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Changes in habitat suitability over a two decade period before and after Asian elephant recolonization



Dinesh Neupane^{a, b, *}, Youngsang Kwon^c, Thomas S. Risch^d,
Ronald L. Johnson^d

^a Resources Himalaya Foundation, Naya Bato, Lalitpur, Nepal

^b Graduate Program of Environmental Sciences, Arkansas State University, State University, Arkansas, USA

^c Department of Earth Sciences, The University of Memphis, Memphis, TN, USA

^d Department of Biological Sciences, Arkansas State University, State University, Arkansas, USA

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ABSTRACT

Habitat degradation has caused a significant threat to wildlife, particularly to megafauna including the Asian elephant that has a large home range. Recolonization of Asian elephants in 1994 in and around Bardia National Park (BNP) has provided a unique study setting to address habitat change over two decades (1990–2013). Elephant presence data in 2013 was modeled using Ecological Niche Factor Analysis (ENFA), which identified the influential ecogeographical variables for elephant habitat. These variables were further used in a regression model to determine habitat suitability for 1990. We found that elephant suitable habitat has been lost between pre-recolonization (1990) and the year 2013 in and around BNP. Unsuitable elephant habitat increased overall by 22% in Bardia District and 20% inside BNP. Central to elephant habitat loss has been a large human population growth, re-forestation efforts with an increase in sal forests, and elephant alteration of vegetation by grazing. Available suitable habitat for elephants in and around BNP should be conserved and managed to prevent further degradation for the maintenance of the elephant population, which will help mitigate human-elephant conflict in the region.

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1. Introduction

Climate change and land use change interact to alter biodiversity and wildlife distribution (Oliver and Morecroft, 2014; Hansen et al., 2001). Migratory species in particular have shown adjustments to effects of climate change by shifting their habitat ranges towards northern latitudes or upslopes (Bellard et al., 2012; Robinson et al., 2009). Human land use practices and encroachment to natural habitat exacerbate climate change effects, forcing migratory wildlife to further modify their travelling routes.

Migratory wildlife change their habitat seasonally based on productivity of the location (Robinson et al., 2009). For example, moving towards waterbodies and wetland habitat during dry periods has been observed in megafauna including the Asian elephant (*Elephas Maximus*) (Neupane et al., 2019; Rood et al., 2010; Sukumar 1990), the African elephant (*Loxodonta*

* Corresponding author. GPO Box 2448, Naya Bato, Sanepa-3, Lalitpur, Nepal.

E-mail address: dineshkneupane@gmail.com (D. Neupane).

Africana) (Okello et al., 2015) and the one-horned rhinoceros (*Rhinoceros Unicornis*) (Sarma et al., 2012). Similarly, forest buffalo (*Syncerus caffer nanus*) in Africa was observed moving long distances into forests from clear areas during the dry season (Melletti et al., 2007).

Expansions and contractions of ranges of animal populations commonly occur and are often driven by changes in population size and varying resource availability. Thus, a species' recolonization of areas previously occupied is a natural phenomenon. However, recolonization behaviors may also be the result of habitat degradation caused by land use alterations that are a consequence of human population growth. For example, urbanization and agriculture expansion in Asia has caused habitat fragmentation and degradation, which impacts most wildlife, but is particularly problematic for large mammals such as Asian elephants (Neupane et al., 2017a, 2017b; Sukumar 1989).

Residential Asian elephants were almost extirpated from southwestern Nepal including Bardia National Park (BNP) in the 1980s (Lister and Blashford-Snell, 2000), due to habitat encroachment, fragmentation, and hunting. Historically, southern Nepal was densely forested and offered suitable habitat for roaming megafauna such as the Asian elephant, one-horned rhinoceros, and Bengal tiger (*Panthera tigris tigris*).

BNP is connected with Indian forests to the south by way of forested corridors. An estimated 12 elephants used to visit BNP seasonally prior to 1994 (Bolton, 1976). In 1994, over 45 individuals visited and re-colonized BNP from Indian national parks (Velde, 1997). Although the current population of elephants in BNP is unknown, their numbers may have peaked near 80 in 2004 (Pradhan et al., 2007). In addition to these recolonized residential elephants, seasonal trans-country movement of mobile Asian elephants has continued to be common (Neupane et al., 2017b; Pradhan et al., 2007). During this same period, humans in both Nepal and India have expanded their farmlands and settlements and have replaced much of the historical lowland forests and grasslands.

Prior to the 2000s, human-elephant conflict (HEC) in Nepal was not regionally problematic (Shrestha et al., 2007). However as large areas of natural elephant habitats were cleared for the growing of crops, elephants have episodically responded to dwindling resources by encroaching on these settlements and surrounding croplands. HEC has become increasingly common since 2001 in southern Nepal (Neupane et al., 2014; Shrestha et al., 2007).

This unique history of a known recolonization event in BNP allows us to explore how suitable habitat for elephants has changed in and around BNP over a two decade period. African elephants cause habitat change in Africa that result in decreasing habitat quality for the African elephant (*Loxodonta africana*) (Staub et al., 2013; Laws, 1970). However, habitat change due to megafauna has not been studied well in Asia. The challenge to understanding the dynamic nature of habitat changes is lack of spatially explicit data sets on elephant movement and historical land cover. The destabilization of elephant habitat would exacerbate their movement patterns and increase the chances of HEC in the region.

Therefore, the objective of this study was to better understand the current status of elephant habitat in and around BNP relative to habitat available prior to their recolonization. We attempted to overcome data privation on both historic elephant's records and related land covers in the past by scrutinizing the elephant's current habitat preference using ecological niche factor analysis (ENFA), then extrapolating the results of ENFA to the year 1990 using Landsat images and aerial photography through a GIS-based regression approach. ENFA is one of the presence-only approaches that has been widely used in habitat analysis of various wildlife, including bearded vultures in the Swiss Alps (Hirzel et al., 2004) and Asian elephants in Indonesia (Rood et al., 2010). The significance of using ENFA is its flexibility in methodology, which allows for various quantifications of eco-geographic variables to be tested, as well as its simplicity in interpretation. We present habitat changes associated with the elephants' recolonization over a 20 year period, and thus provide valuable information for the formulation of a long-term conservation plan for elephants in BNP.

2. Materials and methods

2.1. Study area

The Terai is a flat plain area in the southern belt of Nepal. The study area of Bardia District is located in the western Terai, which includes Bardia National Park (BNP) in the northern half of the district. Land cover in Bardia District is predominantly forested, followed by agricultural lands. BNP (area: 968 sq. km) is the largest protected area in southern Nepal, and home for diverse wildlife including the Asian elephant, one-horned rhinoceros, and the Bengal tiger. Residential elephants are confined to BNP due to the establishment of human settlements in and around BNP; northward range expansion of elephants within BNP is prevented by steep terrain (Neupane et al., 2019).

2.2. Field surveyed presence data

Elephant presence locations (dung) were collected as per Neupane et al. (2019). Briefly, we conducted a centerline transect ($n = 15$ transects, approximately covering 10 km long and 100 m wide) survey in BNP and southwest Bardia District, including locations of elephant presence in Khata Corridor and surrounding forests. Transect length varied from 8 km to 15 km depending on the landscape, and 12 transects were located inside BNP and three transects covered both BNP and the surrounding corridor forests in Bardia. Each transect was sampled twice by five survey teams (each team was comprised of two members), first during the fall and later during the winter 2012 (late September - early December) over a total of 180 field days. A total of 429 elephant dung presence locations were processed under the UTM 44 N reference system (WGS 1984

datum) and converted to a Boolean raster with 30 m by 30 m pixel resolution; presence cells were coded as 1 and absence cells were coded as 0.

2.3. Environmental predictors

Following our previous study (Neupane et al., 2019), we identified ecologically relevant variables that could be used as determinants of the elephants' distribution (hereafter referred to as ecogeographical variables, EGVs) (Hirzel et al., 2002). EGVs were categorized into four groups: land cover, topography, landscape metric and anthropogenic groups (Table 1). As we heavily relied on land covers and their configuration as habitat determinants, four Landsat images (each for November and March of both 1990 and 2013, respectively) (path 144, row 040), as well as high resolution aerial photography provided by ArcGIS online (ESRI ArcGIS) were utilized to improve land cover classification. The months of March and November were supplementary to one other in classifying forest types, as March is one of the hot dry months of the year, whereas November represents a cool dry month.

We used unsupervised Interactive Supervised Classification (ISO) Cluster classification (20 iterations) and six land covers were classified: mixed forest, sal-dominated forest, riverine forest, grassland, waterbodies, and floodplain. Based on the land cover classification, we developed two continuous frequency-based land cover variables (hereafter frequency variables) and one distance-based land cover variable (distance variable) to see if the choice of quantification methods produced any difference in the result of habitat preferences. Using a moving average window, the frequency variables were calculated at radii of 500 m and 1 km. The rationale for the choice of these radii was that elephants walked approximately 500 m between two defecation periods, typically defecate 16–18 times a day (Choudhury et al., 2008), and can walk up to 2 km per day in continuous forest (Alfred et al., 2012). The distance-based variable was calculated as the Euclidean distance from a focal land cover. We used the DistAn module in the Biomapper software package for the distance-based variable quantification (Hirzel et al., 2007).

For topography group variables, we derived elevation, slope, terrain ruggedness and curvature from the Shuttle Radar Topography Mission (SRTM) digital elevation model (DEM) downloaded from the Global Landcover Facility (<http://www.landcover.org>). The ruggedness of the terrain was calculated by the standard deviation of elevation within a 1 km distance of each cell. The landscape curvature was calculated by subtracting the elevation of each cell from the mean of 10 adjacent pixels. Low values of curvature corresponded to valleys whereas higher values represented areas of higher elevation.

For landscape metric group variables, we calculated perimeter-area ratio (PA ratio) and the Shannon diversity index using a radius of 1 km moving average windows. PA ratio variables for each land cover accounted for the amount of patch area exposed to edges, which was calculated by dividing the border length by the area. The Shannon diversity index (Shannon and Weaver, 1963) was calculated to represent habitat (i.e., land cover) heterogeneity.

Lastly, for the anthropogenic group, human settlements including narrow roads were manually digitized for 2013 by using high-resolution aerial photographs while human settlements for 1990 were downloaded from the Nepal Department of Survey 1992 data. Human settlements included agricultural areas, although agricultural lands represented a small fraction of those areas surveyed. Then we calculated the distance-based human settlements variable as the Euclidean distance from a human settlement using the DistAn module in Biomapper. All aforementioned EGVs for 1990 and 2013 were normalized by using box-cox transformation and resampled at 30 m by 30 m to match resolution of the species presence map.

Table 1

Categorization of ecogeographical variables (EGVs) associated with Asian elephant habitat in and around Bardia National Park.

Topography group (4 variables)	Land cover group (18 variables): Two frequency-based (at two scales) and one distance-based variables	Landscape metrics group (7 variables)	Anthropogenic group
1 Slope	1 Flood plain (two frequency variables: 1) at 500 m radius and 2) at 1 km radius, and one distance variable)	1 Perimeter-area ratio for six land covers: Flood plain, Grassland, Mixed forest, Riverine forest, Sal forest, Waterbodies	1 Human settlements (distance-based)
2 Elevation			
3 Terrain ruggedness			
4 Terrain curvature	2 Grassland (two frequency variables: 1) at 500 m radius and 2) at 1 km radius, and one distance variable)	2 Shannon Index	
	3 Mixed forest (two frequency variables: 1) at 500 m radius and 2) at 1 km radius, and one distance variable)		
	4 Riverine forest (two frequency variables: 1) at 500 m radius and 2) at 1 km radius, and one distance variable)		
	5 Sal forest (two frequency variables: 1) at 500 m radius and 2) at 1 km radius, and one distance variable)		
	6 Waterbodies (two frequency variables: 1) at 500 m radius and 2) at 1 km radius, and one distance variable)		

2.4. Ecological niche factor analysis (ENFA) modelling

We applied ecological niche factor analysis (ENFA) using Biomapper ver. 4.0 software (<http://www2.unil.ch/biomapper>; Hirzel et al., 2007) to describe elephant habitat suitability (HS) for the year 2013 and then extrapolated the results of ENFA to the year 1990 using a GIS-based regression approach. ENFA is a niche-based predictive HS analysis, which has been widely used in species distribution modelling (see Hirzel et al., 2002 for a full review). In brief, ENFA examines the species-specific habitat requirements from a set of EGVs by utilizing an approach similar to principal component analysis (PCA), resulting in two main uncorrelated, ecologically meaningful factors: marginality and specialization (Hirzel and Le Lay, 2008, Hirzel et al., 2002, 2006). Marginality, the first factor, is a vector which describes the ecological distance between the species optimum of an EGV and the mean habitat in the study area (Calenge, 2006; Santos et al., 2006). Specialization, all subsequent factors in PCA, is about niche narrowness of species compared to the available habitat, calculated as the ratio of ecological variance of the mean habitat to the observed habitat for the species (Calenge and Dufour, 2006; Hirzel et al., 2002). To interpret overall habitat characteristics, a global marginality (M) and tolerance (T) value was calculated, with a larger marginality value indicating that the focal species has habitat requirements that differ from the average conditions available and a high tolerance value indicating that within a given study area, the species occupies a relatively wide niche (Engler et al., 2004; Reutter et al., 2003).

We first ran ENFA using all 30 EGVs (Table 1) as an exploratory step to examine autocorrelations among EGVs. Based on the initial ENFA results, we selected only the highest variable among different quantification methods of variables (i.e., two frequency variables and one distance variable) and second, a variable was removed if its absolute coefficients to both the first and second factors were less than 0.2; lastly, if the bi-variate correlation between any two variables exceeded a threshold of 0.7, the variable with the lower contribution to marginality was discarded. Since most of the variance was explained by a few of the first factors, only those shown significant by comparison with Mac-Arthur's Broken-stick distribution (Hirzel et al., 2002) were kept for the final HS maps.

Based upon the above approach, a total of 12 EGVs (Table 2) were selected out of 30 EGVs from the initial ENFA analysis of the 2013 data (Supplementary Data 1). The terrain ruggedness variable was removed from the final model as it was strongly correlated to the slope variable (Pearson's $R = 0.70$). Frequency variables at a radius of 1 km were selected for all land cover group variables, as they consistently showed higher coefficients to the first and second factors than the other two quantification methods (i.e., frequency variable calculated at a radius of 500 m and a distance-based method). From the landscape metrics group, only floodplain was selected, as all other land covers exhibited less than 0.2 absolute correlation coefficients to the first and second factors.

We used the median algorithm in Biomapper to compute HS values ranging from 0 to 100. The median algorithm assumes that the best habitat is at the median of the species distribution on each factor, and that these distributions are symmetrical. The validation of the HS model was evaluated by a Boyce Continuous Index (BCI), a jack-knife cross-validation procedure (Fielding and Bell, 1997) using the VALIDATE function in Biomapper (Boyce et al., 2002). In addition, following the approach of Strubbe and Matthysen (2009), BCIs were used as guidelines to reclassify HS maps into meaningful bins. We used a 90% confidence interval around the BCI curve to find the non-overlapping HS classes (Hirzel et al., 2006). The BCI ranges from 0 to

Table 2

Correlations between the ENFA factors and the ecogeographical variables (EGVs) for Asian elephants in Bardia District, Nepal. The amount of specialization accounted for is given in parentheses.

EGVs	Amount of Specialization explained by the first five factors				
	Factor 1 (100% Marginality) (0.33)	Factor 2 (0.21)	Factor 3 (0.16)	Factor 4 (0.12)	Factor 5 (0.03)
Topography					
Elevation	–	***	*	**	**
Slope	–	**	*	**	****
Terrain curvature	–	*	*	0	0
Landscape metrics					
Flood plain (Perimeter-area ratio)	++	*	0	0	0
Shannon Index	+++	0	0	0	0
Land covers (frequency variable)					
Flood plain	++++	**	0	0	**
Grassland	++	*	*	**	**
Mixed forest	–	*	*	**	**
Riverine forest	+	0	*	**	**
Sal forest	–	0	*	**	0
Waterbodies	+++	*	0	*	*
Anthropogenic variable					
Human settlements	–	**	**	*	**
Total variance explained	85%				

Marginality (M): 1.67, Tolerance (T): 0.37.

1; a value closer to 1 represents a better model (Hirzel and Le Lay, 2008). The Index is a correlation of the HS values and the frequency of presence points relative to area measured (Boyce et al., 2002).

2.5. Habitat suitability comparison between 1990 and 2003

ENFA models are difficult to extrapolate to past environmental conditions or different areas because they are based on the comparison between the specific area with presence locations and the available background habitat. Since elephant presence records (geographic coordinates) for 1990 were unavailable, we developed a two-step comparison approach (Fig. 1). First, we created a multiple regression equation using EGVs for 2013 as independent variables and HS values from the ENFA results for 2013 as dependent variables. Second, we computed GIS-based HS values for 1990 by applying the regression coefficients calculated in the first step, with EGVs measured in 1990. Topography group variables for 1990 were the same as for 2013 whereas land cover related and anthropogenic variables were obtained from 1990. Finally, we compared GIS-based HS maps between 2013 and 1990. Here, GIS-based HS models were used to compare quality of habitat between the two periods based on the 2013 ENFA results with known elephant presence locations; thus a limitation of this approach is that the accuracy of HS for 1990 cannot be directly assessed. We also report area changes in terms of HS classes followed by simple land cover changes between the two periods.

3. Results

We focus on predictive HS outputs and development of our extrapolation method over a 20- year period following elephant recolonization, whereas the description of ENFA results in this section are intentionally brief because our previous study (Neupane et al., 2019) detailed elephant habitat preference in 2013.

3.1. Land cover changes between 1990 and 2013

Analyses of land cover, and ultimately HS, were performed for the entirety of Bardia District (including BNP) and also separately for BNP. BNP is a protected national park with no settlements whereas outside the park population growth has been substantial. Land cover has changed dramatically in Bardia District over the 23 year period between 1990 and 2013 and the composition of land cover changes was surprisingly similar for Bardia District and BNP (Fig. 2). Over the period, the net area of mixed forest in Bardia District had gained by 231.6 sq. km (138%) while other land covers decreased (Fig. 2). The major contributors to the net increase in mixed forest over the period were declines in sal forest, floodplain, and riverine forest (including water bodies): the sal forest area decreased by 86 sq. km (23%), the floodplain area decreased by 108 sq. km (51%), and riverine areas and waterbodies declined together by 82 sq. km (31.8%) during this period. Within BNP, about 31% of the

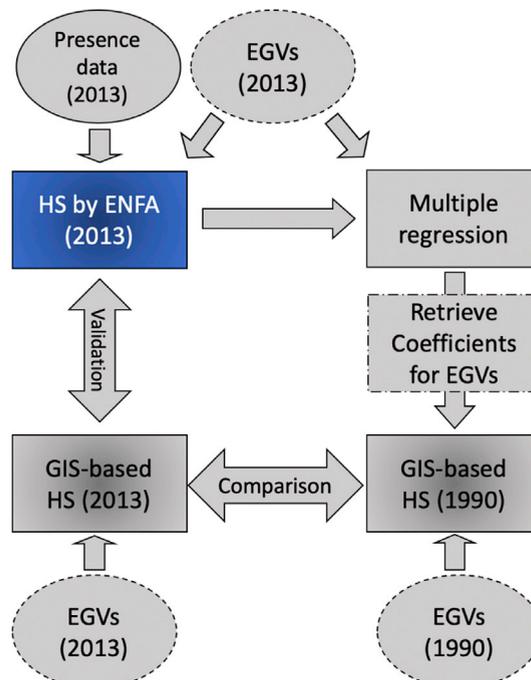


Fig. 1. Work flow to compare HS between 2013 and 1990.

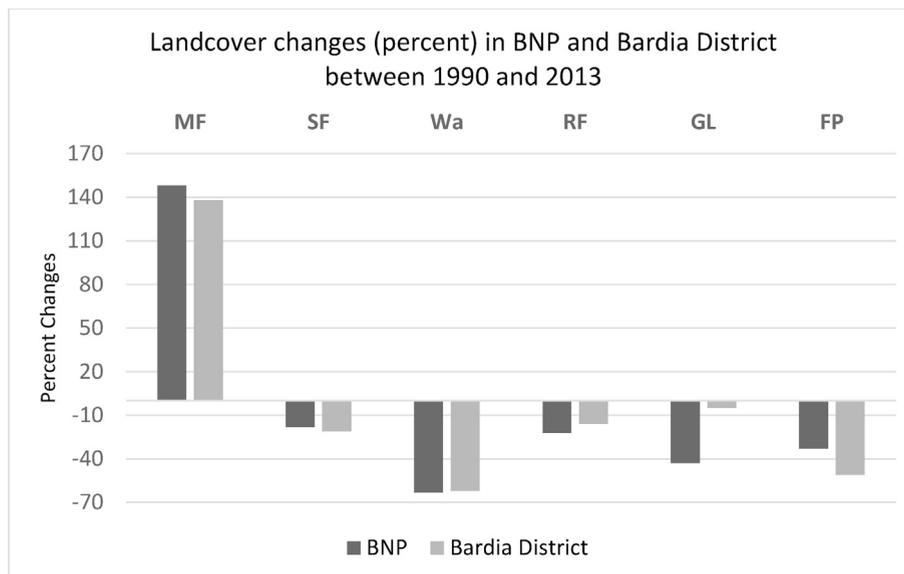


Fig. 2. Percentages of landcover changes in BNP and Bardia District between 1990 and 2013. Legend: Mixed forest (MF); Sal forest (SF); Waterbodies (Wa); Riverine forest (RF); Grassland (GL); and Floodplain (FP).

park was grassland in 1990 whereas grassland comprised about 17% of area in 2013. The primary differences in changes for Bardia District and BNP were a greater loss of grassland in BNP compared to a greater loss of floodplain in Bardia District (Fig. 2).

3.2. ENFA model evaluation

A marginality (M) value of 1.67 and the tolerance (T) value of 0.37 suggested that Asian elephants had a tendency to have a restricted range of habitat that differed from the average available habitat. They also tended to occur in a relatively narrow range of conditions. Briefly, elephants preferred small patches of floodplain or locations near water with more diverse land covers in addition to avoiding human settlements and high relief areas.

3.3. Habitat suitability

Based on the MacArthur's broken-stick distribution of the ENFA eigenvalues, HS values for 2013 were first computed using five factors which explained 100% of the marginality and 85% of the specialization (Table 2). The BCI value was 0.65 ± 0.11 , indicating accuracy in the model prediction. We evaluated the distribution of HS values from the validation set (25% of the presence locations) and 81% of the presence cells predicted HS greater than 0.65, which differed significantly ($p < 0.0001$, bootstrap test) from the value of 14% as expected if cells were randomly chosen from the global distribution.

Then, using HS values from ENFA as the dependent variables and EGVs as independent variables, a GIS-based multiple regression model developed for the year 2013 showed good predictive power (adjusted $R^2 = 0.81$, $p < 0.01$, Table 3). The regression coefficient showed a similar pattern with the marginality coefficient from ENFA that lack of slope and frequent riverine forest were the two most significant variables in positively explaining HS. All topography group variables, land cover variables of sal forest and mixed forest, and human settlements showed negative HS coefficients whereas floodplain (including PA ratio), grassland, water, and Shannon Index were positively correlated. Therefore, elephants were associated with a higher diversity of vegetation.

The GIS-based HS maps for 2013 and 1990, by reclassifying HS values into three classes as unsuitable (HS: 0–30), marginal (HS: 31–70) and suitable (HS: 71–100), showed that most of the highly suitable habitats were along the western and southern borders of BNP, and the Khata Corridor connecting to Indian forests (Fig. 3a). The northern border of BNP was found unsuitable as it is comprised of highly elevated areas.

The comparison between GIS-based HS maps showed degradation of elephant habitat both inside and outside BNP over the 23 year period between 1990 and 2013. A total area of unsuitable habitat increased overall by 22% in Bardia District and 20% in BNP in 2013 (Fig. 4a). Habitat in Bardia District and BNP that was considered suitable in 1990 became marginal, and marginal habitat became unsuitable by 2013, representing a greater degradation of habitat even beyond the margins, and extending to the interior of the park.

Table 3

Multiple regression results developed for the year 2013 habitat suitability study in Bardia District. Coefficient and the standard error for EGVs were calculated using EGVs as independent variables and HS values from ENFA as dependent variables.

EGVs	Coefficient	Std. Error
Intercept	25.22	5.883
Slope	-1.34***	0.102
Elevation	-0.13**	0.001
Curvature	-0.05*	0.001
Floodplain	0.27**	0.032
Grassland	0.11*	0.472
Mixed forest	-0.12*	0.008
Riverine	0.66***	0.018
Sal forest	-0.30*	0.031
Water	0.11*	0.029
Floodplain (PA ratio)	0.14**	0.022
Human Settlements	-0.38*	0.014
Shannon Index	0.11*	0.020

***p < 0.001 **p < 0.01 * P < 0.05, Adjusted R² = 0.81.

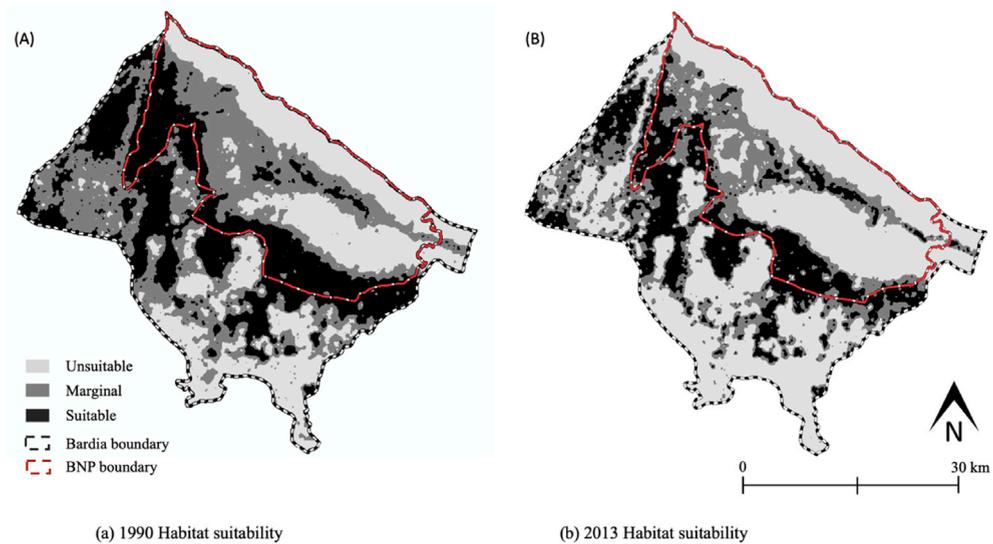


Fig. 3. Asian elephant habitat suitability (HS) map in Bardia District as determined by GIS-based regression approach for (a) 1990 and (b) 2013. The unsuitable habitat in the northern rim of Bardia District and the large oval of eastern portion of BNP is due to the presence of large hills and densely forested sal forest area, respectively.

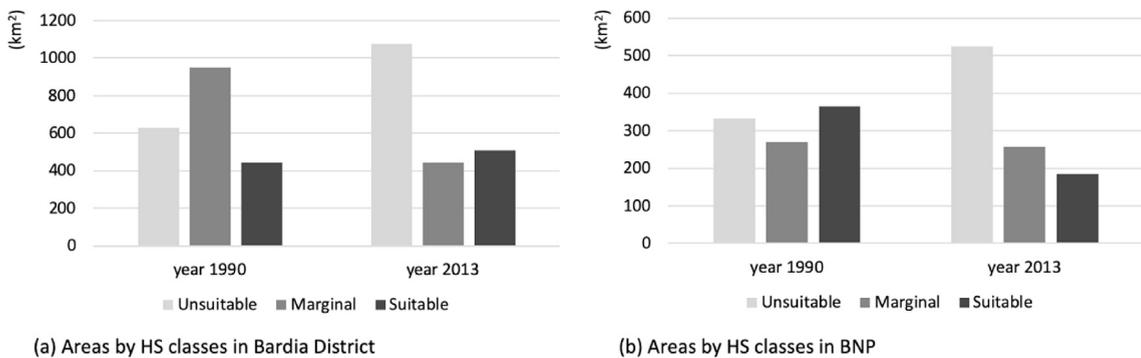


Fig. 4. Area comparison of habitat suitability (HS) between 1990 and 2013 for (a) Bardia District and (b) Bardia National Park.

4. Discussion

This study compared suitable habitats for elephants in and around BNP for 1990 and 2013. Loss of grassland, floodplain, and waterbodies and/or conversion of these land covers into mixed forest occurred in and around BNP over the past two decades. Since elephants prefer grasslands and waterbodies (Neupane et al., 2019; Pradhan et al., 2007; Steinheim et al., 2005), alteration of these land covers affects the carrying capacity of elephants locally. Elephants also avoid human settlements and steep slopes (Neupane et al., 2019), so are restricted to the grasslands in the extreme western and southern borders of BNP and the adjoining corridor in western Bardia District.

Declines in native food supplies have exacerbated HEC. For the past decade, elephants have episodically entered human settlements and farm lands for their dietary needs, especially during the dry season (Neupane et al., 2014; Shrestha et al., 2007; Velde, 1997). Primary agricultural products such as rice and maize provide easy and rich food sources for elephants (Neupane et al., 2017a).

The ENFA results are consistent with findings from the previous General Niche-Environment System Factor Analysis (GNESFA) modelling framework as ENFA is a special case of GNESFA (see Neupane et al., 2019). Marginal habitat was converted to unsuitable habitat in Bardia District during that period, and although BNP is protected, suitable habitat became marginal and marginal habitat became unsuitable within the park. Large portions of the western and southern borders of BNP and a narrow strip in central Bardia District were identified as suitable areas for both 2013 and 1990. The northern border of BNP was found unsuitable as it is comprised of highly elevated areas.

Three primary factors are driving these reductions in suitable elephant habitat over the two decades following elephant re-introduction. First, outside of BNP the local human population has almost doubled (46.94% increase) over the 20 year period between 1991 and 2011 in Bardia District (CBS/GoN, 2014). Associated with this increase in human population is the pressure to convert historic grasslands and riverine forests to farmlands and infrastructure development such as the construction of roads. Regionally, Chaudhary et al. (2016) estimated a 17% forest loss between 1984 and 2010/2011 in the Terai districts of Nepal, with Bardia District being one of the districts that experienced the highest loss of forest during this period (FRA/DFRS 2014). Within Bardia District, forest lands along the edges of national forests were lost due to human encroachment, and few areas in the southern portion of district continue to maintain some forested areas (FRA/DFRS 2014).

Second, conservation efforts within and outside BNP have been introduced to re-establish the historic forests. As part of a broader conservation goal, forests can enhance the biological diversity regionally, yet management is often not species-specific. Re-forestation efforts in Nepal have included the Forest Act of 1993 in addition to a community forestry program, which is a participatory conservation approach with the involvement of local residents (Luintel et al., 2018). Community forests typically hold higher tree species diversity than national or government-owned forests (Pandey, 2007); however, the community forestry program has primarily focused on preserving high-value timber products and removing climbers and other species having low economic value (Shrestha et al., 2010). The borders of the park and the adjoining forest along the southwestern corridor are now predominantly sal (59.4%) and mixed hardwood forests (18%) (Pradhan et al., 2007). Since elephants tend to avoid sal forests (Neupane et al., 2019; Steinheim et al., 2005; Williams et al., 2008), mobile herds of Asian elephants use the adjoining community forests near human settlements in the corridor as travelling routes (Neupane et al., 2019; Shrestha et al., 2007; Velde, 1997), exacerbating HEC regionally. Importantly, degradation of suitable habitats into marginal and unsuitable habitats in and around the boundary of BNP has also interlinked with increased incidences of HEC in recent years. Thus, providing technical skills to park managers on maintaining preferred tree species of elephants within the community forests would be beneficial to promote suitable habitat regionally.

Third, elephants as large herbivores often are disruptive to available flora (Guldmond and Van Aarde, 2010; Laws, 1970; Staub et al., 2013). Areas along the southern and western areas of the park are now highly reduced in their suitability as elephant habitat. The influence of elephants as herbivores may explain our finding that habitat degradation was worse inside BNP than district-wide over this period.

5. Conservation recommendations

Estimates for annual home ranges for Asian elephant herds are highly variable, with estimates of 18–24 km² in and around Rajaji National Park of northern India (Joshi and Singh, 2009), and up to 250–400 km² in continuous forests in Rajaji and Corbett national parks, India (Williams, 2004). As availability of resources and size of natural habitat combined with population size determines the home range (Whyte, 1996), even with the smaller range estimate stated above, a current available area of suitable habitat (185 km²) in BNP by itself may not be sufficient to support both residential and visiting mobile elephant populations. With these constraints, elephants periodically leave BNP, particularly to forests within the Khata Corridor, where there is greater risk of human encounters (Neupane et al., 2017a; Shrestha et al., 2007). However, elephants avoid human settlements (Neupane et al., 2019), particularly female elephants with calves (Williams et al., 2008). As long as mobile elephants visit BNP seasonally and breed with residing elephants the risk of inbreeding depression is lowered in this population (Pradhan et al., 2007). Thus, connectivity among forests in the Khata Corridor and also with BNP is important for the management of these herds of elephants in the Indo-Nepal trans-border area of western Nepal.

Identification of spatial habitat use by elephants within their range provides critical information to park officials in the formulation of effective management plans. Available suitable habitat for elephants in and around BNP should be conserved

and managed to prevent further habitat degradation for the maintenance of the population. In addition to the reforestation efforts discussed above, maintenance of grasslands and waterbodies both within and adjacent to BNP are critical.

Declaration of competing interest

There are no competing interests in the publication of this manuscript.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.gecco.2020.e01023>.

For the marginality factor (Factor 1), the symbol + means that the elephant was found in locations with higher values than average. The symbol - means the elephant was found with lower values than the average occurring. The greater the number of symbols, the greater the correlation. 0 indicates a very weak correlation. For the specialization factors, the symbol * means the elephant was found occupying a narrower range of values than available. The greater the number of asterisks, the narrower the range. 0 indicates a very low specialization (Hirzel et al., 2002).

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