Global Ecology and Conservation 17 (2019) e00570

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

Habitat use by Asian elephants: Context matters

Dinesh Neupane [a,*], Youngsang Kwon [b], Thomas S. Risch [c], A. Christy Williams [d], Ronald L. Johnson [c]

[a] Graduate Program of Environmental Sciences, Arkansas State University, State University, AR, USA
[b] Department of Earth Sciences, The University of Memphis, Memphis, TN, USA
[c] Department of Biological Sciences, Arkansas State University, State University, AR, USA
[d] WWF-Myanmar, Myanmar

A R T I C L E I N F O

Article history:
Received 3 December 2018
Received in revised form 17 February 2019
Accepted 18 February 2019

Keywords:
Asian elephant
Nepal
Habitat use
GNESFA
Ecogeographical variables

A B S T R A C T

Asian elephants are isolated in fragmented habitat patches in and around Bardia National Park (BNP), Nepal. To describe habitat use patterns and ecogeographical variables (EGVs) that determine an elephant's niche in BNP, we used a General Niche-Environment System Factor Analysis (GNESFA) modeling framework. Novel to our study was the comparison of niche requirements between core (residential) and corridor (travel corridor) areas to elucidate site-specific preferences of Asian elephants in BNP. A total of 13 EGVs (four topographic variables, six land covers, heterogeneity index and two anthropogenic variables) were examined. We implemented a 'bias file' approach to address potential sampling bias in the transect survey methods for presence records. Our study illustrated that, regardless of study area, elephants' habitat use was positively influenced by presence of grasslands, mixed forest, and landscape heterogeneity, whereas use was restricted by the topographic variables of slope and elevation. Results also demonstrated different habitat preferences between elephants in the core and corridor, which may be attributed to differences in potential dangers posed in these areas; in the core, elephant habitat preference was mainly associated with food resources such as grassland or mixed forest, whereas in the corridor, where elephants are more likely to encounter human conflict, the anthropogenic factor of distance to human settlements contributed the most in predicting elephant presence. Correlations among significant factors from the three methods (FANTER, ENFA, and MADIFA) demonstrated the consistent and reliable results of these approaches. While these methods complemented each other by providing different points of view, FANTER was especially useful when bimodal niches were analyzed. We suggest a detailed conservation plan for the small populations of elephants in BNP and surrounding areas, while considering the protection of travel routes from human activities in the corridor habitats, and lastly, maintaining grasslands and waterholes in core habitats.

1. Introduction

Conservation of a species requires detailed knowledge of how populations interact with their environment. Ecologists have recognized for decades that habitat use by animals is influenced by the context in which the animal exists. Classic

* Corresponding author. PO Box 599, State University, Jonesboro, AR, 72467, USA.
E-mail address: dineshkneupane@gmail.com (D. Neupane).

https://doi.org/10.1016/j.gecco.2019.e00570

models of habitat use have considered resource acquisition (e.g., MacArthur and Pianka, 1966; Charnov, 1976), competition between/among species (e.g., Rosenzweig, 1974, 1981), and/or the distribution of available resources (e.g., Rosenzweig, 1981). Habitat use is often examined in relation to specific periods of an animal's life-history, most prominently via studies of breeding habitats (e.g., Custer and Osborn, 1978; Saab, 1999), wintering habitat (e.g., Steenhof et al., 1980; Larsen and Guillemette, 2007), whereas habitat use during periods when animals are highly mobile, for example, during bird migration, has received less attention (Keller et al., 2009; Webb et al., 2010; De Groeve et al., 2016). As uses of habitats differ by species seasonally (Keller et al., 2009), an understanding of habitat use in specific temporal and spatially contexts is essential for the conservation of a species.

Human activities result in dramatic changes of habitats. Landscape alteration by humans poses the greatest threat to many wildlife species. The destruction of habitat is especially problematic for Asian elephants (*Elephas maximus*), because elephants require large areas (Williams et al., 2008; Alfred et al., 2012) to meet their ecological requirements (Rood et al., 2010; Steinheim et al., 2005). Thus, habitat loss jeopardizes this species more so than species having smaller ranges. For example, within southern Nepal, the malaria eradication campaign by the government of Nepal in the 1950's (Mills et al., 2008) involved the draining of marshland and its conversion to farmland and human settlements. The three-fold increase in the human population regionally during this same period (GON/MOHP, 2011), has resulted in severe habitat loss for elephants (Neupane et al., 2014, 2017a, 2017b).

Further, remaining native elephant habitats are fragmented and sub-optimal, and may not provide adequate food resources year-round (Leimgruber et al., 2003; Shannon et al., 2009). To complicate matters, primary human crops (e.g., rice, wheat, sugar cane etc.) are cultivated grasses, which also have high nutritional value to elephants (Sukumar, 1990). Thus, elephants often enter and damage farmlands where they are considered agricultural pests both in Africa (Löyttyniemi and Mikkola, 1980) and Asia (Bandara and Tisdell, 2005; Neupane et al., 2014, 2017b). The lack of connectivity of these forests in Nepal often results in human-elephant conflict (HEC) (Neupane et al., 2014). HEC is the biggest threat to Asian elephants locally and throughout its range (Choudhury et al., 2008; Neupane et al., 2014). Nonetheless, understanding habitat use patterns by Asian elephants in Nepal as a means to potentially reduce HEC have not been critically examined.

Bardia National Park (BNP) in Nepal provides a unique setting for studying remaining native elephants' habitats of two differing types of herds exhibiting differing behaviors; BNP holds a large population of residential elephants (n~80) as well as itinerant herds of elephants that travel north from Indian forests (Pradhan et al., 2007). The western boundary of BNP is a lowlands floodplain (hereafter corridor) that serves as a route for elephants to move from BNP to Indian forests, whereas the interior of the park is preserved natural habitat with dense forest and limited human accessibility (hereafter core). Thus, BNP offers the opportunity to study habitat use and niche requirements of both mobile and residential elephants.

Species distribution models have been conducted using two basic approaches: presence-only and presence-absence. A presence-only approach predicts species' distribution by relating a species' presence to location, and the ecogeographic characteristics of that location. In contrast, a presence-absence approach requires both the study of where a species is known to be and where it is known not to be with respect to particular habitats. However, a limitation of the presence-absence approach is that it is difficult to demonstrate the absence of a species using field data, particularly for large mobile animals (Pearce and Boyce, 2006). Moreover, studying wide-ranging species can result in false absence data due to the logistic challenges of locating animals over large areas (Brotons et al., 2004), which in turn degrades model quality (Engler et al., 2004). With the growing availability of georeferenced data, presence-only models such as the maximum-entropy approach (Maxent; Phillips et al., 2017) demonstrated successful habitat predictions with mobile animals including the one-horned rhinoceros *Rhinoceros unicornis* in Nepal (Kafley et al., 2009) and elephants (*Loxodonta africana*) in Ghana (Ashiagbor and Danquah, 2017). Nevertheless, the Maxent model may produce biased results, as it tends to overestimate the probability of occurrence beyond the species' known extent of habitat (Gomes et al., 2018).

The General Niche-Environment System Factor Analysis (GNESFA) is an extensive presence-only modeling framework to examine habitat use patterns, as it includes three complementary methods with each offering different analytical approaches for the data (Calenge and Basille, 2008). Advantages of using GNESFA are that it is exploratory by nature, easy to perform, and interpretation is transferable to ecologists, as this analysis is based on Hutchinson's concept of the ecological niche (Calenge and Basille, 2008). Additionally, GNESFA is more appropriate for mobile animals like elephants where it is difficult to collect absence data of such animals, as illustrated by Caruso et al. (2015) studying the Puma (*Puma concolor*).

The objectives of this study are to examine elephant habitat use through a General Niche-Environment System Factor Analysis (GNESFA) modeling framework, with the aim of identifying important ecogeographical variables comparing two contexts (a core area containing a residential herd of elephants, and a corridor area containing mobile elephants) in and around Bardia National Park (BNP), Nepal.

2. Materials and methods

2.1. Study area

Bardia National Park (Area: 968 km^2), located in southwest Nepal (Fig. 1), is home to approximately 80 residential Asian elephants (Pradhan et al., 2007), with another 40–50 elephants crossing the Indo-Nepal border seasonally from adjacent Indian forests (Pradhan et al., 2011; Neupane et al., 2014). Bardia National Park is directly connected to the Katarniaghat Wildlife Sanctuary in India through the Khata Corridor.

2.2. Field surveys

We focused our surveys on habitat use in areas of known elephant activity based upon interviews with local park officials and elephant mahouts. Mahouts use domestic elephants to track and monitor wildlife deep in the park, and thus have current knowledge of local elephant distributions. Based on the information provided, we identified three study locations (the Karnali floodplain, the Ramvapur Forest, and the Babai Valley; Fig. 2) having potential elephant activity. The Karnali floodplain is located along the western boundary of the park, and includes both BNP and the neighboring buffer zones within the Khata Corridor. Ramvapur Forest and the Babai Valley as comprising the core areas are located near the center of BNP (Fig. 2). The corridor includes adjacent forests where human activity is prevalent, whereas the core is largely undisturbed. Elephants in these two areas use their habitat in two differing contexts, as elephants reside in the core for longer periods, whereas the corridor is used by mobile herds for moving between India and Nepal (D. Neupane, pers. observation; Pradhan et al., 2007).

Each location was surveyed using a center-line transect ($n = 15$ transects; each approximately 10 km long and 100 m wide). Five survey teams, each comprised of two surveyors, were employed for 36 days. Within a transect, a survey team walked along trails, fire breaks, roads, or creek beds in search of elephant sign (dung, tracks, or damage). In addition to basic transect line surveys, whenever elephant sign was encountered, we further searched a 500-m radius area from the presence locations because we estimated that elephants walked approximately that distance (500 m) between defecation periods. This additional effort resulted in a greater likelihood in delineating habitat use by elephants. By focusing on information provided by the mahouts as to probable elephant activity we sampled approximately 80% of BNP. Each transect was sampled twice (18 field days each period), once during the fall (September/October) and later during the winter (November/December) of 2012. These sampling months were chosen as they represent periods of greatest elephant movement in the study area. Bardia experiences HEC year-round with December and January representing HEC peaks; the remaining months have low to moderate HEC (Neupane et al., 2014, 2017b). Tracks and signs of elephant damage were used to help locate dung samples; however, only dung piles were considered for presence data. Presence locations were recorded using GPS (model: GPSMAP®64ST, accuracy ±10m) based on the UTM 44N reference system (WGS, 1984 datum).

2.3. Model development

2.3.1. Species presence and background condition

A total of 429 elephant dung sample locations were converted to a raster of 30 m by 30 m grids matching the spatial resolution of Landsat images used for land cover classification and other ecogeographical variables (EGVs) described in Section 2.3.2.

As with most presence-only species distribution models, GNESFA requires additional data representing the range of environmental conditions available for the species in the modeled region, called background (or pseudo-absence data). Background, usually drawn at random from the entire study region, is different from absence data as it doesn't mean absence

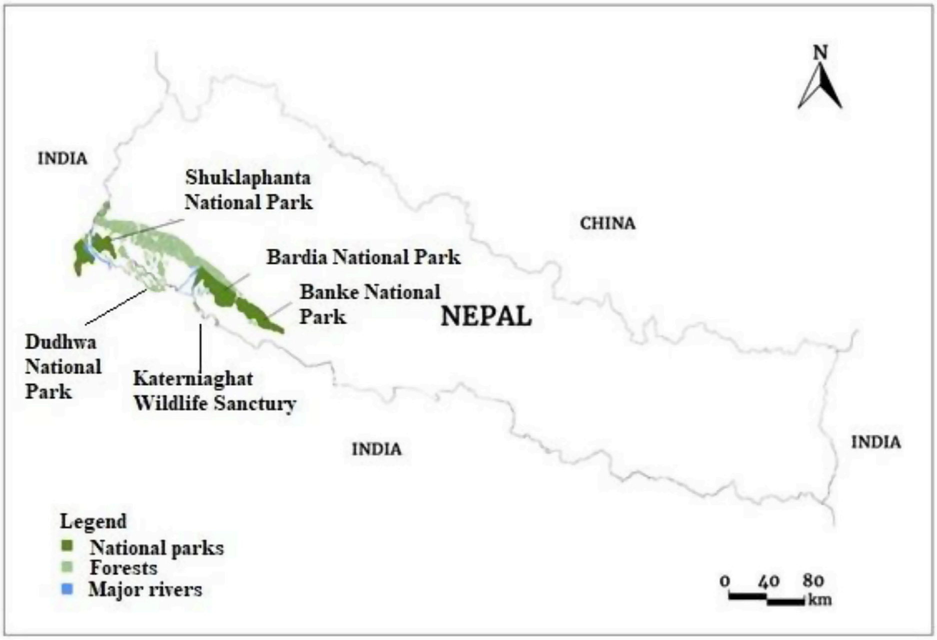

Fig. 1. Map of Nepal showing the national parks, major rivers, and surrounding forests of southwestern Nepal and adjacent protected areas of India.

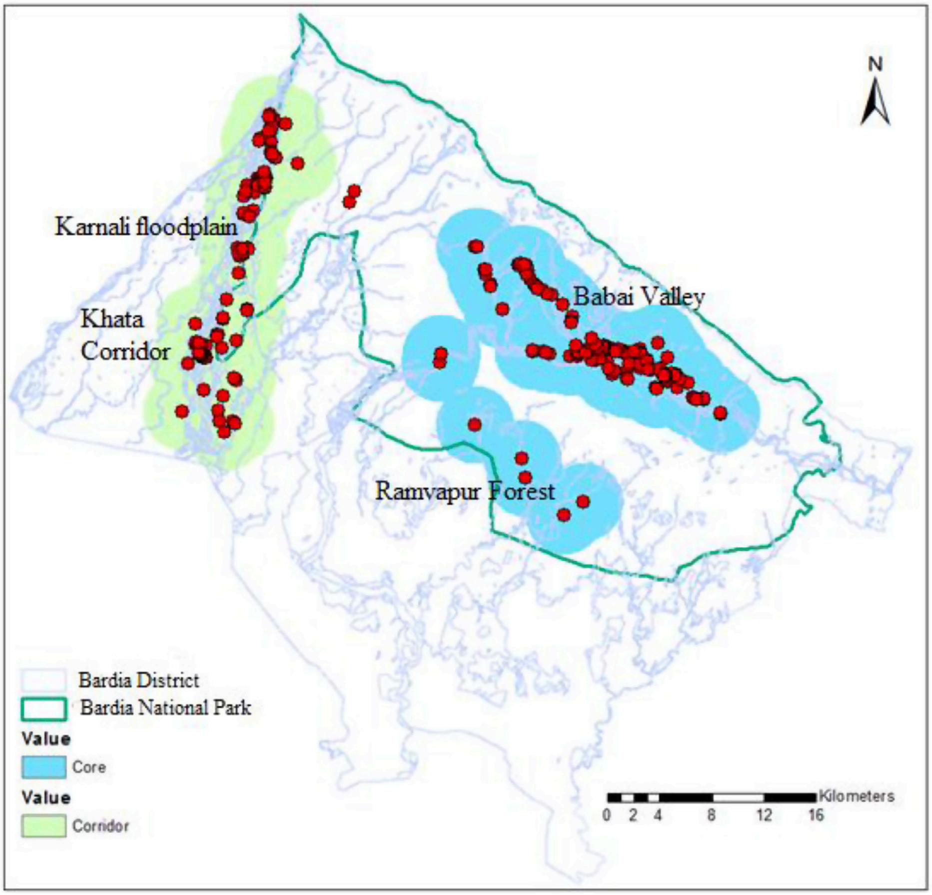

Fig. 2. Map showing locations of elephant dung locations (red) in the core (blue) and corridor (green) areas in and around Bardia National Park. Gray lines indicate river and landscape features. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

of a species' occurrence (Phillips et al., 2009). We applied a background sampling treatment using a '*bias file*' approach to account for spatial sampling bias introduced from our transect survey, following methods suggested by Kramer-Schadt et al. (2013) and Phillips et al. (2009). This approach corrects for bias in presences by introducing the similar kind of bias in background, thus the two biases cancel one another. A *bias file* was created by intersecting transect lines on a 30 m by 30 m grid, with each cell intersecting transect lines given a value of 1; we then subsequently summed the number of records across the 70 by 70 pixels (approximately 2 km width) of each grid. If there was no transect line, a cell was assigned the value 0.1, indicating a tenth of the sampling effort of 1. The basis for this available background area estimation (2 km buffer) is two-fold: first, north of BNP is delimited by high elevation with steep slope where elephants can not access. From the transect survey lines, the distance to those inaccessible areas is approximately 2–4 km. Thus the 2 km distance is to avoid artificially inflated test statistics when data are drawn from too large area (Anderson and Raza, 2010). Second, elephants can typically walk up to 2 km per day in continuous forest (Alfred et al., 2012), and defecate 16 to 18 times a day (Choudhury et al., 2008).

2.3.2. *Eco-geographical variables (EGVs)*

EGVs were categorized into three groups (see Table 1 for details) as a land cover-related group, a topographical group and an anthropogenic group. To classify land covers that are most relevant to the elephant's ecological niche in BNP, two Landsat images (March and November of 2013) (path 144, row 040) were used together with high-resolution aerial photographs from Digital Globe taken during 2012 provided by ArcGIS as supplemental data. The month of March represents one of the hot dry months of the year, whereas November represents a cool month; images from different seasons complement each other to improve vegetation classification accuracy. For example, deciduous forest was less distinguishable in March than November, whereas evergreen forest was better discerned in March. We used the unsupervised ISO Cluster classification method, as it outperformed the supervised classification method. A total of six mutually exclusive land covers were identified to characterize potential habitats in study areas: mixed forest, sal forest, riverine forest, grassland, waterbodies, and floodplain. A sal forest is characterized by the deciduous species *Shorea robusta* found in the lowlands and foothills of Nepal. We used field-survey of land cover and random points identified by aerial photographs as ground truth references to calculate an error matrix of the classification map.

Table 1
Description of each ecogeographical variable (EGVs) used in the analysis.

Variables		Description
Topography variables		
Elevation		Elevation from sea level
Slope		Slope of the terrain
Terrain ruggedness		Standard deviation within a 1 km distance of each cell
Curvature		Difference between the elevation of each cell and the average of 10 adjacent pixels
Land cover variables		
Sal forest	**Distance-based**	Dominant six land cover types in the area by the shortest distance of sample location from the target land cover
Riverine forest		
Grassland	**Frequency-based**	Dominant six land cover types in the area by the frequency of land cover in 7 by 7 window
Water bodies		
Floodplain		
Mixed forest		
Shannon index (Heterogeneity index)		Proportion of land cover in a reference unit of 7 by 7 windows
Anthropogenic variables		
Distance to roads		Roads identified by aerial photographs
Distance to human settlements		Houses and man-made agricultural features identified by aerial photographs

To develop land cover-related EGVs, the six land covers were transformed into both distance-based and frequency-based variables. A distance-based variable simply measures the distance from a given land cover pixel, whereas the frequency-based variable calculates the proportion of pixels from a given land cover within an area of 7 by 7 pixels around the focal pixel. We tested both the distance-based (distance of sample points from land cover types) and frequency-based (land cover frequencies) quantification methods and chose the EGVs with higher explanation power determined by correlation coefficients to the first and second factors of ecological-niche factor analysis (ENFA, see Section 2.3.3). When distance-based variables show positive correlations with marginality of bi-plots (see Section 2.3.3), the interpretation is a species' avoidance to that class, whereas frequency-based variables are a species' preference of that class. The Shannon diversity index was calculated to determine land cover heterogeneity by using a 7 by 7 moving window. The formula for the Shannon index (Shannon and Weaver, 1963) is expressed as:

$$\text{Shannon Index} = -\sum_i \text{p}i \ln(pi)$$

where pi is the proportion of land cover i in a reference unit of 7 by 7 pixels.

Four topography-related variables (elevation, slope, ruggedness, and curvature) were derived from the Shuttle Radar Topography Mission (SRTM) digital elevation model downloaded from the Global Land Cover Facility (http://www.landcover.org). Following Rood et al. (2010), we quantified the ruggedness of the terrain by using the standard deviation of elevation within a 1 km distance of each cell. Landscape curvature was calculated as the difference in elevation between the focal cell and the average of 10 adjacent pixels. Low values of curvature corresponded to valleys and higher values for landscape curvature represented areas of higher elevation.

Two anthropogenic variables (closest distance to roads and distance to human settlements) were manually digitized by using high-resolution aerial photographs, as Landsat images failed to detect scattered houses and narrow roads near the park boundary.

2.3.3. General Niche-Environment System Factor Analysis

We used General Niche-Environment System Factor Analysis (GNESFA) following Calenge and Basille (2008) to study the factors affecting the use of ecological space in two different locations (core and corridor areas) in BNP. Central to GNESFA is a factor analysis to create a multidimensional ecological space using EGVs and it encompasses three methods by the choice of one of two distributions - focus distribution (FD) or reference distribution (RD) for the graphical exploration of the relationships between distribution of the species occurrences and its available background conditions: Factor Analysis of the Niche Taking the Environment as the Reference (FANTER), Mahalanobis Distances Factor Analysis (MADIFA) and Ecological-Niche Factor Analysis (ENFA). If the presence distributions are chosen as FD and the available background as RD, the resulting analysis is called FANTER. This method examines deviates of FD from the centroid of RD in multidimensional space, namely the ecological space. FANTER provides a detailed exploratory analysis of the habitat patterns taking the environment as the reference in the ecological space as in classic habitat selection studies.

On the other hand, if the presence distributions are chosen as RD and the available background chosen as FD, the approach is called MADIFA. This method examines deviates of RD from the centroid of FD in the ecological space and compares the available background to habitat used by the species as in habitat suitability studies (Calenge and Basille, 2008). MADIFA finds the direction of the ecological space in which the background is most different from the distribution of used habitats, identifying the most suitable environment conditions available for that species.

Lastly, if two distributions (presence and background) are symmetrically chosen as both the RD and FD by centering both the centroids of RD and FD in the ecological space, this symmetrical point of view is called ENFA. This method measures a vector connecting the centroids of RD and FD by maximizing the overall characteristics of a species' niche (i.e., marginality (M) formally measured as the absolute difference between global mean, divided by 1.96 standard deviation of global distribution) and the narrowness of that niche (i.e., specialization (S) formally measured as the ratio of the standard deviation of the global distribution to that of the focal species). ENFA has been widely used in habitat studies (e.g., Hirzel and Arlettaz, 2003; Cianfrani et al., 2010; Rood et al., 2010), taking advantage of formal measures of M and S, and being an intermediate approach between FANTER and MADIFA. However, this method alone may cause erroneous interpretation when the marginality is not significant, resulting in biased characteristics of specialization due to the orthogonality constraints in factor analysis (Calenge and Basille, 2008).

In practice, we first normalized all EGVs using Box-Cox transformation. A total of 1000 raster pixels were then randomly selected from background to define the available background environment. In each approach of GNESFA, factors (i.e., principal components) from PCA analysis were selected by evaluating eigenvalues (γ) of each factor compared to MacArthur's Broken-stick distribution (Hirzel et al., 2002) using the Monte-Carlo randomization procedure with 1000 permutations. If the eigenvalue of a particular factor was larger than what would have been obtained randomly (i.e., broken-stick distribution), it was considered a significant factor and was therefore included in each method for the graphical (i.e., bi-plots) interpretation. The biological meaning of principal components from GNESFA can be derived from the correlations between the EGVs and the selected factors of each analysis (FANTER, ENFA, MADIFA).

ENFA distinguishes the marginality and the specialization of a species based on the assumption that both the presence and the available background are symmetrical and unimodal (Hirzel et al., 2002). Therefore, FANTER is complimentary to ENFA, as it can identify bimodal niches (as demonstrated by Calenge and Basille, 2008) and the MADIFA is useful in that it combines the marginality and the specialization of a species into a unique measure of habitat suitability. FANTER tends to maximize the marginality on the first factor and the specialization on the last factor, whereas MADIFA combines the marginality and the specialization into one single measure of niche restriction (see Calenge et al. (2008) for the mathematical explanation of this approach).

We present a series of bi-plots projecting both the ecological niche and the EGVs on the subspace defined by the two axes of significant factors developed using each of the three methods of GNESFA. The strength and direction of the correlations between selected factors and the EGVs used in the analyses allowed us to assign biological significance to the principal factors. Additionally, we present histograms of available background and utilized niche by elephants plotted against the background using the first factor of FANTER to examine the shape of niche. GNESFA analysis was performed using the package “adehabitatHS” (e.g., Calenge, 2016) in R software (R Development Core Team, 2007).

3. Results

Six land covers classified by two Landsat images produced an overall accuracy of 83.2%, with a Kappa coefficient value calculated as 0.79, assuring accuracy of our land cover classes used in the study area. For both the core and corridor, two land cover groups of EGVs (grassland and floodplain) were quantified using the frequency-based approach and four other land covers (sal forest, riverine forest, mixed forest, and waterbodies) were used as distance-based variables determined by correlation coefficients of the first and second axes of the initial ENFA. The summary of GNESFA results (the two strongest influential EGVs to significant factors) are presented in Table 2 and the subsequent interpretations of bi-plots are presented separately for core (Section 3.1.) and corridor (Section 3.2.) areas.

3.1. Core area

The randomization test for FANTER indicated significant eigenvalues in the core area for the first ($\gamma_1 = 2.65$, $p < 0.01$) and the last factors ($\gamma_{13} = 0.55$, $p < 0.01$). The first factor (abscissa in a bi-plot; maximized marginality) of FANTER was primarily correlated with grassland (i.e., preference of grassland), and to a lesser extent, mixed forest (negative correlation to distance to mixed forest, and thus preference of mixed forest) (Fig. 3a), indicating elephants' presence was near grassland and mixed forest more frequently than the average available background condition. For example, 30% of the dung samples were located

Table 2
Summary of primary EGVs to selected factors using three approaches (FANTER, ENFA, and MADIFA) in the core and corridor of BNP under the GNESFA framework. The sign in the parentheses indicates whether that EGV is preferred (+) or in avoidance (−) to habitat preference. ‘M’ indicates the marginality factor and ‘S’ indicates the specialization factor in ENFA. Legend: FP - floodplain; GS - grassland; Sal - sal forest; MF - mixed forest; RF - riverine forest; Water − water bodies; Elev. - elevation; HS, human settlements; and, Shannon - Shannon index.

	FANTER	ENFA	MADIFA
Core	1st factor: GS (+); MF (+)	M: MF (+); Water (+)	1st factor: Sal; GS
	Last factor: Elev.; Slope	S: Slope; Sal	2nd factor: Elev.; Water
Corridor	1st factor: HS (−); Shannon (+)	M: HS (−); RF (+)	1st factor: HS; RF
	Last factor: Shannon; RF	S: Shannon; Sal.	Not significant

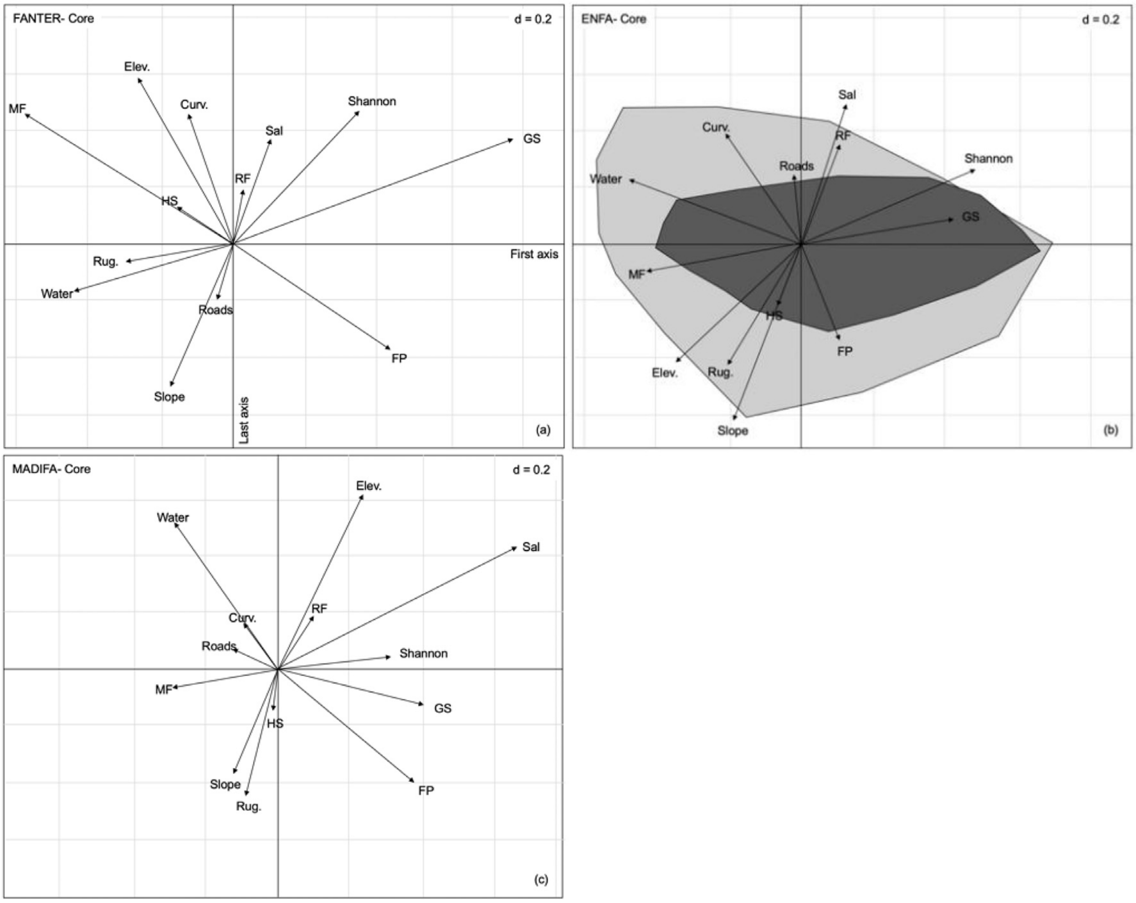

Fig. 3. Biplots of GNESFA for the core area; (a) FANTER in the plane formed by first (X-axis) and last factor (Y-axis); (b) ENFA in the plane formed by marginality (X-axis) and specialization (Y-axis). The light and dark areas in ENFA correspond to the minimum convex polygon enclosing all the projections of the available background and presence points, respectively; and (c) MADIFA in the plane formed by first (X-axis) and second factor (Y-axis). Grid lines (separated by a distance of 0.2) can be used to measure the correlations between EGVs and significant factors (i.e., abscissa and ordinate axes) on the graph for each analysis. Legend: GS, frequency of grassland; FP, frequency of floodplain; Sal, distance to sal forest; MF, distance to mixed forest; RF, distance to riverine forest; Elev., elevation; Curv., curvature; Rug., ruggedness; Slope, slope; Water, distance to water; Shannon, Shannon index, HS, distance to human settlements; and Roads, distance to roads.

in sites with more than 50% comprised of grassland; in contrast, this vegetation class represented only 14% of the study area. The last factor of FANTER (ordinate in a bi-plot; maximized specialization) exhibited strong correlations with elevation and slope (Fig. 3a), indicating elephants' habitats were utilized in a narrower range of topographic variables of elevation and slope than available background. The niche distribution was bimodal against the first factor of FANTER; there was a first mode around the origin and a second peak on the positive side of this factor (Fig. 4a). The eigenvalues of ENFA indicated that two factors - the marginality (M) and the first factor of specialization (S) - accounted for 71% of the variances in the core area. The distance between the centroid of elephants' niche and the centroid of available habitat was quite high, resulting in a pronounced marginality value ($M = 0.43$, $p < 0.01$, via the randomization test), which reflects that an elephant's probability of presence in a habitat was different from the mean available condition. The eigenvalue (γ) of the first factor of specialization was 3.16 ($p < 0.01$), which reflects that the variance of the available background is more than three times the variance of the used habitat; thus the ecological niche is much narrower than the available background habitat. Determined by the correlations between EGVs and two axes (i.e., marginality (abscissa) and specialization (ordinate) in the bi-plot), preference to waterbodies contributed the most to the marginality, followed by the Shannon index (preference to land cover heterogeneity), and to a lesser extent, the preference to grassland and mixed forest. The slope and sal forest were two primary variables which contributed the most to the specialization (ordinate in a bi-plot, Fig. 3b), indicating that elephants were not tolerant to the variation of slope and distance to sal forest (i.e., elephants were restricted on a limited range on these variables) with a mean shift toward low slope area and slightly avoiding sal forest.

The results of MADIFA identified additional significant EGVs in the core area, as it identified the directions of the ecological space where Mahalanobis distances were the largest, corresponding to the environmental conditions scarcely used by elephants. The randomization tests of the first and second eigenvalues of MADIFA were significant ($\gamma_1 = 3.23$, $p < 0.01$, and $\gamma_2 = 1.66$, $p < 0.01$). The first axis (abscissa) of MADIFA was strongly correlated with sal forest and the second axis (ordinate) was correlated with elevation (Fig. 3c), which reflects sal forest and elevation were primary variables affecting the position of

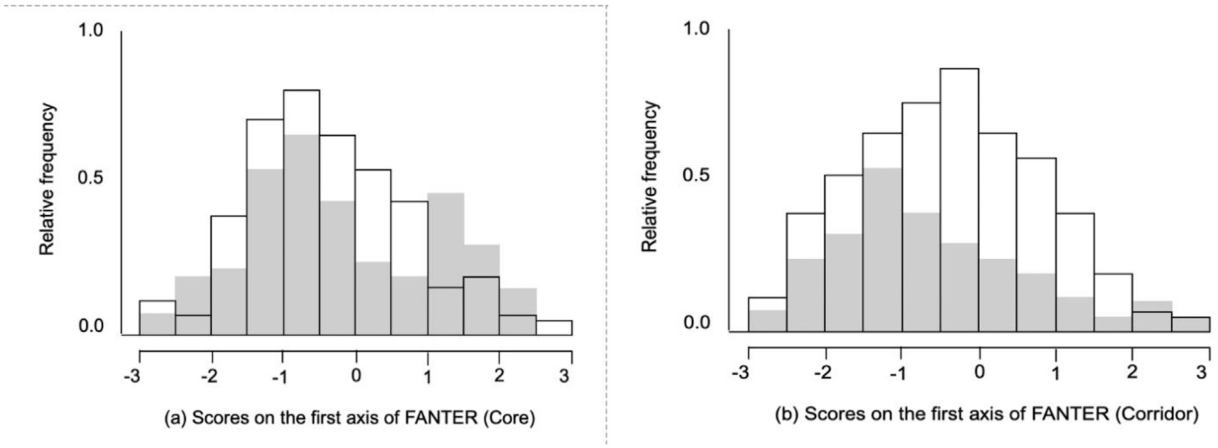

Fig. 4. Histograms of the coordinates of the available background (white bars) and of the used habitats (gray bars) on the first component of the FANTER for (a) core and (b) corridor.

the availability niche in relation to the used niche for the first and second factors, respectively. Only 5% of the elephants' dung sample locations occurred within a 30 m distance of sal forest, whereas this forest type represented 45% of the study area. We observed an extensive internal coherence among the different factors of the three approaches. The first and last factors from FANTER were highly correlated to both ENFA marginality and specialization and the first factor from MADIFA (Table 3), confirming the consistent, reliable patterns of these results.

3.2. Corridor area

The randomization tests for FANTER indicated significant eigenvalues in the corridor area for the first ($\gamma_1 = 3.53$, $p < 0.01$) and the last factors ($\gamma_{13} = 0.58$, $p < 0.01$). The first axis (i.e., abscissa in a bi-plot; maximized marginality) of FANTER was mainly correlated with distance to human settlements (positive correlation to distance to human settlements and thus avoidance to human settlements, followed by the Shannon index (preference to land cover heterogeneity) (Fig. 5a), indicating elephants' avoided human settlements and were near land cover heterogeneity more frequently than the average available background conditions. Over 40% of the elephants' dung samples were located within a 1 km distance of human settlements, while this distance class represented 20% of the study area. The last axis of FANTER was mainly correlated with the Shannon index and riverine forest (Fig. 4a), indicating elephants' habitats were utilized in a narrower range of land cover heterogeneity and riverine forest than the available background. The niche distribution was unimodal, showing a peak on the negative side of the origin against the first factor of FANTER (Fig. 4b).

The results of ENFA within the corridor were consistent with FANTER. Two factors (the marginality and the first factor of specialization) of ENFA together explained 67% of the total variances. The marginality value ($M = 0.53$, $p < 0.01$, via the randomization test) indicates an elephant's probability of presence was significantly different from the mean available conditions. The eigenvalue of the first axis of specialization was 5.31 ($p < 0.01$), indicating that the variance of the available background is more than five times the variance of the used habitat. The correlations between significant factors (i.e., marginality and specialization) and the EGVs showed that distance (avoidance) to human settlements was the most influential EGV to the marginality, followed by preference to riverine forest and mixed forest. The Shannon index and sal forest were the two primary variables that contributed the most to the specialization (ordinate in a bi-plot, Fig. 5b), indicating the elephants were not tolerant to the variation of land cover heterogeneity and distance to sal forest (i.e., elephants were restricted on a limited range on these variables), with a mean shift toward land cover heterogeneity and slightly avoiding sal forest.

Table 3
Pearson's correlation coefficient among factors from the three models: FANTER (F), ENFA (E), and MADIFA (M) under GNESFA in BNP. Each of the correlations is significant at $p < 0.01$. Letters in parenthesis represent marginality (M), specialization (S), first factor (1st), and last factor (last).

Site	Pearson's correlation coefficient	
Core	F (1st) vs. E (M)	R = 0.81
	F (last) vs. E (S)	R = - 0.71
	M (1st) vs. E (S)	R = 0.78
	M (1st) vs. F (last)	R = 0.77
Corridor	F (1st) vs. E (M)	R = 0.88
	F (last) vs. E (S)	R = - 0.72
	M (1st) vs. E (S)	R = 0.82

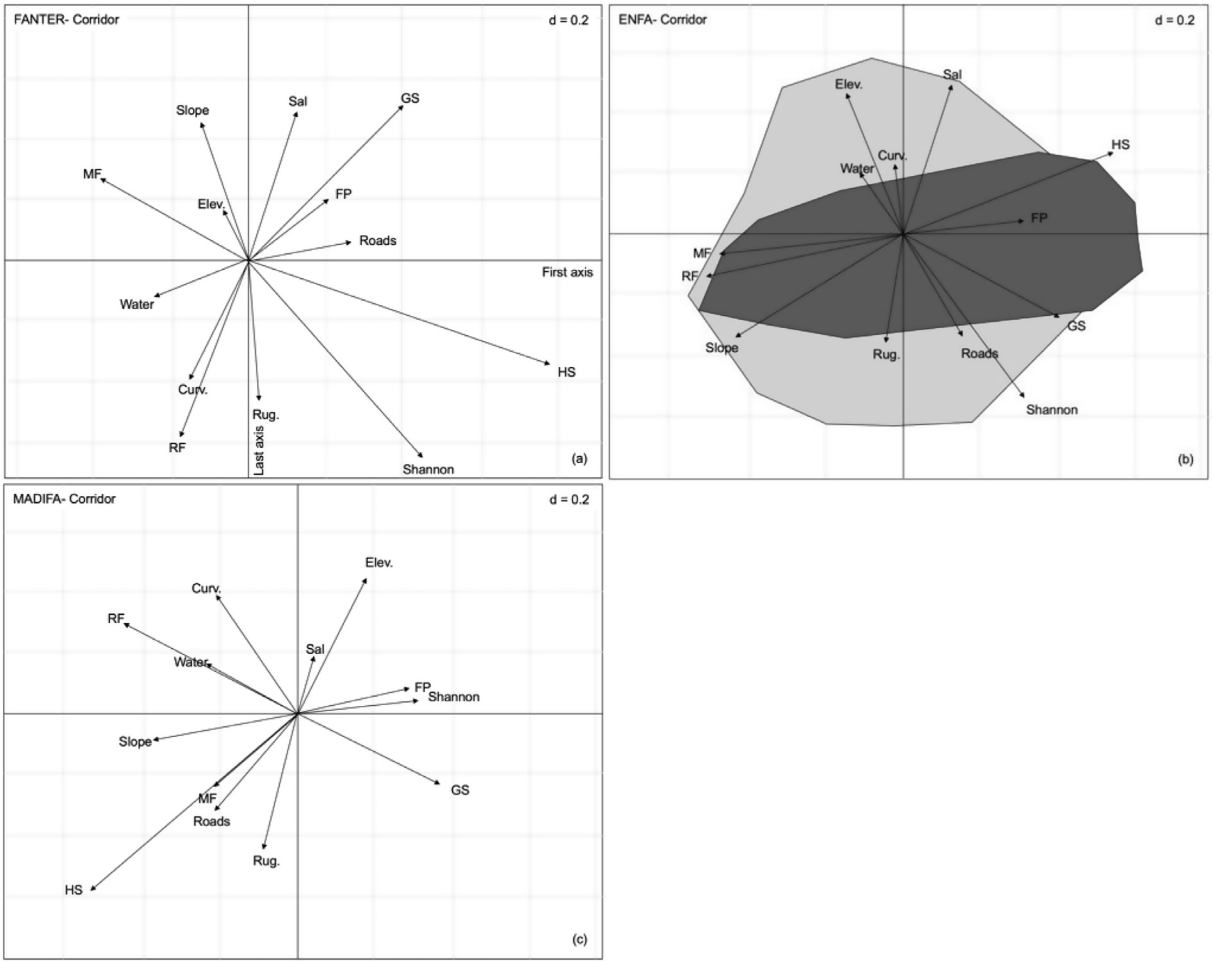

Fig. 5. Biplots of GNESFA for the corridor; (a) FANTER in the plane formed by first (X-axis) and last factor (Y-axis); (b) ENFA in the plane formed by marginality (X-axis) and specialization (Y-axis). The light and dark areas in ENFA correspond to the minimum convex polygon enclosing all the projections of the available background and presence points, respectively; and (c) MADIFA in the plane formed by first (X-axis) and second factor (Y-axis). Grid lines (separated by a distance of 0.2) can be used to measure the correlations between EGVs and significant factors (i.e., abscissa and ordinate axes) on the graph for each analysis. Legend: GS, frequency of grassland; FP, frequency of floodplain; Sal, distance to sal forest; MF, distance to mixed forest; RF, distance to riverine forest; Elev., elevation; Curv., curvature; Rug., ruggedness; Slope, slope; Water, distance to water; Shannon, Shannon index, HS, distance to human settlements; and Roads, distance to roads.

The results of MADIFA were consistent with FANTER and ENFA for analyzing the corridor. The randomization test for the first eigenvalue of MADIFA was significant ($\gamma_1 = 3.88$, $p < 0.01$) but the subsequent factors were not significant. The first factor of MADIFA was highly correlated with distance to human settlements, and to a lesser extent, riverine forest (Fig. 5c), which reflects human settlements and riverine forest as two primary variables affecting the position of the availability niche in relation to the used niche for the first factor. Similar to that identified for the core, the correlation coefficients among significant factors from the three analyses of GNESFA showed strong internal coherence, which further confirmed the consistency of the analytical approaches (Table 3).

4. Discussion

4.1. Ecogeographical variables and elephant niche in BNP

Although there were different EGVs identified affecting an elephant's niche between the core and corridor of BNP, several EGVs commonly appeared as important habitat determinants in both areas: grassland, mixed forest, water bodies, the Shannon index of land cover heterogeneity, and topographical factors such as slope and elevation. These habitat requirements of elephants in Nepal are consistent with previous research for both Asian elephants (Indonesia, Rood et al., 2010; India, Sukumar, 1989; Desai and Baskaran, 1996; Areendran et al., 2011; Sri Lanka, Fernando et al., 2008; and China, Zhang et al., 2015) and African elephants (South Africa, Smit et al., 2007; Southern Africa, Harris et al., 2008). A higher marginality score for elephants' preferences for grasslands provides a similar outcome to vegetation association studies previously done in Nepal by Steinheim et al. (2005) and Pradhan et al. (2007), as grasslands provide a higher nutritional source for herbivores than other vegetation types (Anderson and Briske, 1995; Steinheim et al., 2005).

A higher marginality explained by the Shannon index in our model indicated that elephants preferred areas with a greater land cover diversity. Species richness is positively correlated with landscape variance (Katayama et al., 2014), and is important to large herbivores such as African elephants in Kenya (Okello et al., 2015) and the one-horned rhinoceros in northern India (Sarma et al., 2012). Mixed forest and riverine forest were preferred by elephants in BNP, different to that identified by Steinheim et al. (2005) in Nepal. Mixed forests provide a greater diversity and seasonal variation of potential food sources, and have higher productivity as compared to homogeneous forests (Gamfeldt et al., 2013). Elephants may retreat to heterogeneous forests (identified by mixed forests or land cover heterogeneity) for cover and/or shade when not feeding on grasses, and/or may travel through these areas while searching for food or avoiding human disturbance while travelling. Additionally, forest edges between grasslands and riverine forests often have abundant secondary regrowth and nutritious foliage (Rood et al., 2010), whereas a closed canopy forest such as the sal forest in our study area provides a low-quality food (Steinheim et al., 2005). Williams et al. (2008) found that Asian elephants used sal vegetation significantly less compared to other vegetation types in India.

Topographic features such as slope and elevation served as basic factors to limit elephant distribution in BNP. Elephant movement and potential escape from human threats is not impeded in areas with less slope, similar to that observed in China (Pan et al., 2009) and in Indonesia, where Asian elephants were prevalent in mountain valleys (Rood et al., 2010).

4.2. Comparisons between core and corridor

Residential (core) and itinerant (corridor) elephants exhibited different habitat preferences, as indicated by different EGVs associated with marginality in BNP. Within the core, habitat preference was mainly associated with feeding such as in grassland or mixed forest, whereas in the corridor, where human disturbances are prevalent, habitat preference was associated with anthropogenic factors such as distance to human settlements. These differences may be attributed to differences in the potential dangers posed to the elephants in these areas. The corridor of BNP is part of the larger Khata Corridor connecting Nepal and India, and close to human settlements (within 3 km radius from the survey lines). In contrast, the core area of BNP is primarily an undisturbed grassland valley with consistent, reliable water resources; the influence of human settlements was negligible in the core. Most locations of human settlements and main roads were more than 10 km away from the presence locations in the core, whereas over two-thirds of the households located near the corridor had reported HEC within the previous five years (Neupane et al., 2017a, 2017b). In the corridor, other than human settlements, elephant niche was determined by preference to riverine forests and land cover heterogeneity (Shannon index). The riverine forests are often located adjacent to the floodplain and provide for an opportunity to escape in case of danger.

4.3. Complementary results of GNESFA

GNESFA using the three methods of FANTER, ENFA, and MADIFA yielded complimentary results and interpretations from the different perspectives of these models. For example, FANTER strongly suggested the importance of grassland in the core area as compared to a much weaker influence of grassland identified by MADIFA and ENFA (Fig. 3). As FANTER provides a view point centered from available background as reference, used habitat by elephants is most different from available habitats in terms of frequency of grassland. Importantly, the niche distribution of the core was bimodal, as identified by the first factor of FANTER. This bimodal shape of niche by elephants can be attributed to, first, the random use of ecological space affected by the same shape of available background and, second, a strong preference to grassland. This bimodal niche distribution is a special case where FANTER is unique among these three approaches; both ENFA and MADIFA assume unimodal niche distributions (Calenge and Basille, 2008). On the other hand, the sal forest was strongly captured by MADIFA yet not by FANTER as a primary EGV in explaining habitat suitability in the core. As MADIFA is oriented towards an elephant's niche as reference, available habitats are most different from the used habitat by elephants in terms of the distance to sal forest. Similarly, the preference for land cover heterogeneity (Shannon index) was a strong EGV only by FANTER in the corridor. Nonetheless, the correlations among the significant factors from the three approaches demonstrated the consistent, reliable patterns of the model outputs; thus, a strength of GNESFA is that the three model outputs complement one other in delineating habitat preferences.

Here, we identify the importance of considering niche requirements both for the home range and those associated with movement patterns for a mobile species. Habitat is used differently depending on the context of the species: mobility vs. non-mobility. This approach can be employed to examine habitat use of other mobile species, including those with regular migratory patterns. Recognizing those habitat use differences occurring during different periods of an animal's life history (e.g., breeding, migration, and wintering) will enable a conservation manager to develop a more comprehensive approach towards that species conservation.

5. Recommendations for management of elephant herds in Nepal

Asian elephants require large home ranges (Williams, 2002); therefore, survival of a viable population depends on the provision of extensive areas of suitable habitat. Specifically, within BNP, conserving the grasslands around river systems and fringe forests around the corridor should benefit those elephants moving long distances within their ranges. Further losses of grasslands due to the conversion to agriculture as has occurred over the past 50 years (Mills et al., 2008) would exacerbate HEC, further challenging the long-term sustainability of these herds. Additionally, since grasslands are invaded by woodlands over time through succession, continual maintenance of available grassland should be a management priority. In corridors, proper management of human-elephant conflict (HEC) is a critical factor, as we identified that scattered human settlements are a primary determinant of elephant habitat use in the corridor area where elephants may move over broad geographical areas. Our results may be applicable to other patch corridor networks used by Asian elephants because Bardia National Park and the Khata Corridor are part of a larger core/corridor network and are connected directly to the Katarniaghat Wildlife Sanctuary in India. As elephant preferences were related to feeding and cover variables in the core, these areas of preferred habitat that we have identified could be targeted with supplemental food and water during periods of low natural availability when elephants are moving through the corridor. Supplemental feeding has been used as a management tool during critical shortages for other types of wildlife such as deer and elk (e.g., Putman and Staines, 2004; Sahlsten et al., 2010; Milner et al., 2014). Similarly, artificial water sources have been established for Asian elephant conservation during dry periods in India (Lakshminarayanan et al., 2016).

We have demonstrated that habitat preferences differ between travel corridors versus core protected habitats in determining the niche requirements of Asian elephants. Thus, conservation officials should consider a more tailored management plan in BNP and surrounding areas. In addition, since elephants share their habitat with other megafauna in BNP, particularly the endangered one-horned rhinoceros (Steinheim et al., 2005), conserving and maintaining existing grasslands should also serve to safeguard other wildlife in this protected area. Unlike other south Asian countries such as south India (Desai and Baskaran, 1996) and Sri Lanka (Fernando et al., 2008), no radio-telemetry work has been performed on Asian elephants of Nepal. We recommend the future use of radio-telemetry, which would provide greater insight into elephant habitat requirements and movement patterns.

Acknowledgements

We would like to thank all paid field assistants especially Shankar Luitel, Bedu Pandey, Bir Bahadur, Ram Krishna, Ram Raj, Khusi Ram, Hemant, and others from Bardia National Park for their help in conducting the survey for this study. We owe thanks to park officials especially Mr. Tika Ram Adhikari, and Mr. Ramesh Thapa, and Mr. Rabin Kadariya and Shree Ram Ghimire from National Trust for Nature Conservation, Bardia. This work was supported by the US Fish and Wildlife Service (Award #F12AP00377) and Arkansas State University.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.gecco.2019.e00570.

References

Alfred, R., Ahmad, A.H., Payne, J., Williams, C., Ambu, L.N., How, P.M., Goossens, B., 2012. Home range and ranging behaviour of Bornean elephant (*Elephas maximus borneensis*) females. PLoS One 7 (2), e31400.
Anderson, R.P., Raza, A., 2010. The effect of the extent of the study region on GIS models of species geographic distributions and estimates of niche evolution: preliminary tests with montane rodents (genus *Nephelomys*) in Venezuela. J. Biogeogr. 37 (7), 1378–1393.
Anderson, V.J., Briske, D.D., 1995. Herbivore-induced species replacement in grasslands: is it driven by herbivory tolerance or avoidance? Ecol. Appl. 5 (4), 1014–1024.
Areendran, G., Raj, K., Mazumdar, S., Munsi, M., Govil, H., Sen, P.K., 2011. Geospatial modeling to assess elephant habitat suitability and corridors in northern Chhattisgarh, India. Trop. Ecol. 52 (3), 275–283.
Ashiagbor, G., Danquah, E., 2017. Seasonal habitat use by elephants (*Loxodonta africana*) in the mole national park of Ghana. Ecol. Evol. 7 (11), 3784–3795.
Bandara, R., Tisdell, C., 2005. Changing abundance of elephants and willingness to pay for their conservation. J. Environ. Manag. 76 (1), 47–59.
Brotons, L., Thuiller, W., Araújo, M.B., Hirzel, A.H., 2004. Presence-absence versus presence-only modelling methods for predicting bird habitat suitability. Ecography 27 (4), 437–448.
Calenge, C., Basille, M., 2008. A general framework for the statistical exploration of the ecological niche. J. Theor. Biol. 252 (4), 674–685.
Calenge, C., 2016. Package 'adehabitatHS': analysis of habitat selection by animals. R package version 3 (1).
Calenge, C., Darmon, G., Basille, M., Loison, A., Jullien, J.M., 2008. The factorial decomposition of the Mahalanobis distances in habitat selection studies. Ecology 89 (2), 555–566.
Caruso, N., Guerisoli, M., Vidal, E.L., Castillo, D., Casanave, E.B., Lucherini, M., 2015. Modelling the ecological niche of an endangered population of *Puma concolor*: first application of the GNESFA method to an elusive carnivore. Ecol. Model. 297, 11–19.
Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. Theor. Popul. Biol. 9 (2), 129–136.
Choudhury, A.L., Choudhury, D.K.L., Desai, A., Duckworth, J.W., Easa, P.S., Johnsingh, A.J.T., Fernando, P., Hedges, S., Gunawardena, M., Kurt, F., Karanth, U., Lister, A., Menon, V., Riddle, H., Rübel, A., Wikramanayake, E., 2008. Elephas maximus. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011. 1. www.iucnredlist.org. (Accessed 12 July 2011).
Cianfrani, C., Le Lay, G., Hirzel, A.H., Loy, A., 2010. Do habitat suitability models reliably predict the recovery areas of threatened species? J. Appl. Ecol. 47 (2), 421–430.
Custer, T.W., Osborn, R.G., 1978. Feeding habitat use by colonially-breeding herons, egrets, and ibises in North Carolina. Auk 95 (4), 733–743.
De Groeve, J., Van de Weghe, N., Ranc, N., Neutens, T., Ometto, L., Rota-Stabelli, O., Cagnacci, F., 2016. Extracting spatio-temporal patterns in animal trajectories: an ecological application of sequence analysis methods. Methods Ecol. Evol. 7 (3), 369–379.
Desai, A.A., Baskaran, N., 1996. Impact of human activities on the ranging behaviour of elephants in the Nilgiri Biosphere Reserve, South India. J. Bombay Nat. Hist. Soc. 93 (3), 559–569.
Engler, R., Guisan, A., Rechsteiner, L., 2004. An improved approach for predicting the distribution of rare and endangered species from occurrence and pseudo-absence data. J. Appl. Ecol. 41 (2), 263–274.

Fernando, P., Wikramanayake, E.D., Janaka, H.K., Jayasinghe, L.K.A., Gunawardena, M., Kotagama, S.W., Weerakoon, D., Pastorini, J., 2008. Ranging behavior of the Asian elephant in Sri Lanka. Mamm. Biol.-Zeitschrift für Säugetierkunde 73 (1), 2–13.
Gamfeldt, L., Snäll, T., Bagchi, R., Jonsson, M., Gustafsson, L., Kjellander, P., Ruiz-Jaen, M.C., Fröberg, M., Stendahl, J., Philipson, C.D., Mikusiński, G., 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nat. Commun. 4, 1340-1340.
Gomes, V.H., IJff, S.D., Raes, N., Amaral, I.L., Salomão, R.P., Coelho, L.S., Matos, F.D.A., Castilho, C.V., Lima Filho, D.A., López, D.C., Guevara, J.E., 2018. Species distribution modelling: contrasting presence-only models with plot abundance data. Sci. Rep. 8 (1), 1003-1003.
GON/MOHP, 2011. Nepal Population Report 2011. Government of Nepal, Ministry of Health and Population, Kathmandu, Nepal.
Harris, G.M., Russell, G.J., van Aarde, R.I., Pimm, S.L., 2008. Rules of habitat use by elephants *Loxodonta africana* in southern Africa: insights for regional management. Oryx 42 (1), 66–75.
Hirzel, A.H., Arlettaz, R., 2003. Modeling habitat suitability for complex species distributions by environmental-distance geometric mean. Environ. Manag. 32 (5), 614–623.
Hirzel, A.H., Hausser, J., Chessel, D., Perrin, N., 2002. Ecological-niche factor analysis: how to compute habitat-suitability maps without absence data? Ecology 83 (7), 2027–2036.
Kafley, H., Khadka, M., Sharma, M., 2009. Habitat evaluation and suitability modeling of *Rhinoceros unicornis* in Chitwan National Park, Nepal: a geospatial approach. In: XIII World Forestry Congress. Buenos Aires, Argentina.
Katayama, N., Amano, T., Naoe, S., Yamakita, T., Komatsu, I., Takagawa, S.I., Sato, N., Ueta, M., Miyashita, T., 2014. Landscape heterogeneity–biodiversity relationship: effect of range size. PLoS One 9 (3) e93359.
Keller, G.S., Ross, B.D., Klute, D.S., Yahner, R.H., 2009. Temporal changes in migratory bird use of edges during spring and fall seasons in Pennsylvania. Northeast. Nat. 16 (4), 535–552.
Kramer-Schadt, S., Niedballa, J., Pilgrim, J.D., Schröder, B., Lindenborn, J., Reinfelder, V., Stillfried, M., Heckmann, I., Scharf, A.K., Augeri, D.M., Cheyne, S.M., 2013. The importance of correcting for sampling bias in MaxEnt species distribution models. Divers. Distrib. 19 (11), 1366–1379.
Lakshminarayanan, N., Karanth, K.K., Goswami, V.R., Vaidyanathan, S., Karanth, K.U., 2016. Determinants of dry season habitat use by Asian elephants in the Western Ghats of India. J. Zool. 298 (3), 169–177.
Larsen, J.K., Guillemette, M., 2007. Effects of wind turbines on flight behaviour of wintering common eiders: implications for habitat use and collision risk. J. Appl. Ecol. 44 (3), 516–522.
Leimgruber, P., Gagnon, J.B., Wemmer, C., Kelly, D.S., Songer, M.A., Selig, E.R., 2003. Fragmentation of Asia's remaining wildlands: implications for Asian elephant conservation. Anim. Conserv. 6 (4), 347–359.
Löyttyniemi, K., Mikkola, L., 1980. Elephant as a pest of pines in Zambia. Int. J. Pest Manag. 26 (2), 167–169.
MacArthur, R.H., Pianka, E.R., 1966. On optimal use of a patchy environment. Am. Nat. 100 (916), 603–609.
Mills, A., Lubell, Y., Hanson, K., 2008. Malaria eradication: the economic, financial and institutional challenge. Malar. J. 7, 1–13.
Milner, J.M., Van Beest, F.M., Schmidt, K.T., Brook, R.K., Storaas, T., 2014. To feed or not to feed? Evidence of the intended and unintended effects of feeding wild ungulates. J. Wildl. Manag. 78 (8), 1322–1334.
Neupane, D., Johnson, R.L., Risch, T.S., 2014. Temporal and spatial patterns of human-elephant conflict in Nepal. In: 2013 International Elephant & Rhino Conservation & Research Symposium Proceedings, pp. 856–888.
Neupane, D., Kunwar, S., Bohara, A.K., Risch, T.S., Johnson, R.L., 2017a. Willingness to pay for mitigating human-elephant conflict by residents of Nepal. J. Nat. Conserv. 36, 65–76.
Neupane, D., Johnson, R.L., Risch, T.S., 2017b. How do land-use practices affect human—elephant conflict in Nepal? Wildl. Biol. 2017, wlb-00313.
Okello, M.M., Njumbi, S.J., Kiringe, J.W., Isiiche, J., 2015. Habitat use and preference by the African elephant outside of the protected area, and management implications in the Amboseli Landscape, Kenya. Int. J. Biodivers. Conserv. 7 (3), 211–226.
Pan, W., Lin, L., Luo, A., Zhang, L., 2009. Corridor use by Asian elephants. Integr. Zool. 4 (2), 220–231.
Pearce, J.L., Boyce, M.S., 2006. Modelling distribution and abundance with presence-only data. J. Appl. Ecol. 43 (3), 405–412.
Phillips, S.J., Anderson, R.P., Dudík, M., Schapire, R.E., Blair, M.E., 2017. Opening the black box: an open-source release of Maxent. Ecography 40 (7), 887–893.
Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19 (1), 181–197.
Pradhan, N.M., Williams, A.C., Dhakal, M., 2011. Current status of Asian elephants in Nepal. Gajah 35, 87–92.
Pradhan, N.M.B., Wegge, P., Moe, S.R., 2007. How does a re-colonizing population of Asian elephants affect the forest habitat? J. Zool. 273 (2), 183–191.
Putman, R.J., Staines, B.W., 2004. Supplementary winter feeding of wild red deer *Cervus elaphus* in Europe and North America: justifications, feeding practice and effectiveness. Mamm Rev. 34 (4), 285–306.
Rood, E., Ganie, A.A., Nijman, V., 2010. Using presence-only modelling to predict Asian elephant habitat use in a tropical forest landscape: implications for conservation. Divers. Distrib. 16 (6), 975–984.
Rosenzweig, M.L., 1974. On the evolution of habitat selection. In: Proceedings of the First International Congress of Ecology, pp. 401–404.
Rosenzweig, M.L., 1981. A theory of habitat selection. Ecology 62 (2), 327–335.
Saab, V., 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecol. Appl. 9 (1), 135–151.
Sahlsten, J., Bunnefeld, N., Månsson, J., Ericsson, G., Bergström, R., Dettki, H., 2010. Can supplementary feeding be used to redistribute moose *Alces alces*? Wildl. Biol. 16 (1), 85–92.
Sarma, P.K., Mipun, B.S., Talukdar, B.K., Singha, H., Basumatary, A.K., Das, A.K., Sarkar, A., Hazarika, B.C., 2012. Assessment of habitat utilization pattern of rhinos (*Rhinoceros unicornis*) in Orang National Park, Assam, India. PACHYDERM 50, 38–44.
Shannon, C.E., Weaver, W., 1963. The Mathematical Theory of Communication. University of Illinois Press, Urbana, IL.
Shannon, G., Matthews, W.S., Page, B.R., Parker, G.E., Smith, R.J., 2009. The effects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. Divers. Distrib. 15 (5), 776–783.
Smit, I.P., Grant, C.C., Devereux, B.J., 2007. Do artificial waterholes influence the way herbivores use the landscape? Herbivore distribution patterns around rivers and artificial surface water sources in a large African savanna park. Biol. Conserv. 136 (1), 85–99.
Steenhof, K., Berlinger, S.S., Frederickson, L.H., 1980. Habitat use by wintering bald eagles in South Dakota. J. Wildl. Manag. 44 (4), 798–805.
Steinheim, G., Wegge, P., Fjellstad, J.I., Jnawali, S.R., Weladji, R.B., 2005. Dry season diets and habitat use of sympatric Asian elephants (*Elephas maximus*) and greater one-horned rhinoceros (*Rhinocerus unicornis*) in Nepal. J. Zool. 265 (4), 377–385.
Sukumar, R., 1989. Ecology of the Asian elephant in southern India. I. Movement and habitat utilization patterns. J. Trop. Ecol. 5 (1), 1–18.
Sukumar, R., 1990. Ecology of the Asian elephant in southern India. II. Feeding habits and crop raiding patterns. J. Trop. Ecol. 6 (1), 33–53.
Webb, E.B., Smith, L.M., Vrtiska, M.P., Lagrange, T.G., 2010. Effects of local and landscape variables on wetland bird habitat use during migration through the Rainwater Basin. J. Wildl. Manag. 74 (1), 109–119.
Williams, A.C., 2002. Elephants (Elephas maximus), Their Habitats in Rajaji-Corbett National Parks. PhD Thesis. Saurashtra University.
Williams, A.C., Johnsingh, A.J., Krausman, P.R., Qureshi, Q., 2008. Ranging and habitat selection by Asian elephants (*Elephas maximus*) in Rajaji national park, north-west India. J. Bombay Nat. Hist. Soc. 105 (1), 24–33.
Zhang, L., Dong, L., Lin, L., Feng, L., Yan, F., Wang, L., Guo, X., Luo, A., 2015. Asian elephants in China: estimating population size and evaluating habitat suitability. PLoS One 10 (5) e0124834.