cell boundary where then calculated and summed (Jenness 2004).
And 8 additional variables by neighbourhood analysis		
SA<scale>	surface area at scales <3,4,6,7,8, 13,21> (dimension in map cells)	Surface area calculated at radius 0.7km, 0.9km, 1.4km, 1.6km, 1.9km, 2.4km, 3.1km, and 4.9km.
SR	surface ratio	Surface ratio calculated by dividing the surface area value of a cell by the planimetric area within that cell (Jenness 2004).
And 8 additional variables by neighbourhood analysis		
SR<scale>	surface ratio at scales <3,4,6,7,8, 13,21> (dimension in map cells)	Surface ratio calculated at radius 0.7km, 0.9km, 1.4km, 1.6km, 1.9km, 2.4km, 3.1km, and 4.9km.
W5_1	ridge at scale 5	Classified if Topographic Position Index (TPI) has the Standard Deviation (SD) > 1 (Weiss 2001) at radius using 235m elevation grid
W5_2	upper slope at scale 5	Classified if TPI has the SD between > 0.5 and <= 1 (Weiss 2001) at radius using 235m elevation grid
W5_3	middle slope at scale 5	Classified if TPI has the SD between > -0.5 and < 0.5 (Weiss 2001) at radius using 235m elevation grid
W5_4	flat slope at scale 5	Classified if TPI has the SD between >= -0.5 and <= 0.5 (Weiss 2001) at radius using 235m elevation grid
W5_5	lower slope at scale 5	Classified if TPI has the SD between >= -1 and < -0.5 (Weiss 2001) at radius using 235m elevation grid

Table 3.1, continued.

Abbreviation	**Variable**	**Definition**
W5_6	valley at scale 5	Classified if TPI has the SD < -1 (Weiss 2001) at radius using 235m elevation grid
W20_1	ridge at scale 20	Classified at the larger scale, 20
W20_2	upper slope at scale 20	Classified at the larger scale, 20
W20_3	middle slope at scale 20	Classified at the larger scale, 20
W20_4	flat slope at scale 20	Classified at the larger scale, 20
W20_5	lower slope at scale 20	Classified at the larger scale, 20
W20_6	valley at scale 20	Classified at the larger scale, 20
DRi	distance to river [m]	Distance to the nearest river within 23.5km.
DRo	distance to road [m]	Distance to the nearest road within 23.5km.
DVi	distance to village [m]	Distance to the nearest village 23.5km.
DnVi3	density of villages at scale 3 [100 km^2]	Density of villages per 100 km² calculated within the specified neighbourhood radius.
And 7 additional variables by neighbourhood analysis		
DnVi<scale>	density of villages at scales <4,6,7,8,10, 13,21> (dimension in map cells)	Density of villages per 100km² calculated at radius 0.9km, 1.4km, 1.6km, 1.9km, 2.4km, 3.1km, and 4.9km.
DnRo3	density of roads at scale 3 [m/km^2]	Density of roads in meter per km² calculated within the specified neighbourhood radius.
And 7 additional variables by neighbourhood analysis		
DnRo<scale>	Density of roads at scales <4,6,7,8,10, 13,21> (dimension in map cells)	Density of roads in meter per km² calculated at radius 0.9km, 1.4km, 1.6km, 1.9km, 2.4km, 3.1km, and 4.9km.
Di	Shannon landscape diversity index at fine scale	Measure of relative landuse diversity; equals 0 when there is only one landuse and increases as the number of landuse types increases. Calculated at fine scale.
And 8 additional variables by neighbourhood analysis		
Di<scale>	Shannon landscape diversity index at scales <3,4,6,7,8, 13,21> (dimension in map cells)	Calculated at radius 0.7km, 0.9km, 1.4km, 1.6km, 1.9km, 2.4km, 3.1km, and 4.9km.

3.2.3.3 Variables quantifying human disturbances

1:50,000 scale topographic maps dated 1971 to obtain the digital vector layers of roads, villages and rivers were used. River vector layer (used as habitat variable not as human disturbance) included rivers and all other perennial water sources. Roads included national and state highways, district and village roads, and cattle cart ways. Distances to the nearest road, village and water source were calculated within a searching radius of 100 grid cells of the 235m grid. Additionally neighbourhood variables giving the density of villages, water bodies, and roads were calculated at a specified radius (see section "*Large scale variable*"). Because human impact in the TAL usually results in a diversification of land cover types, I also used the Shannon diversity index, based on the eight land cover classes, as indicator for human disturbance.

3.2.3.4 Large scale variables

The eight land cover variables and the data on roads, villages and rivers describe only local (5.5ha) properties of the landscape, but they do not contain information at larger spatial scales. However, such larger-scale properties may be important for the habitat of the four ungulate species. For example, individuals may perceive connectivity of landscape features (e.g., forest cover) at scales above one cell, and human activity may diffuse from focal points (e.g., villages) into neighbouring cells. To consider such neighbourhood effects I followed the approach taken in Schadt *et al*. (2002), Naves *et al*. (2003), Vezzani *et al*. (2005), and Aguayo *et al*. (2007) and calculated, from the original 235m × 235m raster data sets, scale- dependent neighbourhood variables that represented the original variables at larger scales. The neighbourhood variables were calculated by taking the mean value of the variable within a circle with specified radius around the target cell, reflecting the extent and connectivity of that specific landcover type at the specified scale. Because I did not know *a priori* the critical spatial scales for the four target species, I calculated the neighbourhood variables for eight different randomly selected scales (d = 3 (1.6 km^2), 4 (2.8 km^2), 6(6.2 km^2), 7(8.5 km^2), 8(11.1 km^2), 10(17.4 km^2), 13(29.3 km^2) and 21(76.5 km^2) grid cells) (Table 3.1).

ArcInfo 9.1 (ESRI, Redlands, California, USA) was used to calculate the means and percentages of vegetation and elevation variables, and calculations using distances and densities in the presence and absence locations. The variables of slope degree, slope aspects, surface area and ratio, and slope position classification were calculated using extensions (Directional Slopes v.1.2a, Surface Areas and Ratios from Elevation Grid v.1.2, Topographic Position Index (TPI) v.1.3a) available from Jenness Enterprises for Arc/View 3.x (http://www.jennessent.com).

3.2.4 Statistical analysis and model design

3.2.4.1 Variable and data reduction

Before constructing the set of alternative models, data points and variables were eliminated to reduce spatial autocorrelation of the dependent variable and to remove variables, which did not show differences between presence and absence, and to remove highly auto correlated independent variables. In a first step I accounted for spatial autocorrelation in the dependent variable which can lead to pseudo replication problems because data are not independent (Clifford *et al*. 1989; Lennon 1999). Because presence and absence data were collected every 250m in transects, some autocorrelation were expected in the dependent variables. I, therefore, quantified the spatial autocorrelation for each dependent variable using the common *Pearson* correlation coefficient between two variables v_i and m_i taken over all transect points i, where v_i is the value of the binary variable "presence-absence" in a given cell i, and m_i the mean value of this variable within a ring of radius d and width 1 around cell i. To reduce problems with severe spatial correlation between sites, I determined the spatial lag r at which locations were not strongly correlated (i.e., $c(r) < 0.7$) and selected only those cells which were sufficiently separated (e.g. Schadt *et al*. 2002; Naves *et al*. 2003).

In a second step, I used descriptive univariate analyses to test if the different variables were able to discriminate presence and absence locations before entering them into the generalized linear models (GLM). Univariate statistical differences between presence and absence locations were tested using the Kruskal-Wallis test (Sokal and Rohlf 1995) and variables which did not show a significant difference were removed.

In a third step, I reduced the high number of possible models and grouped the variables into different blocks that corresponded to different a priori selected hypotheses. To this end all predictor variables were grouped under the two categories; habitat and disturbance (Table 3.1). These categories represent my basic hypotheses about the determinants of species occurrence. Among each of these two categories, variables with the same neighbourhood scale were further grouped into separate blocks. I thus treat each scale as a separate hypothesis. In case of disturbance variables each neighbourhood scale block additionally contained the distance variables and the Shannon landscape diversity index. All blocks of the habitat category were again grouped under the small and large scales of slope position classification variables resulting in a total of 27 models for each species (Fig. 3.2).

In a fourth step I tested for correlation between the independent variables within each variable block. Correlation matrix was calculated among all independent variables within a block using Spearman rank coefficients (Sokal and Rohlf 1995). Among strongly correlated variables ($r > 0.6$), I retained those with the greatest explanatory effects in the univariate analysis on the dependent variable (Schadt *et al*. 2002).

3.2.4.2 Model construction

For each block of predictive variables, I fitted one model using a GLM with binary error distribution and logit link (R Project for Statistical Computing, http://www.r-project.org/) in which all predictors entered the equations simultaneously. Models for a given species and variable type (i.e., habitat variables and disturbance variables) were compared through the hierarchical ordering based on the scores of Akaike's Information Criterion (AIC). The most parsimonious model (lowest AIC value) was selected by comparing the AIC values within and among the habitat and disturbance categories.

The primary interest was in determining the most parsimonious (biologically interpretable) model for describing the habitat suitability for a given ungulate species, and not to identify the model which received, among a set of *a priory* defined models, most support from the data.

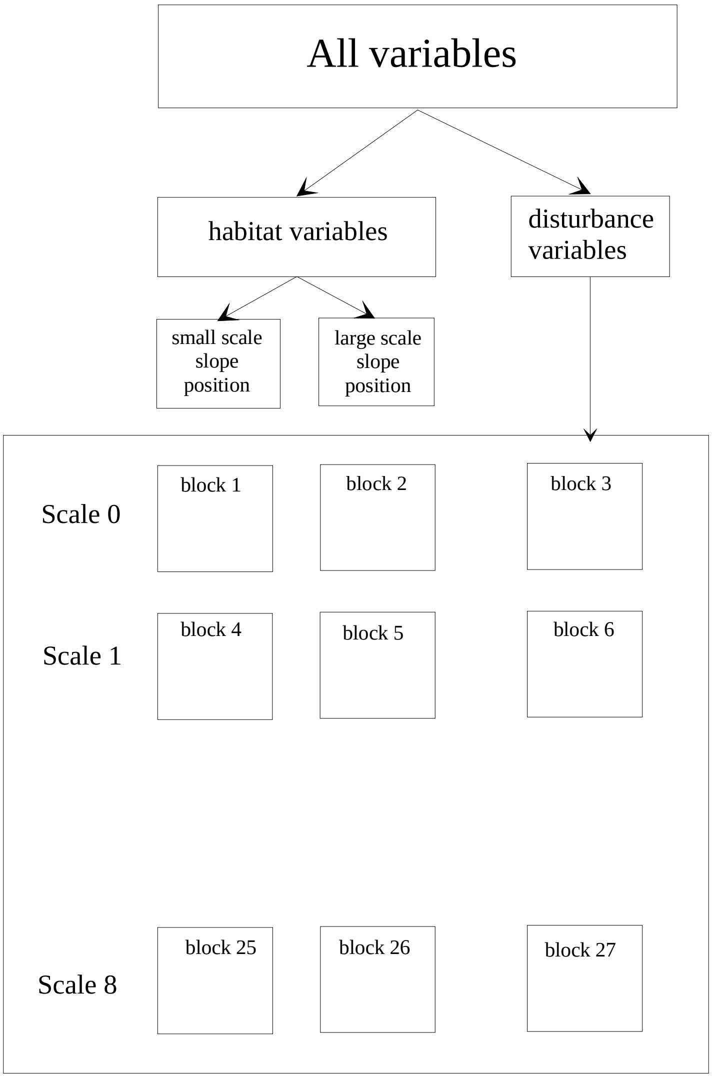


Figure 3.2 Model selections. Independent variables were grouped into 27 blocks and run for each block one GLM model. Blocks were defined due to a hierarchical classification of the variables into habitat and human associated variables, slope position model, and neighborhood scale.

I therefore combined, if appropriate, in a subsequent step models with similar support into a final model and removed non-significant variables. Models were combined by joining their independent variables which were not highly correlated and I eliminated the remaining predictors which were not significant at $p < 0.05$ manually step by step from the selected model.

However, combining models and removing variables implies that I theoretically tested a high number of models which may result in overfitting. To test for potential overfitting I used a cross-validation procedure for the final model (Fernandéz *et al*. 2003). The original data set was divided into 10 parts, called folds. Nine of the folds were combined and used for fitting the model and the remaining fold was used for testing the model. This was then repeated for a total of 10 times. In each iteration, an estimate of accuracy (ranged between 0 and 1) was calculated and the results were averaged over the 10 runs. Statistics were performed with R release 2.3.1 (function "cv.binary", package "DAAG").

3.3 Results

3.3.1 Variable and data reduction

3.3.1.1 Spatial autocorrelation

As expected, the dependent variable showed relatively high spatial autocorrelation at small lag distances; it was strongest for nilgai and sambar, intermediate for wild pig and chital (Fig. 3.3). However, at spatial lag of three cells the correlation coefficient dropped below values of 0.7. I therefore eliminated the data points corresponding to two nearest neighbour segments on the transects in every direction. This reduced the number of data points from initially 4465 to 1489.

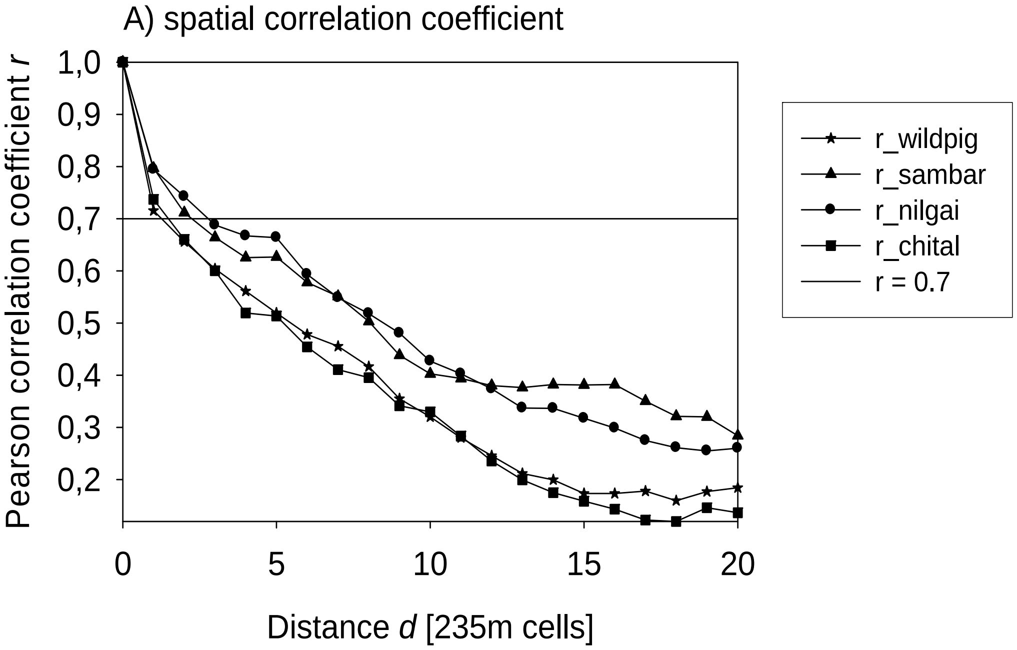


Figure 3.3 Spatial autocorrelation of the presence/absence data at the 250m segments in the transects for each target species in relates to distance (*d*). The Pearson correlation coefficient was high for sambar and nilgai and intermediate for chital and wild pig.

3.3.1.2 Univariate analyses

The univariate analysis revealed significant differences between presence and absence locations for most variables (Appendix I-IV). For sambar 149 of the 163 variables showed significant differences (Appendix I), but most notably no significant differences were found for percentage water bodies at all neighbourhood scales. The largest differences were found for percentage tall grass, short grass, and agricultural and human habitation which were at most neighbourhood scales on average about 10, 3, and 4 times higher at sambar absences than at presences, respectively. On the other hand, percentage forest cover, elevation, and elevation range was on average about 2 or 3 times higher at sambar presences than at absences.

For chital, 128 of the 163 variables showed significant differences (Appendix II), but for range elevation, slope degree and aspects, surface area, and surface ratio no significant difference was found. Proportion dense forest cover, proportion tall grass, and elevation were on average higher at chital presences, but the proportion of most other landcover types was lower.

For nilgai, 132 of the 163 variables showed significant differences (Appendix III), but percentage scrub cover, density of villages and roads, and percentage agricultural and human habitation showed at most neighbourhood scales no significant difference. Proportion open and disturbed forest and proportion tall grass were at most neighbourhood scales about two times as high at nilgai presence than at absence, and elevation was about half at presence.

For wild pig, 136 of the 163 variables showed significant differences. The largest differences were found for proportion tall grass which was higher at presences, and maximum elevation was lower. Notably, proportion dense forest at larger neighbourhood scales did not show significant differences between presence and absence locations (Appendix IV).

3.3.1.3 Correlation between predictive variables

Several habitat variables were strongly correlated to each other. Dense, open and disturbed forests were negatively correlated at all neighbourhood scales (correlation coefficients r_P ranged between -0.75 and -0.85, all $p < 0.01$). Dense forest also correlated negatively with short grass at neighbourhood scales between $d = 6$ and 21 cells (r_P ranged between -0.7 and -0.8, all $p < 0.01$), and short grass with scrub cover at all neighbourhood scales (all r_P between 0.7 and 0.8, all $p < 0.01$) and with barren land at scale $d = 3$ ($r_P > 0.72$, $p < 0.01$). Maximum elevation was strongly correlated with minimum, mean and range elevations, slope degree, surface area and surface ratio at all scales (all r_P between 0.7 and 1, all $p < 0.01$).

Among the variables in the disturbance category, strong positive correlation was detected between habitat diversity and agricultural land at all neighbourhood scales (all r_P between 0.7 and 0.85, all $p < 0.01$). Strong positive correlations were also detected between minimum distance to road and density of road at all neighbourhood scales (all r_P between -0.7 and -0.9, all $p < 0.01$). Minimum distance to villages strongly positively correlated with density of roads at scales between $d = 6$ and 13 (all r_P between -0.7 and -0.9, all $p < 0.01$).

3.3.2 Predictive models

3.3.2.1 Sambar

Model selection using AIC showed that models constructed with disturbance variables received little support compared to models constructed with natural habitat variables (Fig. 3. 5, Table 3.2). For natural models, there was a clear effect of neighbourhood scale with a pronounced minimum at the small neighbourhood scale 3 cells (Fig. 3.5). Generally, there were only small difference (but with ΔAIC > 2) between the slope position classification groups where the small scale slope position classification yielded slightly smaller AIC values.

Table 3.2 Summary of logistic predictive models for sambar distribution, and model selection estimators; -2 log(*L*) = -2 log-likelihood estimates; AIC = Akaike's Information Criterion.

Model	**-2log(*L*)**	**AIC**	**Ranking**
Habitat category – small scale (slope position classification)			
1. Intercept only (Null model)	1829.9	1831.9	10
2. C1, C2, C3, C6, MAE, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	532.2	572.2	7
3. F3C1, F3C2, F3C3, F3C4, MAE3, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	364.0	404.02	1
4. F4C1, F4C2, F4C3, F4C4, MAE4, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	377.9	417.9	2
5. F6C1, F6C2, F6C3, F6C4, MAE6, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	433.7	473.7	3
6. F7C1, F7C2, F7C3, F7C4, MAE7, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	460.1	500.1	4
7. F8C1, F8C2, F8C3, F8C4, MAE8, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	486.3	526.3	5
8. F10C1, F10C2, F10C3, F10C4, MAE10, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	526.4	566.4	6
9. F13C1, F13C2, F13C3, F13C4, MAE13, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	575.8	615.8	8
10. F21C1, F21C2, F21C3, F21C4, MAE21, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	644.7	684.7	9
Habitat category – large scale (slope position classification)			
1. Intercept only (Null model)	1829.9	1831.9	10
2. C1, C2, C3, C6, MAE, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W20_1, W20_3, W20_4, W20_5, W20_6, DRi	532.8	572.8	7
3. F3C1, F3C2, F3C3, F3C4, MAE3, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W20_1, W20_3, W20_4, W20_5, W20_6, DRi	369.5	409.5	1
4. F4C1, F4C2, F4C3, F4C4, MAE4, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W20_1, W20_3, W20_4, W20_5, W20_6, DRi	384.7	424.7	2
5. F6C1, F6C2, F6C3, F6C4, MAE6, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W20_1, W20_3, W20_4, W20_5, W20_6, DRi	440.8	478.8	3
6. F7C1, F7C2, F7C3, F7C4, MAE7, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W20_1, W20_3, W20_4, W20_5, W20_6, DRi	466.1	504.1	4
7. F8C1, F8C2, F8C3, F8C4, MAE8, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W20_1, W20_3, W20_4, W20_5, W20_6, DRi	488.4	528.4	5

Table 3.2, continued.

Model	**-2log(*L*)**	**AIC**	**Ranking**
Habitat category – large scale (slope position classification)			
8. F10C1, F10C2, F10C3, F10C4, MAE10, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W20_1, W20_3, W20_4, W20_5, W20_6, DRi	524.6	564.6	6
9. F13C1, F13C2, F13C3, F13C4, MAE13, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W20_1, W20_3, W20_4, W20_5, W20_6, DRi	567.4	607.4	8
10. F21C1, F21C2, F21C3, F21C4, MAE21, SE, SNE, SN, SNW, SSE, SS, SW, SSW, W20_1, W20_3, W20_4, W20_5, W20_6, DRi	627.1	667.1	9
Disturbance category			
1. Intercept only (Null model)	1829.9	1831.9	10
2. DRo, DVi, C8	1238.5	1250.5	9
3. DRo, DVi, F3C8, DnVi3	1143.9	1157.9	8
4. DRo, DVi, F4C8, DnVi4	1121.9	1135.9	7
5. DRo, DVi, F6C8, DnVi6	1071.5	1085.5	6
6. DRo, DVi, F7C8, DnVi7	1058.4	1072.4	5
7. DRo, DVi, F8C8, DnVi8	1048.2	1062.2	4
8. DRo, DVi, F10C8, DnVi10	1034.4	1048.4	3
9. DRo, DVi, F13C8, DnVi13	1012.6	1026.6	2
10. DRo, DVi, F21C8, DnVi21	964.1	978.1	1
Final combined model			
F3C1, F3C2, F3C3, F3C4, MAE3, W5_3, W5_6, DRi	372.8	390.8	

See Table 3.1 for model definitions.

From the best model identified by the model selection procedure I eliminated manually step by step the non significant variables related with slope aspects and ridge, upper and lower slopes of slope position classification (Weiss 2001). Combining the best models from the natural and the disturbance category did not improve the model since the disturbance predictors were not significant at $p < 0.05$ in the model. Final model had eight variables (Table 3.6). To evaluate the final model, model predictions were classified as occurrences for $P \geq 0.5$ and absences for $P < 0.5$. I used receiver operating characteristic (ROC; Fielding and Bell 1997; Guisan and Zimmermann 2000; Schadt *et al*. 2002) to determine the optimal cutoff. Because the optimal cutoff was with $P = 0.556$ close to the commonly used 0.5 cutoff I used the 0.5 cutoff. The final model classified 93% of all observed presences and absences correctly. The cross-validation test confirmed that no overfitting occurred; mean classification accuracy was with 92% very close to the value of the final model.

3.3.2.2 Chital

Model selection showed that AIC values of models constructed with disturbance variables had a similar range as models constructed with natural habitat variables, although natural models were somewhat better supported by the data (Fig. 3.5, Table 3.3). For natural models, there was a clear effect of neighbourhood scale with a pronounced minimum at neighbourhood scale 8 cells (Fig. 3.5) and for disturbance variables the model with neighbourhood scale 6 received most support.

Table 3.3 Summary of logistic predictive models for chital distribution, and model selection estimators; -2 log(*L*) = -2 log-likelihood estimates; AIC = Akaike's Information Criterion.

Model	**-2log(*L*)**	**AIC**	**Ranking**
Habitat category – small scale (slope position classification)			
1. Intercept only (Null model)	1982.4	1984.4	10
2. C1, C3, C5, C6, C7, MIE, SNW, DRo	1329.6	1347.6	9
3. F3C1, F3C3, F3C5, F3C7, MIN3, SNW, DRo	1250.0	1266.0	8
4. F4C1, F4C3, F4C5, F4C7, MIN4, SNW, DRo	1235.7	1251.7	6
5. F6C1, F6C3, F6C6, F6C7, MIN6, SNW, DRo	1221.0	1237.0	4
6. F7C1, F7C3, F7C6, F7C7, MIN7, SNW, DRo	1215.7	1231.7	2
7. F8C1, F8C3, F8C6, F8C7, MIN8, SNW, DRo	1211.3	1227.3	1
8. F10C1, F10C3, F10C6, F10C7, MIN10, SNW, DRo	1214.0	1230.0	3
9. F13C1, F13C3, F13C6, F13C7, MIN13, SNW, DRo	1226.8	1242.8	5
10. F21C1, F21C3, F21C6, F21C7, MIN21, SNW, DRo	1263.0	1277.0	7
Disturbance category			
1. Intercept only (Null model)	1982.4	1984.4	10
2. DRo, DVi, C8	1272.8	1284.8	9
3. DnRo3, DVi, F3C8, DnVi3	1246.0	1260.0	3
4. DnRo4, DVi, F4C8, DnVi4	1246.8	1260.8	4
5. DnRo6, DVi, F6C8, DnVi6	1243.4	1257.4	1
6. DnRo7, DVi, F7C8, DnVi7	1245.3	1259.3	2
7. DRo, DVi, F8C8	1261.6	1273.6	5
8. DRo, DVi, F10C8	1262.3	1274.3	6
9. DRo, DVi, F13C8	1263.0	1275.0	7
10. DRo, DVi, F21C8	1266.1	1278.1	8
Final combined model			
F8C1, F8C3, MIE8, SNW, DVi	1188.6	1200.6	

See Table 3.1 for model definitions.

Combining the best natural model with the best disturbance model decreased the AIC value considerably (Fig. 3.5, Table 3.3) and I considered the combined model for the final selection. I stepwise eliminated the non significant variables like barren land, percentage of water source and minimum distances to river from the model. The final model comprised five variables (Table 3.6) and classified with a 0.5 cutoff 73.4% of all observed presences and absences correctly. The estimated optimal cutoff for this model was 0.493. Because the optimal cutoff was close to the commonly used 0.5 cutoff I used the 0.5 cutoff. The cross-validation test confirmed that no overfitting occurred; the mean classification accuracy was 73%.

3.3.2.3 Nilgai

Model selection showed that AIC values of models constructed with natural variables received at smaller neighbourhoods considerably more support than models with disturbance variables (Fig. 3.5, Table 3.4). The models with the lowest AIC occurred at neighbourhood scale of 6 cells and were similar for both slope position classifications (ΔAIC < 1.3).

After combining the two best natural models each with the best disturbance model and removing non significant variables, I obtained the final model at small scale slope classification that retained both, natural and disturbance variables. The final model comprised six variables (Table 3.6) and classified with a 0.5 cutoff 75% of all observed presences and absences correctly. The estimated optimal cutoff for this model was 0.561. Because the optimal cutoff was close to the commonly used 0.5 cutoff I used the 0.5 cutoff. The cross-validation test confirmed that no overfitting occurred; the mean classification accuracy was 75%.

Table 3.4 Summary of logistic predictive models for nilgai distribution, and model selection estimators; -2 log(*L*) = -2 log-likelihood estimates; AIC = Akaike's Information Criterion.

Model	**-2log(*L*)**	**AIC**	**Ranking**
Habitat category – small scale (slope position classification)			
1. Intercept only (Null model)	1899.2	1901.2	10
2. C2, C3, C7, MEE, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	1193.0	1215.0	9
3. F3C2, F3C3, F3C4, F3C7, MEE3, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	1135.7	1159.7	3
4. F4C2, F4C3, F4C5, F4C7, MEE4, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	1129.9	1153.9	2
5. F6C2, F6C3, F6C5, F6C7, MEE6, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	1126.4	1150.5	1
6. F7C2, F7C5, F7C7, MEE7, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	1156.7	1178.7	8
7. F8C2, F8C5, F8C7, MEE8, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	1155.1	1177.1	7
8. F10C2, F10C5, F10C7, MEE10, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	1150.8	1172.8	6
9. F13C2, F13C5, F13C7, MEE13, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	1142.5	1164.5	5
10. F21C2, F21C5, MEE21, W5_1, W5_2, W5_3, W5_5, W5_6, DRi	1139.8	1159.8	4
Habitat category – large scale (slope position classification)			
1. Intercept only (Null model)	1899.2	1901.2	10
2. C2, C3, C7, MEE, W20_1, W20_3, W20_4, W5_5, DRi	1195.6	1215.6	9
3. F3C2, F3C3, F3C4, F3C7, MEE3, W20_1, W20_3, W20_4, W20_5, DRi	1136.4	1158.4	3
4. F4C2, F4C3, F4C5, F4C7, MEE4, W20_1, W20_3, W20_4, W20_5, DRi	1131.6	1153.6	2
5. F6C2, F6C3, F6C5, F6C7, MEE6, W20_1, W20_3, W20_4, W20_5, DRi	1127.9	1149.9	1
6. F7C2, F7C5, F7C7, MEE7, W20_1, W20_3, W20_4, W20_5, DRi	1159.9	1179.9	8
7. F8C2, F8C5, F8C7, MEE8, W20_1, W20_3, W20_4, W20_5, DRi	1158.0	1178.0	7
8. F10C2, F10C5, F10C7, MEE10, W20_1, W20_3, W20_4, W20_5, DRi	1153.4	1173.3	6
9. F13C2, F13C5, F13C7, MEE13, W20_1, W20_3, W20_4, W20_5, DRi	1145.0	1165.0	5
10. F21C2, F21C5, MEE21, W20_1, W20_3, W20_4, W20_5, DRi	1141.6	1159.6	4
Disturbance category			
1. Intercept only (Null model)	1899.2	1901.2	10
2. Di, DRo, DVi	1281.8	1293.8	7
3. Di3, DnRo3, DVi	1289.8	1301.8	9
4. DnRo4, F4C8, DVi	1288.3	1300.3	8
5. DnRo6, F6C8, DVi	1267.4	1279.4	6
6. DnRo7, F7C8, DVi	1259.5	1271.5	5
7. DRo, F8C8, DVi	1234.4	1246.4	4
8. DRo, F10C8, DVi	1216.3	1228.3	3
9. DRo, F13C8, DVi	1194.8	1206.8	2
10. DRo, F21C8, DVi	1154.5	1166.5	1

Table 3.4, continued.

Model	**-2log(*L*)**	**AIC**	**Ranking**
Final combined models			
1. F6C2, F6C3, MEE6, W5_4, DRi, DRo	1129.3	1143.3	
2. F6C2, F6C3, MEE6, W20_4, DRi, DRo	1129.9	1143.9	

See Table 3.1 for model definitions.

3.3.2.4 Wild pig

The models for wild pig received relatively little support from the data. Proportion dense forest was not included in the models of the habitat category at neighbourhoods larger than 7 cells because the mean differences were not significant between presence and absence locations (Appendix I). Even though a model without the dense forest predictor had the lowest AIC value (Table 3.5), I considered the two best model with dense forest (models 5 and 6 in the ranking) for the final selection by taking into consideration their relatively small difference in AIC to the best model (ΔAIC = 4.6 and 6.6, respectively) and the biology of the target species.

Combining the best natural models with the best disturbance model and removing non significant variables yielded a model with AIC 6.5 units smaller than the best model from the habitat category. The final model contained six variables (Table 3.6) and classified with 0.5 cutoff 64% of all observed presences and absences correctly. The estimated optimal cutoff for this model was 0.529. Because the optimal cutoff was close to the commonly used 0.5 cutoff I used the 0.5 cutoff. The cross-validation test confirmed that no overfitting occurred; mean classification accuracy was 64%.

Table 3.5 Summary of logistic predictive models for wild pig distribution, and model selection estimators; -2 log(*L*) = -2 log-likelihood estimates; AIC = Akaike's Information Criterion.

Model	**-2log(*L*)**	**AIC**	**Ranking**
Habitat category – small scale (slope position classification)			
1. Intercept only (Null model)	2085.0	2087.0	10
2. C1, C3, C5, C6, MAE, SE, SNE, SN, SNW, SSE, SSW, W5_3, W5_5, W5_6, DRi	1557.3	1589.3	9
3. F3C1, F3C3, F3C5, F3C7, MAE3, SE, SNE, SN, SNW, SSE, SSW, W5_3, W5_5, W5_6, DRi	1539.5	1571.5	8
4. F4C1, F4C3, F4C5, F4C7, MAE4, SE, SNE, SN, SNW, SSE, SSW, W5_3, W5_5, W5_6, DRi	1538.1	1570.1	7
5. F6C1, F6C3, F6C6, F6C7, MAE6, SE, SNE, SN, SNW, SSE, SSW, W5_3, W5_5, W5_6, DRi	1531.3	1563.3	6
6. F7C1, F7C3, F7C6, F7C7, MAE7, SE, SNE, SN, SNW, SSE, SSW, W5_3, W5_5, W5_6, DRi	1529.3	1561.3	5
7. F8C2, F8C3, F8C5, F8C7, MAE8, SE, SNE, SN, SNW, SSE, SSW, W5_3, W5_5, W5_6, DRi	1526.8	1558.8	4
8. F10C2, F10C3, F10C5, F10C7, MAE10, SE, SNE, SN, SNW, SSE, SSW, W5_3, W5_5, W5_6, DRi	1524.4	1556.4	3
9. F13C2, F13C3, F13C5, F13C7, MAE13, SE, SNE, SN, SNW, SSE, SSW, W5_3, W5_5, W5_6, DRi	1524.0	1556.0	2
10. F21C2, F21C3, F21C5, F21C7, MAE21, SE, SNE, SN, SNW, SSE, SSW, W5_3, W5_5, W5_6, DRi	1523.2	1555.2	1
Habitat category – large scale (slope position classification)			
1. Intercept only (Null model)	2085.0	2087.0	10
2. C1, C3, C5, C6, MAE, SE, SNE, SN, SNW, SSE, SSW, W20_3, W20_4, W20_5, DRi	1552.8	1584.8	9
3. F3C1, F3C3, F3C5, F3C7, MAE3, SE, SNE, SN, SNW, SSE, SSW, W20_3, W20_4, W20_5, DRi	1534.2	1566.2	8
4. F4C1, F4C3, F4C5, F4C7, MAE4, SE, SNE, SN, SNW, SSE, SSW, W20_3, W20_4, W20_5, DRi	1532.3	1564.3	7
5. F6C1, F6C3, F6C6, F6C7, MAE6, SE, SNE, SN, SNW, SSE, SSW, W20_3, W20_4, W20_5, DRi	1526.2	1558.3	6
6. F7C1, F7C3, F7C6, F7C7, MAE7, SE, SNE, SN, SNW, SSE, SSW, W20_3, W20_4, W20_5, DRi	1524.7	1556.7	5
7. F8C2, F8C3, F8C5, F8C7, MAE8, SE, SNE, SN, SNW, SSE, SSW, W20_3, W20_4, W20_5, DRi	1522.6	1554.6	4
8. F10C2, F10C3, F10C5, F10C7, MAE10, SE, SNE, SN, SNW, SSE, SSW, W20_3, W20_4, W20_5, DRi	1521.1	1553.1	1
9. F13C2, F13C3, F13C5, F13C7, MAE13, SE, SNE, SN, SNW, SSE, SSW, W20_3, W20_4, W20_5, DRi	1521.3	1553.3	2
10. F21C2, F21C3, F21C5, F21C7, MAE21, SE, SNE, SN, SNW, SSE, SSW, W20_3, W20_4, W20_5, DRi	1521.3	1553.4	3
Disturbance category			
1. Intercept only (Null model)	2085.0	2087.0	9
2. C8, DRo, DVi	1757.5	1765.5	8
3. F3C8, DRo, DVi	1757.5	1765.5	8
4. F4C8, DRo, DVi	1756.7	1764.7	6
5. F6C8, DRo, DVi, DnVi6	1753.9	1763.9	3
6. DRo, DVi, DnVi7	1756.8	1764.8	7
7. DRo, DVi, DnVi8	1756.2	1764.2	5

Table 3.5, continued.

Model	**-2log(*L*)**	**AIC**	**Ranking**
8. DRo, DVi, DnVi10	1755.8	1763.8	2
9. DRo, DVi, DnVi13	1756.0	1764.0	4
10. DRo, DVi, DnVi21	1755.1	1763.1	1
Final combined model			
F7C1, F7C3, MAE7, W20_3, W20_4, DVi	1536.2	1550.2	

See Table 3.1 for model definitions.

3.3.3 Habitat mapping

3.3.3.1 Models for the four study species

I applied the final models shown in Table 3.2 to the 42,700km^2 study area to assess the spatial distribution of suitable habitat for sambar, chital, nilgai and wild pig (Fig. 3.5). All three national parks contained suitable areas ($P > 0.5$) for sambar and chital (Fig. 3.5). The sambar had highly suitable habitats in the hilly terrains, Shivalik and bhabar areas, and some areas in the lowland (terai) habitats (Fig. 3.5). Chital had highly suitable habitats in the terai as well as hilly habitats but avoided higher elevated areas (Fig. 3.5). Not surprisingly, the nilgai which preferred open and disturbed forest and tall grass areas had very little suitable habitats in the NPs except the boundary regions of Dudhwa, Corbett and Rajaji NPs. The high suitable areas for nilgai occurred in the lower hill areas and also some areas in the terai habitats (Fig. 3.5). Dudhwa NP lying in the terai habitat contained high suitable habitat for wild pig compare to hilly terrains in Rajaji and Corbett NPs. The lowland, terai habitats were more suitable than the hilly terrain for wild pig in the model.

Table 3.6 Summary of the final logistic predictive models for sambar, chital, nilgai, and wild pig with presence-absence data.

						Goodness-of-fit				
Species	**Variable**	**Symbol**	**ß**	**SE**	***p***	***X*²**	**df**	***p***	**AIC**	**Predicted**
Sambar						1112.45	8	<0.001	390.8	93 %
	dense forest (%) at scale *d* = 3	F3C1	0.072	0.012	<0.001					
	open and disturbed forest (%) at scale *d* = 3	F3C2	-0.057	0.013	<0.001					
	tall grass (%) at scale *d* = 3	F3C3	-0.543	0.101	<0.001					
	short grass (%) at scale *d* = 3	F3C4	-0.131	0.036	<0.001					
	maximum elevation at scale *d* = 3	MAE3	0.005	0.001	<0.001					
	middle slope at scale *d* = 5	W5_3	-0.355	0.001	0.023					
	valley at scale *d* = 5	W5_6	-0.249	0.092	0.007					
	minimum distance to river	DRi	$-4.14e^{-04}$	$1.49e^{-04}$	0.006					
	constant	C	-1.909	1.076	0.076					
Chital						427.60	5	<0.001	1200.6	73.4%
	dense forest (%) at scale *d* = 8	F8C1	0.039	0.003	<0.001					
	tall grass (%) at scale *d* = 8	F8C3	0.071	0.013	<0.001					
	minimum elevation at scale *d* = 8	MIE8	0.002	0.001	<0.004					
	northwest slope aspect	SNW	-0.033	0.013	0.015					
	minimum distance to village	DVi	$2.33e^{-04}$	$4.62e^{-05}$	<0.001					
	Constant	C	-3.215	0.226	<0.001					
Nilgai						418.52	6	<0.001	1143.3	74.9%
	open and disturbed forest (%) at scale *d* = 6	F6C2	0.042	0.005	<0.001					
	tall grass (%) at scale *d* = 6	F6C3	0.073	0.014	<0.001					
	mean elevation at scale *d* = 6	MEE6	-0.003	0.001	<0.001					
	flat slope at scale *d* = 5	W5_4	0.113	0.045	0.011					
	minimum distance to river	DRi	$3.98e^{-04}$	$7.68e^{-05}$	<0.001					
	minimum distance to road	DRo	$-2.01e^{-04}$	$5.17e^{-05}$	<0.001					
	constant	C	-0.728	0.310	0.019					

Table 3.6, continued.

						Goodness-of-fit				
Species	**Variable**	**Symbol**	**ß**	**SE**	***p***	X^2	**df**	***p***	**AIC**	**Predicted**
Wild pig						160.35	6	<0.001	1550.2	63.3%
	dense forest (%) at scale *d* = 7	F7C1	0.011	0.003	<0.001					
	tall grass (%) at scale *d* = 7	F7C3	0.077	0.015	<0.001					
	maximum elevation at scale *d* = 7	MAE7	-0.001	0.000	<0.001					
	middle slope at scale *d* = 20	W20_3	-0.163	0.072	0.023					
	flat slope at scale *d* = 20	W20_4	0.094	0.037	0.011					
	minimum distance to village	DRi	$9.36e^{-02}$	$3.67e^{-02}$	0.026					
	constant	C	-0.552	0.194	0.005					

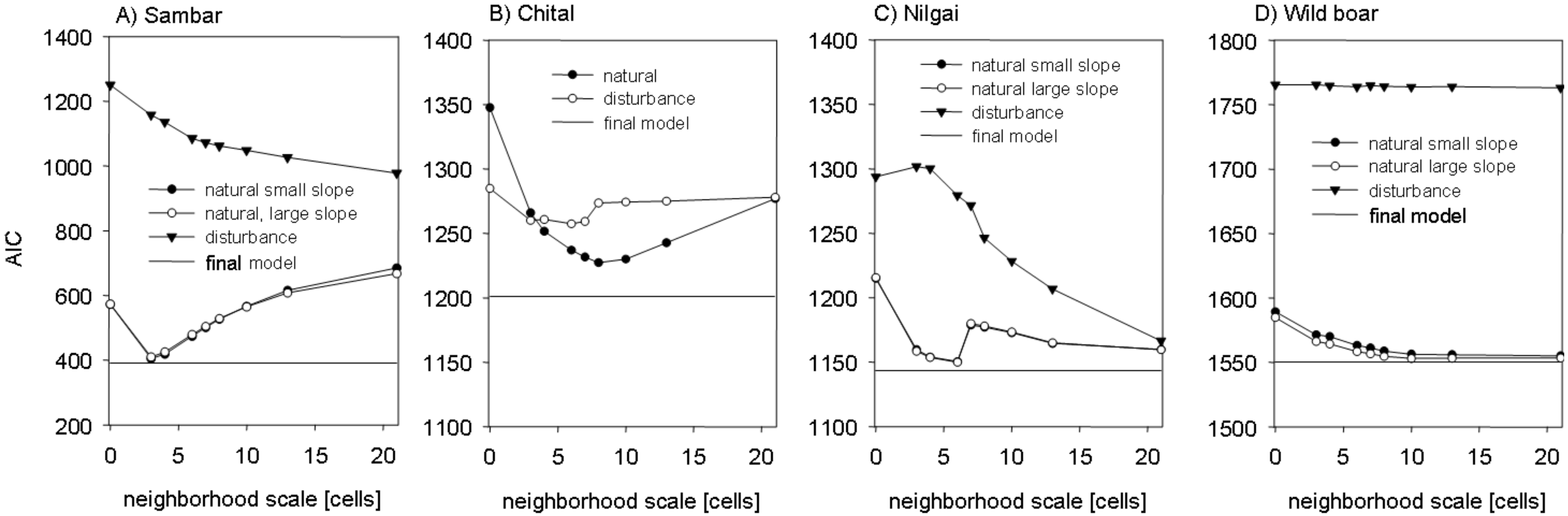


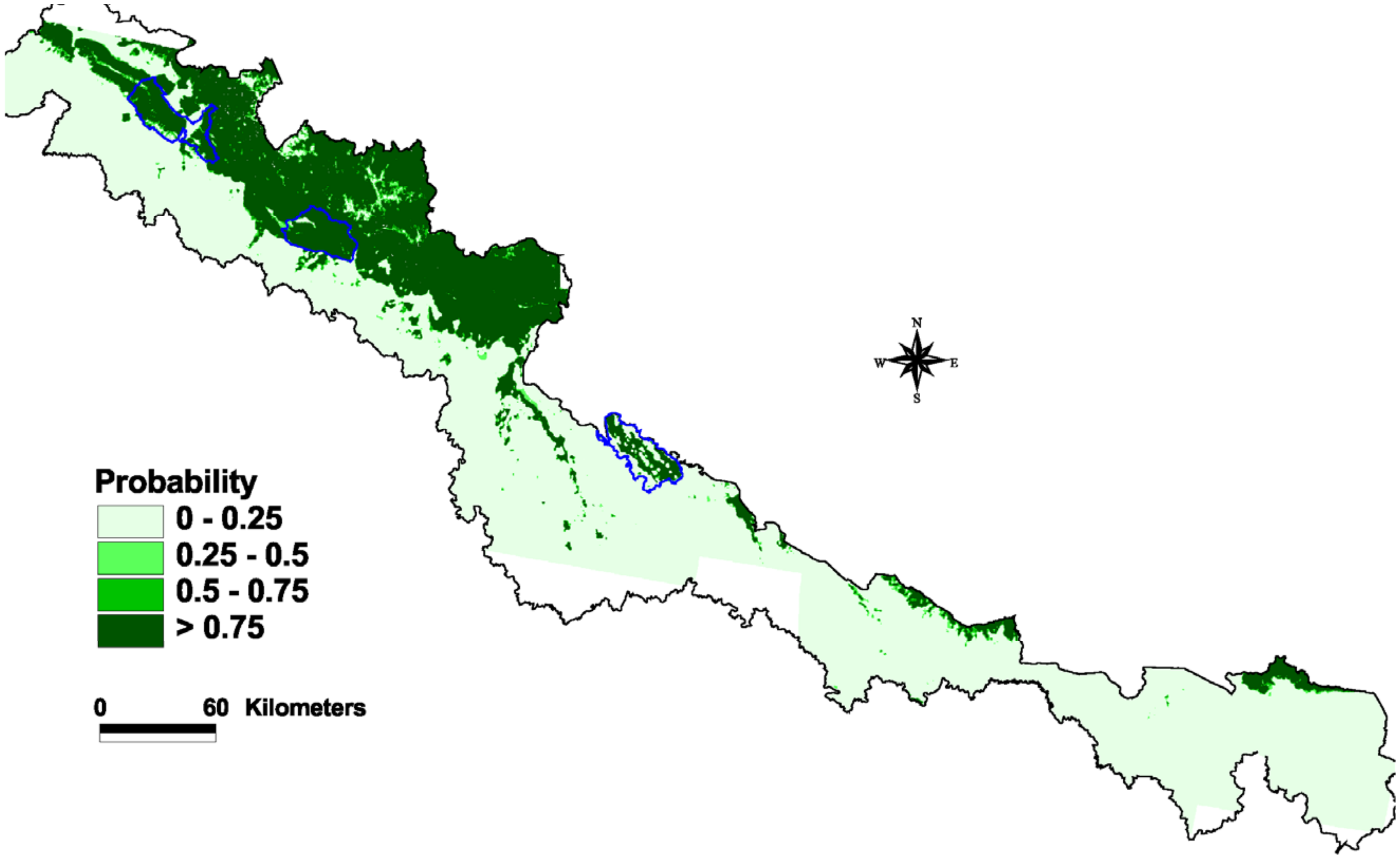
Figure 3.4 Results of model selection for the four ungulate species in dependence on the neighbourhood scale.

To assess wrong classifications caused by of animals moving occasionally into habitat of low suitability, I calculated the distance between false positives (i.e., absence classified as presence) and the nearest cell predicted as suitable habitat (Fig. 3.7). For sambar, 19 out of 33 false positives were within distance of 470m of predicted suitable habitat, and only 4 false negatives were further away than 940m. For chital, 32% of all false negatives were within 470m from predicted suitable habitat and 80% within 2.8km. For nilgai, 50% of all false negatives were located within 1.1km from predicted suitable habitat and 80% within 2.8km. In case of the wild pig one third of all false negatives were within 1km from suitable habitat and 80% within 3.8km.

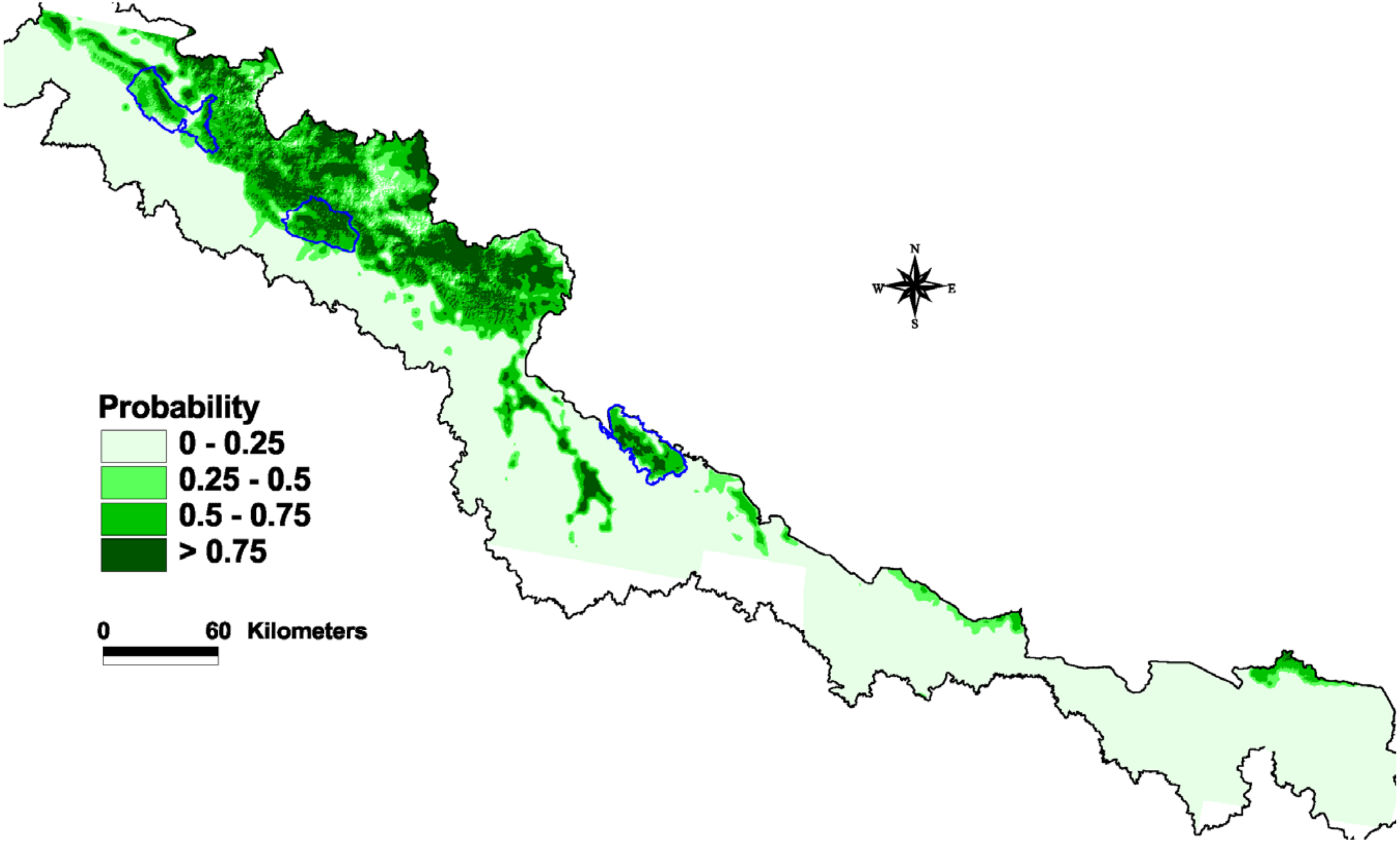
3.3.3.2 Overall map for the four study species

Final models indicated that different factors determined habitat suitability for the four study species. Consequently, I found that they segregate considerably in space. I therefore combined the resulting habitat suitability maps of four ungulate species (by counting the number of species for which the final model predicts $p > 0.5$) to assess the habitat separation among the species (Fig. 3.6). The combination of two species dominated the two national parks and the surrounding areas in the hilly, medium elevated areas, approximately below 1200m, in the study area (Fig. 3.6). The higher elevated areas were patchily occupied by a single species (Fig. 3.6). The disturbed forests in the low elevated areas were also occupied by a single species. The major part of the terai habitats was occupied by a combination of three species (Fig. 3.6).

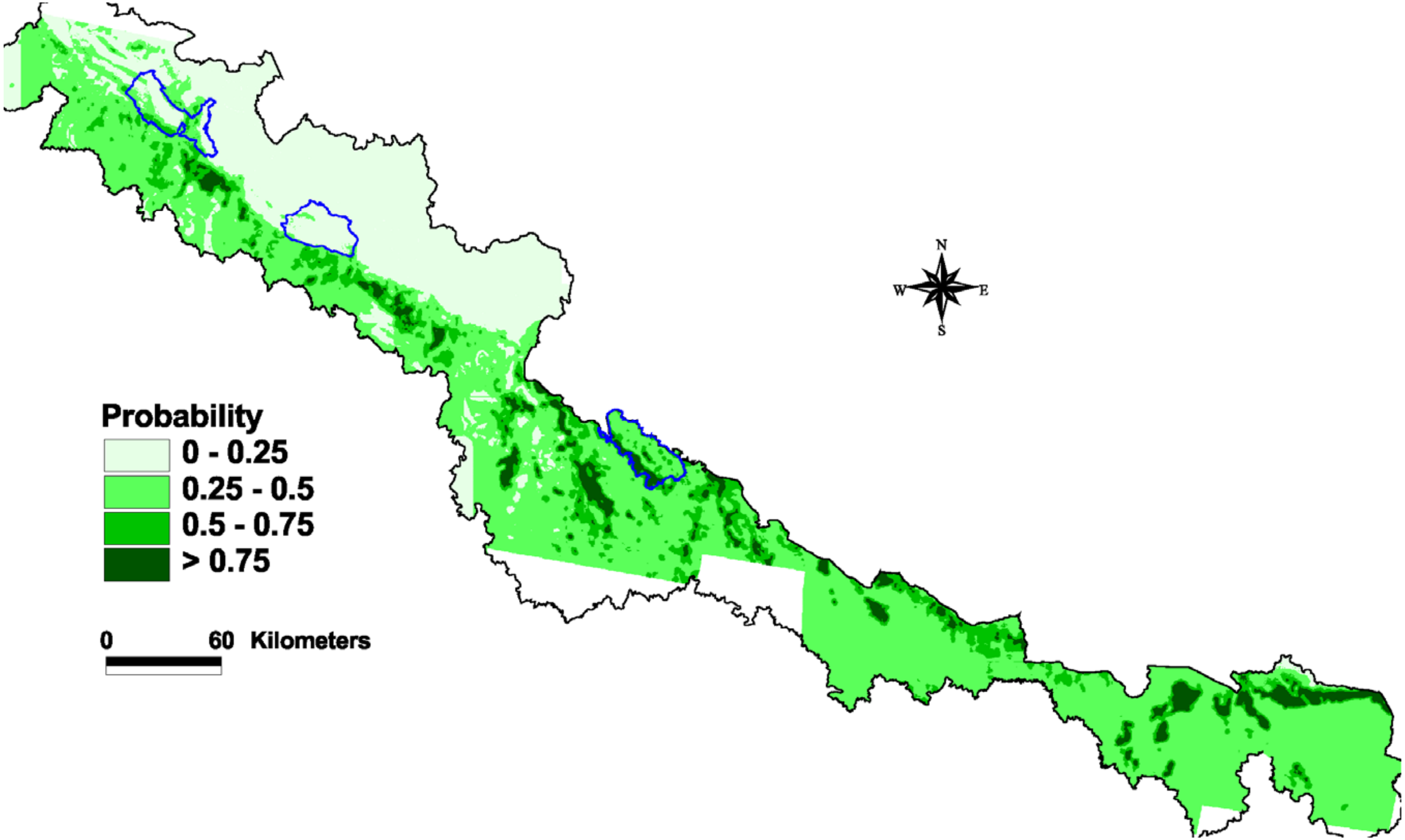
Figure 3.5 Maps of predicted habitat suitability for sambar (A), chital (B), nilgai (C) and wild pig (D) in the Indian part TAL.



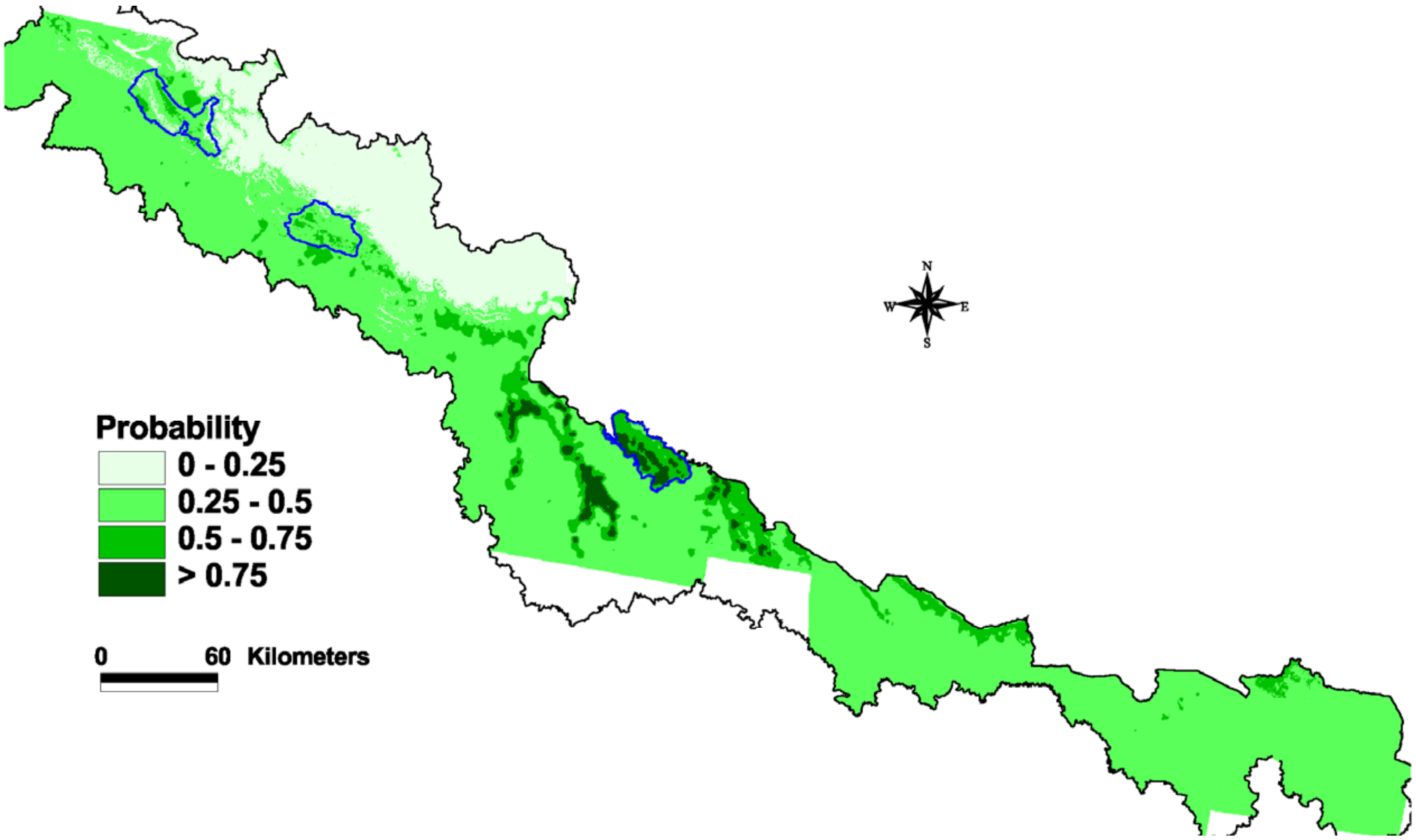
A) Sambar



B) Chital



C) Nilgai



D) Wild pig

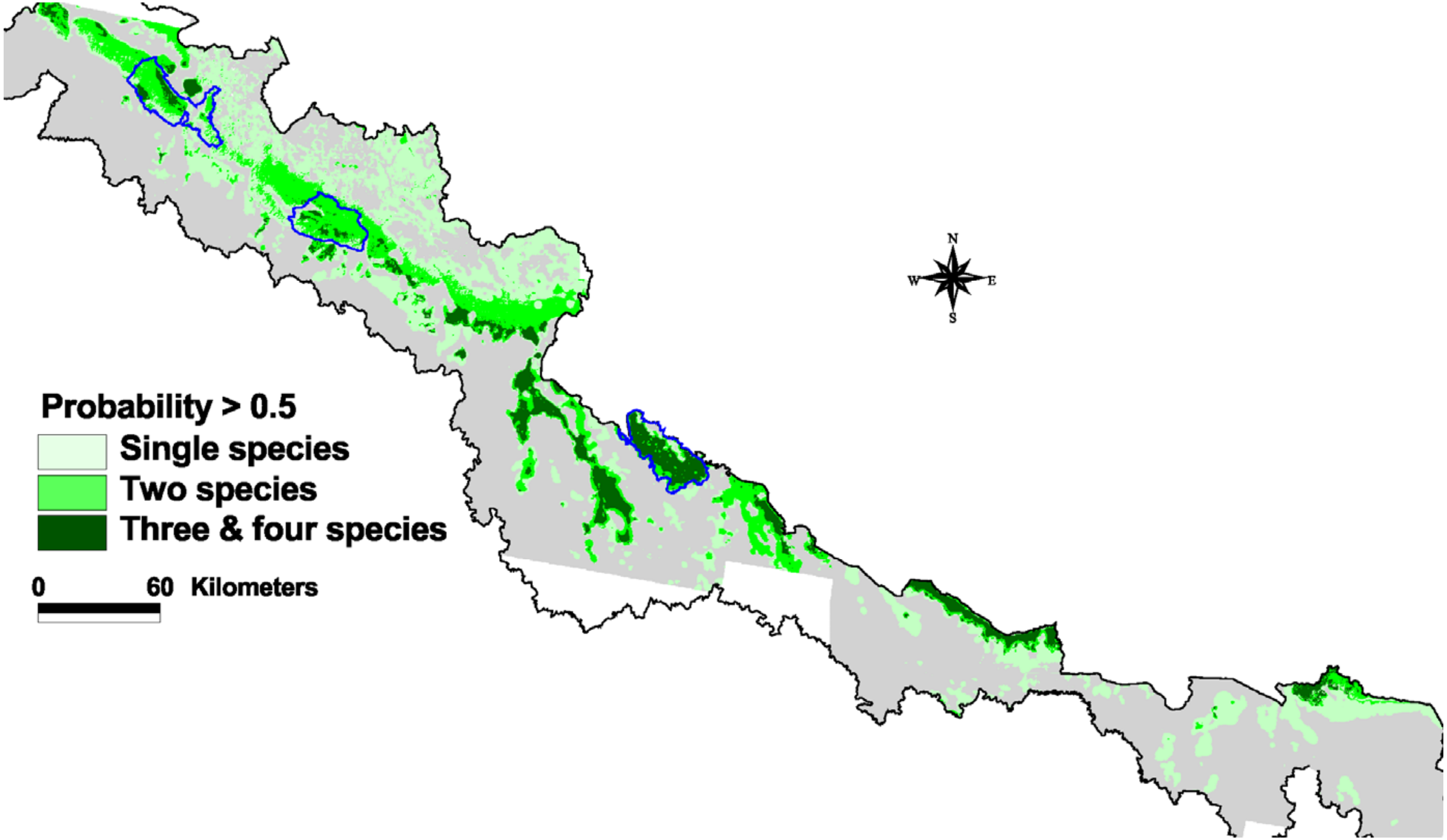


Figure 3.6 Combined habitat suitability map of all four ungulate species showing areas where 1, 2, or 3 or 4 species had a probability of occurrence larger than 0.5.

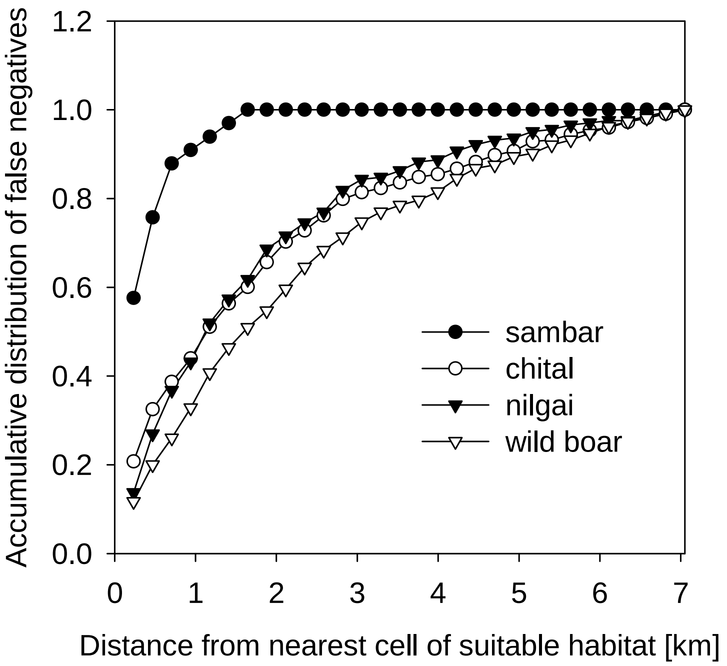


Figure 3.7 Accumulative distributions of distances in km between false negatives and nearest cell of predicted suitable habitat for the four study species.

3.4 Discussion

I have presented here habitat suitability models, each explicitly assessing natural habitat characteristics and anthropogenic factors at various neighbourhood scales, to reveal factors which determine habitat suitability and to describe the distribution of suitable habitat and its overlap for four ungulate species in the heterogeneous TAL landscape in northern India. In this multi scale modelling approach, I explicitly accounted for larger-scale properties of the environmental variables and examined their effects in predicting ungulates' distributions. In the following sections I will discuss the contribution of this approach to the ecological understanding of the interaction between the ungulate species and landscape heterogeneity, the habitat overlaps between the ungulate species, and the regional level management of these species, especially in respect to tiger conservation and the avoidance of human-wildlife conflicts.

3.4.1 Sambar

Model revealed that sambar prefers disturbance free areas of the hilly terrains but that terai areas were less suitable. At altitudes above 1200m the model predicts a patchy distribution because of the higher levels of human disturbances and less dense forests in these areas. These results are in accordance with previous studies (see section '*Study species*'). I found that the probability of sambar occurrence was positively related with amount of dense forest, with elevation, and proximity of rivers (Mathur 1991) whereas open and disturbed forest, tall grass and short grass were avoided (Sankar 1994). Interestingly, the transition between matrix areas (i.e., $p < 0.25$) and highly suitable areas (i.e., $p > 0.75$) was very sharp with little intermediate areas in between (Fig. 3. 5A), pointing to a clear pattern of local habitat selection. Twenty-four percent of the area of the study area and 78% of the NPs were predicted as suitable for sambar at the probability of > 0.5 (Table 3.7).

I found a strong effect of the neighbourhood scale at which the proportion of the different land cover classes was measured. The neighbourhood scale of $d = 3$ cells (≈ 1.6 km^2) was best supported by the data. This scale is close to the estimated mean annual home range of female sambar (Shea *et al*. 1990; Sankar 1994). Similar results were obtained in habitat models by Naves *et al*. (2003) for brown bears (*Ursos arctos*) in Spain and Schadt *et al*. (2002) for European lynx (*Lynx lynx*) where neighbourhood scale corresponded to typical home range sizes. Although the model predicted that most of the hilly terrain would be suitable for sambar, I expect its abundance to be lower outside the National Parks than inside because of its preference of disturbance free areas.

Table 3.7 Amount of favourable habitat available for the study ungulates within the National Parks and in the TAL.

Probability	% of Habitat Area							
	Sambar		Chital		Nilgai		Wild pig	
	SA[#]	NP*	SA	NP	SA	NP	SA	NP
> 0	74	19	80	11	29	49	17	7
> 0.25	3	3	8	22	57	37	74	53
> 0.5	3	5	9	50	10	8	8	29
> 0.75	21	73	2	17	4	6	2	10

% of habitat area in the study area (TAL).
% of habitat area within the National Park, the most strictly protected area.

3.4.2 Chital

Chital presence was positively related to proportion of dense forest and proportion of tall grass within an $11km^2$ neighbourhood and negatively related to northwest slope aspect and distance to villages (Table 3.6). This is consistent with the knowledge on this species (see section '*Study species*'; Bhatt and Rawat 1995). As a result of these characteristics, chital showed preference for lowland *terai* habitats and also shares the lower elevated hilly terrains with sambar. Accordingly, 11% of the study area and 67% of the national parks were classified as suitable habitat for chital (Table 3.7).

There was a strong effect of the neighbourhood scale on AIC with a clear minimum at a neighbourhood scale of d = 8 ($11.1km^2$). This neighbourhood is bigger than typical home ranges of chital (see section '*Study species*'). One possible explanation for this is that this scale does not reflect home-range but larger-scale processes of population dynamics e.g., related with the herd building of this species. Another explanation would be that chital, unlike sambar with very specialized habitat preferences, uses more diverse vegetation and landscape types and that the larger neighborhood areas are required to capture this variability in predicting chital occurrence.

3.4.3 Nilgai

The presence of nilgai was positively related to lower elevation, flat slopes and the proportions of open and disturbed forest and tall grass at a neighbourhood of $6.2km^2$. This coincides well with previous knowledge (see section '*Study species*'). The $6.2km^2$ neighbourhood scale coincides with the home range size of an adult radio-collared female nilgai and her associated group members in the Royal Bardia NP lowland in Nepal (Subedi 2001). The seasonal home ranges ranged between 5.6 km^2 and 10.0 km^2.

The negative response to rivers can be explained by nilgai's being antelope and less dependent on water and for preference of open habitats (which are normally close to human habitation) and high human disturbances in the river beds. Nilgai have the tendency of defecating in the forest roads that could be responsible for the positive effect of proximity of roads on nilgai occurrence.

Because of the avoidance of dense forests and hilly terrain, which characterize especially Rajaji and Corbett NPs, only 14% of the areas of all national parks were classified as suitable at probability > 0.5 for nilgai. Overall, about 14% of the area of the study area was classified as suitable habitat for nilgai (Table 3.7).

3.4.4 Wild pig

The predictive power of the final model for wild pig was with 63% correct classifications much lower than the models for the other species. It could be because of low presence points for wild pig compare to other study species and its low abundance in the hilly terrain habitats in the study area (Johnsingh *et al.* 2004). More intensive surveys, especially in the hilly areas, are required to increase the predictive power of the model developed for the entire TAL.

3.4.5 Habitat overlaps between ungulates

It has been postulated that assemblages of similar species may partition in ecological communities three types of resources: space (or habitat), food and time (Pianka 1973; Schoener 1974). Coexisting species may reduce niche overlap through ecological character displacement and interspecific differences in responses to habitat factors may influence the community structure especially in heterogeneous landscapes (Gabor *et al*. 2001). Here I investigated the ecological distribution of four coexisting herbivore species in a heterogeneous landscape in terms of habitat preferences.

Model predicted most of the terai habitats to be suitable for 3 ungulate species (chital, nilgai and wild pig) and the hilly terrain habitats, bhabar and Shivaliks, suitable for chital and sambar. More quantitatively, about 38% (*c*.16200sq.km) of the study area was suitable for at least one of four prey species, but in 58% (*c*.9400sq.km) of this area only one species would occur, in 29% (*c*.4700sq.km) two species and in 13% (*c*.2100sq.km) three species (Table 3.8). The two important "axes" of spatial separation were landscape heterogeneity in terms of topography and type of vegetation, which were superposed by differential responses to human disturbances. All four models contained one variable which was related to topography and all four models contained variables which indicated preference or avoidance of certain vegetation types such as dense forest, tall grass, or open and disturbed forest.

Table 3.8 Amount of overlapping favourable habitat for the four study species within the National Parks and in the TAL.

Species	% of Habitat Area			
	Rajaji NP	Corbett NP	Dudhwa NP	SA#
0*	10	5	5	63
1	31	16	11	22
2	46	70	21	11
3 and 4	13	10	63	5

* unsuitable habitats for all four study species
\# % of habitat area in the study area (TAL).

As a result of this, the two deer species, sambar and chital, showed some overlapping of suitable areas in the hilly terrain and the dense forests habitats in the western part of the study area that includes Rajaji and Corbett NPs and the eastern part that includes Valmik TR and Suhelwa WLS. However, the suitable areas for chital and sambar were only partly overlapping in the terai habitats that include Dudhwa NP, Kishanpur and Katerniaghat WLSs, and Pilibhit FD and surrounding areas. Higher elevated areas were avoided by chital but used by sambar and terai habitats were avoided by sambar but used by chital.

The areas predicted to be suitable for the antelope nilgai and for sambar largely segregated, except few areas in Corbett and Dudhwa NPs. Nilgai avoided dense forest and preferred the plains and low hills with shrubs. However, nilgai which has a preference for areas with abundant grass and shrub cover for forage showed some overlap with chital and wild pig, especially in the terai habitats. Rodgers (1988), Sankar (1994) and Bagchi *et al*. (2003) found overlap in food habits by chital and nilgai caused by their generalized diet choice.

Several additional factors may promote coexistence of the four species in TAL. For example, competition and predation played an important role in the niche separation of a closely related ungulate community (Sinclair 1985). However, competition occurs only when the resources in question are in short supply (Leuthold 1978). The terai areas comprise fertile grasslands mixed with woodlands and scrublands that provide abundant food resources which should allow chital and nilgai, which show a more generalized diet (Rodgers 1988; Sankar 1994; Bagchi *et al*. 2003), to coexist with wild pig. Moreover, sambar are browsers as well as grazers, depending on season. This may additionally reduce competition with chital because differential use of shared resources is a principal factor which allows species to co-exist (Schoener 1974). Although sambar and chital show niche overlap in space in most of the bhabar and Shivalik habitats, sambar prefers rugged hilly terrain, which is normally avoided by chital (Schaller 1967; Khan 1996).

Another factor which is known to structure ungulate communities is predation. The TAL is home of two endangered top carnivores, tiger and leopard. Sinclair (1985) observed that zebra are using wildebeest to obtain protection from predators in the African ungulate community. However, further studies are required to explain how this ungulate community assemblages themselves to escape from the potential predation.

3.4.6 Application of the distribution map to identify conservation hotspots

As a result of the conquest of malaria, establishment of numerous settlements and a subsequent increase in human population in the TAL has become highly fragmented and degraded (Johnsingh *et al*. 2004). Management in such landscapes requires consideration of the spatial location of potentially available natural habitats as well as quantification of anthropogenic impacts on species distributions. Accordingly, I considered the effect of natural habitat variables and anthropogenic factors separately during model development. Results indicated that the ungulates responded mostly negative to indicators of human disturbances such as distance to villages or roads. Interestingly, the final model for sambar was based solely on natural habitat characteristics which indicated that this species has habitat preferences which keep them away from human disturbance. The coexistence of chital, nilgai, wild pig and sambar in the lowland (terai) areas (includes Dudhwa NP, Kishanpur and Katerniaghat WLSs, and Pilibhit FD) indicate the importance of this high quality habitat for tiger conservation in the TAL. However, the negative influence of anthropogenic factors in the models suggests that a reduction of human disturbances, especially from villages and roads, would be a top priority in this area. Models also indicate the fragmented available potential habitats for ungulates and also highlight the possible connectivity areas between the fragmented suitable habitats and assist in identifying conservation priority areas and designing management strategies in a spatial context.

This study is a significant step to an understanding of the role of landscape heterogeneity for ungulate habitat suitability. In the TAL, this is especially important because it is home to the endangered tiger which uses the study species as preferred prey species. In this multi-scale modelling approach, I explicitly included the neighbourhood information of natural habitats and anthropogenic factors at various neighbourhoods and examined their ability in predicting the ungulates distributions. The inclusion of such variables is important for capturing the organism's perception of landscape structure above the grain of the landscape map, which is often arbitrarily defined (Schadt *et al*. 2002), and for correcting systematic errors introduced when the scale of the analysis does not match the relevant spatial scale of the underlying ecological processes.

Models used relatively coarse land cover types, and land cover measured over relatively large neighbourhoods predicted the observations best. On the other hand it would be desirable to consider information on finer scale habitat use and on consumption of specific food species to improve the understanding of habitat needs and for recommending specific management actions (Fernandez *et al*. 2003). However, fine grained information over large areas, as would be required for the study landscape, is rarely available for the species of high conservation value (Fernandez *et al*. 2003). For conservation in landscapes like the Terai Arc which are rapidly changing due to human pressure it is vital to provide significant results speedily. The methods presented here meet this goal and can be easily applied for the development of landscape-level conservation strategies in other rapidly changing landscapes.

3.5 Summary

- Understanding factors affecting distribution and habitat suitability of species is critical for conservation, especially for endangered carnivore species but also for its main prey species. I present a spatial habitat modelling approach to assess habitat requirements of four coexisting herbivores (sambar *Cervus unicolor*, chital *Axis axis*, nilgai *Boselaphus tragocamelus*, and wild pig *Sus scrofa*), which are important prey species of tiger (*Panthera tigris*), in order to quantify habitat suitability and its main environmental determinants, to examine how habitat requirements of 4 species differed, and to identify the areas of high conservation value and to highlight critical areas where conservation measures are needed.

- Data on presence/absence of four ungulates were collected in two phases during the period between 2002 and 2006. Remote sensing and topographic data were used to develop spatial layers of land use, vegetation characteristics and topography. I integrated the presence and absence information with landscape characteristics and indices of human disturbance using Generalized Linear Models at different neighbourhood scales.

- The resulted models agreed well with previous knowledge on species' habitat selection and yielded model accuracy greater than 73%, except for wild pig. The final models indicated that different factors determined habitat suitability for four study species and quantifying habitat suitability over entire TAL showed that they segregate considerably in space. The combination of two species dominated two national parks and surrounding areas in the hilly, medium elevated areas. The major part of low land terai habitats was occupied by a combination of three species. More quantitatively, about 38% (*c*.16200sq.km) of the study area was suitable for at least one of four prey species, but in 58% (*c*.9400sq.km) of this area only one species would occur, in 29% (*c*.4700sq.km) two species and in 13% (*c*.2100sq.km) three species. Overall, 63% of the TAL was classified as unsuitable and only 16% (*c*.6800sq.km) of the landscape was suitable for more than one species. Therefore, there is a need to undertake habitat restoration and minimizing the level of disturbance to maintain TAL as a functional unit for tiger conservation.

- Habitat suitability maps point to specific areas where habitat conservation actions, including reduction of human disturbances, are needed. Additionally, conservation actions are needed in forests surrounding protected areas (national parks and tiger reserves) that would strengthen the connectivity between the high quality habitats as evident from the resulting habitat maps. The approach presented here can be applied to rapidly changing landscapes where information must be compiled speedily for developing landscape-level conservation strategies.

CHAPTER 4

ASSESSING HABITAT SUITABILITY FOR TIGER

4.1 Introduction

Fragmentation and loss of natural habitats are recognized as major threats to the viability of endangered species and has become an important subject of research in ecology (Forman 1996; Hanski 2005). This is especially true for large carnivore species which are highly vulnerable to extinction in human-altered habitats because of their large area requirements and strong dependence on prey species (Noss *et al*. 1996; Crooks 2002; Karanth *et al*. 2004). A prerequisite for conservation efforts and management is to identify the factors which affect the distribution and abundance of the species of interest (Scott and Csuti 1997). However, the required monitoring for addressing these issues is especially difficult for large carnivores of high conservation concern due to their large spatial requirements (Gese 2001). Therefore, specific methods are required to make the most put of the limited existing data.

The tiger (*Panthera tigris*), a top predator with large home ranges, which requires abundant large wild ungulate prey and undisturbed habitats is especially prone to human caused habitat alteration. As a consequence, it resides today in only a small fraction of its historical range (Dinerstein *et al*. 2007). For example, the Terai Arc Landscape (TAL) contains the Global and Regional Tiger Conservation Landscape Priorities (Sanderson *et al*. 2006), but this landscape has become highly fragmented and degraded after the conquest of malaria induced a substantial increase in human population. Although a network of protected areas (PAs) was established, it did not stop degradation of tiger habitat outside the protected areas (Smith *et al.* 1998). Facing this situation, an assessment of the potential habitat patches and the quality of corridors which may link these patches is required (Smith *et al.* 1998; Wikramanayake *et al*. 2004; Carroll and Miquelle 2006; Linkie *et al*. 2006; Sanderson *et al*. 2006; Dinerstein *et al*. 2007).

One powerful approach for assessment and mapping of suitable habitat is statistical habitat modelling e.g., using ecological niche factor analysis (ENFA; Hirzel *et al*. 2002) or generalized linear models (GLM; Boyce and McDonald 1999; Guisan *et al.* 2002). The basic idea of most habitat models is to predict the probability of occupancy from a set of landscape-scale explanatory variables and 'presence-only' or presence/absence data (Manly *et al.* 1993; Hirzel *et al*. 2002). 'Presence-only' modelling techniques (e.g. ENFA) have the advantage that they do not require absence data, which is, in many cases, either unavailable or unreliable. Presence-only techniques combined with GLM are powerful tools for habitat-modelling of rare and endangered species (Hirzel *et al*. 2002; Engler *et al.* 2004). A deeper analysis of habitat selection, however, often requires more specific analyses. First, a better understanding of habitat selection involves evaluation of different hypotheses on factors that may influence habitat suitability. This can be accomplished by adopting an information-theoretic approach to determine the relative support gained by each of these hypotheses given the data (e.g., Fernandez *et al*. 2003). Second, it is well known that different factors determine large carnivore mortality (human disturbances) and recruitment (natural habitat factors; Woodroffe and Ginsberg 1998; Naves *et al*. 2003). In this situation, the development of a two-dimensional habitat model is required where one axis describes suitability for recruitment and the second axis for survival (Naves *et al*. 2003). This allows identifying critical areas for management as "attractive sinks" (i.e., good natural suitability but high levels of human disturbance). Third, because animals perceive landscape structure at certain critical scales, assessment of habitat selection requires determination of critical spatial scales (Schadt *et al*. 2002). This can be accomplished within a hierarchic information theoretic approach by treating models of different spatial scales as different hypotheses.

In this study, I apply recent techniques of statistical habitat modelling to tiger and prey species presence data. The objectives are (1) to identify the factors which affect the distribution of tigers, (2) to map potentially suitable habitats and to assess the quality of potential corridors linking suitable habitat, and (3) to identify critical areas for conservation with the ultimate aim to assess landscape management needs for the conservation of tiger in the TAL. I use a hypothesis testing framework and contrast several *a priori* models based on the available knowledge about tiger biology to the data.

4.2 Materials and methods

4.2.1 Species data

Data on tiger presence within our study area were obtained based on indirect evidences (scat and pugmark) and identified individuals from camera-traps. All data were from Indian part of the TAL and collected during the period between November 2005 and December 2008. Surveys were carried out in river beds, dirt forest roads, seasonal streams and culverts. Length and route of the sign surveys were identified in the field with the help of existing spatial data and administrative maps of the forest department. Surveys were carried out by 2-3 well trained research fellow and field assistants by foot, except in Dudhwa national park where we collected the data on indirect evidence by travelling in a vehicle within a speed of 15-20km/hr along the forest roads, along the survey routes at a time.

All survey routes were intensively searched for the evidences of tiger presence in the early morning before they get disturbed by human activity which is quite common in habitats outside the protected areas (Johnsingh *et al*. 2004). We put maximum effort to cover all possible survey routes in any given forest patch during the survey. Additionally, transects were also laid along with sigh survey routes in order to maximize our efforts particularly in non-protected areas as a previous study in this landscape revealed a low use of reserve forests by tigers outside the protected areas (Johnsingh *et al*. 2004). Length of these transects ranged between 0.5 and 3.25km depending on the accessibility of the area because of rugged terrain in the study area. GPS reading was noted whenever the evidence was encountered during the survey. We also included the locations of six identified individual tigers in the data set based on a camera-trap study in Rajaji NP (see Harihar *et al*. 2009). Additionally, we included indirect evidences of tiger presence observed on transects laid for prey species pellet groups (see description below). Out of

185 locations that were collected from Corbett tiger reserve, 138 locations were opportunistic locations based on indirect evidences (scat and pugmark) and direct sightings of tiger (*personal communication* with Dr. Hemsingh Gehlot). These 138 presences were from Corbett NP. Although tiger observations in this particular case were based on opportunistic evidence, the observations remaining after stratification (to avoid autocorrelation, see below) covered the entire Corbett NP. Ninety-seven percent of the 4.5km × 4.5km grid cells used for stratification that represented Corbett NP contained tiger presence (Fig. 4.1).

Presence data on prey species were taken from 443 10m radius circular plots laid for collection of ungulates' fecal pellet groups. These plots were located at every 250m along 2km transects, which were randomly laid with minimum distance of 2km between two transects, covering hilly and low land terai habitats (Table 4.1, Fig. 4.1). I included the prey species which had a broad distribution across the entire study area (e.g. Johnsingh *et al.* 2004) (i.e., sambar and chital, 50 and 64, respectively).

4.2.2 Stratifying species data

To reduce potential autocorrelation among nearby tiger presence locations (i.e., pseudo replicates), I superposed the data with a grid with a cell size of 4.5km × 4.5km. This cell size was selected to match the average home range size of female resident tigers in Royal Chitwan NP in the Nepal part of TAL (Smith 1993). If more than one observation was located within one grid cell, I randomly selected one observation. This procedure eliminated 257 data points, resulting in 98 valid occurrences (Fig. 4.1). To avoid autocorrelation in the observation data of the prey species, I stratified these locations within a grid with a cell size of 2km × 2km, corresponding roughly to the prey species' home range size (Moe and Wegge 1994; Sankar 1994). This data reduction resulted in 64 and 50 occurrences for chital and sambar, respectively across the landscape in the Indian side.

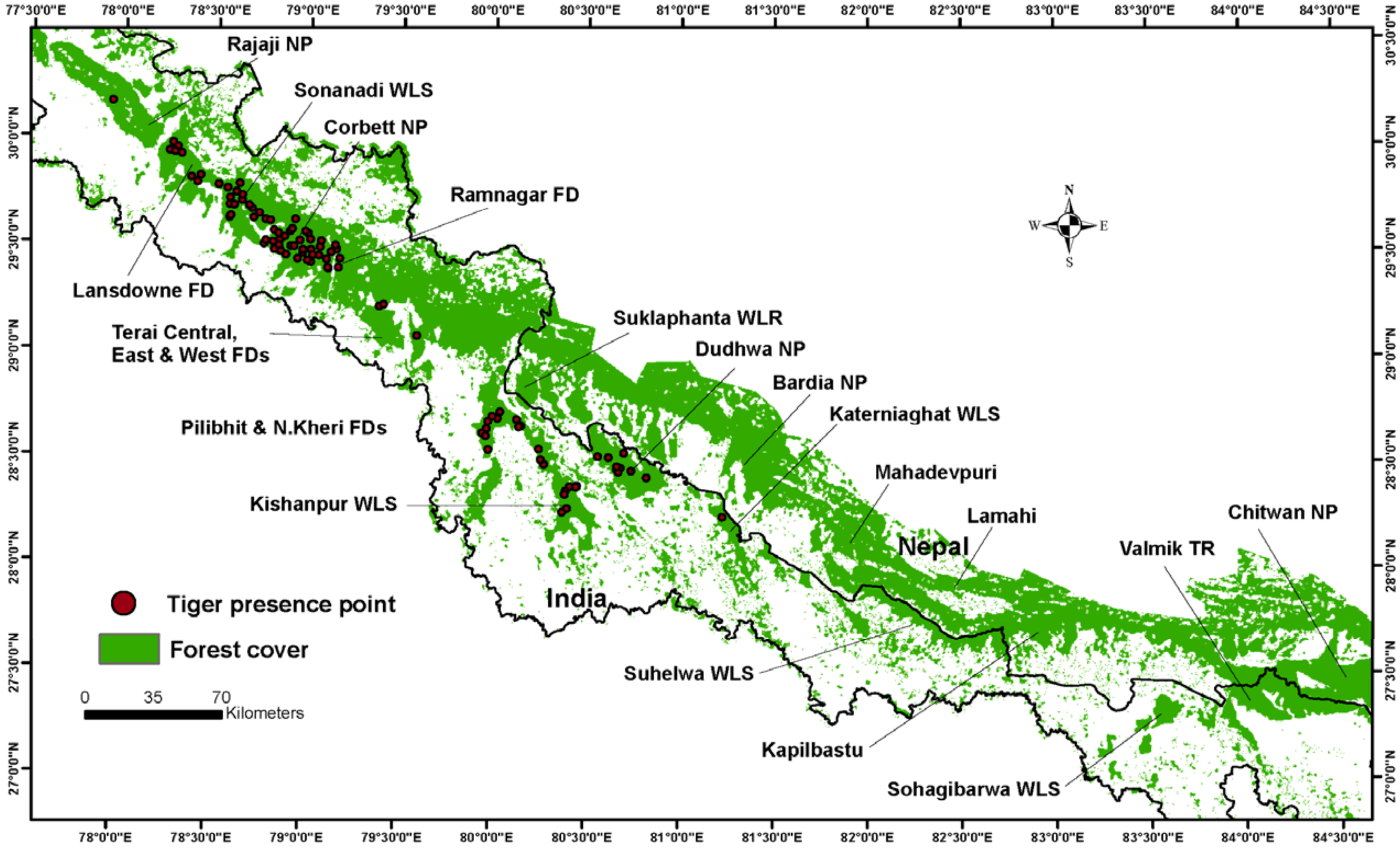


Figure 4.1 The Terai Arc Landscape in India and Nepal with the Indian TAL border (black boundary line), the locations of tiger presence points (red dots), reserve forests (FD, forest division) and protected areas (TR, tiger reserve; NP, national park; WLS, wildlife sanctuary; WLR, wildlife reserve). Forest cover includes all natural forests.

Table 4.1 Efforts and tiger presence occurrences used for the habitat suitability analysis in the TAL.

Surveyed area	Transects[a]		Transects		Sign surveys		Approx. total distance (km)	No. of tiger locations
	Total no.	Distance (km)	Total no.	Distance (km)	Total no.	Approx. distance (km)		
Reserved forest								
Lansdowne FD	35	70	-	-	22	70	140	43
Ramnagar FD	5	10	15	30	6	22	62	17
Terai Central FD	6	12	25	40	10	28	80	2
Terai East FD	11	22	29	45	14	50	117	1
Pilibhit FD	-	-	7	12	6	26	38	45
North Kheri FD	-	-	5	8	2	14	22	0
Protected area								
Rajaji NP[b]	-	-	-	-	-	-	-	6
Corbett TR[c]	13	18	-	-	9	25	43	185
Kishenpur WLS	-	-	-	-	4	22	22	14
Dudhwa NP[d]	-	-	-	-	5	30	30	38
Katerniaghat WLS	-	-	7	12	7	20	32	4
Total	**70**	132	**88**	147	**85**	307	**586**	**355**

[a] Transects used for estimation of ungulates' pellet groups and vegetation parameters (see section "*Species Data*" above).

[b] Data obtained from camera-trap study (Harihar *et al*. 2009).

[c] 138 locations collected from Corbett national park (see section "*Species Data*" above).

[d] Data collected by vehicle survey (see section "*Species Data*" above).

4.2.3 Environmental variables

4.2.3.1 Land cover variables

For mapping forest cover and landscape pattern, I first performed an unsupervised classification in Erdas Imagine 9.x of the two scenes of Landsat GeoCover ETM+ 2000 Edition Mosaics (456 m resolution) (MDA Federal 2004). I ran 15 iterations of 50 classes and grouped them into nine habitat categories: (1) dense forest, (2) open and disturbed forest, (3) degraded forest and plantation, (4) tall grass, (5) short grass or open area with sparse vegetation, (6) scrub land, (7) barren or open area, (8) water bodies and (9) human habitation and agriculture based on the information from the vegetation sampling plots, information on villages and roads, and experience in the field in the Indian side of TAL (Table 4.2). I used the best available digital vector layers of roads and villages with the scale of 1:1,000,000 (uncertainty is about 2km) downloaded from the Digital Chart of the World Data Server (http://www.maproom.psu.edu/dcw/).

4.2.3.2 Topographic and human disturbance variables

Elevation data (85m resolution) was downloaded from Seamless Data Distribution System (SDDS), U.S. Geological Survey (http://seamless.usgs.gov) and converted into 456m resolution of the land cover data by re-sampling using nearest neighbour method in Arc/View 3.x. The variables of slope degree, surface area and surface ratio were calculated from it using the extension Surface Areas and Ratios from Elevation Grid v.1.2 (http://www.jennessent.com). Because human impact in the TAL usually results in a diversification of land cover types, I calculated the Shannon diversity index to describe land use diversity and used it together with the variables agriculture and human habitation and absence of PA as indicators for human disturbances (Table 4.2).

4.2.3.3 Neighbourhood variables

The environmental variables (with 456m resolution), however, are not necessarily related to the critical spatial scales at which tiger perceive the landscape. I therefore followed the approaches taken in Schadt *et al*. (2002), Naves *et al*. (2003), and Wiegand *et al.* (2008) and transformed the data into a set of derivative neighbourhood variables. A neighbourhood variable was the mean of the original variable within a circle with specified radius around the target cell. For GLM analyses, I calculated neighbourhood variables for six different radii (*d* = 1, 3, 5, 7, and 9 grid cell) representing an area of 1.8km², 7.6km², 20.2km², 36.8km², and 60.9km², respectively using the module 'CircAn' of software Biomapper (Hirzel *et al.* 2005). For ENFA, I calculated neighbourhood variables using 2 and 5 grid cell radius circular windows for prey species and tiger, respectively, corresponding roughly to the home range sizes.

Table 4.2 List of predictor variables (excluding neighbourhood variables) used for the spatial models. The resolution of the data is 456 m × 456 m.

Abbreviation	**Variable**	**Definition**
A) Land cover variables†.		
V1*	dense forest	Frequency of occurrence of the focal feature within the neighbourhood scale
V2*	open and disturbed forest	
V3*	degraded forest and plantation	
V4*	tall grass	
V5*	short grass	
V6*	scrub land	
V7*	barren land	
V8*	water body	
V9*	agricultural and human habitation	
B) Topographic variables‡		
MEE*	mean elevation	Mean elevation
SD*	slope degree [°]	Slope in degrees calculated from MEE
SA*	surface area [m]	Surface area calculated from MEE§
SR*	surface ratio	Surface ratio§
C) Human disturbance variables		
Di*	Shannon landscape heterogeneity index	Measure of relative land use diversity; equals 0 when there is only one land use and increases as the number of land use types increases
PAREA	presence of Protected Area	Binary variable (1-presence, 0-absence)
D) Prey species variables		
PC*	chital habitat model	Probability of occurrence based on ENFA
PS*	sambar habitat model	Probability of occurrence based on ENFA

†Classification of 456m × 456m Landsat satellite data.

‡ Mean elevation (MEE) on a 456m × 456m resolution was calculated from the original data with 85m × 85m resolution.

*variables for which the neighbourhood scales were calculated (5 scales; 1,3,5,7 and 9 grid cells).

§I used the method of Jenness (2004).

In total, 14 variables for chital and sambar and 17 variables were derived for tiger for ENFA normalized through Box-Cox algorithm (Sokal and Rohlf 1995). All ENFA analyses were performed using Biomapper.

4.2.4 Statistical analyses

4.2.4.1 ENFA habitat suitability maps

The principles and procedure of ENFA, which is based on the niche concept by Hutchinson (1957), have been described in detail in Hirzel *et al*. (2002 and 2004). ENFA needs a set of presence data (no absences are required) and a set of environmental variables and computes suitability functions by comparing the species distribution in the variable space with that of the whole set of cells. The overall information is summarized under two types of components. The first component, the "marginality" factor, describes the degree to which the species' mean within the variable space differs from the global mean. A value close to 1 indicates that the species' requirements differ considerably from the average habitat conditions in the study area. The second and subsequent components are called "specialization" factors and describe the species' variance relative to the global variance. A high specialization indicates that a species has a restricted ecological tolerance compared with the overall range of conditions that prevail in the study area. The computation of a habitat suitability (HS) index from the marginality and specialization factors is a rather complex procedure. I used the median algorithm for this purpose.

HS maps were derived using ENFA for prey species (i.e., sambar and chital) and included them as predictor variables in ENFA and GLM of tiger. 10-fold cross-validation was used based on partitioning of the original data (Fielding and Bell 1997; Boyce *et al*. 2002) to evaluate the accuracy of the ENFA habitat suitability models. To this end, I divided the presence data set evenly, but randomly, into 10 partitions. Each partition was used in turn to evaluate the predictions computed by a model derived from the data of the other nine partitions. This process provided 10 values for each evaluation measure, summarized by their mean and standard deviation. I used three standard presence-only evaluation measures; the Absolute Validation Index (AVI), the Contrast Validation Index (CVI), and the Boyce index for validation. The AVI and the CVI use an arbitrary threshold to distinguish between areas predicted to be suitable and unsuitable (habitat suitability = 50) to determine how good the model discriminates presence and absence. The AVI is the proportion of the observation data of the evaluation partition that have a habitat suitability value greater than 50. This index varies between 0 and 1. The CVI quantifies how much the AVI differs from what would have been obtained with a random model. i.e., $\text{CVI} = \text{AVI} - \text{AVI}_{\text{random}}$. CVI ranges between 0 and AVI.

The Boyce index provides a more continuous assessment of model predictive power. For each partition an ENFA model was calculated from the remaining 9 partition. The study area was then classified according to this model and binned into the four categories unsuitable, marginal, suitable and optimal habitat. For each observation reserved for validation, the habitat suitability index was calculated and the frequency of observations within a given class, adjusted for area, were determined and plotted with increasing ENFA score. For a good model one would expect that more observations are made in classes with increasing ENFA score, thus the area-adjusted frequencies should be highly correlated with the ENFA scores if the ENFA model would indeed predict the relative probability of occurrence of the organisms on the landscape. I used Spearman-rank correlation, which ranges between -1 and 1 as evaluation measure.

4.2.4.2 GLM and generation of pseudo-absences

GLM are an extension of classic linear regression models (McCullagh and Nelder 1989). To account for the data structure, I used logistic regression. All GLM were fitted within the R software (R 2.8.1; A language and environment for statistical computing ©2008).

To use GLM with ‘presence-only’ data, I followed an approach by Engler *et al.* (2004) that first involves generation of ENFA model, which is then used as weight for the selection of random pseudo-absences. To generate pseudo-absence data, I used the same grid with a cell size of 4.5km × 4.5km as used for stratification of presence data, allowing only for one data point per cell. The random pseudo-absences were chosen only in areas where predictions by the ENFA model for tiger were lower than 1 and if they were located in forest areas. Additionally, I demanded that they were located within 15 km from suitable habitats because generating pseudo-absences from environmental regions further away from the optimum established by presence data may increase over-prediction of the model (Chefaoui and Lobo 2008). The threshold 1 was chosen because it was the lowest ENFA prediction associated with observed presences (Engler *et al*. 2004). The number of generated pseudo-absences was similar to the number of real presences.

4.2.4.3 Model selection

Analyses were based on information-theoretic methods where ecological inference with statistical models is approached by weighting the evidence for multiple working hypotheses simultaneously (Johnson and Omland 2004). Following this approach, I derived a set of alternative, *a priori* hypotheses on tiger habitat selection in a first step. In a second step, I tested the relative support gained by each of these models, given the data, by fitting the models to species distribution data and examining penalized maximum-likelihood estimates (e.g., Fernandez *et al*. 2003).

Similarly to Fernandez *et al*. (2003) I considered several working hypotheses (Table 4.3) on tiger habitat selection derived from previous knowledge of basic aspects of tiger ecology. To this end, I grouped the variables in a way that each group represents a different hypothesis. If possible, I also defined a “minimal” model for each hypothesis that contained only those variables expected to be the most important ones. Second, I further specified my hypotheses by applying them separately for the different neighbourhood scales (all variables of a given neighbourhood scale and hypothesis are called “block”). Finally, I performed a variable reduction procedure within each block to remove variables that were highly correlated or variables that did not show significant differences between tiger presence and absence. For variable reduction within a given block I tested for statistical differences in the value of the variables between presence and absence locations using the Kruskal-Wallis test (Sokal and Rohlf 1995). Variables which did not show significant differences were removed. Next, I calculated a correlation matrix among all remaining predictor variables using Spearman rank coefficients (Sokal and Rohlf 1995) and from highly correlated predictors ($r > 0.7$) the ones with the weaker univariate difference were not included in the model. Because each data point was at least 4.5km apart spatial autocorrelation was not an issue here. I also assembled a “global model” that included all variables for a given neighbourhood scale that remained after variable reduction from combining the protective habitat, the prey species, and the human disturbance hypotheses.

In total, 8 models (one protective habitat, three prey species, two prey and protective cover, one human disturbance and one global) were confronted with 5 neighbourhood scales, yielding a total of 40 *a priori* models to the data. I fitted the candidate models to the tiger presence and ENFA-weighted pseudo-absence data. To evaluate the performance of the final models for each hypothesis I used a cross-validation. The most parsimonious model (i.e., having the lowest AIC value), was selected by comparing through the hierarchical ordering of the sets of fitted candidate models based on the scores of Akaike’s Information Criterion (AIC). To evaluate the performance of the final models for each hypothesis I used a cross-validation procedure (Fernandéz *et al*. 2003). The original data set was divided into 10 parts, called folds. Nine of the folds were combined and used for fitting the model and the remaining fold was used for testing the model. This was then repeated for a total of 10 times. In each iteration, an estimate of prediction accuracy (ranged between 0 and 1) was calculated and the results were averaged over the 10 runs. Statistics were performed with R software; function “cv.binary”, package “DAAG”).

Table 4.3 Hypotheses, based on available knowledge of tiger biology, used to contrast several *a priori* models with the data.

Hypothesis name	**Description**	**Reference**
"protective habitat hypothesis"	tiger need dense forest cover to rest, breed and for hunting. I used the land cover variables and the topographic variables (Table 4.2) to construct these blocks.	supported by data from 26 radio-collared tigers in the Nepal part of the TAL landscape (Smith 1993; Smith *et al.*1998).
"prey species hypothesis"	tiger presence is largely mediated by the presence of its ungulate prey. I used the ENFA habitat maps for the three main prey species chital and sambar as variables for this hypothesis.	(Karanth *et al*. 2004)
"disturbance hypothesis"	human proximity, infrastructure, habitat alteration for agricultural purpose, and extensive forestry are detrimental for tigers because they produce higher mortality, cause disturbances, and degrade the original biologically rich habitats of the TAL.	(Mountfort 1981; Thapar 1992; Jackson and Kempf 1994; Johnsingh *et al*. 2004)
natural habitat hypothesis	includes variables that describe natural habitat suitability and combines the "protective habitat" and "prey species" hypotheses.	

4.2.4.4 Assessing source, sink, attractive sink, and refuge habitats

To develop a two-dimensional habitat model (Naves *et al*. 2003) I used the best model of the “natural habitat hypothesis” as first axis and the best model of the “disturbance hypothesis” as second axis. This scheme allows classifying the area into attractive sink, refuge, avoided matrix, and sink using appropriate cut-off values for each axis. Because the resulting categories were not based on actual demographic data (i.e., mortalities and reproduction), but indirectly assessed via “human” and “natural” variables, I called the resulting categories “attractive sink-like” or “avoided matrix-like”.

4.3 Results

4.3.1 ENFA

The high global marginality values of 1.239 and 1.351 for chital and sambar, respectively, indicate that these species used a narrow range of habitat conditions compared to those available. They preferred non-degraded forests and tall grass but avoided agricultural and human habitations (Table 4.4). The high tolerance index of 0.245 for chital, compared to the value of 0.213 for sambar, indicates that chital is more tolerant towards deviations from its optimal habitat than sambar. This is because the later showed additionally preference for high elevated areas in relatively undisturbed habitats (Table 4.4).

Applying MacArthurs’s broken-stick rule (Hirzel *et al*. 2002), two factors explaining 92.1% of the information for chital and four factors explaining 97.2% of the information for sambar were used for calculating the HS index. The HS maps indicated that sambar preferred high elevated hilly areas and avoided the low land *terai* habitats whereas chital preferred low land *terai* habitats and low elevated areas (Fig. 4.2).

Table 4.4 Results of ENFA habitat models. Correlations between the ENFA factors and the environmental variables for chital, sambar and tiger. Factor 1 explains 100% of the marginality. The percentages indicate the amount of specialization accounted for by the factor.

A) Chital*

	Factor 1^1 (22%)	Factor 2^2 (62%)
Dense forest frequency	+ + + +	0
Open and disturbed forest frequency	+ + +	0
Degraded forest and plantation frequency	− −	0
Tall grass frequency	+ + + +	0
Short grass frequency	−	0
Scrub land frequency	− −	0
Barren land frequency	− − −	0
Agricultural and human habitation frequency	− − − − − −	0
Elevation mean	+	0
Slope mean	+ +	0
Surface area mean	−	* * * * * * *
Surface ratio mean	−	* * * * * * *
Shannon landscape diversity index	− −	0

B) Sambar*

	Factor 1^1 (65%)	Factor 2^2 (17%)	Factor 3^2 (7%)	Factor 4^2 (5%)
Dense forest frequency	+ + + +	0	0	0
Open and disturbed forest frequency	+ + + + +	0	0	0
Degraded forest and plantation frequency	−	0	0	0
Tall grass frequency	+ + +	0	0	0
Short grass frequency	−	0	0	0
Scrub land frequency	−	0	0	0
Agricultural and human habitation frequency	− − − − −	0	*	0
Elevation mean	+ + +	0	* * *	*
Slope mean	+ + + +	0	* * *	0
Surface area mean	+ +	* * * * * * *	* * * * * *	* * * * * * *
Surface ratio mean	+ +	* * * * * * *	* * * * * * *	* * * * * * *
Shannon landscape diversity index	0	0	*	0

C) Tiger§

	Factor 1^1 (72%)	Factor 2^2 (17%)	Factor 3^2 (4%)
ENFA suitability map for chital	+ + + +	0	* *
ENFA suitability map for sambar	+ + +	0	0
ENFA suitability map for barking deer	+ + +	0	* * *
Dense forest frequency	+ + +	0	0
Open and disturbed forest frequency	+ +	0	0
Degraded forest and plantation frequency	− −	0	0
Tall grass frequency	+ +	0	*
Short grass frequency	− −	0	0

Table 4.4, continued.

	Factor 1[1] (72%)	Factor 2[2] (17%)	Factor 3[2] (4%)
Scrub land frequency	−	0	0
Barren land frequency	− −	0	0
Agricultural and human habitation frequency	− − − −	0	*
Elevation mean	+	0	* * *
Slope mean	+ +	0	* * * * *
Surface area mean	0	* * * * * * *	* * * * * *
Surface ratio mean	0	* * * * * * *	* * * * *
Shannon landscape diversity index	− −	0	*

[1] Marginality factor. The symbols + and - mean that the species was found in locations with higher and lower values than the average cell, respectively. The greater the number of symbols, the higher the correlation; 0 indicates a very weak correlation.

[2] Specialization factor. Any number > 0 means the species was found occupying a narrower range of values than available. The greater the number of symbols, the narrower the range; 0 indicates a very low specialization.

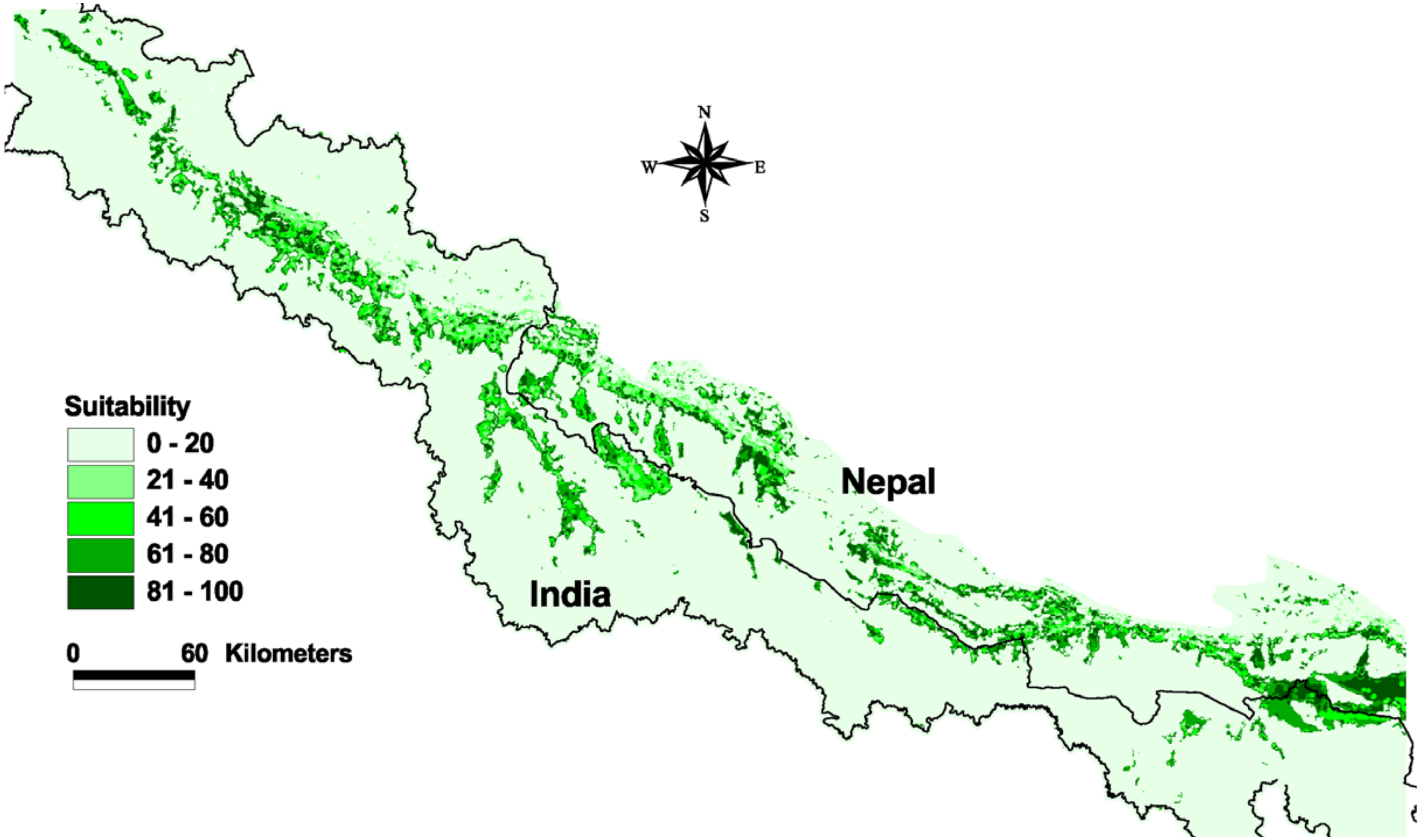
*Variables calculated for 4km^2 neighbourhood area scale.

[§] Variables calculted for 20km^2 neighbourhood area scale.

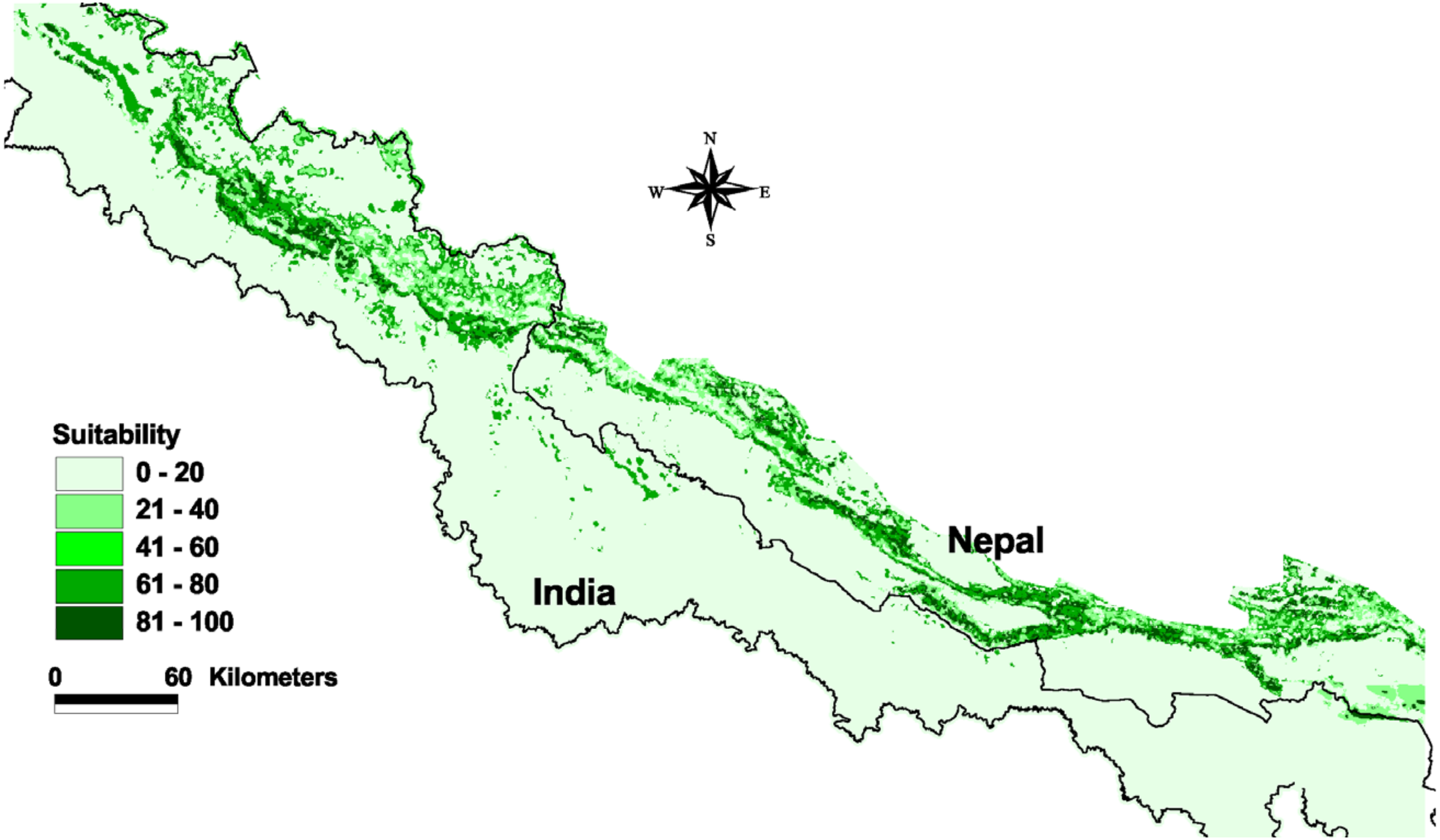
A high marginality value of 1.864 and low tolerance of 0.178 for tiger indicated that this species used very particular habitats compared to habitats available in the reference area and showed low tolerance towards deviations from its optimal habitat (Table 4.4). Tiger preferred habitats with high suitability for their main prey species with dense forests and avoided areas with agricultural use and human habitation (Table 4.4). Based on three factors totalling 96.2% of overall information, the HS map (Fig. 4.3) indicated that favourable tiger habitats are distributed in the low land terai habitats and low elevated hilly terrains.

Three indices; AVI, CVI and Boyce Index, were used to evaluate the HS models (Table 4.5). For all three models, more than 50% of the observations were located in areas with an ENFA HS index > 50 (i.e., AVI > 0.5) indicating a high consistency with the evaluation data sets. Mean CVI values of 0.464 and 0.507 for the two prey species and tiger, respectively, indicated that the ENFA suitability maps differed substantially from a purely random model, thus indicating appropriate maps.

Figure 4.2 Habitat suitability maps, as computed from ENFA, for chital and sambar showing the spatial distribution of predicted suitable habitats in the TAL.


N
W
E
S
Suitability
0 - 20
21 - 40
41 - 60
61 - 80
81 - 100
0
60
Kilometers
India
Nepal

Chital


N
W
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Suitability
0 - 20
21 - 40
41 - 60
61 - 80
81 - 100
0
60 Kilometers
India
Nepal

Sambar

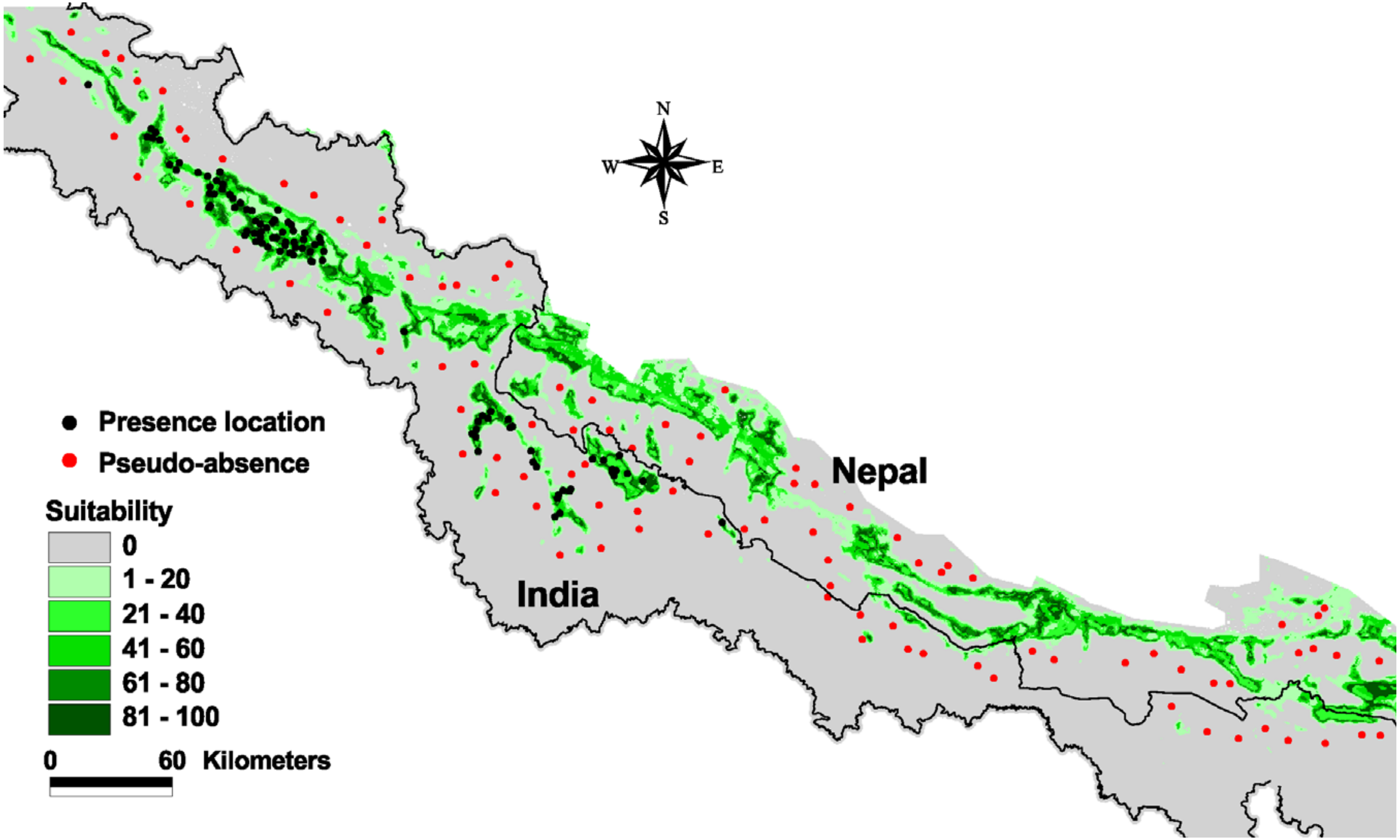


Figure 4.3 Habitat suitability map, as computed from ENFA, for tiger showing the locations of tiger presence and ENFA-weighted random pseudo-absences. Pseudo-absence locations were randomly selected with minimum distance of 4.5km between points using the areas classified <1 suitable by ENFA.

Table 4.5 Model evaluation indices for the habitat suitability maps of chital, sambar and tiger, computed with 10-fold cross-validation. High mean values indicate a high consistency with the evaluation data sets. The lower the standard deviation, the more robust the prediction of habitat quality.

Species	Absolute validation Index (AVI)[1]	Contrast validation index (CVI)[2]	Boyce index[3]
Chital			
Mean	0.521 ± 0.197	0.401 ± 0.180	0.933 ± 0.107
Sambar			
Mean	0.618 ± 0.358	0.507 ± 0.348	0.911 ± 0.115
Tiger			
Mean	0.595 ± 0.186	0.507 ± 0.183	0.956 ± 0.094

[1]AVI varies from 0 to 1. [2]CVI varies from 0 to AVI. [3]Boyce's index varies from -1 to 1.

The Boyce indices for tiger, sambar and chital (0.956 ± 0.094, 0.911 ± 0.115 and 0.933 ± 0.107, respectively) were high indicating that the species were relatively more often observed in areas classified with higher habitat suitability, thus attesting good predictive power. However, the large standard deviation for sambar was a symptom of low robustness

4.3.2 GLM

4.3.2.1 Predictive models

All eleven hypotheses yielded models with excellent classification accuracy with >90% of all cases correctly classified (Table 4.7 and see Table 4.6 for the list of all models). I also found clear scale effects; in general, models comprising variables measured at neighbourhood scales ≥20km^2 performed better (Fig. 4.4).

The most parsimonious model (thereafter called final model) was selected from the "prey species" hypothesis (Table 4.7) based on the lowest Akaike information criterion (AIC) and comprised the two variables ENFA habitat suitability (HS) index for chital and sambar at an approximate 37km^2 neighbourhood (Table 4.8). This neighbourhood is slightly bigger than the home ranges of female tigers in Chitwan NP. As expected, both variables entered the model with positive sign (Table 4.8).

Table 4.6 Summary of logistic predictive models for tiger distribution, and model selection estimators; -2log(*L*) = -2 log-likelihood estimates; AIC = Akaike's Information Criterion.

Model*	**-2log(L)**	**AIC**	**Model Ranking**
Protective habitat			
0. Intercept only (Null model)	296.7	298.7	6
1. V1F1, V3F1, V4F1, V6F1, V7F1, MEE1, MEE1^2, PAREA	29.7	47.7	5
2. V1F3, V3F3, V4F3, V6F3, V7F3, MEE3, MEE3^2, PAREA	9.8	27.8	2
3. V1F5, V3F5, V4F5, V6F5, V7F5, MEE5, MEE5^2, PAREA	16.1	34.1	4
4. V1F7, V3F7, V4F7, V6F7, V7F7, MEE7, MEE7^2, PAREA	12.8	30.8	3
5. V1F9, V3F9, V4F9, V6F9, V7F9, MEE9, MEE9^2, PAREA	8.7	26.7	1
Prey species – Model type I			
0. Intercept only (Null model)	296.7	298.7	6
1. PS1	183.4	187.4	5
2. PS3	172.8	176.8	4
3. PS5	170.0	174.0	3
4. PS7	166.0	170.0	1
5. PS9	167.1	171.1	2
Prey species – Model type II			
0. Intercept only (Null model)	296.7	298.7	6
1. PC1	30.8	34.8	5
2. PC3	22.0	26.0	4
3. PC5	9.5	13.5	2
4. PC7	9.1	13.1	1
5. PC9	11.6	15.6	3
Prey species – Model type III			
0. Intercept only (Null model)	296.7	298.7	6
1. PC1, PS1	21.1	27.1	5
2. PC3, PS3	14.8	20.8	4
3. PC5, PS5	6.2	12.2	2
4. PC7, PS7	**4.5**	**10.5**	**1**
5. PC9, PS9	7.4	13.4	3
Prey and Protective habitat – Model type I			
0. Intercept only (Null model)	296.7	298.7	6
1. PS1, V1F1, V3F1, V4F1, V6F1, V7F1, MEE1, MEE1^2, PAREA	15.8	35.8	4
2. PS3, V1F3, V3F3, V4F3, V6F3, V7F3, MEE3, MEE3^2, PAREA	22.2	42.2	5
3. PS5, V1F5, V3F5, V4F5, V6F5, V7F5, MEE5, MEE5^2, PAREA	13.7	33.7	3
4. PS7, V1F7, V3F7, V4F7, V6F7, V7F7, MEE7, MEE7^2, PAREA	10.0	30.0	1
5. PS9, V1F9, V3F9, V4F9, V6F9, V7F9, MEE9, MEE9^2, PAREA	13.0	33.0	2
Prey and Protective habitat – Model type II			
0. Intercept only (Null model)	296.7	298.7	6
1. PS1, V1F1	81.5	87.5	5
2. PS3, V1F3	59.6	65.6	4
3. PS5, V1F5	47.5	53.5	3
4. PS7, V1F7	41.8	47.8	1
5. PS9, V1F9	44.0	50.0	2

Table 4.6, continued.

Model*	**-2log(L)**	**AIC**	**Model Ranking**
Human disturbance			
0. Intercept only (Null model)	296.7	298.7	6
1. V9F1, Di1, PAREA	50.5	58.5	5
2. V9F3, Di3, PAREA	45.2	53.2	4
3. V9F5, Di5, PAREA	32.1	40.1	3
4. V9F7, Di7, PAREA	**27.6**	**35.6**	**1**
5. V9F9, Di9, PAREA	27.6	35.6	2
Global model			
0. Intercept only (Null model)	296.7	298.7	6
1. PS1, V1F1, V3F1, V4F1, V6F1, V7F1, MEE1, MEE1², PAREA, Di1	17.1	39.1	5
2. PS3, V1F3, V3F3, V4F3, V6F3, V7F3, MEE3, MEE3², PAREA, Di3	16.7	38.7	4
3. PS5, V1F5, V3F5, V4F5, V6F5, V7F5, MEE5, MEE5², PAREA, Di5	10.3	32.3	1
4. PS7, V1F7, V3F7, V4F7, V6F7, V7F7, MEE7, MEE7², PAREA, Di7	11.1	33.1	2
5. PS9, V1F9, V3F9, V4F9, V6F9, V7F9, MEE9, MEE9², PAREA, Di9	11.6	33.6	3

* See Table 4.2 for variable defenition

Table 4.7 Summary of selected logistic predictive models for tiger distribution, and model selection estimators; -2log(*L*) = -2 log-likelihood estimates; AIC = Akaike's Information Criterion. CV = cross validation. For models see Table 4.6 and for variable definitions see Table 4.2.

Model	**-2log(L)**	**AIC**	**Model Ranking**	**Predicted (%)**	**CV (%)**
Null model					
0. Intercept only	296.7	298.7	9		
Protective habitat					
1. V1F9, V3F9, V4F9, V6F9, V7F9, MEE9, MEE9², PAREA	8.7	26.7	3	99.0	96.4
Prey species					
2. PS7	166.0	170.0	8	79.6	79.1
3. PC7	9.1	13.1	2	99.0	99.0
4. PC7, PS7	4.5	10.5	1	99.0	98.5
Prey and Protective habitat					
5. PS7, V1F7, V3F7, V4F7, V6F7, V7F7, MEE7, MEE7², PAREA	10.0	30.0	4	99.0	97.4
6. PS7, V1F7	41.8	47.8	7	95.4	94.9
Human disturbance					
7. V9F7, Di7, PAREA	27.6	35.6	6	96.9	95.4
Global model					
8. PS5, V1F5, V3F5, V4F5, V6F5, V7F5, MEE5, MEE5², PAREA, Di5	10.3	32.3	5	99.0	99.5

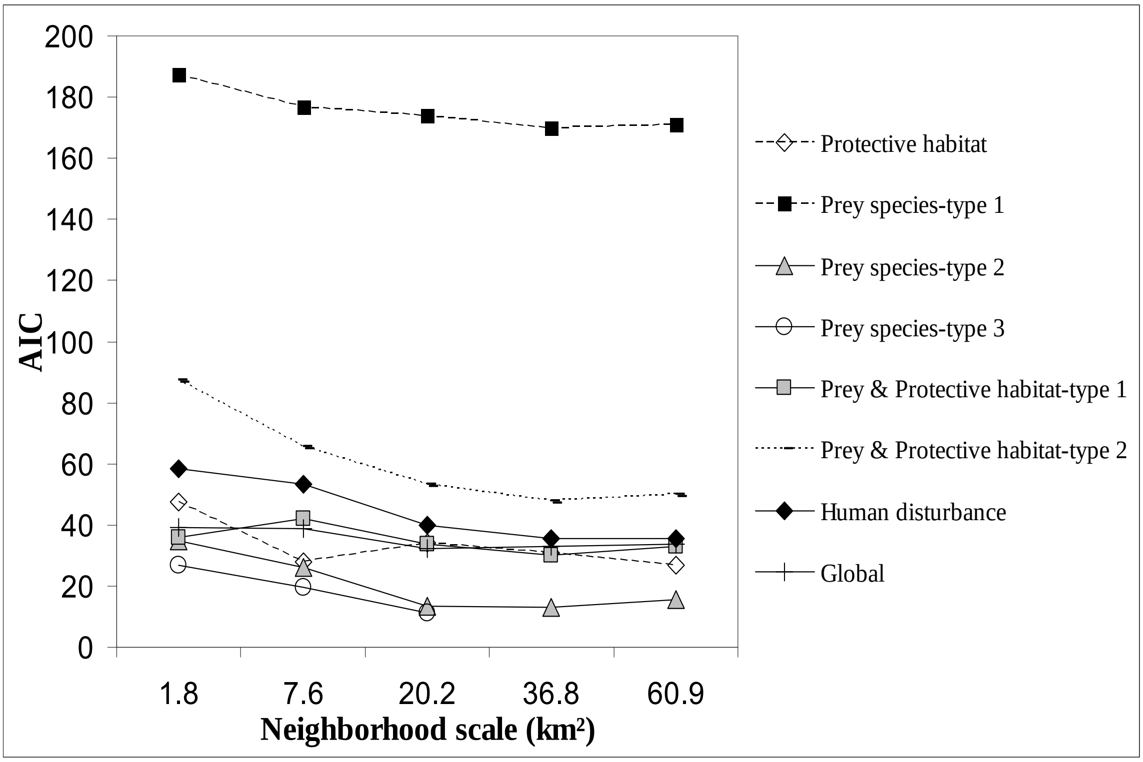


Figure 4.4 Comparison of the AIC value of the different candidate models shown as function of neighbourhood scale. The full models (i.e., protective habitat, prey & protective habitat 1, human disturbance, and global model) comprise all variables of a block (i.e., corresponding to one of my hypotheses and one neighbourhood scale) which passed the variable reduction procedure. The minimal models (i.e., prey species 1, 2 and 3 prey & protective habitat 2) comprises only those variables of a given block which were a priory selected as the most important variables, based on tiger biology.

For the human disturbance hypothesis I found two models (scale 36.8km² and 60.9km²) with minimal AIC value (35.6) but I selected the model with the 36.8km² scale (Tables 4.6, 4.7 and 4.8) because of the lower standard error. The selected model comprised three variables, proportion of agricultural and human habitation, the Shannon landscape diversity index, and protective area status of the habitat. The first two variables entered with negative sign and the protection status with a positive sign. The cross-validation of the best model of each hypothesis (Table 4.7) yielded estimates of prediction accuracy close to that of the model. Thus, no over fitting occurred.

Table 4.8 Summary of the final logistic models for tiger constructed with presence and pseudo absence data. SE = standard error, AIC = Akaike’s Information Criterion, CV = cross validation.

Variable	Symbol	ß	SE	*p*	AIC	Predicted	CV
Model - Final	Tn				10.5	99.0%	98.5%
chital habitat suitability based on ENFA	PC7	0.235	0.058	<0.001			
sambar habitat suitability based on ENFA	PS7	0.101	0.053	0.061			
constant	C	-7.968	2.502	0.001			
Model - Human disturbance	Th				35.6	96.9%	95.4%
agricultural and human habitation (%)	V9F7/V9F9	-0.212/-0.218	0.058/0.057	<0.001/<0.001			
Shannon landscape diversity index	Di7/Di9	-4.246/-6.513	1.572/1.967	0.006/<0.001			
presence of protected area	PAREA	3.268/3.213	1.602/1.656	0.041/0.052			
constant	C	7.875/11.689	2.044/2.990	<0.001/<0.001			
Model - Protective habitat	Tp				26.7	99.0%	96.4%
dense forest (%)	V1F9	0.279	0.100	0.005			
plantation and degraded forest (%)	V3F9	0.056	0.105	0.592			
tall grass (%)	V4F9	0.035	0.094	0.708			
scrub land (%)	V6F9	-0.963	0.454	0.033			
barren land (%)	V7F9	-1.636	0.714	0.022			
elevation (mean)	MEE9	0.003	0.006	0.607			
elevation (mean)-qudratic term	MEE9^2	-8.9e^{-}07	2.9e^{-}06	0.763			
presence of protected area	PAREA	10.680	4.118	0.009			
constant	C	-3.312	2.285	0.172			

4.3.2.2 Habitat mapping

I applied the final model to the TAL, using a cut-off of $P > 0.5$ for suitable habitat (Fig. 4.5). The suitable habitat forms a narrow belt, mostly comprising lowland terai and Shivaliks forests. A notable result of this analysis is that the predicted probability of occurrences is almost a binary function predicting either a high (> 0.9) or a low (< 0.25) probability of tiger occurrence (Fig. 4.5). In between values occurred only at the edges of highly suitable areas. All PAs, other hilly terrains and terai habitats comprise large suitable patches.

To apply the framework of Naves *et al*. (2003) for further habitat classification I used thresholds of 0.01 to separate barrier from matrix, a threshold of 0.25 for human and natural models to separate matrix from poor quality habitat and a threshold of 0.9 to separate poor quality habitat from good quality habitat. Note that the Naves scheme has the purpose of showing tendencies within the main habitat categories. To best visualize these tendencies given the almost binary response of habitat suitability, I selected the high 0.9 threshold. The PAs in India and Nepal form large blocks of good habitat, but a substantial proportion of the areas outside PAs classified by the final model as suitable habitat appear to be “attractive sink-like”, i.e., they show a high natural suitability but also relatively high levels of human disturbance (Fig. 4.6).

4.3.2.3 Corridor assessment

I used the results of the predictive habitat mapping for habitat quality assessment of corridors identified in the TAL (Johnsingh *et al*. 2004; Wikramanayake *et al*. 2004) that could potentially link the different large patches of suitable habitats (Fig. 4.5). Only three corridors located at the western part of the study area (Kosi river, Rajaji-Corbett, and Nihal-Boar-Gola) comprise more than half of its area as suitable habitat (Table 4.9). However, the Naves scheme indicates that most of the good quality habitat of these corridors may be attractive sink-like, thus having a high level of human disturbance (Table 4.9). For the other corridors barrier and matrix dominate (Table 4.9).

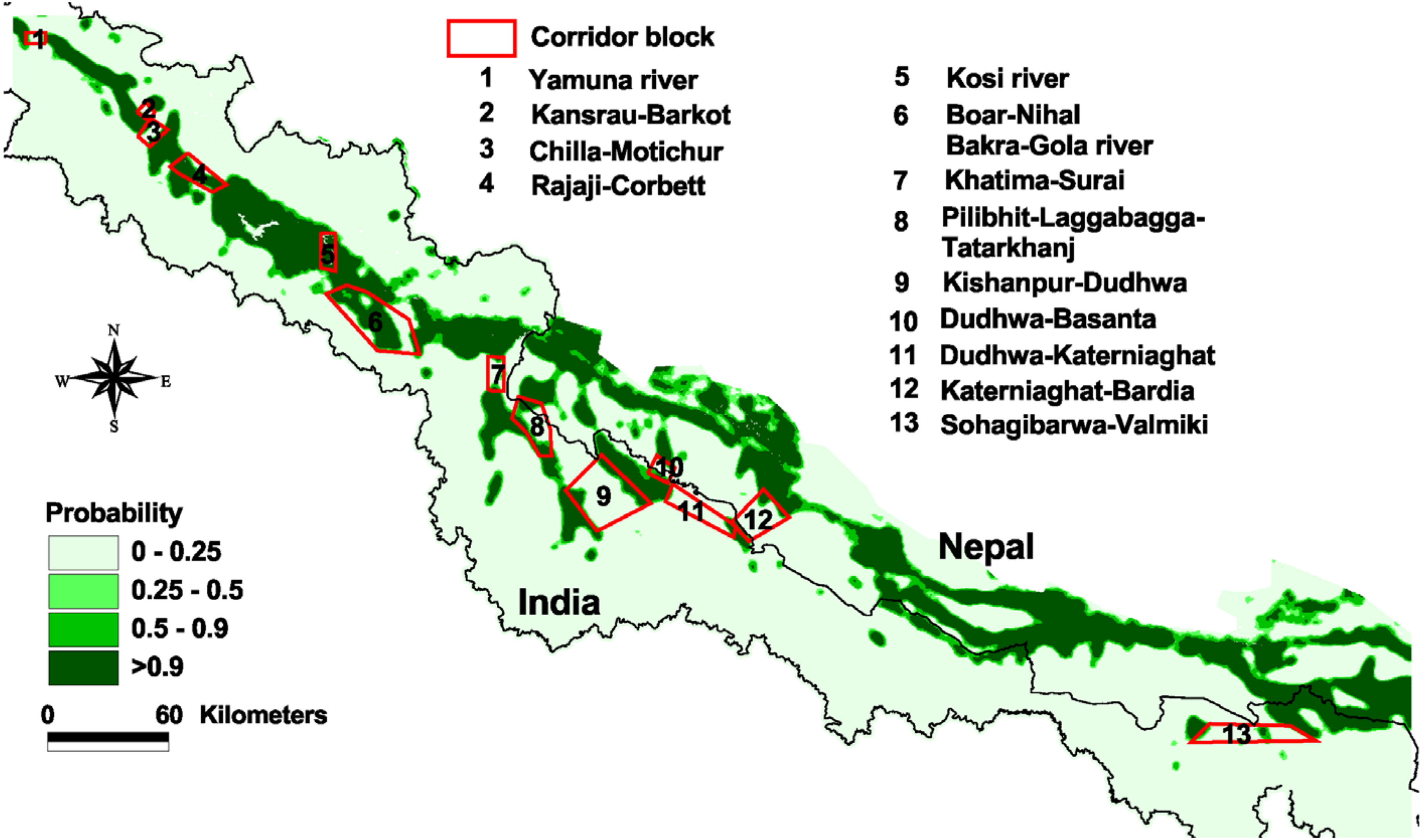


Figure 4.5 Maps of predicted habitat suitability (probability) for tiger in the TAL based on the final model (Table 4.8).

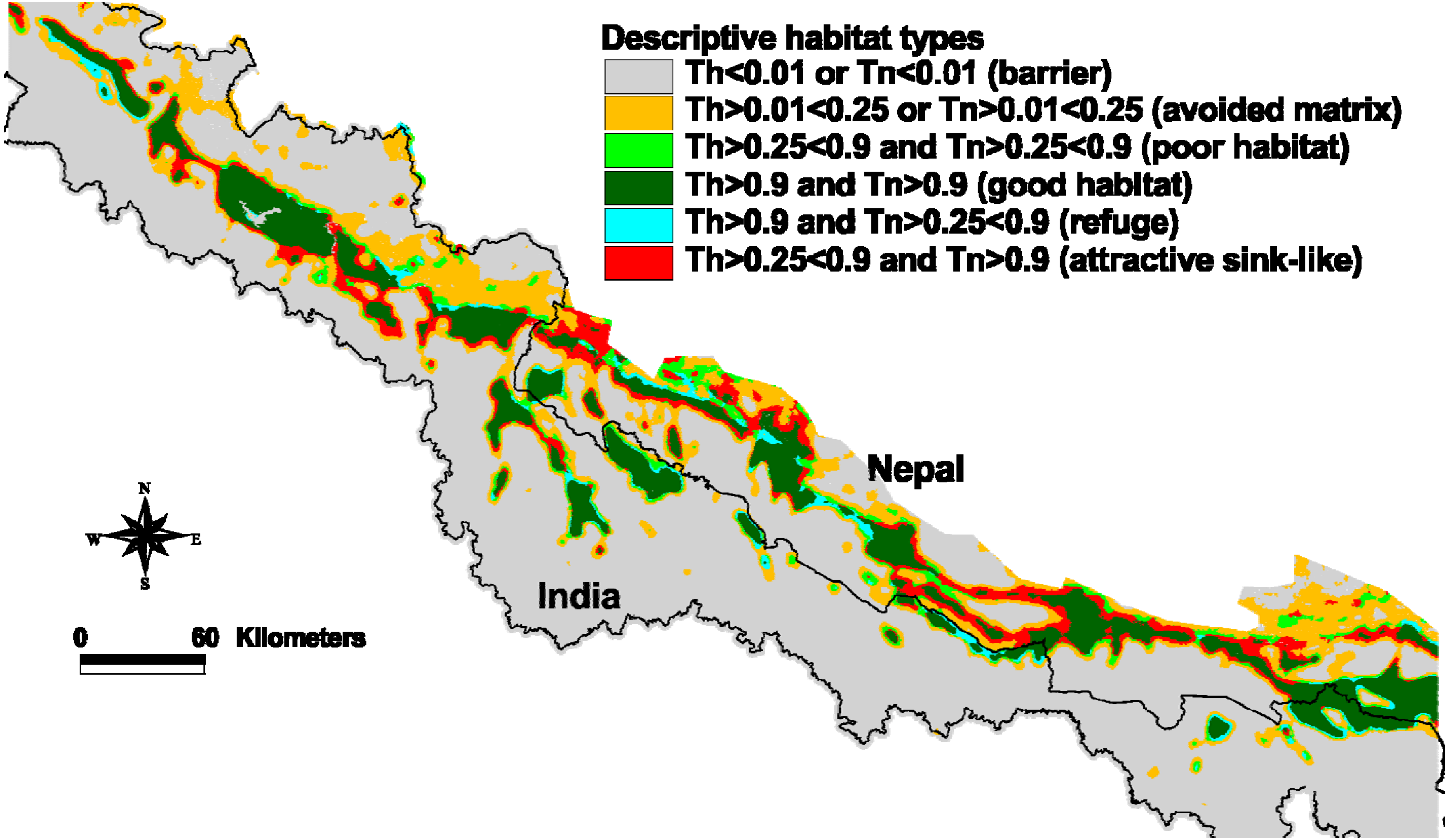


Figure 4.6 Classification of habitat quality into avoided matrix-like, poor habitat-like, good habitat-like, refuge-like, and attractive sink-like in the TAL based on the final model (Tn) and human disturbance model (Th) (Table 4.8).

Table 4.9 Available amount of different quality habitats and suitable areas in potential corridors for tiger in TAL.

Corridor	**Area (km^2)**	**% cover of different habitat types**						**% of suitable area***			
		Barrier	**Matrix**	**Poor habitat**	**Good habitat**	**Refuge-like**	**Attractive sink-like**	**≥0 <.25**	**>.25 <.50**	**>.50 <.75**	**>.75 ≤1**
Yamuna river	52.4	38	47	4	0	6	5	67	10	14	9
Kansrau-Barkot	42	32	48	6	3	0	11	57	9	17	16
Chilla-Motichur	102.7	28	26	15	20	3	7	52	8	12	28
Rajaji-Corbett	221.9	16	29	3	21	0	30	17	5	12	66
Kosi river	131	10	6	0	53	0	30	10	0	1	89
Nihal-Boar-Gola	769.8	25	24	4	15	0	32	26	5	13	56
Khatima-Surai	130	34	47	10	1	0	8	66	12	13	9
Kishanpur-Dudhwa	805.3	58	12	6	20	3	1	68	3	8	21
Dudhwa-Katerniaghat	277.4	76	9	4	8	2	0	84	3	4	9
Pilibhit-Laggabagga	341	19	31	13	20	3	15	41	9	15	35
Dudhwa-Basanta	97.3	19	38	18	11	9	5	48	13	24	16
Katerniaghat-Bardia	353.1	65	14	3	10	3	5	73	4	8	15
Sohahibarwa-Valmiki	418.37	54	25	7	4	9	2	77	6	11	6

* based on the habitat suitability index of the final model (Table 4.8)

4.4 Discussion

In this study, I obtained an understanding of the factors and critical scales of landscape perception that determine habitat selection of tiger in the TAL. Such an understanding is urgently needed given the current population fragmentation and dramatic decline of tigers in this landscape (e.g., Smith *et al.* 1998; Wikramanayake *et al*. 2004; Dinerstein *et al*. 2007). I combined recent techniques of habitat modelling with information theoretic approaches in a novel way and contrasted several *a priori* hypotheses on tiger habitat selection with the data. This modelling approach revealed that habitat degradation outside the protected areas and especially in the corridor linkages is the predominant threat to long-term tiger survival, which helps focussing future management actions.

4.4.1 Gains and shortcomings of the modelling approach

The GLM habitat models shared an unusual feature of an almost binary function classifying the TAL as either highly suitable (e.g., cut-off $P > 0.9$) or highly unsuitable (e.g., cut-off $P < 0.25$) with abrupt boundaries between those categories (e.g., Fig. 4.5). This suggests that tiger show a very clear pattern of habitat selection in this landscape; they prefer dense forest, areas with high likelihood of finding their main prey species, but avoid areas with dense road networks, agriculture and human habitation. This pattern of tiger habitat selection is not particularly new and confirmed the expectations based on previous studies (e.g., Smith *et al.* 1998; Karanth *et al*. 2004; Carroll and Miquelle 2006). However, this study provided a statistical quantification of this knowledge, allowed for an assessment of the relative importance of different hypotheses on tiger habitat selection, and facilitated for a rigorous assessment of the critical spatial scales at which tigers perceive their environment, thus basing further conservation actions on a sound basis.

Information-theoretic model selection showed that the “prey species” hypothesis received most support from the data (Fig. 4.4, Table 4.7), followed by the “protective habitat” hypothesis. These results clearly showed that prey and protective habitat play an important role in tiger habitat selection.

Nevertheless, the human disturbance hypothesis also yielded a model with high classification accuracy (>90%). The positive effect of presence of PA in the model shows the importance of PAs for the survival of tigers in the TAL. Interestingly, as for example demonstrated by the Naves scheme (Fig. 4.6), the differences among the predictions of the models resulting from the different hypotheses where really small indicating that the models are quite robust.

Assessment of critical spatial scales for habitat selection is an important, albeit often overlooked issue in studies of statistical habitat modelling (but see Schadt *et al*. 2002; Boyce *et al*. 2003). For example, one would expect that territorial species select areas at which their requirements are matched at the spatial scale of their home range (Schadt *et al*. 2002). Results of this study confirmed the power of this approach and revealed for protective habitat and human disturbance hypotheses a critical neighbourhood scale of 37km^2, which approximates the size of female tiger home ranges in the Nepal part of TAL (Smith *et al.*1987). The AIC values for smaller scales were in most cases substantially larger, but more or less equal for >60.9 km^2 neighbourhood scale (Fig. 4.4). This indicates that measuring environmental variables at too small neighbourhood scales, i.e., below the typical home range size, produces poorer models because they miss the critical scale of habitat selection.

This approach combined the gains of two powerful approaches in statistical habitat modelling, ENFA and GLM, to optimally use a data set on tiger occurrence for multi-scale assessment of the importance of natural habitat characteristics and anthropogenic factors for tiger habitat suitability. Such approaches are needed when dealing with critically endangered species for which lack of valid absence data seriously constrains traditional approaches (Engler *et al.* 2004). Application of the Naves scheme gave this approach additional power, allowing a more sophisticated look at habitat suitability than usually possible with traditional one-dimensional approaches ranking suitability from poor to good. The categorization of the TAL into six demographically motivated habitat categories further allowed for an assessment of the composition of different previously identified corridors (Table 4.9, Fig. 4.6).

4.4.2 Management recommendations

The model predicted that 24% (c.18500 km²) of the study area was suitable for tiger (cut-off *P* > 0.5), out of which approximately 7% of the area was under PAs. This approach also revealed that only 12% of the habitat area was good quality habitat to be considered as source patches, out of which 6% was protected in the study area (Fig. 4.6). Within the PAs, 67% of the area was assigned good quality habitat and only 1.5% as attractive sink-like habitat, indicating the low level of disturbances in the PAs. However, when considering the remaining study area outside PAs, only 13% of the habitat was predicted as good quality habitat out of which 6% are attractive sink-like habitats indicating the high level of human disturbances in the good habitat outside the PAs. This sets clear objectives of where to strengthen conservation actions.

This approach also revealed large areas of matrix, poor habitats and attractive sink-like habitats as those dominated by forest monoculture plantations of softwood and hardwood, which replaced the mixed forests and grassland habitats in the 1960s to meet industrial needs (Johnsingh & Negi 2003) in the Rajaji-Corbett Conservation Unit (Fig. 4.6). It exposed the areas of attractive sink-like habitats in the Kosi river and Nihal-Boar-Gola corridors (Johnsingh *et al*. 2004) and in the narrow Rajaji-Corbett corridor, which is a vital habitat link between Rajaji NP and Corbett TR (Johnsingh and Negi 2003), especially in the critical areas where disturbance in this narrow corridor arises largely from Kotdwar town and adjacent villages (Johnsingh and Negi 2003). These corridors are currently used by tigers (Johnsingh *et al*. 2004), but the identification as attractive sink-like habitat highlights the importance of reducing the human disturbance in these areas; failure of this might destroy these corridors and jeopardize the connectivity in this most intact and extensive forest block in the TAL with 4053.5km^2 of potential habitat for tiger in the near future (Johnsingh *et al.* 2004).

Physical connectivity between suitable areas in India and Nepal is reduced by the presence of barrier and avoided matrix habitats in the potential corridor areas (Fig. 4.6). In the eastern part of TAL, areas connecting the populations of Suhelwa in India and Lamahi, Mahadevpuri and Kapilbastu in Nepal suffered from the presence of attractive sink-like and avoided matrix habitats. These populations separated from Chitwan population by the presence of attractive sink-like and poor habitats.

In summary, reducing the human disturbance espicially in corridor habitats and increasing the connectivity between habitat patches by strengthening the corridors will be critical for connecting tiger habitats of Corbett NP, and the Pilibhit forest region in India with the Nepal side of TAL. Dispersal is a key process for the survival of these spatially structured fragmented tiger subpopulations. Quantitative estimates of dispersal probability between habitat patches and successful production of emigrants can adequately explain whether a given landscape configuration is good enough for the long-term population survival (Jepsen *et al*. 2005). Hence, for future research, it will be important to derive quantitative estimates of connectivity between suitable patches in order to ensure the long term survival of tiger in this fragmented and heterogeneous landscape.

4.5 Summary

- Tiger (*Panthera tigris*) populations have dramatically declined in the Terai Arc Landscape (TAL; India and Nepal), and the current populations are highly fragmented and endangered. The overall objective is to aid tiger management in identifying critical areas for conservation. To this end, I aimed to (1) identify the factors which affect the distribution of tigers in the TAL and (2) to map potentially suitable habitats and to assess the quality of potential corridors linking suitable habitat.

- I used an approach based on presence and pseudo-absence data, combing ecological niche factor analysis (ENFA) and generalized linear models (GLM). An information-theoretic approach of model selection was used to confront the data on tiger presence to hypotheses on tiger habitat selection (i.e., protective habitat, prey species, human disturbance, and natural habitat) at several spatial neighbourhood scales.

- All hypotheses yielded models with high prediction accuracy (> 90%). The most parsimonious model supported the “prey species” hypothesis and contained two variables characterizing the prey species habitat suitability within a 37km^2 neighbourhood. The best model of the human disturbance hypothesis suggested that the presence of agriculture land and human habitation and absence of protected areas had a significant negative effect on tiger distribution.

- More detailed assessment of the potentially suitable areas using an extended source-sink approach suggested that most of the habitats outside the protected areas were attractive sink-like habitats, i.e., they showed high “natural” quality but suffered from high levels of human disturbance. Potential corridors had generally a low proportion of suitable habitat and showed high levels of human disturbance. The key management recommendations for tigers in the TAL stress the importance of reducing the human disturbance outside the protected areas, especially in potential corridors, to maintain connectivity between subpopulations located in India and Nepal. More widely, this study also shown that combining ENFA-generated pseudo-absence, GLM, and neighbourhood variables is a powerful approach that could be widely applied to quantify factors and critical scales of habitat selection for species with scarce data.

CHAPTER 5

ASSESSING INTER-PATCH CONNECTIVITY FOR TIGER

5.1 Introduction

Studies on dispersal and connectivity have become a central issue in conservation biology and are of vital importance to the conservation of threatened species world-wide (Simberloff 1988; Crooks and Sanjayan 2006; Revilla and Wiegand *in press*). Landscape connectivity is defined as “the degree to which the landscape facilitates or impedes movement among resource patches” (Taylor *et al.* 1993). Depending on the spatial scale and the management question, connectivity may be assessed with regard to the entire landscape as typically done in landscape ecology (e.g., Tischendorf and Fahrig 2000), or with regard to specific patches (i.e., “inter-patch connectivity”) as typically done in metapopulation studies (e.g., Moilanen and Hanski 2001) or case studies for specific species (Ferreras 2001; Kramer-Schadt *et al*. 2004; Graf *et al*. 2007).

Dispersal success and therefore inter-patch connectivity depends on both, the spatial structure of the landscape and the behavior of the dispersing species in response to landscape heterogeneity (Revilla *et al*. 2004). An assessment of dispersal success is especially complicated in intensively used landscapes due to movement barriers imposed by humans (Kramer-Schadt *et al*. 2004). Additionally, field studies on dispersal are very time consuming and expensive, especially for large carnivores because of high tracking-costs of individual animals. As a result, my current understanding on dispersal of such species is limited and alternative approaches are required to complement the assessment of connectivity (Zollner and Lima 1999; Revilla *et al*. 2004; Graf *et al*. 2007).

One approach to describe dispersal and estimate inter-patch connectivity is to use models. Depending on the landscape structure, the scientific question and the organism of interest, several approximations to the complex problem of estimating patch connectivity have been proposed. For example, the incidence metapopulation model (Hanski 1994; Moilanen and Nieminen 2002) describes connectivity between two patches as a function that declines exponentially with distance between the patches without taking into account details of landscape structure. Similar simplifying assumptions are made in graph-based landscape connectivity indices (e.g., Keitt *et al*. 1997; Urban and Keitt 2001; Pascual-Hortal and Saura 2006; but see O'Brien *et al*. 2006). Least-cost analysis, on the other hand, explicitly considers the impact of landscape structure to find the optimal movement path between two patches that minimizes a given cost criterion. However, this method cannot directly include dispersal behavior (Gonzales and Gergel 2007). Instead, friction values that represent the resistance to movement through different landscape elements (i.e., the cost) implicitly represent behavioral decisions regarding movement through particular landscape features (Schadt *et al*. 2002).

Spatially explicit simulation models (Dunning *et al*. 1995; Kramer-Schadt *et al*. 2004; Wiegand *et al*. 2004b; Graf *et al*. 2007; Revilla and Wiegand *in press*) overcome the limitations of landscape connectivity indices and cost-path analysis. They simulate dispersal explicitly using an individual-based approach (Grimm and Railsback 2005) where behavioral movement rules describe how organisms interact with landscape structure and are therefore especially suitable for evaluation of dispersal success and connectivity between specific habitat patches in situations where details of landscape structure matter. This type of model has been successfully used in several studies on animals and birds (e.g., Iberian lynx (*Lynx pardinus*)), Eurasian lynx (*Lynx lynx*), capercaillie (*Tetrao urogallus*)) to explain dispersal behavior and estimate connectivity between habitat patches (e.g., Revilla *et al*. 2004; Kramer-Schadt *et al.* 2004; Tracey 2006; Graf *et al*. 2007; Revilla and Wiegand *in press*).

Large carnivores are particularly vulnerable to extinction in fragmented landscapes because of their low population density, wide ranges, broad resource requirements, low fecundity, and direct persecution by humans (Noss *et al*. 1996; Crooks 2002). A typical example is a (meta) population of tiger (*Panthera tigris*) that exist in the Terai Arc Landscape (TAL) along the Himalayan foothills in India and Nepal. The terai forests and tall grasslands that lie at the base of the Himalaya once supported a rich ungulate biomass that a female tiger in many areas here needs only 20 km² to live and raise her young compare to other areas, e.g., a female needs 500 km² in the temperate forest of Russian Far East (Seidensticker *et al*. 1999). This top priority landscape for tiger conservation was once continuous across the Himalayan foothills but is now highly fragmented and most of the remaining large, intact habitats are located within protected areas (Wikramanayake *et al*. 2004). As tigers cannot sustain viable populations in small habitat fragments (Johnsingh and Negi 1998; Seidensticker *et al*. 1999) an assessment of potential connectivity among the remaining habitat patches is required (Smith *et al*. 1998; Wikramanayake *et al*. 2004; Dinerstein *et al*. 2007) to assess possibilities to ensure the creation of a single functioning unit for tiger.

In this study, I used a simple individual-based and spatially explicit dispersal model to (1) assess the inter-patch connectivity among the major (protected) habitat patches for dispersal of tiger in the complex and heterogeneous TAL and (2) to investigate the effect of potential initiatives to restore identified potential corridors for dispersal. To overcome the problem of scarce data in parameterizing the dispersal model, which is common in endangered species (Wiegand *et al*. 2004b; Kramer-Schadt *et al*. 2007), exhaustive sensitivity analyses were conducted. Finally, I discuss my results in respect to tiger management in the TAL.

5.2 Materials and methods

5.2.1 The habitat map

To represent the TAL with the eye of dispersing tigers I used categorical habitat maps with a cell size of 500 m × 500 m that were derived by generalized linear models (GLM) and ecological niche factor analysis as described in Chapter 4. I divided the TAL into the four functional habitat types breeding habitat, dispersal habitat, matrix and barrier (e.g., Kramer-Schadt *et* *al*. 2004; Revilla *et al*. 2004; Revilla and Wiegand, *in press*). In this model, the movement decisions of tigers depend directly on these four categories (see below "*Correlated habitat-dependent walk*"). These habitat types were defined by the three threshold values 0.75, 0.5, 0.25 dividing the probability-of-use given by GLM into four classes. However, because of uncertainties associated with these cut-off values I repeated all analyses for three additional habitat maps obtained by modification of these probability cut-off levels (Figs 5.1, 5.2 and 5.4). These maps used the following cut-off values: (0.75, 0.35, 0.10), (0.75, 0.30, 0.05), (0.75, 0.30, 0.02). I derived an additional habitat suitability map (*hq*) which describes human disturbances (see Table 4.8 in Chapter 4 and Fig. 5.3). I used this map to determine stochastic mortality during dispersal (see below "*Mortality during dispersal*").

Twelve source and target patches for the connectivity analysis were defined based on the distribution of breeding habitats and their protected area status (Fig. 5.1). Here, I studied the connectivity among 10 important patches (Fig. 5.1): Rajaji National Park (NP) west (2), Chilla range of Rajaji National Park east (3), Corbett Tiger Reserve (TR) (4), Pilibhit Forest Division (5), Suklaphanta Wildlife Reserve (WLR) (6), Basanta forest block I (7), Dudhwa National Park (8), Basanta forest block II (9), Katerniaghat Wildlife Sanctuary (WLS) (11), and Bardia National Park (12).

5.2.2 Least cost-path analysis

For least cost-path analysis I created for a given habitat map a cost grid based on the four habitat types with a high cost value for barrier (100) and a low cost value for breeding habitat (1). For matrix and dispersal habitat values 50 and 25 were assigned, respectively. I then defined manually a starting and end points at the source and target patch, respectively, located close to the corridor and used the ArcView 3.x extension, cost distance grid tools, to determine the least cost path and the associated cost value. I then compared the cost values of all patch pairs and landscape maps with the respective connectivity values that resulted from the simulation model analysis. If both methods are in agreement both values will show a high negative correlation since a high cost value implies low connectivity.

5.2.3 Dispersal corridor scenarios

5.2.3.1 Scenario 1: corridor creation based on natural vegetation

Dispersing tigers avoid cultivated areas, but may use degraded forest habitats (Smith 1993). I thus manipulated the landscape structure in the model for five important potential corridor areas between suitable patches (Johnsingh *et al*. 2004) to physically link target patches. To this end I used the satellite images that were used to develop the habitat suitability maps (see Chapter 4) and classified all cells having natural (or semi-natural) vegetation and being located between the two target patches as dispersal habitat. This landscape modification created corridors that were composed of very thin degraded natural forests (< 2 km width; Figs 5.2 and 5.4).

5.2.3.2 Scenario 2: increased width of corridors

Wider corridors may have the highest potential to facilitate dispersal between suitable habitat patches and could be more effective than narrow but continuous conduits that connect two patches (Wikramanayake *et al*. 2004). I therefore increased the width of corridors created in scenario 1 by including a 500 m buffer area around each side of the corridor that was assigned status of dispersal habitat (Figs 5.2 and 5.4).

Figure 5.1 Spatial structure of tiger habitat, source and target patches, and corridor areas used for measuring inter-patch connectivity in the study area. Dark-grey areas are matrix, medium-grey areas represent habitat suitable for dispersal and light-grey areas represent barrier. The patches studied here are selected from available suitable patches marked with grey shading: 2,3,4,5,6,7,8,9,11 and 12. The corridor blocks show the corridors for which analyzed the effect of landscape manipulations (i.e., scenarios 1 and 2).

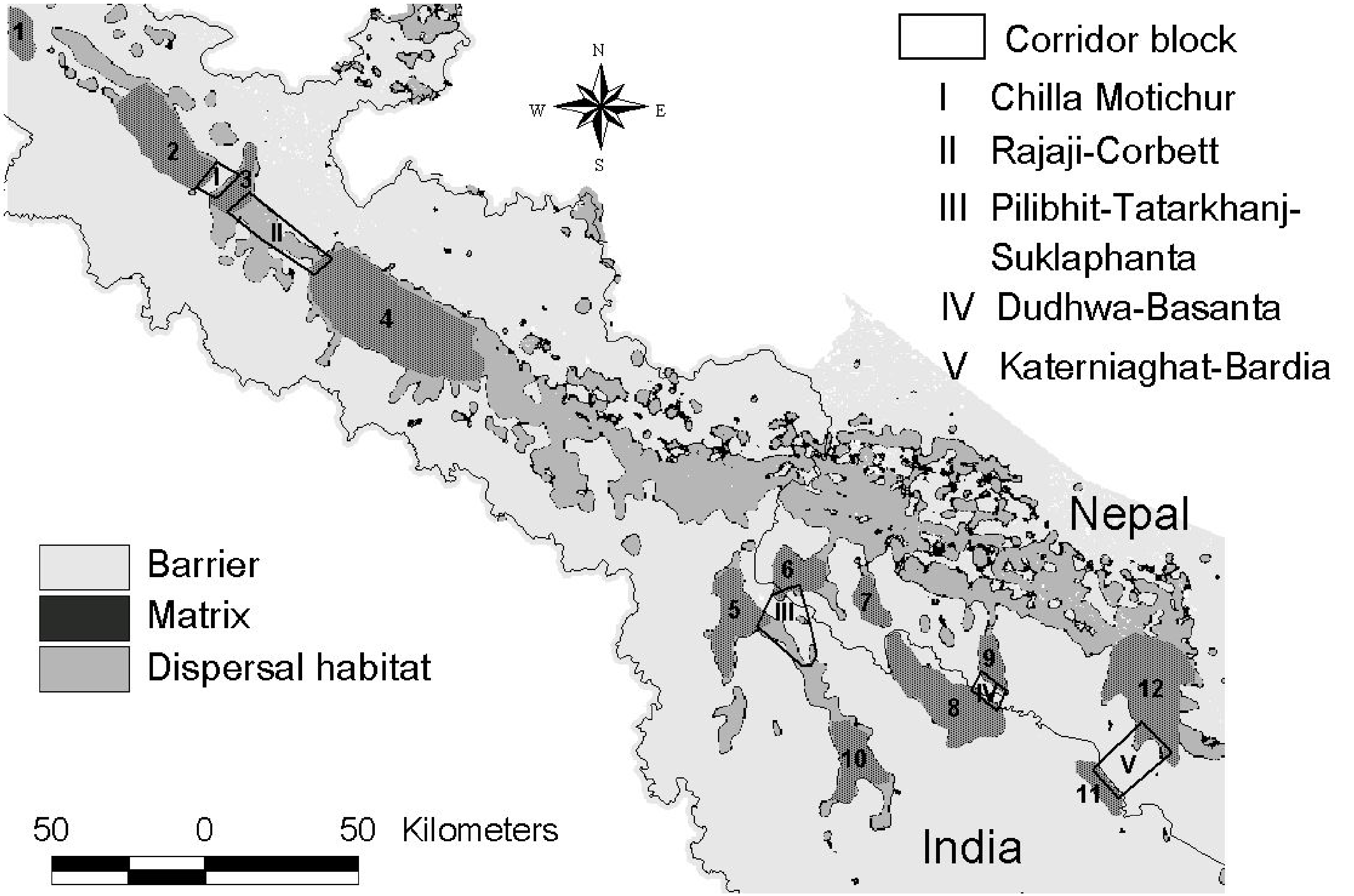

Corridor block
I Chilla Motichur
II Rajaji-Corbett
III Pilibhit-Tatarkhanj-Suklaphanta
IV Dudhwa-Basanta
V Katerniaghat-Bardia
N
W
E
S
1
2
3
4
5
6
7
8
9
10
11
12
I
II
III
IV
V
Nepal
India
Barrier
Matrix
Dispersal habitat
50 0 50 Kilometers

Figure 5.2 Manipulated corridors between suitable patches both in scenarios 1 and 2: (A) Chilla range of Rajaji NP-Rajaji NP west corridor, (B) Dudhwa NP –Basanta forest corridor, (C) Katernighat WLS-Bardia NP corridor, (D) Pilibhit FD-Suklaphanta WLR corridor and (E) Chilla range of Rajaji NP-Corbett TR corridor. The light-grey areas represent barrier, black areas are matrix, medium-grey areas represent dispersal habitat, dark-grey areas represent manipulated corridor (scenario 1) and black border around the corridor represent 500m buffer area (scenario 2).

Landscape map type based on different cut-off values

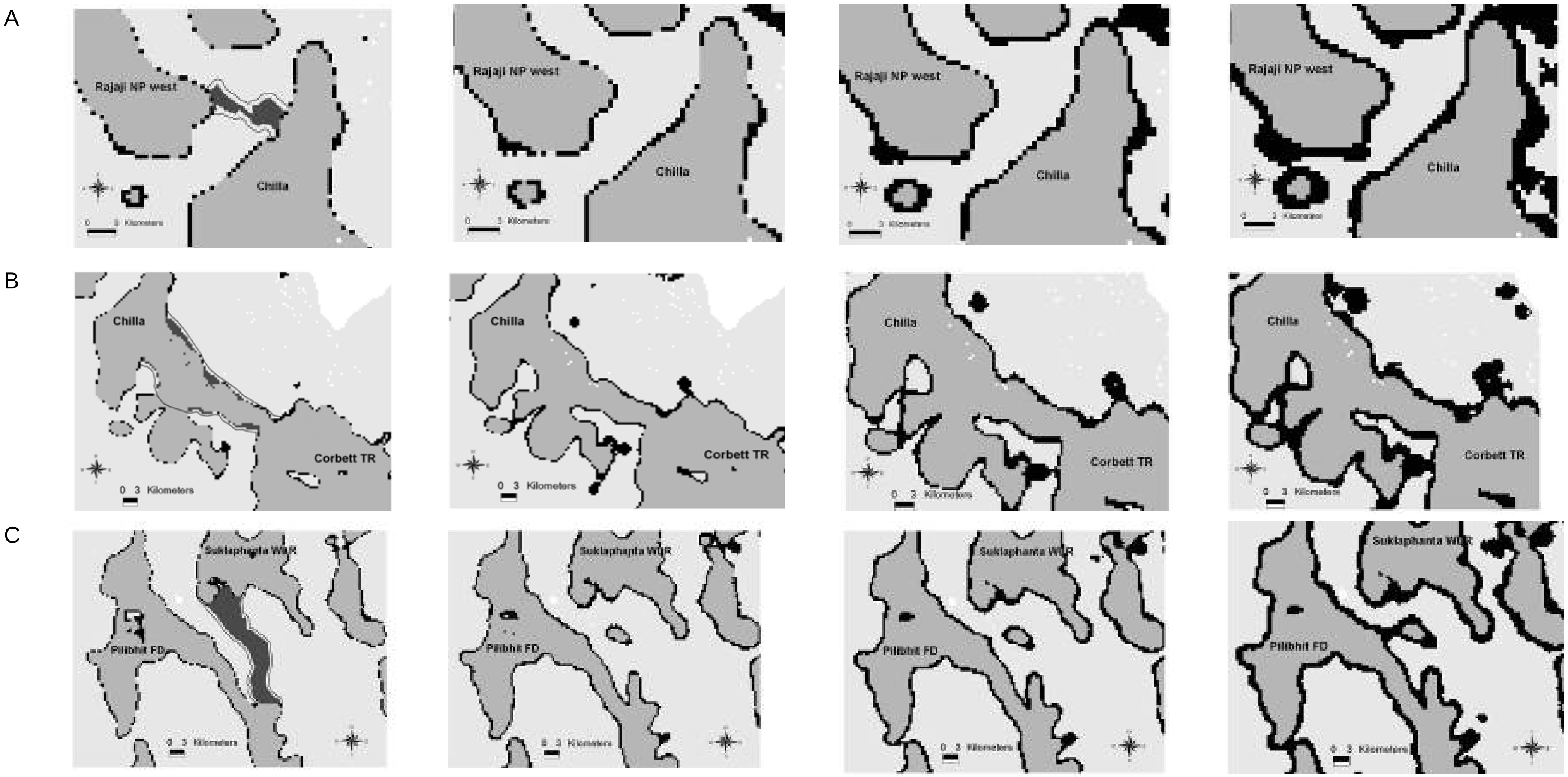
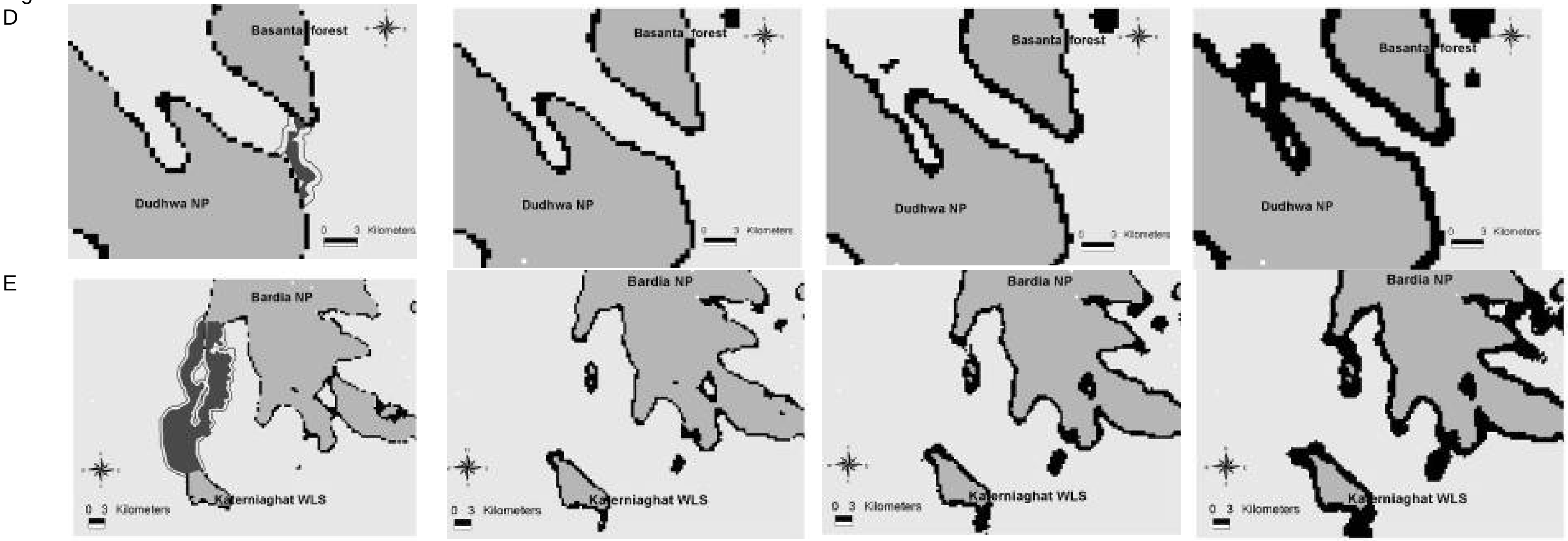


Figure 5.2 continued.



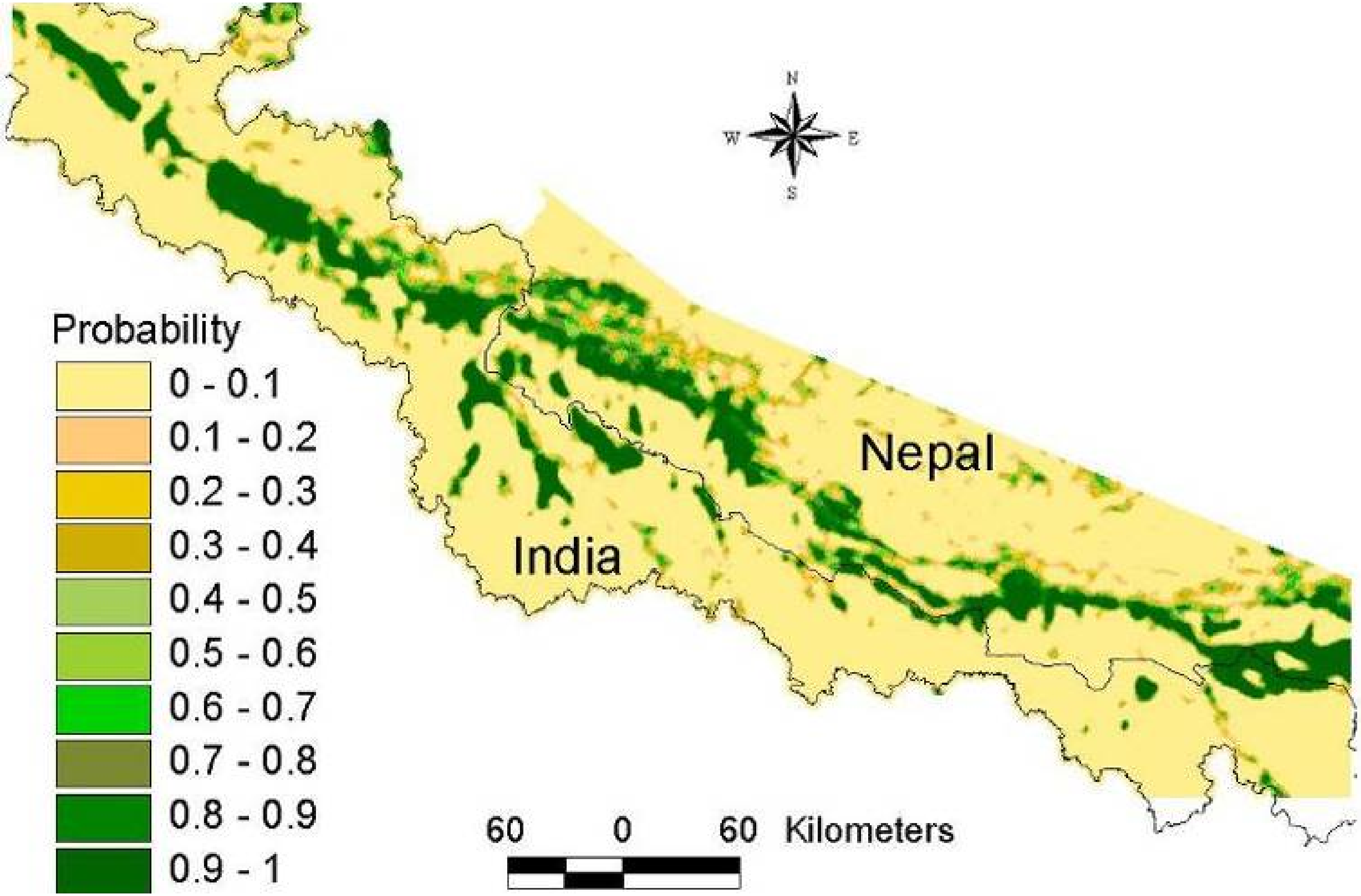


Figure 5.3 Habitat suitability map derived from GLM for tiger using the variables describing human disturbances for entire TAL.

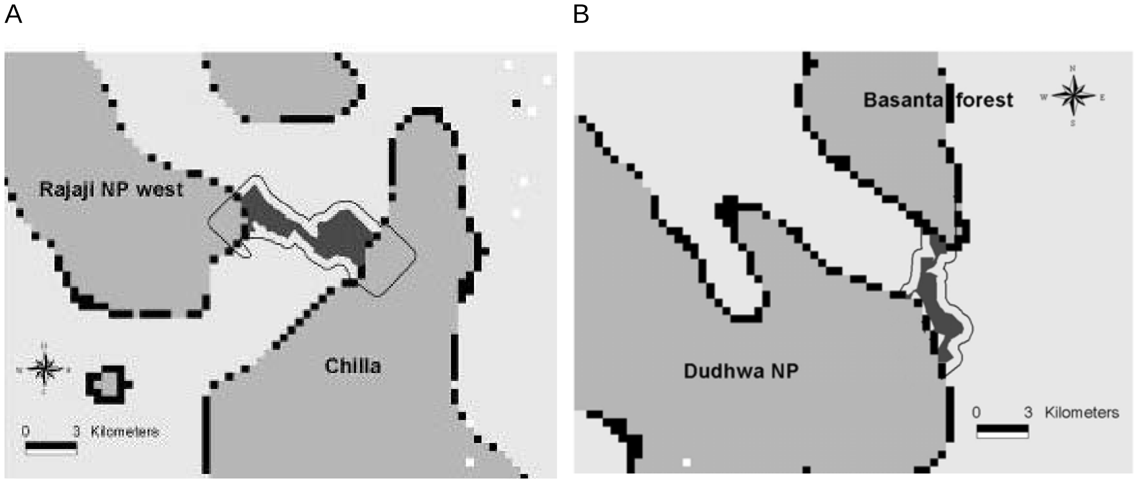


Figure 5.4 Two examples showing landscape manipulations to create corridors between physically non-connected suitable patches: (A) Chilla (patch 3, see Fig. 5.1) - Rajaji National Park west (patch 2) corridor (I) and (B) Dudhwa National Park (patch 8)-Basanta forest block II (patch 9) corridor (IV). The light-grey areas represent barrier, black areas are matrix, medium-grey areas represent dispersal habitat, and the dark-grey areas show cells where I “restored” barrier or matrix habitat (having natural vegetation) into dispersal habitat (scenario 1) and black border around the corridor of restored dispersal habitat represent the 500m buffer area which was restored in scenario 2 (additionally to the manipulation of semi natural vegetation in scenario 1) to reach status of dispersal habitat.

5.2.4 Dispersal model

I developed a spatially explicit and individual-based dispersal model (SEDM) based on simple behavioral rules that operated on an intraday time scale, where the response of the animal to the landscape configuration took place. The rules were based on general knowledge of dispersal of tiger (e.g. Smith 1993; Ahearn *et al*. 2001), and implemented similarly to models of other carnivores (Kramer-Schadt *et al*. 2004; Revilla *et al*. 2004).

The dispersal movement during a given day consists of a series of steps to one of the eight neighbored 500 m × 500 m cells surrounding the current location of the tiger. The actual movement decision for one step is stochastic, but depends on the habitat type of the neighboring cells and on the degree of autocorrelation in the movement.

5.2.4.1 Intraday number of steps

Each day I assigned a dispersing tiger a certain number of movement steps, *s*, based on a probability distribution *P*(*s*), using a power function with an exponent, *x*, as described in Kramer-Schadt *et al*. (2004, their Fig. 5.4):

$$P(s) = \frac{(s_{\max} - s)^x}{\sum_{s=1}^{s_{\max}} (s_{\max} - s)^x} \qquad (1)$$

parameter $s_{\max}$ gives the maximum number of steps that a dispersing tiger could cover during one day. Low values of the exponent yield linear daily step distributions, whereas high exponent values raise the probability of a small number of movement steps. Note that $P(s = 0) > 0$, that means the tiger may not move every day.

I explored the parameter range for the maximum number of steps during one day ($s_{\max}$) between 2.3 and 11.4 km km that allowed the maximum distance traveled by a simulated dispersing tiger to correspond with the distance observed in the wild (Sunquist *et al*. 1999). The exponent x of the power function was varied over a broad range (i.e., 1 - 5) to ensure large variability in step distribution (Table 5.1).

Table 5.1 Parameter ranges of the dispersal model. The column "range explored" refers to the local sensitivity analysis. For each parameter, 21 values were explored. The value of the standard parameterization is given in bold.

Parameter	**Symbol**	**Range explored**	**Number of ANOVA levels and values**
Exponent of power function	x	1 , 1.2. . , **2**, . , 5	4 (1, 2.33, 3.67, 5)
Maximum number of intraday movement steps	$S_{\max}$	5, 6, . , **10**, . , 25	4 (5, 11, 18, 25)
Probability of stepping into matrix	P_{matrix}	0, 0.05, . , **0.3**, . , 1	4 (0, 0.33, 0.67, 1)
Probability of keeping the previous direction	P_c	0, 0.05, . , **0.5**, . , 1	4 (0, 0.3, 0.6, 0.9)
Annual survival probability in optimal habitat	*suv*	0.7, 0.715, . , **0.9**, . , 1	-
Increase in mortality with decreasing habitat quality	b	0.001, 0.00195, . , **0.005**, . , 0.02	4 (0.001, 0.0073, 0.0136, 0.02)

5.2.4.2 Correlated habitat-dependent walk

Individual movement steps were modeled as weighted random walk. The directions to the eight neighbors are numbered (Fig. 5.5A), with the cell of origin being number 0, and the habitat-dependent weights are h^*_1, ..., h^*_8. If a given neighbor *i* has the habitat category ‘barrier’ the associated weight is $h^*_i = 0$, if the neighbor is matrix habitat the associated weight is $h^*_i = P_{matrix}$, and if the neighbor is of breeding or dispersal habitat the associated weight is $h^*_i = 1 - P_{matrix}$. Thus, matrix is avoided if $P_{matrix} < 0.5$. However, to fully explore the behavior of the model I used the full range of this parameter, i.e., $0 < P_{matrix} < 1$ for the sensitivity analysis. Finally I normalize the weights with $h_i = h_i^* / \sum_{j=1}^{8} h_j^*$.

To model autocorrelation in movement, i.e., the tendency of keeping the previous direction *j*, I introduced a second set of weights, d_j (Fig. 5.5B). Note the symmetry in directions, i.e., $d_6 = d_4$, $d_7 = d_3$, and $d_8 = d_2$. The weights were calculated as

$$d_j = Max\left[0, \frac{1.5 + (0.5 - j)P_C}{1.5 - 0.5P_C}\right] \qquad (2),$$

and then normalized to sum up to one. Index $j = 1$ indicates the previous direction; $j = 2 - 8$ are numbered as shown in Figure 5.5A. The parameter P_C determines the degree of autocorrelation. For $P_C = 0$ all eight directions have the same weight (i.e., a random walk), and with increasing value of P_C the weight of the previous direction i increases and for $P_C = 1$ $d_i = 1$ (Fig. 5.5B). I varied the parameter P_C over its full range, i.e., $0 < P_C < 1$.

In cases that habitat preference and the preference for a certain direction were incompatible; the hierarchy was preference of dispersal habitat before correlation in the direction of movement (Kramer-Schadt *et al*. 2004). If at least one cell of dispersal habitat was available, the probability to step into matrix was calculated as $P_{leave} = (n_{matrix} P_{matix})/(9 - n_{barrier})$ where n_{matrix} and $n_{barrier}$ are the number of matrix and barrier cells, respectively. If the tiger decided to step into matrix, one of the n_{matrix} matrix cells was selected, considering their weights d_j of direction preference. Conversely, if the tiger decided to step into dispersal habitat, one of the available cells of dispersal habitat was selected, considering their weights d_j of direction preference.

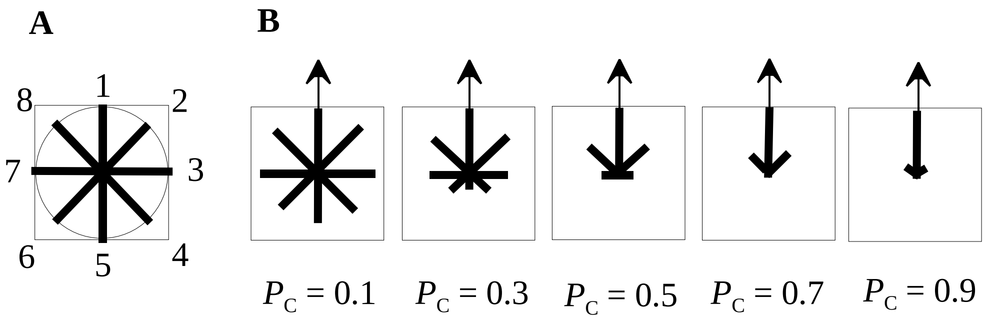


Figure 5.5 Numbering of neighboring cells (A) and impact of parameter P_C, which describes autocorrelation in movement, on the probability to step into one of the eight neighborhood pixels. For $P_C = 0$ there is no preferred direction, and for $P_C = 1$ the previous direction is taken.

5.2.4.3 Mortality during dispersal

For each day I calculated the average habitat quality of the cells the tiger has visited (*q*; taken from the habitat suitability map *hq* derived from variables of human disturbance; see section "*The habitat map*") and calculated the per day mortality P_{mort} as:

$$P_{mort} = (1 - suv^{1/year}) + b(1 - q) \qquad (3)$$

with year = 365 gives the number of days per year. The parameter *suv* is the annual survival probability in optimal habitat (i.e., *q* = 1) and the parameter *b* describes the increase in the daily risk of mortality with decreasing habitat quality. The annual survival probability in the poorest habitat (i.e., *q* = 0) is $(suv^{1/year} - b)^{year}$. I varied the parameter *suv* between 0.7 and 1 and the parameter *b* between 0.001 and 0.02 (Fig. 5.6).

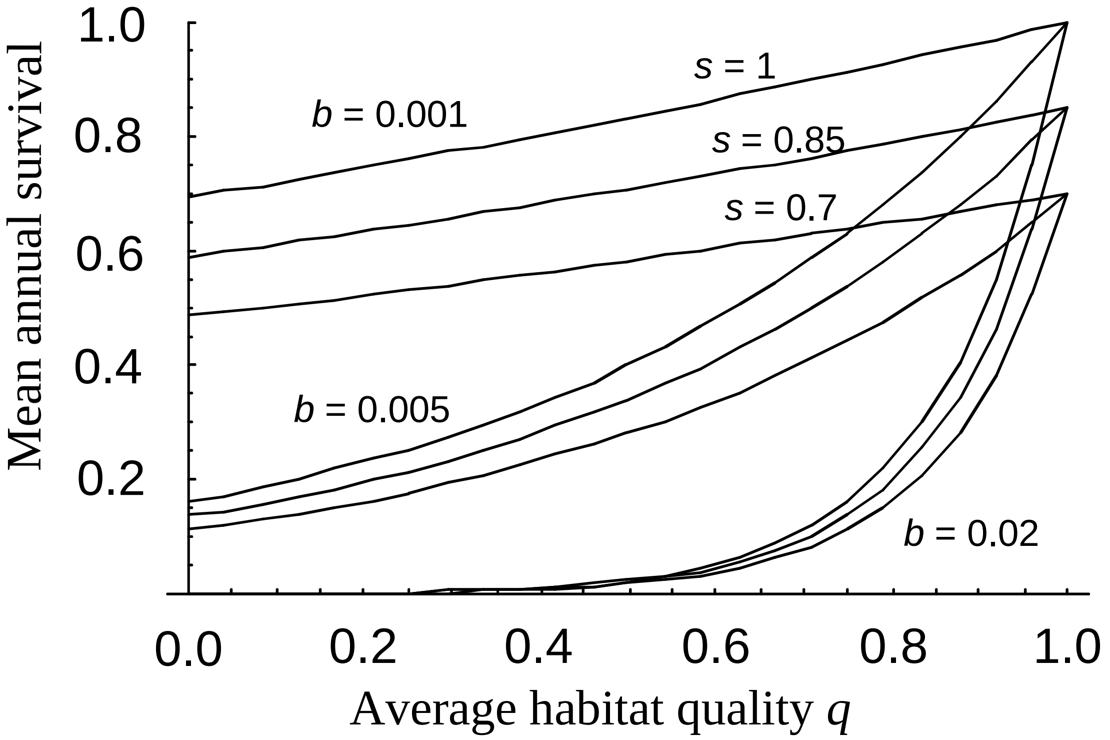


Figure 5.6 Impact of mean habitat quality of pixels used during dispersal on mean annual survival. The parameter *suv* is the annual survival probability in optimal habitat and the parameter *b* describes the increase in the daily risk of mortality with decreasing habitat quality.

5.2.5 Model output

For a given landscape map, model parameterization and start patch (i.e., patches 3, 4, 6, 7, 9, and 12 in Fig. 5.1) one tiger was released and simulated its dispersal movement for one year (i.e., 365 days), or until it died (Fig. 5.7). This simulation was repeated 5000 times to assess patch connectivity. For describing a single dispersal event, I recorded a number of variables. First, all patches the tiger passed during dispersal were recorded. This data is the basis for calculating the connectivity values. Next, I counted the number of times each cell was visited by the dispersing tiger (Fig. 5.7 lower row).

The variables described above were used to calculate, for a given model parameterization and landscape map, several model predictions. I calculated the probability to survive dispersal and conducted a global sensitivity analysis (see section '*Sensitivity analysis*') to explore the response of survived dispersal to variation in individual parameters. I also calculated the connectivity of the source patch to all other target patches being the proportion of cases where a tiger reached a target patch.

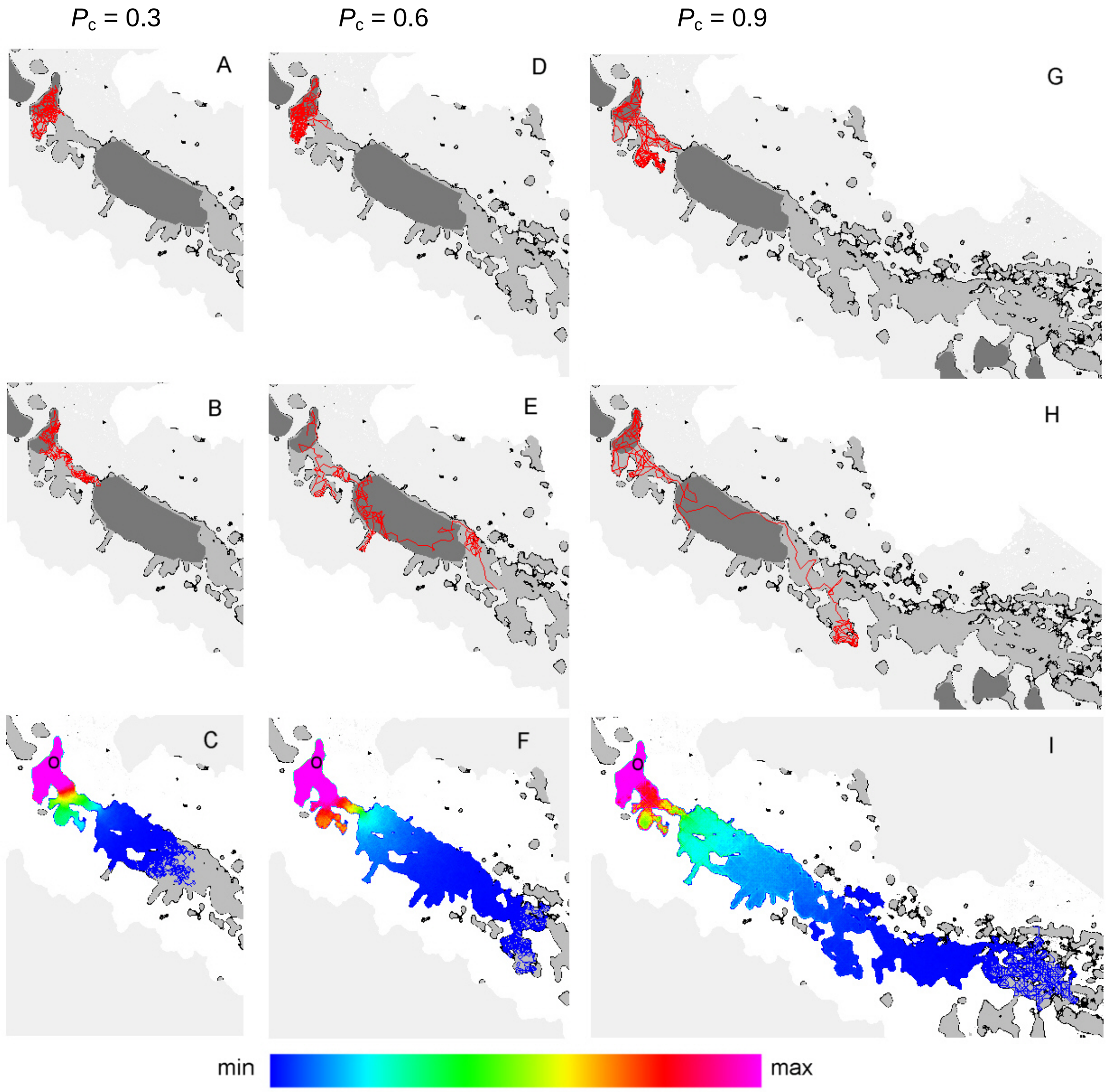


Figure 5.7 Examples of single dispersal events and the resulting probability of use in landscape 1. The dispersing tiger started at the patch 3 (Chilla range of Rajaji NP east), the circles in C, F, and I indicate the release point. Top row: examples of single dispersal events where tigers got trapped in dead ends. Middle row: examples for longer-distance dispersal events. Bottom row: the average probability of use after 5000 simulated dispersal events [blue: lowest density (at least used once), magenta: maximal observed density]. Model parameters were taken from the standard parameterization (Table 1), except S_{max} = 25 and P_C = 0.3 (low autocorrelation in movement; left column), P_C = 0.6 (intermediate autocorrelation in movement; middle column), and P_C = 0.9 (high autocorrelation in movement; right column).

5.2.6 Sensitivity analyses

Based on a “standard parameterization” I varied each parameter over its entire range to explore the response of connectivity to variation in individual parameters (Table 5.1) using linear regression (Fig. 5.8). I used the slope of the linear relationship as sensitivity coefficient, standardized parameter values (between 0-1) and connectivity values without standardization (Wiegand *et al*.

2004a). In case connectivity showed a threshold response, I started regression from the last zero-connectivity value (Fig. 5.8D, J). With this local sensitivity analysis I assess the relative importance of the different parameters and the response of connectivity to changes in the parameters, but it does not consider interactions among parameters.

To assess the relative importance of different parameters and interactions among parameters, I conducted an extensive global sensitivity analysis and explored the full parameter space of the model for those parameters that turned out to be the most important parameters in the local analysis (Wiegand *et al*. 2004b). I explored four values (minimal and maximal value of ranges shown in Table 5.1, and two intermediate values) for each of those *n* parameters and simulated all possible 4^n combinations within the four landscapes. Because of the factorial design of the simulations I used analysis of variance (ANOVA) to analyze the results of the global sensitivity analysis, considering first-order and second-order effects.

5.3 Results

5.3.1 Single simulation run

Landscape structure and autocorrelation in movement have a strong influence on single dispersal events (Fig. 5.7). In this single simulation run example, the dispersing tigers did not always find their way through the relatively narrow corridor II of dispersal habitat that connects the Rajaji National Park with Corbet Tiger Reserve. In many cases they turn or are “trapped” in island-like structures which have no physical connection to the target patch (e.g., Fig. 5.7, top row middle). The density maps that describe the probability that a simulated tiger reaches a given cell show a very steep decline inside the corridor (Fig. 5.7 bottom row).

5.3.2 Sensitivity analyses

5.3.2.1 Local sensitivity analysis

The response of connectivity to changes in the parameter values was mostly linear (Fig. 5.8), except some cases where I observed a threshold behavior which however was linear when omitting the zero values (Fig. 5.8D, J). The connectivity index showed strongly differing sensitivity to changes in the different parameters. In general, I found that the parameter determining autocorrelation in movement P_C was the most sensitive parameter, followed by the number of daily movement steps s_{max} (Fig. 5.8). The model was little sensitive to parameters influencing mortality during dispersal (*b*, and *surv*) and the parameter determining avoidance of matrix (P_{matrix}).

In some situations I observed a strong influence of the landscape composition on connectivity. This happened e.g., in the patch pair 6-7 where patch 7 was only physically linked through a single matrix cell in landscapes 1 and 2, but in landscapes 3 and 4 this corridor was considerably wider (Fig. 5.2C patch in right upper corner in Appendix). As a consequence, connectivity in landscapes 1 and 2 was low (Fig. 5.8G-L) and the avoidance of matrix (P_{matrix}) becomes the most important parameter (Fig. 5.8 I, black dots).

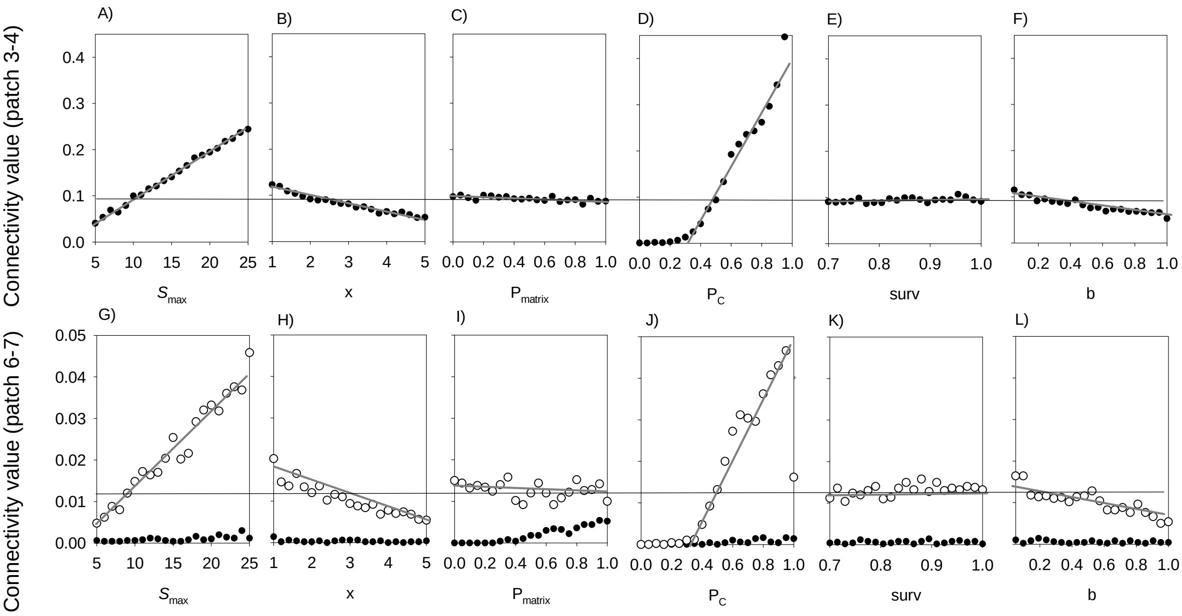


Figure 5.8 Local sensitivity analysis. Examples for the estimated connectivity values between patch 3 and 4 (top) and 6 and 7 (below). The x-axis represents the explored range of parameter to estimate connectivity (see Table 5.1 for parameter definitions). Black dots are for landscape 1 and open circles for landscape 4. The gray lines show the linear regression. I used the (x-axis normalized) slope as index of sensitivity of a given connectivity to the parameter.

5.3.2.2 Global sensitivity analysis: scenario without landscape rehabilitation

The full design for the global sensitivity analysis required 57344 runs for the real landscape (Table 5.2; 4 habitat maps, 5 parameters with 4 levels and 14 patch pairs: $4 \times 4^5 \times 14 = 57344$) and 81920 runs for the two scenarios (Table 5.3; 4 habitat maps, 5 parameters with 4 levels and 10 patch pairs: $4 \times 4^5 \times 10 = 40960$ for each scenario). The global sensitivity analysis largely confirmed the results of the local sensitivity analysis, but detected additional aspects.

Patch pairs with low connectivity (i.e., pairs 6-9, 6-12, 7-9, 7-12) showed a different sensitivity behavior than patch pairs with relatively high connectivity values (i.e., > 0.01; pairs 3-4, 6-7, and 9-12). For pairs of patches with relatively high connectivity (i.e., 3-4, 4-3, 6-7, 7-6, 9-12, 12-9) I found that the parameter P_C was clearly the most important factor, explaining between 32% and 67% of the total sum of squares (Table 5.2), followed by the number of maximal movement steps per day (S_{max}) and an interaction between P_C and S_{max}. An exception was the pair 6-7. In this case I found that the landscape (factor l) and an interaction between landscape and P_C where the next most important factors that followed the parameter P_C. This is because of the narrow corridor connecting in landscapes 1 and 2 the island-like patch 7 which becomes wider for landscapes 3 and 4 (Fig. 5.2C).

In cases where connectivity was low, however, the dominance of the parameter P_C was reduced and other factors and interactions determined connectivity. In this case, connectivity was mostly determined by factors and interactions which influence the distribution of steps moved per day (x and S_{max}) and the straightness of movement (P_C; Table 5.2). This hierarchy in sensitivity behavior is understandable. Fig. 5.1 shows that patch pairs with lower connectivity (i.e., 6-9, 6-12, 7-9, 7-12) were “island-like” patches which were not directly connected via a corridor, but indirectly via a longer distance through the large areas of dispersal habitat located in non-protected mountain areas in Nepal. Conversely, patch pairs with higher connectivity were closer together and/or connected via a direct corridor.

5.3.2.3 Global sensitivity analysis: creating corridors through landscape rehabilitation

The parameter P_C was the dominating parameter accounting for more than 60% of the sum of squares in most corridors (Table 5.3). A notable exception was corridor IV where landscape structure, interactions with landscape structure, and matrix avoidance (P_{matrix}) were dominant for scenario 1. This is because for landscape 1 and 2 and scenario 1 there is no physical connectivity between patches 8 and 9, for landscapes 3 and 4 of scenario 1 it is very weak, but for scenario 2 there is a wide corridor > 1km of dispersal habitat. Interestingly, the decline in survival with habitat quality (b) became important for corridors I and V. This is because the corridor goes through highly populated (and disturbed) areas.

Connectivity values were not symmetric for most corridors (Fig. 5.10). For example, connectivity from patch 2 (Rajaji NP west) to patch 3 (Chilla range of Rajaji NP east) is much higher than from patch 3 to patch 2 (Fig. 5.10). This is because tigers are more likely to move from patch 3 into the southeast direction than through the narrow corridor in northwest direction. The same applies for corridor V (Fig. 5.10).

In case of survival dispersal, for a given model parameterization and landscape map, the largest contribution came from the parameter b that describes the increase in the daily risk of mortality with decreasing habitat quality (Table 5.4). The second most important contribution is coming from the parameter S_{max} and then P_c. Interestingly, mortality is driven by different parameters than connectivity and is not primarily important for connectivity.

Table 5.2 Global sensitivity analysis for the unmodified landscapes using ANOVA. The table shows for each of the seven pairs of patches with non-zero connectivity the total sum of squares and percentage of the total sum of squares explained by a given factor or interaction. The factorial design for each patch pair included 4 habitat maps and 5 parameters with 4 levels, thus requiring 4 × 4^5 = 4096 individual analyses.

	Patch pair													
	3-4	**4-3**	**6-7**	**7-6**	**6-9**	**9-6**	**6-12**	**12-6**	**7-9**	**9-7**	**7-12**	**12-7**	**9-12**	**12-9**
S.of squares	102.8	11.3	1.6	3.4	0.11	0.34	0.10	0.01	0.14	0.21	0.12	0.01	12.5	0.61
P_C	67	60	32	38	28	29	21	22	22	23	17	18	44	37
S_{max}:$\mathrm{P_C}$	6	11	7	9	19	15	21	21	15	9	17	15	15	16
S_{max}	8	11	8	11	9	12	11	11	15	9	8	10	15	13
x:P_C	2	3	2	3	9	6	11	13	7	5	8	10	5	7
x	3	4	3	4	9	6	11	7	7	5	8	6	5	7
P_c:l	0	0	15	6	5	6	1	1	8	14	8	11	0	1
l	0	0	15	7	3	3	1	1	7	9	8	6	0	0
S_{max}:x	1	1	1	1	3	3	11	7	3	2	8	5	2	3
P_C:b	4	2	2	4	3	3	3	2	3	5	3	2	3	2
b	5	2	2	5	2	3	2	1	3	2	2	1	3	2
S_{max}:l	0	0	3	1	2	3	1	1	4	5	4	6	0	0
P_{matrix}:Pc	2	2	1	1	1	3	2	4	0	1	1	1	2	5
P_{matrix}:l	0	0	4	4	2	3	0	0	2	5	1	2	0	0
S_{max}:b	1	1	1	2	1	3	2	1	2	1	2	1	2	2
P_{matrix}	1	2	1	1	0	1	1	2	0	1	0	1	2	3
x:l	0	0	1	1	1	1	0	0	2	2	2	3	0	0
x:b	0	0	1	1	1	1	2	1	1	1	1	1	1	0
b:l	0	0	1	1	0	0	0	0	1	1	1	1	0	0
S_{max}:P_{matrix}	0	0	0	0	0	0	1	2	0	0	0	0	0	2
x:P_{matrix}	0	0	0	0	0	0	0	1	0	0	0	0	0	1
P_{matrix}:b	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Table 5.3 Global sensitivity analysis for the landscape restoration scenario 1/scenario 2 using ANOVA. The table shows for each rehabilitated corridor (which had before connectivity of zero) the total sum of squares (T_{SSQ}) and percentage of the total sum of squares explained (%$_{EX}$) by a given factor. The factorial design for each patch pair included 4 habitat maps and 5 parameters with 4 levels, thus requiring $4 \times 4^5 = 4096$ individual analyses.

	corridor I		**corridor II***		**corridor III**		**corridor IV**		**corridor V**	
	2-3	**3-2**	**3-4**	**4-3**	**5-6**	**6-5**	**8-9**	**9-8**	**11-12**	**12-11**
T_{SSQ}	144/149	9/71	103/119 /105	11/15 /17	14/17	17/19	7/170	11/162	294/339	13/18
%$_{EX}$:										
P_C	83/78	61/74	67/71/75	60/63/65	57/58	63/62	14/71	8/80	67/70	62/60
l	0/1	2/0	0/0/0	0/0/0	0/0	0/0	27/0	39/2	0/0	0/0
S_{max}	7/10	13/10	8/7/6	11/10/10	12/12	10/10	4/12	2/5	7/7	10/11
b	2/4	10/9	5/5/5	2/2/3	3/3	5/5	1/1	2/1	12/6	5/13
S_{max}:P$_c$	2/1	2/1	6/4/4	11/10/10	12/11	8/8	2/6	0/0	3/2	8/8
P_c:l	0/0	1/0	0/0/1	0/1/1	0/0	1/0	19/0	9/1	0/0	1/1
P_{matrix}:l	0/0	0/0	0/0/0	0/0/0	0/0	0/0	9/0	14/0	0/0	0/0
P_{matrix}	1/1	1/0	1/1/0	2/1/1	1/1	1/0	7/1	13/2	0/0	1/1
x	2	4	3/2/2	4/3/3	4	3	1	1	2	3
P_C:b	1	2	4/4/4	2/3/3	3	4	0	0	7	4
P_{matrix}:Pc	0	0	2/1/1	2/2/1	1	1	5	3	0	1
x:P_c	1	1	2/1/1	3/3/3	4	2	1	0	1	2
S_{max}:l	0	0	0/0/0	0/0/0	0	0	5	2	0	0
S_{max}:b	0	1	0/1/1	0/1/1	1	1	0	0	1	1
S_{max}:x	0	1	0/0/0	0/1/1	1	1	0	0	0	1
b:l	0	0	0/0/0	0/0/0	0	0	1	3	0	0
x:l	0	0	0/0/0	0/0/0	0	0	2	1	0	0
S_{max}:P_{matrix}	0	0	0/0/0	0/0/0	0	0	1	1	0	0
x:b	0	0	0/0/0	0/0/0	0	0	0	0	0	0
P_{matrix}:b	0	0	0/0/0	0/0/0	0	0	0	1	0	0
x:P_{matrix}	0	0	0/0/0	0/0/0	0	0	0	0	0	0

*Here given the results for no landscape manipulation, scenario 1 and scenario 2.

Table 5.4 Global sensitivity analysis of the survival of dispersing tiger from source patch for a given model parameterization and landscape map for the landscape restoration scenario 1 / scenario 2 using ANOVA. The table shows for each source patch the total sum of squares (T_{SSQ}) and percentage of the total sum of squares explained ($\%_{EX}$) by a given factor.

	Source patch							
	2	**3**	**5**	**6**	**8**	**9**	**11**	**12**
T_{SSQ}	190/192	284/272	198/206	261/267	124/144	268/245	303/316	208/216
$\%_{EX}$:								
b	51/56	60/65	45/45	55/57	31/33	63/64	67/70	32/33
S_{max}	22/22	20/19	23/23	24/23	21/22	19/19	10/9	24/23
P_{c}	10/8	4/2	10/10	5/5	8/12	0/0	12/11	21/22
x	5/5	5/4	6/6	6/5	6/6	4/4	2/2	6/6
S_{max}:b	5/5	4/4	5/5	5/4	5/5	4/4	1/1	5/5
P_{c}:b	3/2	1/1	2/3	1/1	3/3	0/0	3/2	5/5
x:b	1/1	1/1	1/1	1/1	1/1	1/1	0/0	1/1
S_{max}:$\mathrm{P_c}$	1/0	0/0	0/0	0/0	1/1	0/0	3/4	1/1
P_{matrix}	1/0	2/2	3/2	1/1	8/6	3/3	0/0	2/1
l	1/0	2/1	2/2	1/0	7/5	2/3	0/0	1/1
P_{matrix}:l	0/0	1/1	1/1	0/0	3/2	0/1	0/0	0/0
S_{max}:x	0/0	1/1	0/0	1/1	0/0	1/1	0/0	0/0
x:P_{c}	0/0	0/0	0/0	0/0	0/0	0/0	1/1	0/0
P_{matrix}:b	0/0	0/0	1/1	0/0	2/1	1/1	0/0	0/0
b:l	0/0	0/0	1/0	0/0	2/1	0/1	0/0	0/0
P_{matrix}:Pc	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
P_{c}:l	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
S_{max}:l	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
S_{max}:P_{matrix}	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
x:l	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0
x:P_{matrix}	0/0	0/0	0/0	0/0	0/0	0/0	0/0	0/0

5.3.3 Connectivity values

The global sensitivity analyses revealed that almost all uncertainty in the connectivity values was controlled by the parameter P_C that determines the autocorrelation in the movement (Figs. 5.9 and 5.10). In most cases, the variability introduced by all other parameters and the four alternative landscapes was remarkably low. On the first view this contradicts the result that P_C becomes less dominant in cases where connectivity was low, however, even in this case connectivity appeared in interaction terms (Tables 5.2 and 5.3). Thus, although I lack data to precisely parameterize the dispersal model, I obtained robust connectivity estimates where almost all uncertainty is concentrated into a single unknown parameter.

As already observed in the local sensitivity analysis (Fig. 5.8D, J), the response of connectivity to the parameter P_C is characterized by threshold behavior. Clearly, the autocorrelation in movement determines the maximum distance moved, and patches can only become connected if a tiger is at least occasionally able to cover the distance the two patches are apart. However, once the movement is directed enough to reach the target patch, connectivity increases monotonously with parameter P_C. In most cases, the threshold value was at about $P_C = 0.3$ (Table 5.5), which coincides with the value in P_C where the probability to return becomes low (Fig. 5.5B). With $P_C \leq 0.3$ the movement patch is rather curvy and undirected (see Fig. 5.7).

Landscape manipulation that restored natural or semi-natural vegetation to reach the status of dispersal habitat (i.e., scenario 1) was sufficient for all corridors to produce positive connectivity values if the movement was sufficiently autocorrelated (Fig. 5.10). In all cases with P_C = 0.6 and 0.9, connectivity was larger than 0.0075, meaning that at least one of every 133 dispersing tigers may reach the target patch (Fig. 5.10).

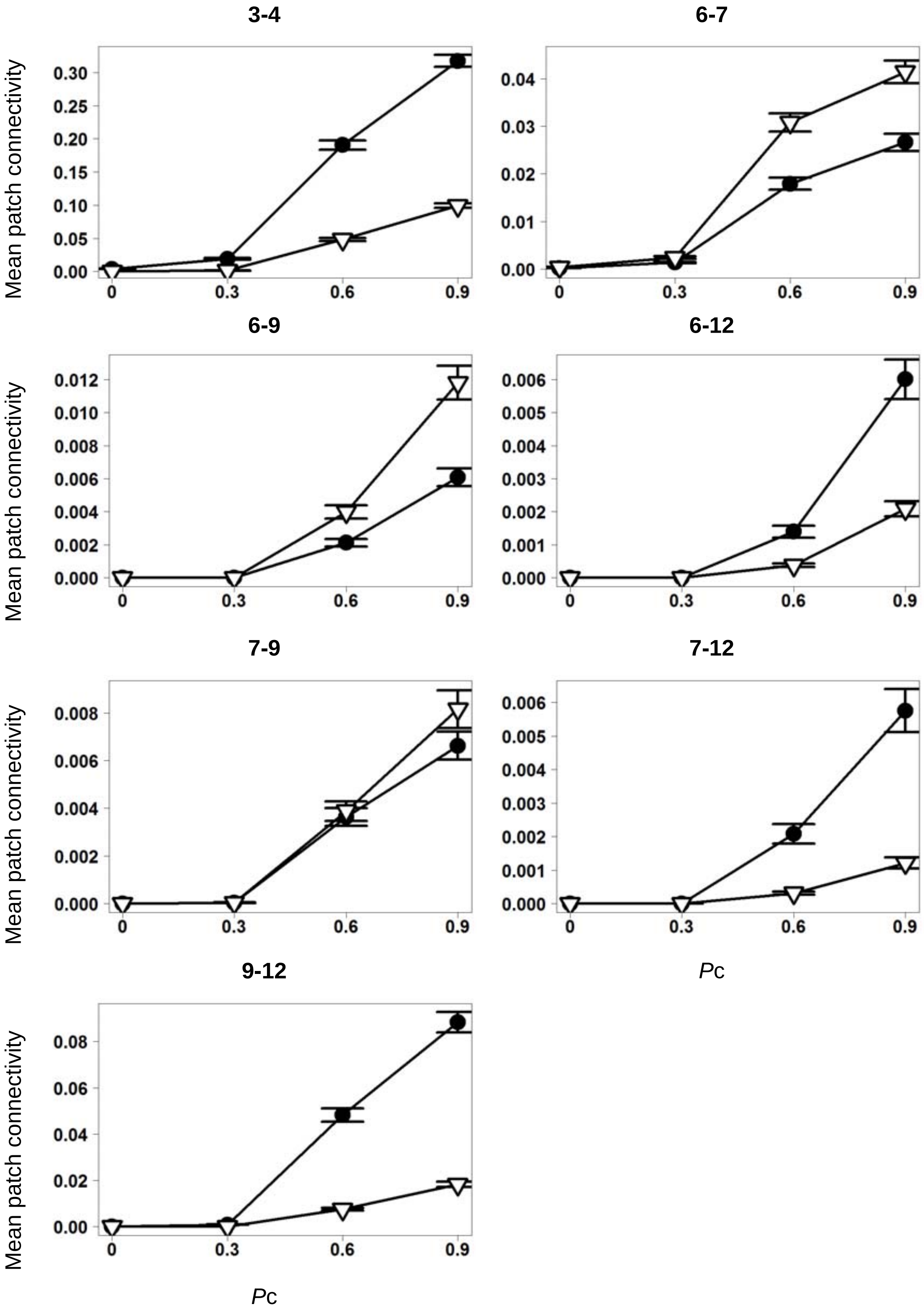


Figure 5.9 Average connectivity and 95% CI intervals for non-manipulated landscapes. Average connectivity values were calculated based on all simulations of the global sensitivity analysis for landscapes without corridor restoration but separately for the four values of the parameter P_C that controls the autocorrelation in the movement. Dark circles represent the animal movement in the direction pointed out in the corridor title. Inverted open triangles represent the opposite direction.

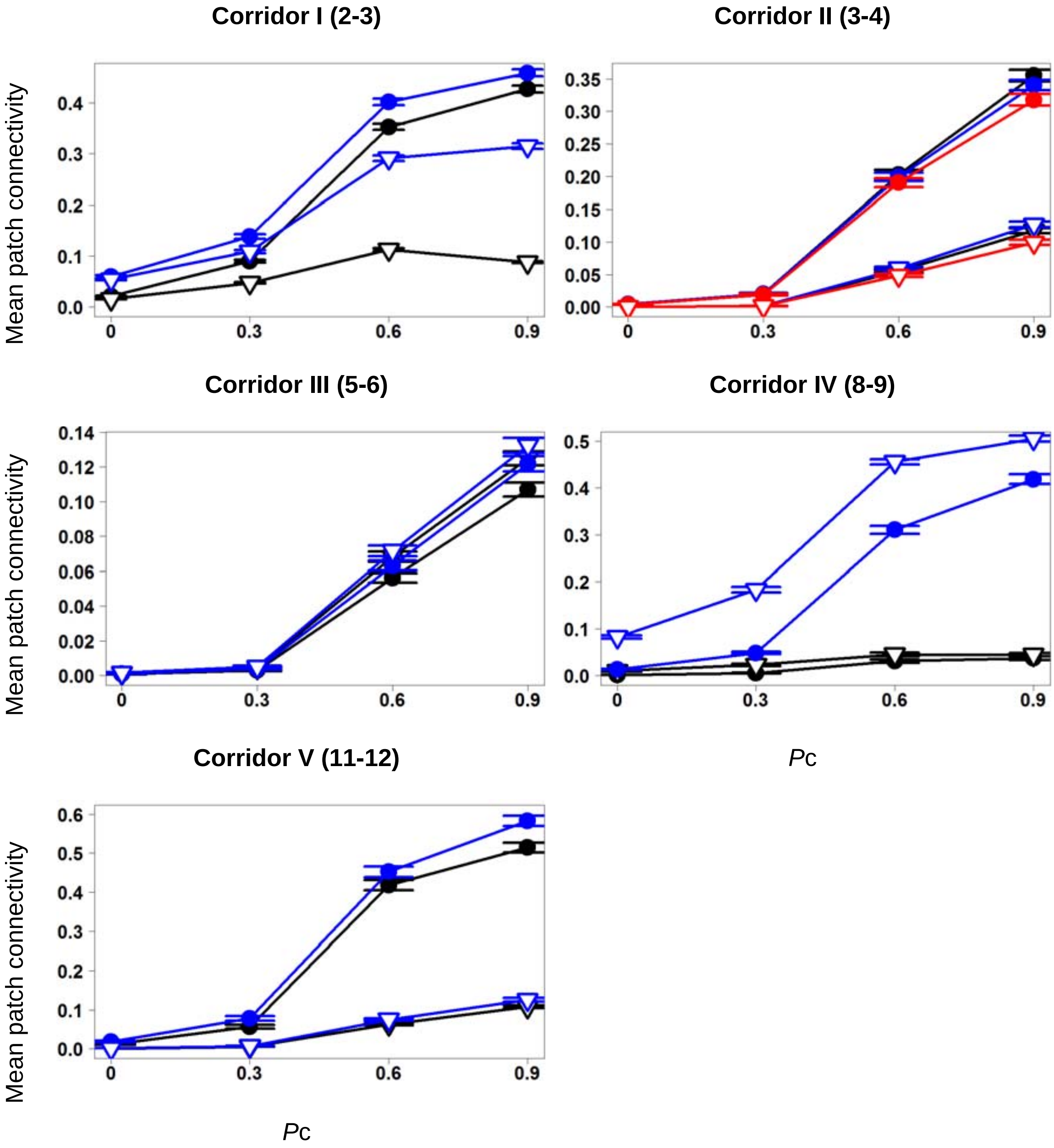


Figure 5.10 Average connectivity and 95% CI intervals for the scenarios with corridor restoration. Average connectivity values were calculated based on all simulations of the global sensitivity analysis for landscapes manipulation scenario 1 (black) and scenario 2 (blue), but separately for the four values of the parameter P_C that controls the autocorrelation in the movement. Dark circles represent the animal movement in the direction pointed out in the corridor title. Inverted open triangles represent the opposite direction. For comparative purpose I show for corridor II also the results of the analyses without corridor restoration.

Corridors I and V facilitated high connectivity. For corridor I this was true for both directions, but for corridor V only in one direction from patch 11 to 12 (island to mainland), but not in the other direction from patch 12 to patch 11 (mainland to island) where connectivity was much lower. Corridors III and IV, although involving short distances between patches, facilitated fewer successful dispersal events.

The 0.5km buffer around the restored dispersal habitat did not substantially enhance connectivity. For corridors I, III, and V, no positive change were observed, but a slight decline in corridor I moving from patch 3 to patch 2. This happened because tigers could now also use the escape via corridor II in southeast direction which was also improved. Only corridor IV improved considerably for scenario 2, compared with scenario 1 (see section "*Global sensitivity analysis: creating corridors through landscape rehabilitation"*).

In all cases of P_C there is a negative correlation between the cost values and the connectivity values as higher cost means lower connectivity. The correlations were relatively high: the rank correlation coefficient was r = 0.7 for $P_C = 0$ and 0.3, and r = 0.6 for $P_C = 0.6$ and 0.9. Negative exponential regression gave good fit ($r^2 > 0.55$) at low P_C values ($<= 0.6$) but it was low ($r^2 < 0.5$) for high values of this parameter (Fig. 5.11). However, especially note for $P_C = 0.6$ and 0.9 the wide range of least cost values that result for smaller values of simulated connectivity (i.e., connectivity < 0.15; Fig. 5.11) which indicate for certain circumstances substantial differences in the predictions between these two methods.

Table 5.5 Local sensitivity analysis showing the threshold value of the parameter, P_c for connectivity between different patch pairs. Response of connectivity to variation in parameter *P*c was explored as a function of slope in linear regression. Threshold value in which the connectivity value started increasing below that value connectivity was zero.

Patch pairs	**Habitat map**	***P*c- threshold value**
3-4	1	0.3
3-4	2	0.3
3-4	3	0.25
3-4	4	0.3
4-3	1	0.35
4-3	2	0.35
4-3	3	0.35
4-3	4	0.35
6-7	1	0.3
6-7	2	0.3
6-7	3	0.3
6-7	4	0.3
6-9	1	0
6-9	2	0
6-9	3	0
6-9	4	0
6-12	1	0
6-12	2	0
6-12	3	0
6-12	4	0
7-6	1	0.25
7-6	2	0.35
7-6	3	0.25
7-6	4	0.25
7-9	1	0
7-9	2	0
7-9	3	0
7-9	4	0
7-12	1	0
7-12	2	0.3
7-12	3	0
7-12	4	0.5
9-6	1	0
9-6	2	0.4
9-6	3	0
9-6	4	0
9-7	1	0
9-7	2	0
9-7	3	0
9-7	4	0.35
9-12	1	0.35
9-12	2	0.35
9-12	3	0.35
9-12	4	0.35

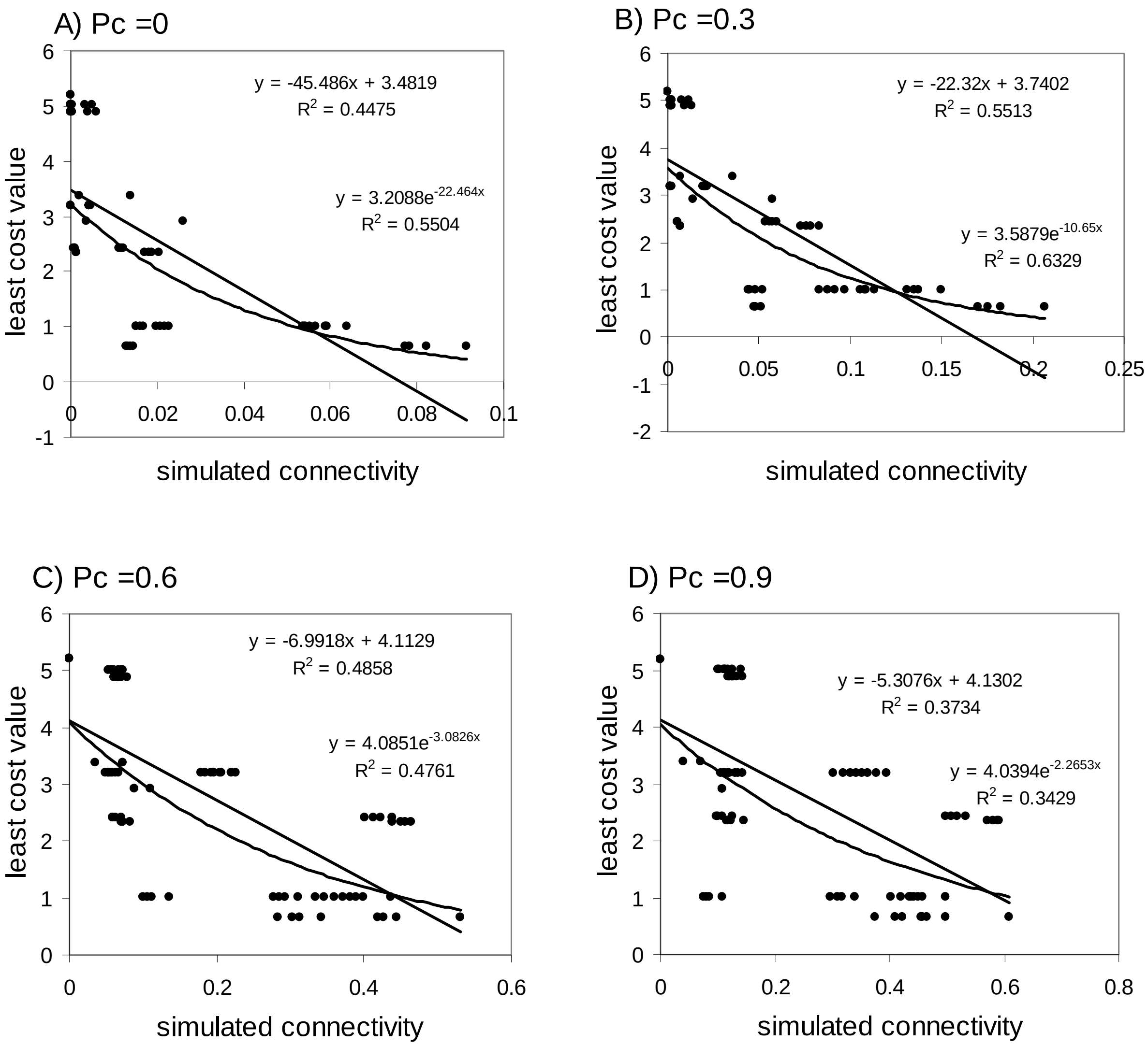


Figure 5.11 Comparison of cost value of shortest path calculated by the least cost-path analysis for each corridor in the scenarios 1 and 2 and the respective connectivity value from simulation at each level of parameter P_c used in global sensitivity analysis. The least cost values were normalized to compare with the simulated connectivity values.

5.4 Discussion

This study showed that individual-based dispersal models can produce robust estimates of patch connectivity within complex landscapes and allows for an assessment of the effect of potential landscape restoration on connectivity. Assessment of inter-patch connectivity is currently one of the major challenges in conservation biology and landscape management (Revilla *et al*. 2004; Tracey 2006; Vuilleumier and Metzger 2006). This approach can address this management question even if data are limited and could therefore be applied for a variety of species with similar management problems.

5.4.1 Modelling issues

In this modelling approach, I constructed a relatively simple individual-based dispersal model based on published data on behavior of dispersing tiger (e.g. Smith 1993) and other carnivores (Revilla *et al*. 2004) to address my management motivated questions concerning inter-patch connectivity in the fragmented TAL landscape. To overcome the problem of parameter uncertainty which arises for this cryptic and endangered species, I conducted extensive sensitivity analyses to compensate for lack of field data for parameter estimation. Note that dispersal models are only one component of a spatially-explicit population model and have therefore usually much less parameters. This allowed for a complete sensitivity analysis involving variation of all parameters of the model simultaneously.

I combined both local and global methods for assessing the sensitivity of inter-patch connectivity to model input parameters. A somewhat surprising outcome of the global sensitivity analysis is the overpowering effect of the parameter P_C that controls the autocorrelation in movement. I found that the simulated inter-patch connectivity values were essentially determined by this parameter whereas all other parameters (and different underlying landscapes) only caused small to moderate variations. This result is good news since it demonstrates that this model is robust against variation in almost all parameters and that I have to deal essentially with one unknown factor. The underlying reason for this effect is the strong correlation between the autocorrelation in movement and maximum dispersal distance resulting from stochastic simulation of the model for a given parameterization. However, for this model which includes complex landscape structure, mortality, and behavioural movement rules I initially expected that other factors would interact to a much larger extent. Models of individual dispersal have often used a strong directionality in the movement (e.g., Schippers *et al*. 1996; Letcher *et al*. 1998; Zollner and Lima 1999), but Revilla *et al*. (2004) found relatively low degree of autocorrelation in intraday movement. This model therefore points to a need to address this general aspect of animal movement in further field studies.

5.4.2 Inter-patch connectivity

This approach clearly showed that connectivity is not solely a function of distance between patches. In simulations, which are based on real landscape structure, I found that the simulated tigers may become frequently trapped in dead ends of the landscape. This trapping effect reduces the net flux into the real corridor and can substantially reduce inter-patch connectivity. I also found clear evidence for asymmetrical inter-patch connectivity which has been previously observed in simulation studies (e.g., Gustafson and Gardner 1996; Schippers *et al.* 1996; Revilla *et al.* 2004) and field studies (e.g., Ferreras 2001). In this study, asymmetrical inter-patch connectivity arose because landscape structure could have both canalizing and diffusing effects on movement, which depended strongly from the context of the start patch.

When analyzing factors that influenced connectivity by means of a sensitivity analysis, I found that patch pairs with low connectivity showed somewhat different sensitivity behaviour than patch pairs with relatively high connectivity values. The dispersal corridors between patches with high connectivity were in general simple, often providing a direct linkage between patches. In contrast, corridors between patches with lower connectivity were often only linked via narrow corridors which were difficult to find, or the patches were “island-like” patches which were only indirectly linked by the larger blocks of dispersal habitat located in non-protected mountain areas in

Nepal. Clearly, the more complex the landscape structure a dispersing tiger must cross to reach a patch, the more complex the interactions between landscape structure and movement become in determining connectivity.

Results of this study outline that the details of landscape structure, such as dead ends, island patches, or matrix and its interactions with species specific behaviour may matter substantially in determining inter-patch connectivity and that simplifying approaches may not be able to effectively capture this complexity. These results are thus in concert with recent studies on connectivity based on individual-based model that showed that including the behavioural ecology of the target species and the landscape structure are imperative when assessing connectivity (Gustafson and Gardner 1996; Gardner and Gustafson 2004; Revilla *et al*. 2004; Kramer-Schadt *et al*. 2004; Wiegand *et al*. 2004b; Graf *et al*. 2007; Revilla and Wigand, *in press*) rather than considering it purely a function of distance (Revilla *et al*. 2004).

I also found that inter-patch connectivity may be more complex than conceptualized by least-cost analysis, a method that has been used frequently in the fields of landscape ecology and conservation planning to assess connectivity between suitable patches (e.g., Adriaensen *et al*. 2003; Nikolakaki 2004; Wikramanayake *et al*. 2004; Gonzales and Gergel 2007). Models based on least-cost path analysis only provide an indication of pathways with the lowest relative costs without explicitly considering the dispersing animal behaviour in the model (Wikramanayake *et al*. 2004; Gonzales and Gergel 2007). I found that animals may not find the optimal path (or even an approximately optimal path) in some situations, but may become trapped in specific landscape structures. If there is a big difference between the optimal path and alternative paths connectivity will be severely overestimated by the least cost path. Thus, cost path may work well in simple landscapes for nearly random walks but it fails in more complicated landscapes with narrow passages, dead ends etc. which are, however, the ones of interest for conservation.

5.4.3 Management implications

Most of the remaining large patches of intact habitat in the TAL are located within protected areas because the forests outside become increasingly disturbed by human activity. Although tigers occur at relatively high densities in these protected areas, these refuges are fast becoming insular, and there are indications of inbreeding depression in populations isolated within reserves (Smith and McDougal 1991). Patch-level effects of habitat fragmentation on population persistence may only become manifest some decades after this process started and, possibly, after a certain threshold value is surpassed (Fahrig 2001). Thus, it is imperative to initiate management actions before isolation critically affects the persistence of populations. The persistence of tiger populations within protected areas can be enhanced if these populations are managed as a metapopulation (Wikramanayake *et al*. 2004).

Results of this study showed that several of these habitat patches may be island-like and already effectively isolated. This applies for patches located between Nepal and India (corridor III-V) and also to patches on the Indian side of the landscape (corridor I: Chilla Motichur area, Dudhwa NP- Kishanpur WLS (patch 10), and Corbett TR-Pilibhit FD). A landscape manipulation in terms of corridor restoration may be a relatively cheap management action. I found that most of the patches in India and between India and Nepal could become connected under this scenario. Moreover, an additional 0.5km buffer around the restored dispersal habitat did not substantially enhance connectivity, which makes this management action even more sensible.

Connectivity between protected areas is crucial for effective and sustainable landscape level conservation. Twenty years ago an exercise proposing a network of protected areas connected by corridors as a conservation strategy in India (Rodgers and Panwar 1988; Sukumar 1991) resulted in highlighting the importance of Chilla-Motichur and Rajaji-Corbett corridors for large mammal conservation in the Rajaji and Corbett NP areas (Johnsingh *et al*. 1990; Johnsingh 1992; Sunderraj *et al*. 1995). Despite the fact that the Chilla- Motichur corridor was identified in the early 1980s, its conservation status has constantly declined over time (Johnsingh *et al*. 1990; Johnsingh 1992), subsequently resulting in considerable loss of corridor area (Nandy *et al*. 2007). However, results of this study showed that improving the quality of currently remaining degraded corridor habitats by reducing the anthropogenic disturbances may result in regaining the lost connectivity for tiger in Rajaji NP. Although connectivity in the already good habitat quality Rajaji-Corbett corridor area did not improve under the scenarios, it is recommended to reduce the anthropogenic disturbance in there to ensure that dispersing tiger reaching the another protected area successfully (Johnsingh *et al*. 2004). By doing so, ensuring connectivity in these corridors would enable to create a single large block of a functioning unit (4052 km²) for tiger in the Indian side of TAL (Johnsingh *et al*. 2004).

The three functional trans-boundary dispersal corridors, Pilibhit-Suklaphanta, Dudhwa-Basanta and Katerniaghat-Bardia, between India and Nepal are vital for creating a single landscape level functioning unit of the entire TAL. These corridors connect India’s Dudhwa NP, Katerniaghat and Kishanpur WLSs and Pilibhit FD with the Nepal’s Bardia NP and Suklaphanta WLR through the Churia foothill forests. Results show that improving the quality of the remaining degraded habitats and adding the 0.5km buffer area in case of Dudhwa-Basanta corridor may create a single functional unit of these fragmented habitats through improved connectivity. Although different habitat blocks showed connectivity under the landscape restoration scenarios, there are no protected areas in the long forest stretch between Corbett NP in India and Sulaphanta WLR in Nepal and Bardia NP and Sukalphanta WLR in Nepal. Further human disturbance and habitat fragmentation in these areas could potentially mitigate the successful dispersal of tiger (Johnsingh *et al*. 2004; Wikramanayake *et al*. 2004).

Dispersal model assessed the permeability of the linkage habitat and estimated the connectivity values in the TAL. But it is essential to conduct a future study that considers the functional level of connectivity that not only depends on the permeability of the linkage habitat, but also upon conditions in the source and destination patches, such as the production of sufficient potential dispersers (Kramer-Schadt *et al*. 2005; Crooks and Sanjayan 2006; Revilla and Wiegand, *in press*). Therefore, a spatially explicit population model to assess the functional connectivity by examining the roles of all landscape elements in promoting or hindering effective dispersal is recommended.

5.5 Summary

- Most rare and endangered species such as tiger exist in human-dominated landscapes as small, fragmented and isolated populations across its range. The Terai Arc Landscape (TAL) is one of the top priority landscapes for tiger conservation that was once continuous across the Himalayan foothills but is now highly fragmented and most of the remaining large, intact habitats are located within protected areas and in stepping stone population model. Connectivity between tiger populations occupying the remaining fragments is a key factor for persistence.

- I describe an individual-based, spatially explicit dispersal model of dispersing tiger behaviour to (1) assess the inter-patch connectivity among the major (protected) habitat patches for dispersal of tiger in the complex and heterogeneous TAL and (2) to investigate the effect of potential initiatives to restore identified potential corridors for dispersal.

- Model clearly revealed that connectivity is not solely a function of distance between patches, but an outcome of the interplay between behaviour and landscape matrix, with asymmetric connectivity explained by canalizing or diffusing effects of the landscape, and depending on the landscape context of the starting patch. The most important model parameter determining patch connectivity was the autocorrelation in movement, followed by the daily movement capacity.

- Results have consequences for the conservation of tiger populations, since several of the habitat patches are likely to be island-like and already effectively isolated for dispersal. However, most of the patches in India and between India and Nepal could become connected under the simulated scenarios of corridor restoration. Ensuring this may mitigate the genetic consequences of small population size and effective isolation on tiger populations in this landscape. More widely, this study has shown that combining habitat models with individual-based and spatially explicit dispersal models is a powerful and robust approach that could be widely applied to quantify patch connectivity even for species with scarce data.

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APPENDICES

Appendix I Statistical comparisons for landscape variables for sambar between presence and absence locations. For variable definitions see Chapter 3.

Variable	Presence	Absence	Univariate tests†		
			X^2	*P*	
C1	76.31 ± 0.97	23.34 ± 1.03	252.27	< 0.01	*
F3C1	76.06 ± 0.68	25.98 ± 0.83	313.60	< 0.01	*
F4C1	75.74 ± 0.66	26.81 ± 0.84	327.02	< 0.01	*
F6C1	74.88 ± 0.62	27.94 ± 0.85	363.55	< 0.01	*
F7C1	74.33 ± 0.62	28.13 ± 0.85	375.35	< 0.01	*
F8C1	73.61 ± 0.61	28.27 ± 0.85	385.92	< 0.01	*
F10C1	72.13 ± 0.61	28.32 ± 0.84	408.28	< 0.01	*
F13C1	69.92 ± 0.60	28.37 ± 0.83	432.79	< 0.01	*
F21C1	64.92 ± 0.59	27.91 ± 0.77	492.70	< 0.01	*
C2	14.69 ± 0.61	41.77 ± 1.24	69.48	< 0.01	*
F3C2	15.25 ± 0.49	40.64 ± 0.97	118.35	< 0.01	*
F4C2	15.38 ± 0.48	40.00 ± 0.94	123.80	< 0.01	*
F6C2	15.77 ± 0.47	38.52 ± 0.88	132.07	< 0.01	*
F7C2	15.95 ± 0.46	37.96 ± 0.86	133.19	< 0.01	*
F8C2	16.14 ± 0.46	37.34 ± 0.84	131.71	< 0.01	*
F10C2	16.44 ± 0.44	36.20 ± 0.80	123.95	< 0.01	*
F13C2	16.75 ± 0.42	34.55 ± 0.75	113.39	< 0.01	*
F21C2	17.27 ± 0.37	30.52 ± 0.61	80.27	< 0.01	*
C3	0.41 ± 0.07	6.73 ± 0.69	104.72	< 0.01	*
F3C3	0.41 ± 0.04	5.81 ± 0.48	87.11	< 0.01	*
F4C3	0.44 ± 0.04	5.57 ± 0.45	82.46	< 0.01	*
F6C3	0.50 ± 0.05	5.06 ± 0.40	85.55	< 0.01	*
F7C3	0.53 ± 0.05	4.88 ± 0.38	88.82	< 0.01	*
F8C3	0.58 ± 0.06	4.69 ± 0.36	89.23	< 0.01	*
F10C3	0.68 ± 0.07	4.38 ± 0.33	90.88	< 0.01	*
F13C3	0.83 ± 0.09	4.03 ± 0.30	94.56	< 0.01	*
F21C3	0.94 ± 0.10	3.49 ± 0.25	97.21	< 0.01	*
C4	2.88 ± 0.26	10.64 ± 0.62	20.97	< 0.01	*
F3C4	2.87 ± 0.14	10.22 ± 0.39	54.56	< 0.01	*
F4C4	2.99 ± 0.14	10.20 ± 0.36	77.52	< 0.01	*
F6C4	3.22 ± 0.13	10.58 ± 0.33	137.07	< 0.01	*
F7C4	3.36 ± 0.13	10.81 ± 0.32	160.07	< 0.01	*
F8C4	3.56 ± 0.14	11.08 ± 0.31	179.86	< 0.01	*
F10C4	4.01 ± 0.14	11.60 ± 0.30	213.12	< 0.01	*
F13C4	4.71 ± 0.15	12.40 ± 0.29	253.93	< 0.01	*
F21C4	6.48 ± 0.16	14.29 ± 0.27	341.82	< 0.01	*
C5	2.13 ± 0.19	4.65 ± 0.33	0.00	0.95	
F3C5	1.98 ± 0.09	4.75 ± 0.20	0.02	0.88	
F4C5	2.00 ± 0.08	4.77 ± 0.19	0.53	0.47	
F6C5	2.06 ± 0.08	4.97 ± 0.17	11.00	< 0.01	*
F7C5	2.11 ± 0.07	5.05 ± 0.17	18.05	< 0.01	*
F8C5	2.18 ± 0.07	5.14 ± 0.16	27.73	< 0.01	*
F10C5	2.36 ± 0.07	5.33 ± 0.15	48.64	< 0.01	*
F13C5	2.69 ± 0.08	5.53 ± 0.14	71.73	< 0.01	*
F21C5	3.52 ± 0.08	5.85 ± 0.12	89.16	< 0.01	*
C6	1.49 ± 0.24	3.86 ± 0.41	8.56	< 0.01	*

Appendix I continued.

Variable	Presence			Absence			Univariate tests†			
							X^2		*P*	
F3C6	1.45	±	0.14	3.96	±	0.26	5.58		0.01	*
F4C6	1.40	±	0.13	3.90	±	0.24	12.68	<	0.01	*
F6C6	1.37	±	0.11	3.97	±	0.22	46.39	<	0.01	*
F7C6	1.40	±	0.10	4.03	±	0.21	65.61	<	0.01	*
F8C6	1.46	±	0.10	4.11	±	0.21	85.20	<	0.01	*
F10C6	1.56	±	0.10	4.34	±	0.20	119.70	<	0.01	*
F13C6	1.78	±	0.10	4.67	±	0.19	153.31	<	0.01	*
F21C6	2.32	±	0.10	5.65	±	0.18	250.48	<	0.01	*
C7	1.15	±	0.25	5.71	±	0.69	0.24		0.62	
F3C7	1.11	±	0.15	5.23	±	0.44	0.30		0.58	
F4C7	1.19	±	0.14	5.19	±	0.41	0.14		0.71	
F6C7	1.30	±	0.14	4.98	±	0.36	0.00		0.97	
F7C7	1.36	±	0.14	4.91	±	0.35	0.04		0.84	
F8C7	1.44	±	0.14	4.82	±	0.33	0.08		0.77	
F10C7	1.61	±	0.15	4.66	±	0.30	0.10		0.75	
F13C7	1.83	±	0.17	4.43	±	0.27	0.67		0.41	
F21C7	2.31	±	0.17	4.30	±	0.21	2.08		0.15	
MAE	455.41	±	8.02	203.00	±	4.59	719.01	<	0.01	*
MAE3	550.11	±	9.90	224.03	±	5.74	723.46	<	0.01	*
MAE4	575.85	±	10.44	229.78	±	6.09	722.99	<	0.01	*
MAE6	628.52	±	11.53	241.37	±	6.76	724.53	<	0.01	*
MAE7	646.91	±	11.82	246.74	±	7.06	723.45	<	0.01	*
MAE8	670.57	±	12.33	251.77	±	7.31	721.63	<	0.01	*
MAE10	716.97	±	13.22	262.70	±	7.86	714.47	<	0.01	*
MAE13	775.65	±	14.24	278.88	±	8.75	705.11	<	0.01	*
MAE21	931.12	±	16.52	319.82	±	10.79	688.52	<	0.01	*
MIE	418.59	±	7.09	196.65	±	4.35	705.85	<	0.01	*
MIE3	369.26	±	5.55	183.25	±	4.17	681.34	<	0.01	*
MIE4	360.75	±	5.35	179.55	±	4.14	675.32	<	0.01	*
MIE6	344.47	±	5.04	172.15	±	4.11	656.84	<	0.01	*
MIE7	338.99	±	4.96	168.69	±	4.12	649.59	<	0.01	*
MIE8	332.41	±	4.85	164.41	±	4.14	642.85	<	0.01	*
MIE10	320.62	±	4.72	158.24	±	4.15	613.70	<	0.01	*
MIE13	306.96	±	4.57	150.92	±	4.11	591.13	<	0.01	*
MIE21	281.88	±	4.24	137.43	±	4.05	582.05	<	0.01	*
MEE	436.13	±	7.55	199.64	±	4.44	714.04	<	0.01	*
MEE3	443.39	±	7.37	202.33	±	4.59	720.79	<	0.01	*
MEE4	446.61	±	7.36	203.21	±	4.64	722.77	<	0.01	*
MEE6	452.38	±	7.36	204.76	±	4.73	725.82	<	0.01	*
MEE7	454.21	±	7.37	205.24	±	4.75	726.24	<	0.01	*
MEE8	455.92	±	7.38	205.71	±	4.78	725.91	<	0.01	*
MEE10	458.42	±	7.40	206.61	±	4.82	724.79	<	0.01	*
MEE13	461.04	±	7.41	207.93	±	4.88	722.05	<	0.01	*
MEE21	470.11	±	7.43	211.16	±	5.04	719.16	<	0.01	*
RE	37.69	±	1.63	6.89	±	0.83	583.68	<	0.01	*
RE3	181.63	±	5.60	41.29	±	2.82	617.87	<	0.01	*
RE4	215.88	±	6.48	50.72	±	3.31	621.80	<	0.01	*
RE6	284.80	±	8.13	69.71	±	4.13	639.13	<	0.01	*
RE7	308.66	±	8.55	78.53	±	4.50	638.29	<	0.01	*

Appendix I continued.

Variable	Presence			Absence			Univariate tests†			
							X^2		P	
RE8	338.89	±	9.25	87.83	±	4.87	640.98	<	0.01	*
RE10	397.05	±	10.48	104.92	±	5.52	642.46	<	0.01	*
RE13	469.38	±	11.89	128.41	±	6.51	641.15	<	0.01	*
RE21	649.87	±	14.79	182.81	±	8.79	619.08	<	0.01	*
SD	6.34	±	0.25	1.41	±	0.12	563.12	<	0.01	*
SE	3.03	±	0.30	0.54	±	0.12	125.08	<	0.01	*
SNE	2.84	±	0.26	0.68	±	0.11	106.38	<	0.01	*
SN	2.78	±	0.30	0.79	±	0.12	101.17	<	0.01	*
SNW	1.96	±	0.31	0.55	±	0.11	53.93	<	0.01	*
SSE	2.34	±	0.29	0.18	±	0.10	79.31	<	0.01	*
SS	0.61	±	0.30	-0.05	±	0.10	19.68	<	0.01	*
SSW	-0.07	±	0.28	0.08	±	0.10	5.90		0.02	*
SW	0.43	±	0.34	0.26	±	0.11	26.19	<	0.01	*
SA	2606.94	±	6.14	2512.41	±	2.50	610.82	<	0.01	*
SA3	2611.57	±	4.97	2511.70	±	1.42	649.82	<	0.01	*
SA4	2612.13	±	4.85	2511.96	±	1.40	658.42	<	0.01	*
SA6	2611.35	±	4.57	2512.23	±	1.33	669.29	<	0.01	*
SA7	2610.80	±	4.45	2512.46	±	1.33	672.52	<	0.01	*
SA8	2610.59	±	4.35	2512.68	±	1.31	675.06	<	0.01	*
SA10	2610.13	±	4.17	2513.13	±	1.27	679.18	<	0.01	*
SA13	2608.78	±	3.95	2513.74	±	1.24	684.06	<	0.01	*
SA21	2606.74	±	3.45	2514.89	±	1.21	678.73	<	0.01	*
SR	1.04	±	0.00	1.00	±	0.00	612.25	<	0.01	*
SR3	1.04	±	0.00	1.00	±	0.00	652.21	<	0.01	*
SR4	1.04	±	0.00	1.00	±	0.00	660.99	<	0.01	*
SR6	1.04	±	0.00	1.00	±	0.00	671.60	<	0.01	*
SR7	1.04	±	0.00	1.00	±	0.00	674.84	<	0.01	*
SR8	1.04	±	0.00	1.01	±	0.00	677.08	<	0.01	*
SR10	1.04	±	0.00	1.01	±	0.00	681.43	<	0.01	*
SR13	1.04	±	0.00	1.01	±	0.00	685.98	<	0.01	*
SR21	1.04	±	0.00	1.01	±	0.00	680.05	<	0.01	*
DRi	688.69	±	32.90	808.94	±	43.14	32.58	<	0.01	*
DRo	1613.24	±	76.96	1227.87	±	94.16	50.62	<	0.01	*
DVi	3049.55	±	90.18	2504.86	±	108.50	12.81	<	0.01	*
DnVi3	4.04	±	0.76	9.18	±	1.22	4.71		0.03	*
DnVi4	4.36	±	0.62	10.73	±	1.08	8.96	<	0.01	*
DnVi6	5.51	±	0.56	12.40	±	0.92	12.61	<	0.01	*
DnVi7	6.36	±	0.57	12.97	±	0.89	13.94	<	0.01	*
DnVi8	7.24	±	0.57	13.50	±	0.87	11.79	<	0.01	*
DnVi10	9.15	±	0.59	14.77	±	0.85	5.87		0.02	*
DnVi13	11.95	±	0.64	16.54	±	0.82	2.96		0.09	
DnVi21	18.15	±	0.70	21.40	±	0.75	0.89		0.35	
DnRo3	429.95	±	26.06	683.10	±	32.27	49.28	<	0.01	*
DnRo4	427.66	±	23.47	673.81	±	29.24	56.56	<	0.01	*
DnRo6	427.34	±	19.85	658.99	±	25.36	59.47	<	0.01	*
DnRo7	430.80	±	18.82	656.62	±	24.04	60.04	<	0.01	*
DnRo8	437.12	±	17.87	657.80	±	22.92	62.32	<	0.01	*
DnRo10	455.19	±	16.54	662.11	±	21.38	61.50	<	0.01	*

Appendix I continued.

Variable	Presence	Absence	Univariate tests†	
			X^2	P
DnRo13	486.28 ± 15.18	668.05 ± 19.58	64.04	< 0.01 *
DnRo21	574.17 ± 14.02	722.77 ± 17.48	57.99	< 0.01 *
C8	0.92 ± 0.10	3.26 ± 0.31	15.85	< 0.01 *
F3C8	0.83 ± 0.05	3.37 ± 0.20	41.00	< 0.01 *
F4C8	0.84 ± 0.05	3.52 ± 0.20	68.79	< 0.01 *
F6C8	0.87 ± 0.05	3.94 ± 0.19	146.82	< 0.01 *
F7C8	0.92 ± 0.05	4.20 ± 0.19	180.45	< 0.01 *
F8C8	1.00 ± 0.06	4.51 ± 0.20	210.86	< 0.01 *
F10C8	1.18 ± 0.07	5.15 ± 0.21	258.17	< 0.01 *
F13C8	1.48 ± 0.08	5.97 ± 0.22	322.30	< 0.01 *
F21C8	2.21 ± 0.10	7.96 ± 0.25	475.58	< 0.01 *
Di	0.55 ± 0.02	0.86 ± 0.02	44.86	< 0.01 *
Di3	0.69 ± 0.02	1.18 ± 0.02	119.96	< 0.01 *
Di4	0.71 ± 0.01	1.21 ± 0.02	148.77	< 0.01 *
Di6	0.75 ± 0.01	1.27 ± 0.01	211.62	< 0.01 *
Di7	0.77 ± 0.01	1.29 ± 0.01	233.28	< 0.01 *
Di8	0.79 ± 0.01	1.31 ± 0.01	251.98	< 0.01 *
Di10	0.84 ± 0.01	1.35 ± 0.01	282.33	< 0.01 *
Di13	0.91 ± 0.01	1.41 ± 0.01	315.72	< 0.01 *
Di21	1.06 ± 0.01	1.52 ± 0.01	406.28	< 0.01 *

Notes: Values are means ± SE. Asterisks indicate significant difference at $P < 0.05$.
† All variables were tested using Kruskal-Wallis.

Appendix II Statistical comparisons for landscape variables for chital between presence and absence locations. For variable definitions see Chapter 3.

Variable	Presence			Absence			Univariate tests†			
							X^2		P	
C1	69.63	±	1.21	36.63	±	1.28	240.97	<	0.01	*
F3C1	70.19	±	0.95	37.30	±	1.11	295.17	<	0.01	*
F4C1	70.07	±	0.91	37.38	±	1.09	298.26	<	0.01	*
F6C1	69.12	±	0.86	37.32	±	1.06	284.07	<	0.01	*
F7C1	68.48	±	0.84	37.17	±	1.05	277.93	<	0.01	*
F8C1	67.69	±	0.84	36.98	±	1.03	270.12	<	0.01	*
F10C1	65.93	±	0.82	36.58	±	1.01	252.78	<	0.01	*
F13C1	63.43	±	0.81	36.14	±	0.98	228.54	<	0.01	*
F21C1	57.69	±	0.79	35.16	±	0.91	178.70	<	0.01	*
C2	16.11	±	0.76	35.87	±	1.17	156.76	<	0.01	*
F3C2	16.37	±	0.60	35.98	±	0.96	219.69	<	0.01	*
F4C2	16.28	±	0.58	35.86	±	0.92	232.70	<	0.01	*
F6C2	16.38	±	0.55	35.25	±	0.86	237.13	<	0.01	*
F7C2	16.44	±	0.54	34.97	±	0.84	237.29	<	0.01	*
F8C2	16.53	±	0.53	34.60	±	0.82	234.90	<	0.01	*
F10C2	16.66	±	0.50	33.78	±	0.78	227.41	<	0.01	*
F13C2	16.75	±	0.46	32.47	±	0.73	219.32	<	0.01	*
F21C2	16.75	±	0.39	29.02	±	0.60	209.66	<	0.01	*
C3	4.78	±	0.53	3.01	±	0.42	21.73	<	0.01	*
F3C3	4.23	±	0.38	2.73	±	0.30	76.05	<	0.01	*
F4C3	4.17	±	0.36	2.65	±	0.28	85.93	<	0.01	*
F6C3	3.98	±	0.32	2.50	±	0.24	89.96	<	0.01	*
F7C3	3.93	±	0.31	2.44	±	0.23	90.98	<	0.01	*
F8C3	3.90	±	0.30	2.37	±	0.22	92.27	<	0.01	*
F10C3	3.91	±	0.29	2.23	±	0.20	90.89	<	0.01	*
F13C3	3.91	±	0.27	2.12	±	0.18	91.66	<	0.01	*
F21C3	3.67	±	0.24	1.97	±	0.15	91.35	<	0.01	*
C4	3.85	±	0.35	8.87	±	0.56	64.13	<	0.01	*
F3C4	3.69	±	0.20	8.57	±	0.36	124.52	<	0.01	*
F4C4	3.77	±	0.19	8.68	±	0.34	128.28	<	0.01	*
F6C4	4.13	±	0.18	9.12	±	0.32	128.02	<	0.01	*
F7C4	4.34	±	0.18	9.35	±	0.31	131.50	<	0.01	*
F8C4	4.61	±	0.18	9.61	±	0.30	131.29	<	0.01	*
F10C4	5.16	±	0.18	10.18	±	0.29	137.99	<	0.01	*
F13C4	6.05	±	0.20	10.95	±	0.29	132.36	<	0.01	*
F21C4	8.24	±	0.22	12.74	±	0.27	113.87	<	0.01	*
C5	1.67	±	0.15	4.49	±	0.32	63.16	<	0.01	*
F3C5	1.66	±	0.09	4.47	±	0.18	199.06	<	0.01	*
F4C5	1.69	±	0.08	4.52	±	0.17	205.65	<	0.01	*
F6C5	1.84	±	0.08	4.69	±	0.16	214.04	<	0.01	*
F7C5	1.92	±	0.08	4.77	±	0.16	217.42	<	0.01	*
F8C5	2.02	±	0.08	4.85	±	0.15	218.08	<	0.01	*
F10C5	2.28	±	0.08	5.00	±	0.14	212.25	<	0.01	*
F13C5	2.63	±	0.08	5.20	±	0.14	203.19	<	0.01	*
F21C5	3.45	±	0.09	5.55	±	0.12	175.52	<	0.01	*
C6	1.41	±	0.24	3.56	±	0.36	52.28	<	0.01	*
F3C6	1.36	±	0.12	3.73	±	0.25	73.70	<	0.01	*

Appendix II continued.

Variable	Presence			Absence			Univariate tests†			
							X^2		P	
F4C6	1.34	±	0.10	3.64	±	0.24	75.82	<	0.01	*
F6C6	1.42	±	0.10	3.67	±	0.21	88.12	<	0.01	*
F7C6	1.49	±	0.10	3.71	±	0.20	86.38	<	0.01	*
F8C6	1.57	±	0.10	3.79	±	0.20	85.05	<	0.01	*
F10C6	1.77	±	0.10	3.98	±	0.19	80.74	<	0.01	*
F13C6	2.12	±	0.10	4.27	±	0.18	69.29	<	0.01	*
F21C6	3.02	±	0.12	5.12	±	0.17	43.56	<	0.01	*
C7	1.55	±	0.30	4.66	±	0.61	18.10	<	0.01	*
F3C7	1.44	±	0.16	4.26	±	0.39	38.32	<	0.01	*
F4C7	1.52	±	0.16	4.21	±	0.36	43.51	<	0.01	*
F6C7	1.65	±	0.17	4.05	±	0.31	37.98	<	0.01	*
F7C7	1.73	±	0.18	3.98	±	0.29	37.44	<	0.01	*
F8C7	1.82	±	0.18	3.92	±	0.28	35.46	<	0.01	*
F10C7	1.99	±	0.18	3.79	±	0.25	30.54	<	0.01	*
F13C7	2.16	±	0.19	3.64	±	0.22	29.15	<	0.01	*
F21C7	2.81	±	0.19	3.45	±	0.17	14.99	<	0.01	*
MAE	333.18	±	8.10	258.16	±	6.60	8.45	<	0.01	*
MAE3	390.64	±	10.29	300.14	±	8.65	6.10		0.01	*
MAE4	407.35	±	10.89	309.60	±	9.12	6.64		0.01	*
MAE6	439.67	±	12.07	329.88	±	10.11	6.66		0.01	*
MAE7	452.24	±	12.49	337.71	±	10.43	6.75		0.01	*
MAE8	465.71	±	13.00	347.08	±	10.86	6.43		0.01	*
MAE10	490.29	±	13.84	368.54	±	11.88	5.36		0.02	*
MAE13	522.68	±	14.79	395.49	±	13.17	4.52		0.03	*
MAE21	618.96	±	17.77	465.62	±	15.90	5.55		0.02	*
MIE	311.49	±	7.15	243.02	±	5.85	9.95	<	0.01	*
MIE3	281.90	±	5.86	222.10	±	5.20	14.06	<	0.01	*
MIE4	276.39	±	5.68	217.09	±	5.12	15.40	<	0.01	*
MIE6	266.59	±	5.42	207.03	±	5.01	18.86	<	0.01	*
MIE7	263.15	±	5.34	202.31	±	4.98	20.89	<	0.01	*
MIE8	258.92	±	5.24	197.56	±	4.94	22.63	<	0.01	*
MIE10	250.32	±	5.11	190.73	±	4.86	22.19	<	0.01	*
MIE13	240.28	±	4.91	182.31	±	4.78	22.43	<	0.01	*
MIE21	219.82	±	4.57	166.11	±	4.65	21.57	<	0.01	*
MEE	321.82	±	7.61	250.16	±	6.19	9.17	<	0.01	*
MEE3	326.28	±	7.60	255.25	±	6.40	8.81	<	0.01	*
MEE4	328.14	±	7.63	256.80	±	6.47	8.83	<	0.01	*
MEE6	331.94	±	7.70	259.34	±	6.58	8.98	<	0.01	*
MEE7	333.26	±	7.73	260.17	±	6.62	9.05	<	0.01	*
MEE8	334.48	±	7.77	260.92	±	6.66	9.18	<	0.01	*
MEE10	336.17	±	7.81	262.29	±	6.72	9.07	<	0.01	*
MEE13	337.94	±	7.85	263.99	±	6.78	8.87	<	0.01	*
MEE21	342.90	±	7.95	269.40	±	6.97	8.15	<	0.01	*
RE	22.32	±	1.47	15.15	±	1.15	0.00		1.00	
RE3	109.33	±	5.29	78.03	±	4.38	0.00		0.95	
RE4	131.54	±	6.13	92.51	±	5.02	0.09		0.77	
RE6	173.64	±	7.73	122.85	±	6.26	0.14		0.71	
RE7	189.65	±	8.24	135.40	±	6.71	0.19		0.66	
RE8	207.34	±	8.89	149.52	±	7.26	0.16		0.69	

Appendix II continued.

Variable	Presence			Absence			Univariate tests†		
							X^2	P	
RE10	240.51	±	9.98	177.81	±	8.48	0.16	0.69	
RE13	282.92	±	11.26	213.18	±	9.92	0.17	0.68	
RE21	399.63	±	14.79	299.51	±	12.96	0.48	0.49	
SD	3.82	±	0.23	2.85	±	0.19	0.04	0.85	
SE	1.78	±	0.24	1.49	±	0.22	0.13	0.72	
SNE	1.71	±	0.21	1.25	±	0.18	0.52	0.47	
SN	1.81	±	0.25	1.25	±	0.18	1.83	0.18	
SNW	1.02	±	0.24	1.03	±	0.19	4.53	0.03	*
SSE	1.24	±	0.22	1.14	±	0.19	2.23	0.14	
SS	0.12	±	0.23	0.41	±	0.18	0.32	0.57	
SSW	0.02	±	0.21	-0.10	±	0.15	0.48	0.49	
SW	0.22	±	0.24	0.43	±	0.18	0.28	0.59	
SA	2562.28	±	5.59	2537.55	±	3.96	0.00	0.96	
SA3	2564.88	±	4.45	2537.59	±	3.18	0.00	0.99	
SA4	2565.37	±	4.31	2537.01	±	3.06	0.02	0.89	
SA6	2565.59	±	4.03	2536.20	±	2.92	0.13	0.72	
SA7	2565.35	±	3.92	2536.07	±	2.86	0.15	0.69	
SA8	2565.12	±	3.81	2536.23	±	2.83	0.16	0.69	
SA10	2564.86	±	3.66	2536.39	±	2.76	0.23	0.63	
SA13	2564.02	±	3.48	2536.53	±	2.69	0.25	0.62	
SA21	2562.87	±	3.17	2537.15	±	2.51	0.32	0.57	
SR	1.02	±	0.00	1.02	±	0.00	0.00	0.99	
SR3	1.03	±	0.00	1.02	±	0.00	0.00	0.98	
SR4	1.03	±	0.00	1.01	±	0.00	0.01	0.92	
SR6	1.03	±	0.00	1.01	±	0.00	0.12	0.73	
SR7	1.03	±	0.00	1.01	±	0.00	0.14	0.71	
SR8	1.03	±	0.00	1.01	±	0.00	0.21	0.65	
SR10	1.03	±	0.00	1.01	±	0.00	0.29	0.59	
SR13	1.03	±	0.00	1.01	±	0.00	0.28	0.59	
SR21	1.03	±	0.00	1.01	±	0.00	0.44	0.51	
DRi	989.43	±	44.13	723.77	±	38.72	29.00	< 0.01	*
DRo	2074.19	±	91.37	1070.24	±	81.33	64.18	< 0.01	*
DVi	3512.88	±	96.25	2354.02	±	95.09	112.23	< 0.01	*
DnVi3	2.78	±	0.58	9.51	±	1.16	31.36	< 0.01	*
DnVi4	4.11	±	0.60	9.58	±	0.93	30.27	< 0.01	*
DnVi6	5.47	±	0.59	10.78	±	0.76	47.52	< 0.01	*
DnVi7	5.85	±	0.57	11.72	±	0.73	64.81	< 0.01	*
DnVi8	6.38	±	0.56	12.47	±	0.72	72.63	< 0.01	*
DnVi10	7.53	±	0.55	14.08	±	0.74	85.42	< 0.01	*
DnVi13	9.41	±	0.55	16.33	±	0.75	87.93	< 0.01	*
DnVi21	14.51	±	0.61	21.85	±	0.71	103.31	< 0.01	*
DnRo3	393.81	±	24.89	699.96	±	30.72	45.50	< 0.01	*
DnRo4	391.96	±	22.37	681.79	±	27.58	51.43	< 0.01	*
DnRo6	384.25	±	19.48	667.09	±	23.59	67.81	< 0.01	*
DnRo7	384.84	±	18.48	666.22	±	22.35	75.97	< 0.01	*
DnRo8	387.93	±	17.62	671.60	±	21.29	83.44	< 0.01	*
DnRo10	406.74	±	16.92	673.72	±	19.56	83.77	< 0.01	*
DnRo13	431.85	±	16.30	688.62	±	17.75	91.83	< 0.01	*

Appendix II continued.

Variable	Presence			Absence			Univariate tests†			
							X^2		P	
DnRo21	507.19	±	16.00	759.13	±	15.81	106.75	<	0.01	*
C8	0.97	±	0.11	2.88	±	0.28	25.30	<	0.01	*
F3C8	1.04	±	0.07	2.93	±	0.19	67.07	<	0.01	*
F4C8	1.14	±	0.08	3.03	±	0.18	66.91	<	0.01	*
F6C8	1.45	±	0.09	3.38	±	0.18	66.82	<	0.01	*
F7C8	1.63	±	0.10	3.58	±	0.18	65.03	<	0.01	*
F8C8	1.84	±	0.11	3.85	±	0.18	63.50	<	0.01	*
F10C8	2.29	±	0.13	4.42	±	0.19	61.44	<	0.01	*
F13C8	2.92	±	0.15	5.18	±	0.20	60.55	<	0.01	*
F21C8	4.37	±	0.19	6.97	±	0.24	51.50	<	0.01	*
Di	0.55	±	0.02	0.78	±	0.02	73.46	<	0.01	*
Di3	0.74	±	0.02	1.05	±	0.02	119.66	<	0.01	*
Di4	0.77	±	0.02	1.09	±	0.02	123.84	<	0.01	*
Di6	0.83	±	0.02	1.15	±	0.02	118.89	<	0.01	*
Di7	0.85	±	0.02	1.17	±	0.01	114.83	<	0.01	*
Di8	0.88	±	0.02	1.19	±	0.01	110.21	<	0.01	*
Di10	0.94	±	0.02	1.24	±	0.01	99.29	<	0.01	*
Di13	1.02	±	0.02	1.30	±	0.01	83.99	<	0.01	*
Di21	1.20	±	0.02	1.41	±	0.01	51.89	<	0.01	*

Notes: Values are means ± 1 SE. Asterisks indicate significant difference at $P < 0.05$.
† All variables were tested using Kruskal-Wallis.

Appendix III Statistical comparisons for landscape variables for nilgai between presence and absence locations. For variable definitions see Chapter 3.

Variable	Presence	Absence	Univariate tests†		
			X^2	*P*	
C1	44.26 ± 1.41	65.65 ± 1.34	8.13	< 0.01	*
F3C1	44.55 ± 1.22	66.35 ± 1.13	16.39	< 0.01	*
F4C1	44.39 ± 1.19	66.47 ± 1.10	20.30	< 0.01	*
F6C1	43.58 ± 1.14	66.19 ± 1.04	30.49	< 0.01	*
F7C1	43.06 ± 1.11	65.82 ± 1.03	34.88	< 0.01	*
F8C1	42.47 ± 1.09	65.31 ± 1.01	39.21	< 0.01	*
F10C1	41.14 ± 1.05	64.27 ± 0.98	48.32	< 0.01	*
F13C1	39.44 ± 0.99	62.73 ± 0.94	60.77	< 0.01	*
F21C1	35.54 ± 0.87	59.20 ± 0.85	98.96	< 0.01	*
C2	34.25 ± 1.27	16.12 ± 0.73	0.63	0.43	
F3C2	34.17 ± 1.08	16.57 ± 0.57	5.59	0.02	*
F4C2	33.79 ± 1.04	16.64 ± 0.56	6.36	0.01	*
F6C2	32.99 ± 0.97	16.82 ± 0.53	9.12	< 0.01	*
F7C2	32.70 ± 0.95	16.90 ± 0.53	10.21	< 0.01	*
F8C2	32.34 ± 0.92	17.00 ± 0.52	10.72	< 0.01	*
F10C2	31.58 ± 0.87	17.13 ± 0.51	10.89	< 0.01	*
F13C2	30.39 ± 0.80	17.24 ± 0.48	9.88	< 0.01	*
F21C2	27.46 ± 0.65	17.14 ± 0.40	10.41	< 0.01	*
C3	5.04 ± 0.53	2.60 ± 0.40	29.80	< 0.01	*
F3C3	4.87 ± 0.40	2.25 ± 0.26	24.08	< 0.01	*
F4C3	4.77 ± 0.38	2.24 ± 0.25	24.05	< 0.01	*
F6C3	4.52 ± 0.34	2.21 ± 0.23	24.82	< 0.01	*
F7C3	4.43 ± 0.33	2.21 ± 0.22	24.84	< 0.01	*
F8C3	4.34 ± 0.32	2.23 ± 0.21	24.59	< 0.01	*
F10C3	4.23 ± 0.31	2.25 ± 0.20	25.00	< 0.01	*
F13C3	4.07 ± 0.29	2.36 ± 0.20	24.36	< 0.01	*
F21C3	3.75 ± 0.25	2.34 ± 0.18	22.09	< 0.01	*
C4	6.99 ± 0.53	5.24 ± 0.41	0.27	0.61	
F3C4	6.65 ± 0.33	5.04 ± 0.29	0.76	0.38	
F4C4	6.87 ± 0.31	5.04 ± 0.27	3.80	0.05	
F6C4	7.57 ± 0.29	5.19 ± 0.25	15.75	< 0.01	*
F7C4	7.89 ± 0.29	5.33 ± 0.25	22.01	< 0.01	*
F8C4	8.26 ± 0.28	5.51 ± 0.25	29.02	< 0.01	*
F10C4	9.03 ± 0.28	5.86 ± 0.24	43.32	< 0.01	*
F13C4	10.17 ± 0.28	6.39 ± 0.24	65.53	< 0.01	*
F21C4	12.76 ± 0.27	7.80 ± 0.23	125.53	< 0.01	*
C5	3.29 ± 0.28	2.58 ± 0.23	1.06	0.30	
F3C5	3.31 ± 0.17	2.46 ± 0.14	6.78	0.02	*
F4C5	3.39 ± 0.17	2.48 ± 0.13	4.57	0.03	*
F6C5	3.65 ± 0.16	2.54 ± 0.12	0.14	0.71	
F7C5	3.77 ± 0.16	2.59 ± 0.11	0.02	0.89	
F8C5	3.89 ± 0.16	2.66 ± 0.11	0.48	0.49	
F10C5	4.15 ± 0.15	2.82 ± 0.10	2.51	0.11	
F13C5	4.50 ± 0.14	3.06 ± 0.10	8.40	< 0.01	*
F21C5	5.20 ± 0.12	3.61 ± 0.09	34.40	< 0.00	*
C6	2.00 ± 0.26	2.47 ± 0.31	2.95	< 0.09	
F3C6	2.14 ± 0.19	2.53 ± 0.20	27.90	< 0.01	*

Appendix III continued.

							Univariate tests†			
Variable	Presence			Absence			X^2		P	
F4C6	2.23	±	0.19	2.39	±	0.17	26.98	<	0.01	*
F6C6	2.49	±	0.19	2.30	±	0.15	14.82	<	0.01	*
F7C6	2.61	±	0.18	2.31	±	0.14	9.30	<	0.01	*
F8C6	2.75	±	0.18	2.34	±	0.14	4.48		0.03	*
F10C6	3.07	±	0.17	2.43	±	0.13	0.43		0.51	
F13C6	3.55	±	0.17	2.60	±	0.13	1.58		0.21	
F21C6	4.75	±	0.16	3.14	±	0.13	17.11	<	0.01	*
C7	2.11	±	0.40	3.60	±	0.54	3.08		0.08	
F3C7	2.10	±	0.24	3.11	±	0.35	26.20	<	0.01	*
F4C7	2.15	±	0.23	3.07	±	0.32	34.12	<	0.01	*
F6C7	2.19	±	0.22	3.00	±	0.28	38.82	<	0.01	*
F7C7	2.22	±	0.21	3.00	±	0.27	36.46	<	0.01	*
F8C7	2.26	±	0.21	3.01	±	0.26	33.47	<	0.01	*
F10C7	2.36	±	0.21	3.03	±	0.24	26.29	<	0.01	*
F13C7	2.45	±	0.20	3.04	±	0.22	21.72	<	0.01	*
F21C7	2.82	±	0.18	3.19	±	0.20	3.56		0.06	
MAE	213.09	±	5.06	378.84	±	9.16	108.03	<	0.01	*
MAE3	234.90	±	6.39	449.21	±	11.35	115.38	<	0.01	*
MAE4	240.69	±	6.78	469.68	±	11.96	118.65	<	0.01	*
MAE6	251.88	±	7.52	510.85	±	13.15	127.15	<	0.01	*
MAE7	256.45	±	7.82	525.20	±	13.49	129.63	<	0.01	*
MAE8	262.75	±	8.42	541.48	±	13.85	132.97	<	0.01	*
MAE10	273.65	±	9.14	575.04	±	14.67	138.92	<	0.01	*
MAE13	288.80	±	9.87	616.53	±	15.81	142.39	<	0.01	*
MAE21	336.39	±	12.22	725.04	±	18.46	147.60	<	0.01	*
MIE	205.53	±	4.67	351.87	±	8.14	104.25	<	0.01	*
MIE3	190.46	±	4.21	315.23	±	6.53	104.98	<	0.01	*
MIE4	186.11	±	4.12	309.13	±	6.31	108.20	<	0.01	*
MIE6	177.36	±	4.03	297.19	±	5.92	112.80	<	0.01	*
MIE7	173.63	±	4.02	292.51	±	5.80	113.19	<	0.01	*
MIE8	170.10	±	4.00	287.22	±	5.70	113.21	<	0.01	*
MIE10	163.82	±	3.98	278.35	±	5.53	115.09	<	0.01	*
MIE13	156.93	±	3.94	266.61	±	5.33	114.88	<	0.01	*
MIE21	140.12	±	3.84	245.71	±	4.90	131.42	<	0.01	*
MEE	209.09	±	4.83	364.83	±	8.64	106.36	<	0.01	*
MEE3	211.28	±	4.95	369.21	±	8.49	109.27	<	0.01	*
MEE4	212.08	±	5.00	371.36	±	8.48	110.55	<	0.01	*
MEE6	213.50	±	5.09	375.59	±	8.50	112.27	<	0.01	*
MEE7	213.87	±	5.11	377.06	±	8.51	113.02	<	0.01	*
MEE8	214.18	±	5.11	378.46	±	8.53	113.79	<	0.01	*
MEE10	214.60	±	5.11	380.78	±	8.55	115.61	<	0.01	*
MEE13	215.02	±	5.09	383.37	±	8.56	117.66	<	0.01	*
MEE21	217.36	±	5.18	391.03	±	8.64	122.63	<	0.01	*
RE	8.57	±	1.00	26.96	±	1.57	111.67	<	0.01	*
RE3	45.40	±	3.21	133.99	±	5.85	112.11	<	0.01	*
RE4	55.52	±	3.82	160.55	±	6.74	115.53	<	0.01	*
RE6	75.44	±	4.89	213.65	±	8.45	125.05	<	0.01	*
RE7	83.72	±	5.30	232.69	±	8.94	127.64	<	0.01	*

Appendix III continued.

					Univariate tests†			
Variable	Presence		Absence		X^2		*P*	
RE8	93.54	± 6.01	254.27	± 9.47	129.84	<	0.01	*
RE10	110.70	± 6.93	296.69	± 10.57	135.24	<	0.01	*
RE13	132.71	± 7.77	349.92	± 12.08	138.27	<	0.01	*
RE21	197.05	± 10.61	479.33	± 15.21	140.97	<	0.01	*
SD	1.62	± 0.13	4.64	± 0.25	94.89	<	0.01	*
SE	0.49	± 0.13	1.96	± 0.29	24.52	<	0.01	*
SNE	0.67	± 0.13	1.98	± 0.25	16.06	<	0.01	*
SN	0.80	± 0.13	2.53	± 0.27	9.59	<	0.01	*
SNW	0.66	± 0.14	1.46	± 0.27	14.70	<	0.01	*
SSE	0.28	± 0.10	1.31	± 0.26	19.88	<	0.00	*
SS	0.02	± 0.10	0.00	± 0.27	4.80		0.03	*
SSW	0.03	± 0.10	-0.25	± 0.24	2.83		0.09	
SW	0.33	± 0.13	0.16	± 0.27	5.29		0.02	*
SA	2515.45	± 2.47	2581.37	± 7.06	120.86	<	0.01	*
SA3	2515.07	± 1.81	2583.48	± 5.35	138.29	<	0.01	*
SA4	2515.13	± 1.79	2583.10	± 5.06	142.74	<	0.01	*
SA6	2515.22	± 1.73	2581.36	± 4.59	150.47	<	0.01	*
SA7	2515.26	± 1.71	2580.86	± 4.44	153.04	<	0.01	*
SA8	2515.33	± 1.69	2580.89	± 4.34	155.39	<	0.01	*
SA10	2515.86	± 1.69	2580.94	± 4.16	157.55	<	0.01	*
SA13	2515.95	± 1.61	2580.56	± 3.96	161.23	<	0.01	*
SA21	2517.31	± 1.59	2579.48	± 3.55	167.85	<	0.01	*
SR	1.01	± 0.00	1.03	± 0.00	119.94	<	0.01	*
SR3	1.01	± 0.00	1.03	± 0.00	137.48	<	0.01	*
SR4	1.01	± 0.00	1.03	± 0.00	141.75	<	0.01	*
SR6	1.01	± 0.00	1.03	± 0.00	150.31	<	0.01	*
SR7	1.01	± 0.00	1.03	± 0.00	152.57	<	0.01	*
SR8	1.01	± 0.00	1.03	± 0.00	155.61	<	0.01	*
SR10	1.01	± 0.00	1.03	± 0.00	158.31	<	0.01	*
SR13	1.01	± 0.00	1.03	± 0.00	162.21	<	0.01	*
SR21	1.01	± 0.00	1.03	± 0.00	167.80	<	0.01	*
DRi	1127.79	± 47.69	706.80	± 37.16	52.75	<	0.01	*
DRo	1238.31	± 70.69	1947.41	± 102.57	6.88		0.02	*
DVi	2682.34	± 83.88	3294.37	± 112.40	2.11		0.15	
DnVi3	5.18	± 0.81	6.12	± 0.99	0.99		0.32	
DnVi4	6.25	± 0.72	6.89	± 0.86	0.65		0.42	
DnVi6	8.71	± 0.70	6.80	± 0.68	0.99		0.32	
DnVi7	9.60	± 0.70	7.37	± 0.66	2.17		0.14	
DnVi8	10.13	± 0.67	8.46	± 0.68	0.68		0.41	
DnVi10	11.92	± 0.71	9.30	± 0.64	1.72		0.19	
DnVi13	14.31	± 0.72	11.14	± 0.65	5.03		0.02	*
DnVi21	20.45	± 0.72	15.42	± 0.63	20.30	<	0.01	*
DnRo3	587.02	± 28.92	460.17	± 27.31	3.01		0.08	
DnRo4	588.39	± 26.85	453.78	± 24.14	3.08		0.08	
DnRo6	583.70	± 23.27	441.70	± 20.61	4.00		0.05	
DnRo7	585.02	± 22.18	439.91	± 19.59	4.68		0.03	*
DnRo8	590.93	± 21.25	443.12	± 18.80	5.55		0.02	*
DnRo10	606.00	± 19.82	450.17	± 17.70	8.37	<	0.01	*
DnRo13	632.65	± 18.22	467.28	± 16.72	14.09	<	0.01	*

Appendix III continued.

Variable	Presence	Absence	Univariate tests†		
			*X*²	*P*	
DnRo21	725.71 ± 17.22	524.38 ± 15.42	27.52	< 0.01	*
C8	2.04 ± 0.23	1.71 ± 0.20	0.04	0.83	
F3C8	2.17 ± 0.16	1.67 ± 0.13	2.39	0.12	
F4C8	2.39 ± 0.16	1.65 ± 0.12	0.44	0.51	
F6C8	2.98 ± 0.16	1.72 ± 0.12	3.04	0.08	
F7C8	3.28 ± 0.17	1.81 ± 0.12	8.29	< 0.01	*
F8C8	3.66 ± 0.18	1.92 ± 0.12	16.50	< 0.01	*
F10C8	4.41 ± 0.19	2.18 ± 0.13	29.40	< 0.01	*
F13C8	5.41 ± 0.21	2.57 ± 0.14	53.06	< 0.01	*
F21C8	7.69 ± 0.25	3.56 ± 0.17	98.64	< 0.01	*
Di	0.68 ± 0.02	0.60 ± 0.02	0.67	0.41	
Di3	0.92 ± 0.02	0.80 ± 0.02	2.74	0.10	
Di4	0.96 ± 0.02	0.82 ± 0.02	5.23	0.02	*
Di6	1.04 ± 0.02	0.87 ± 0.02	12.65	< 0.01	*
Di7	1.07 ± 0.02	0.89 ± 0.02	16.50	< 0.01	*
Di8	1.11 ± 0.02	0.91 ± 0.02	21.17	< 0.01	*
Di10	1.17 ± 0.01	0.95 ± 0.02	30.61	< 0.01	*
Di13	1.26 ± 0.01	1.02 ± 0.02	47.27	< 0.01	*
Di21	1.43 ± 0.01	1.15 ± 0.02	88.68	< 0.01	*

Notes: Values are means ± 1 SE. Asterisks indicate significant difference at $P < 0.05$.
† All variables were tested using Kruskal-Wallis.

Appendix IV Statistical comparisons for landscape variables for wildpig between presence and absence locations. For variable definitions see Chapter 3.

							Univariate tests†			
Variable	Presence			Absence			X^2		P	
C1	55.81	±	1.35	50.27	±	1.34	9.27	<	0.01	*
F3C1	56.67	±	1.13	51.62	±	1.15	10.29	<	0.01	*
F4C1	56.68	±	1.10	51.80	±	1.14	9.13	<	0.01	*
F6C1	55.99	±	1.04	51.88	±	1.11	5.78		0.02	*
F7C1	55.42	±	1.03	51.74	±	1.10	4.43		0.04	*
F8C1	54.73	±	1.01	51.50	±	1.09	3.26		0.07	
F10C1	53.21	±	0.98	50.88	±	1.07	1.52		0.22	
F13C1	51.08	±	0.94	50.02	±	1.03	0.13		0.72	
F21C1	46.23	±	0.87	47.87	±	0.94	2.43		0.12	
C2	22.68	±	0.96	28.32	±	1.03	22.56	<	0.01	*
F3C2	23.03	±	0.80	28.39	±	0.86	27.13	<	0.01	*
F4C2	22.90	±	0.78	28.20	±	0.83	26.67	<	0.01	*
F6C2	22.76	±	0.72	27.68	±	0.79	22.74	<	0.01	*
F7C2	22.71	±	0.71	27.52	±	0.78	21.57	<	0.01	*
F8C2	22.63	±	0.69	27.35	±	0.77	21.07	<	0.01	*
F10C2	22.50	±	0.65	26.90	±	0.73	18.93	<	0.01	*
F13C2	22.16	±	0.61	26.14	±	0.68	16.90	<	0.01	*
F21C2	20.98	±	0.50	24.11	±	0.55	15.51	<	0.01	*
C3	5.68	±	0.55	2.15	±	0.33	44.96	<	0.01	*
F3C3	5.26	±	0.40	1.90	±	0.22	49.30	<	0.01	*
F4C3	5.15	±	0.37	1.86	±	0.21	55.72	<	0.01	*
F6C3	4.92	±	0.34	1.78	±	0.19	63.67	<	0.01	*
F7C3	4.86	±	0.33	1.75	±	0.18	67.17	<	0.01	*
F8C3	4.77	±	0.31	1.73	±	0.18	67.10	<	0.01	*
F10C3	4.69	±	0.30	1.70	±	0.16	68.34	<	0.01	*
F13C3	4.62	±	0.28	1.66	±	0.15	72.47	<	0.01	*
F21C3	4.35	±	0.25	1.55	±	0.13	75.01	<	0.01	*
C4	5.80	±	0.43	7.04	±	0.48	10.18	<	0.01	*
F3C4	5.60	±	0.28	6.47	±	0.31	21.67	<	0.01	*
F4C4	5.69	±	0.26	6.52	±	0.29	15.57	<	0.01	*
F6C4	6.18	±	0.25	6.76	±	0.27	4.86		0.03	*
F7C4	6.46	±	0.25	6.90	±	0.27	2.74		0.10	
F8C4	6.79	±	0.25	7.07	±	0.26	1.19		0.27	
F10C4	7.40	±	0.25	7.51	±	0.26	0.24		0.63	
F13C4	8.35	±	0.25	8.18	±	0.25	0.40		0.53	
F21C4	10.70	±	0.26	9.76	±	0.24	7.47		0.02	*
C5	2.36	±	0.21	3.79	±	0.28	31.85	<	0.01	*
F3C5	2.40	±	0.13	3.60	±	0.15	80.57	<	0.01	*
F4C5	2.48	±	0.13	3.58	±	0.15	69.63	<	0.01	*
F6C5	2.70	±	0.12	3.65	±	0.14	49.19	<	0.01	*
F7C5	2.80	±	0.12	3.70	±	0.13	42.72	<	0.01	*
F8C5	2.92	±	0.12	3.75	±	0.13	36.95	<	0.01	*
F10C5	3.16	±	0.12	3.90	±	0.12	30.11	<	0.01	*
F13C5	3.52	±	0.12	4.10	±	0.11	20.93	<	0.01	*
F21C5	4.33	±	0.11	4.52	±	0.10	3.72		0.05	
C6	2.52	±	0.31	2.85	±	0.33	4.01		0.05	
F3C6	2.19	±	0.16	2.94	±	0.22	32.67	<	0.01	*

Appendix IV continued

							Univariate tests†			
Variable	Presence			Absence			X^2		*P*	
F4C6	2.12	±	0.14	2.89	±	0.21	31.27	<	0.01	*
F6C6	2.18	±	0.13	2.88	±	0.19	19.41	<	0.01	*
F7C6	2.27	±	0.13	2.90	±	0.18	13.51	<	0.01	*
F8C6	2.40	±	0.13	2.92	±	0.17	7.46		0.02	*
F10C6	2.68	±	0.13	3.03	±	0.17	2.71		0.10	
F13C6	3.11	±	0.13	3.25	±	0.16	0.21		0.65	
F21C6	4.22	±	0.14	3.93	±	0.15	4.60		0.03	*
C7	3.15	±	0.46	3.52	±	0.51	0.51		0.48	
F3C7	2.87	±	0.31	3.04	±	0.30	19.90	<	0.01	*
F4C7	2.84	±	0.29	3.07	±	0.28	25.21	<	0.01	*
F6C7	2.76	±	0.25	3.06	±	0.25	25.00	<	0.01	*
F7C7	2.77	±	0.25	3.05	±	0.25	22.19	<	0.01	*
F8C7	2.78	±	0.24	3.05	±	0.24	20.53	<	0.01	*
F10C7	2.83	±	0.23	3.04	±	0.22	18.98	<	0.01	*
F13C7	2.86	±	0.22	3.06	±	0.19	17.22	<	0.01	*
F21C7	3.02	±	0.19	3.33	±	0.18	12.81	<	0.01	*
MAE	260.88	±	6.57	335.39	±	7.67	56.42	<	0.01	*
MAE3	294.36	±	8.12	399.88	±	9.84	63.88	<	0.01	*
MAE4	304.95	±	8.68	415.77	±	10.34	64.07	<	0.01	*
MAE6	324.96	±	9.67	452.11	±	11.59	67.31	<	0.01	*
MAE7	331.93	±	9.94	466.05	±	12.02	68.81	<	0.01	*
MAE8	339.31	±	10.24	483.14	±	12.63	70.58	<	0.01	*
MAE10	355.07	±	10.91	514.96	±	13.65	73.49	<	0.01	*
MAE13	377.24	±	11.87	556.65	±	14.87	76.77	<	0.01	*
MAE21	441.24	±	14.34	664.39	±	17.88	78.49	<	0.01	*
MIE	248.80	±	5.92	311.53	±	6.82	49.25	<	0.01	*
MIE3	230.46	±	5.09	281.57	±	5.79	40.95	<	0.01	*
MIE4	226.83	±	5.01	275.03	±	5.62	39.33	<	0.01	*
MIE6	219.21	±	4.85	263.25	±	5.39	36.07	<	0.01	*
MIE7	216.27	±	4.80	258.84	±	5.32	35.16	<	0.01	*
MIE8	213.05	±	4.76	253.41	±	5.22	33.42	<	0.01	*
MIE10	207.29	±	4.64	244.15	±	5.11	28.40	<	0.01	*
MIE13	199.89	±	4.46	233.61	±	5.01	24.42	<	0.01	*
MIE21	182.57	±	4.27	215.32	±	4.74	26.14	<	0.01	*
MEE	254.53	±	6.22	322.76	±	7.22	52.97	<	0.01	*
MEE3	257.07	±	6.24	330.06	±	7.32	55.29	<	0.01	*
MEE4	258.30	±	6.28	332.44	±	7.36	56.39	<	0.01	*
MEE6	260.69	±	6.38	336.71	±	7.43	57.56	<	0.01	*
MEE7	261.44	±	6.41	338.23	±	7.46	58.25	<	0.01	*
MEE8	262.12	±	6.44	339.64	±	7.50	58.96	<	0.01	*
MEE10	263.24	±	6.48	341.71	±	7.55	60.00	<	0.01	*
MEE13	264.60	±	6.54	343.88	±	7.58	60.78	<	0.01	*
MEE21	268.56	±	6.69	351.09	±	7.70	63.32	<	0.01	*
RE	13.07	±	1.15	23.86	±	1.37	70.55	<	0.01	*
RE3	64.83	±	3.82	118.31	±	5.07	77.59	<	0.01	*
RE4	79.05	±	4.53	140.74	±	5.84	77.98	<	0.01	*
RE6	106.65	±	5.79	188.86	±	7.52	82.28	<	0.01	*
RE7	116.55	±	6.14	207.22	±	8.04	83.15	<	0.01	*

Appendix IV continued

							Univariate tests†			
Variable	Presence			Absence			X^2		P	
RE8	127.14	±	6.53	229.73	±	8.80	85.78	<	0.01	*
RE10	148.64	±	7.41	270.81	±	10.04	90.87	<	0.01	*
RE13	178.20	±	8.70	323.04	±	11.43	95.06	<	0.01	*
RE21	259.46	±	11.64	449.07	±	14.72	100.04	<	0.01	*
SD	2.20	±	0.16	4.29	±	0.22	75.04	<	0.01	*
SE	0.82	±	0.16	2.09	±	0.27	27.42	<	0.01	*
SNE	0.73	±	0.16	2.22	±	0.21	51.13	<	0.01	*
SN	0.85	±	0.17	2.16	±	0.23	40.08	<	0.01	*
SNW	0.51	±	0.16	1.61	±	0.24	14.56	<	0.01	*
SSE	0.67	±	0.16	1.78	±	0.23	7.97	<	0.01	*
SS	0.48	±	0.15	0.17	±	0.24	2.13		0.14	
SSW	0.19	±	0.13	-0.13	±	0.21	5.88		0.02	*
SW	0.11	±	0.16	0.67	±	0.24	1.09		0.30	
SA	2530.39	±	3.97	2565.62	±	5.43	76.57	<	0.01	*
SA3	2532.10	±	2.92	2568.74	±	4.49	84.12	<	0.01	*
SA4	2532.59	±	2.82	2568.21	±	4.32	85.75	<	0.01	*
SA6	2533.40	±	2.74	2566.58	±	3.93	86.86	<	0.01	*
SA7	2533.42	±	2.69	2566.23	±	3.81	87.49	<	0.01	*
SA8	2533.56	±	2.64	2566.01	±	3.71	88.07	<	0.01	*
SA10	2533.81	±	2.57	2565.89	±	3.56	90.28	<	0.01	*
SA13	2533.79	±	2.48	2565.32	±	3.38	91.60	<	0.01	*
SA21	2534.28	±	2.31	2565.00	±	3.02	96.02	<	0.01	*
SR	1.01	±	0.00	1.03	±	0.00	76.26	<	0.01	*
SR3	1.01	±	0.00	1.03	±	0.00	84.11	<	0.01	*
SR4	1.01	±	0.00	1.03	±	0.00	85.70	<	0.01	*
SR6	1.01	±	0.00	1.03	±	0.00	87.03	<	0.01	*
SR7	1.01	±	0.00	1.03	±	0.00	87.81	<	0.01	*
SR8	1.01	±	0.00	1.03	±	0.00	87.45	<	0.01	*
SR10	1.01	±	0.00	1.03	±	0.00	88.54	<	0.01	*
SR13	1.01	±	0.00	1.03	±	0.00	91.23	<	0.01	*
SR21	1.01	±	0.00	1.03	±	0.00	95.71	<	0.01	*
DRi	1000.64	±	42.26	703.71	±	37.63	29.12	<	0.01	*
DRo	1714.65	±	80.20	1366.59	±	85.31	17.69	<	0.01	*
DVi	3154.75	±	90.02	2708.83	±	96.62	19.13	<	0.01	*
DnVi3	5.55	±	0.81	6.31	±	0.95	0.08		0.78	
DnVi4	5.98	±	0.71	7.04	±	0.79	1.06		0.30	
DnVi6	6.89	±	0.63	8.21	±	0.65	5.19		0.02	*
DnVi7	7.13	±	0.59	9.09	±	0.64	7.18		0.02	*
DnVi8	7.70	±	0.57	9.88	±	0.64	8.85	<	0.01	*
DnVi10	8.93	±	0.57	11.32	±	0.66	13.69	<	0.01	*
DnVi13	10.98	±	0.59	13.43	±	0.67	16.18	<	0.01	*
DnVi21	16.09	±	0.60	18.93	±	0.67	14.57	<	0.01	*
DnRo3	488.58	±	26.71	584.05	±	27.73	10.45	<	0.01	*
DnRo4	480.12	±	24.39	579.86	±	24.92	14.40	<	0.01	*
DnRo6	465.30	±	20.94	567.49	±	21.62	15.27	<	0.01	*
DnRo7	468.89	±	20.02	562.28	±	20.45	15.36	<	0.01	*
DnRo8	474.31	±	19.21	564.22	±	19.52	15.61	<	0.01	*
DnRo10	486.59	±	18.21	575.26	±	18.08	17.31	<	0.01	*

Appendix IV continued

							Univariate tests†			
Variable	Presence			Absence			X^2		P	
DnRo13	508.28	±	17.27	595.85	±	16.61	17.82	<	0.01	*
DnRo21	588.76	±	16.69	662.07	±	15.04	16.07	<	0.01	*
C8	1.99	±	0.22	2.03	±	0.21	3.27		0.07	
F3C8	1.96	±	0.15	2.01	±	0.13	26.94	<	0.01	*
F4C8	2.10	±	0.14	2.05	±	0.13	18.62	<	0.01	*
F6C8	2.48	±	0.14	2.28	±	0.13	4.65		0.03	*
F7C8	2.69	±	0.15	2.42	±	0.14	1.58		0.21	
F8C8	2.95	±	0.15	2.60	±	0.14	0.14		0.71	
F10C8	3.50	±	0.16	3.02	±	0.15	0.51		0.47	
F13C8	4.25	±	0.18	3.57	±	0.17	4.02		0.05	
F21C8	6.13	±	0.22	4.90	±	0.20	19.15	<	0.01	*
Di	0.66	±	0.02	0.71	±	0.02	4.88		0.03	*
Di3	0.88	±	0.02	0.94	±	0.02	5.85		0.02	*
Di4	0.91	±	0.02	0.96	±	0.02	3.59		0.06	
Di6	0.98	±	0.02	1.00	±	0.02	0.35		0.56	
Di7	1.01	±	0.02	1.01	±	0.02	0.00		0.98	
Di8	1.04	±	0.02	1.03	±	0.02	0.26		0.61	
Di10	1.10	±	0.02	1.08	±	0.02	1.43		0.23	
Di13	1.18	±	0.02	1.13	±	0.02	5.07		0.02	*
Di21	1.34	±	0.01	1.26	±	0.01	19.85	<	0.01	*

Notes: Values are means ± 1 SE. Asterisks indicate significant difference at $P < 0.05$.
† All variables were tested using Kruskal-Wallis.