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Using presence-only modelling to predict Asian elephant habitat use in a tropical forest landscape: implications for conservation

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ABSTRACT

Aim Asian elephants, *Elephas maximus*, are threatened throughout their range by a combination of logging, large scale forest conversion and conflict with humans. We investigate which environmental factors, both biotic and abiotic, constrain the current distribution of elephants. A spatially explicit habitat model is constructed to find core areas for conservation and to assess current threats.

Location Ulu Masen Ecosystem in the province of Nanggroe Aceh Darussalam on the island of Sumatra, Indonesia.

Methods A stratified survey was conducted at 12 sites (300 transects) to establish the presence of elephants. Presence records formed the basis to model potential habitat use. Ecological niche factor analysis (ENFA) is used to describe their niche and to identify key factors shaping elephant distribution. An initial niche model was constructed to describe elephant niche structure, and a second model focused on identifying core areas only. To assess the threat of habitat encroachment, overlap between the elephants' optimal niche and the occurrence of forest encroachment is computed.

Results Elephants were recorded throughout the study area from sea level to 1600 m a.s.l. The results show that the elephant niche and consequently habitat use markedly deviates from the available environment. Elephant presence was positively related to forest cover and vegetation productivity, and elephants were largely confined to valleys. A spatially explicit model showed that elephants mainly utilize forest edges. Forest encroachment occurs throughout the elephants range and was found within 80% of the elephants' ecological niche.

Main conclusions In contrast to general opinion, elephant distribution proved to be weakly constrained by altitude, possibly because of movement routes running through mountainous areas. Elephants were often found to occupy habitat patches in and near human-dominated areas. This pattern is believed to reflect the displacement of elephants from their former habitat.

Keywords
Distribution, disturbance, ecological niche, ENFA, habitat, marginality, specialization.

INTRODUCTION

Across Southeast Asia, tropical deforestation continues at alarming rates (Santiapillai & Jackson, 1990; Achard *et al.*, 2007; Hansen *et al.*, 2009b; Linkie *et al.*, 2009). Large-bodied mammals, depending on the large areas of suitable habitat to meet their dietary demands, are considered to be particularly vulnerable to the effects of habitat transformation (Leimgruber *et al.*, 2003; Shannon *et al.*, 2009). At the same time, however, the replacement of primary forests, which tend to be low in elephant forage, by farmlands abundant in nutrients and energy-rich crops or secondary forest with higher levels of

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forage may yield benefits to large-bodied herbivores. This apparent dichotomy is well illustrated by the Endangered Sumatran elephant (*Elephas maximus sumatranus*) which has been replaced from its natural habitat by forest conversion and is now considered a farmland pest species throughout its range (Choudhury, 1999; Zhang & Wang, 2003; Rood *et al.*, 2008).

Previous research on Sumatran elephants conducted by Kinnaird *et al.* (2003) found an edge effect with elephants avoiding forest boundaries up to 3 km into the forest interior, suggesting that elephant populations depend on undisturbed forested habitat. Consequently, as the forested landscape is continuously encroached upon by humans and most lowlands are now dominated by agriculture, the availability of suitable habitat has been compromised. As elephant habitat on Sumatra increasingly becomes fragmented, the remaining elephant groups are forced to reside in smaller isolated patches of forest occurring on the higher mountain slopes (Rood *et al.*, 2006).

At present, elephant research and conservation efforts have focused on estimating elephant densities with a variety of field survey and analytical techniques (Walsh *et al.*, 2001; Hedges *et al.*, 2005). Although such studies have been proven to be useful to monitor elephant population trends, they provide limited information on elephant habitat use and range. Knowledge of habitat selection processes and the consequences of habitat transformation on elephant distribution are therefore essential to develop conservation strategies to improve prospects for long-term survival (Leimgruber *et al.*, 2003; Gaucherel *et al.*, 2010).

A recently established statistical technique that can be used for addressing these fundamental conservation and research needs is the ecological niche factor analysis (ENFA: Hirzel & Guisan, 2002; Hirzel *et al.*, 2002). Because this algorithm does not rely on absence data, which is often unavailable because of problems associated with false absences (Hirzel *et al.*, 2002), it is highly applicable to model a cryptic and highly mobile species such as forest elephants. The ENFA algorithm compares the distribution of presence observations in a multidimensional space of environmental variables to the environmental variance across the study area at large. A habitat suitability (HS) index is calculated based on functions that define how the species' mean habitat characteristics differ from (1) the mean available habitat present within the entire area (marginality) and (2) the overall variance of habitat characteristics to the species habitat variance (specialization).

Other methods using presence-only data, such as Maxent (Phillips *et al.*, 2006), garp (Stockwell & Peters, 1999), bioclim (Beaumont *et al.*, 2005) and Mahalonobis factor analysis (Calenge *et al.*, 2008), have recently become increasingly popular tools to model species habitat relations. Generally, there is a high degree of accordance between models, although number of studies showed that more complex methods such as Maxent can produce more accurate predictions of species distributions than e.g. ENFA (Elith *et al.*, 2006; Tsoar *et al.*, 2007). However, ENFA has some marked features making it a more appropriate approach for this study. Firstly, ENFA has been shown to perform well when a species is not in equilibrium with its environment (Hirzel *et al.*, 2001; Cianfrani *et al.*, 2010). Secondly, the results on the ENFA analysis are straightforward and easily interpreted. Hence, the canonical depiction of the species' niche relative to its environment allows to evaluate which part of the available habitat is occupied and to assess to which extend the available habitat is utilized (Titeux *et al.*, 2007; Braunisch *et al.*, 2008).

Because niche models are calculated using raw presence data collected in the field, they are approximations of the realized niche which can substantially differ from the fundamental ecological niche as described by Hutchinson (1957) (Chefaoui & Lobo, 2008). Since elephants are known to move between patches of high suitability (Sukumar, 1989), a number of presence records can be accounted for by movements through areas of low suitability. As such, these records do not describe core niche characteristics necessarily but merely represent an adaptation to local conditions. This effect is expected to be confounded in a highly fragmented or heterogeneous habitat. To delineate areas of core elephant habitat, models should aim to identify and account for presence records that were located within marginal habitats (cf. Titeux *et al.*, 2007).

In this study, we investigate which environmental factors, both biotic and abiotic, constrain the current distribution of elephants in northern Sumatra, Indonesia. Secondly, we assess how elephant presences are distributed in ecogeographical space and identify the ecological niche optimum. Finally, a spatially explicit habitat model is built to establish core habitat areas and to assess the impact of forest encroachment of the prevalence of elephant habitat in Aceh.

METHODS

Study area

Data were collected within the forests of northern Aceh (95°25′E-96°40′E and 05°30′N-04°08′N), also known as the Ulu Masen Ecosystem, spanning an area of 75,000 km^2 of lowland and mountain forests. Altitudes range from sea level to 2697 m a.s.l., with *c.* 50% of the forest occurring below 800 m a.s.l. The geology of the area is predominantly sandstone and granite, but limestone formations are common along the west coast. The vegetation is dominated by dipterocarp forests interspersed with patches of Sumatran pine (*Pinus merkusii*) forest, disturbed or secondary forests characterized by low canopy cover and dense undergrowth, and alang-alang *Imperata cylindrica* dominated grasslands. The climate is typically drier than the rest of the Sumatran mainland, with a mean annual rainfall of 3000–5000 mm year^{-1} along the west coast, decreasing towards the east with increasing elevation. Most of the area has a protected status, but remnants of former commercial logging concessions can be found up to 20 km into the forest. Whilst all commercial logging has been stopped, illegal logging is rampant and patches of previously logged forest are rapidly converted into agriculture (Rood *et al.*, 2009).

Elephant populations within northern Aceh are believed to be fragmented into three distinct subpopulations separated by the Bukit Barisan Mountain Range and areas of human communities (Canney & Jepson, 2002). Even though no current estimates of the population size are available, for the late 1980s Santiapillai & Jackson (1990) estimated the population to comprise 200–300 individuals.

Data collection

Elephant presence data were collected following a stratified sampling design. Hence, the study area was stratified according to four elevation classes (500 m intervals) and three land cover types (forest, non-forest, and plantation) using a geographical information system (GIS) (ESRI ArcGIS 9.3). Initial pilot surveys were conducted from April 2006 to January 2007 across the northern forests, during which five teams were trained in elephant surveying. During February and March 2007, data on elephant distribution were collected over 12 different sites (Fig. 1), in which elephant presence was established by means of strip transects. Within each site, five random plots were selected from which transects were started. Subsequently, five parallel transects were walked each separated by 100 m, resulting in a total of 25 transects per site and 300 transects over the whole study area. Elephant presence was recorded by means of 5-m-wide line transects that varied between 200 and 400 m in length. Presence was confirmed if elephant dung was encountered, and their geographical locations were recorded using global positioning system (GPS). Other elephant sign data were collected in the field, but discarded from the analysis to improve consistency between survey teams.

Data preparation

Spatial autocorrelation, resulting from spatial dependence between elephant presence observations, could potentially increase the risk of type I errors (i.e. falsely rejecting a null hypothesis; Lichstein *et al.*, 2002; Dormann *et al.*, 2007). The occurrence and effect of spatial autocorrelation was tested using the Ripley's *L* statistic (Ripley, 1977; Wiegand & Moloney, 2004) and spatial-correlograms (Bellehumeur & Legendre, 1998). No significant effect of spatial autocorrelation with respect to the data we presented was found (for detailed methods and results see Appendix S1 in Supporting Information).

All presence data were transformed to a 90 × 90 m raster format (WGS84, UTM-46n projection). A total of 160 raster cells were randomly selected from the study area to describe the available background environment and for model validation. Hence, potentially suitable habitat encompassed by the background environment was contrasted against the species optimum leading to a more conservative HS prediction (Chefaoui & Lobo, 2008).

To predict elephant HS and habitat distribution across the study area, a total of twelve habitat variables were used (Table 1) based on their reported relevance to elephant ecology (Sukumar, 1989; Hedges *et al.*, 2005; Pradhan & Wegge, 2007). Forest cover data were derived from three Landsat Enhanced Thematic Mapper Plus satellite scenes from 2005 and 2006 using a classification regression tree algorithm (Lawrence & Wright, 2001; Moisen & Frescino, 2002). Cross-validation of the resulting forest cover maps for 2005 and 2006 proved to be accurate, indicated by both a high total agreement (94% and 89%, respectively) as well as kappa statistic (0.87 and 0.82,

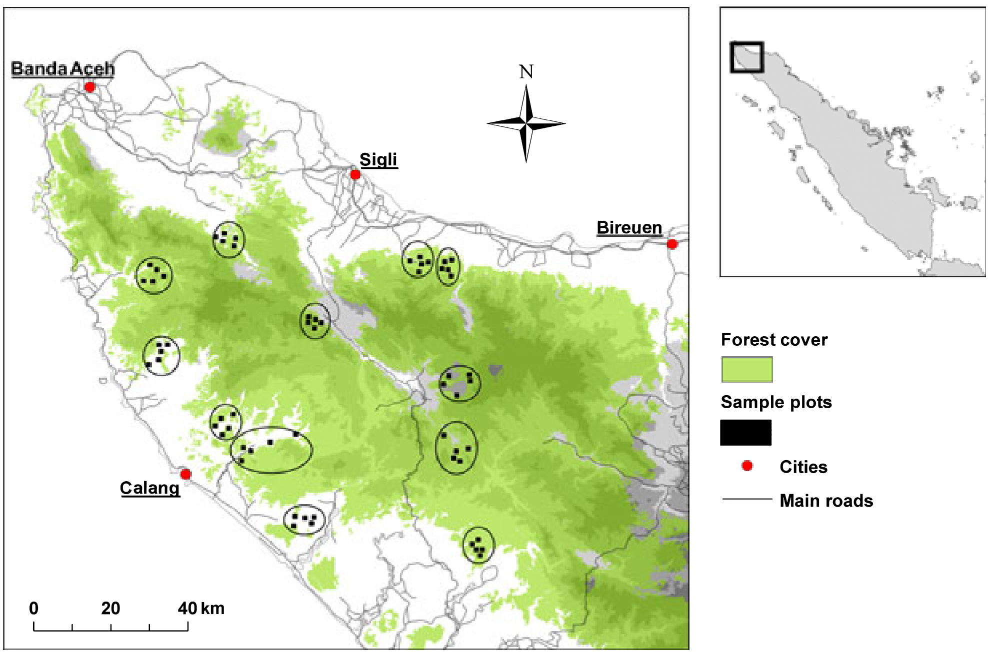

Figure 1 Overview of the study area showing 2006 primary forest cover and elevation (in 500 m intervals). The plot locations within each of the 12 survey sites are encircled. The insert shows the island of Sumatra with Aceh in the north.

Table 1 Description of each habitat variable used in the analysis. Variable standardization and whether a variable was included in the analysis are indicated.

Variable	Description	Standardized	Included
Landscape			
Elevation	Elevation above sea level	Yes	Yes
Slope	Steepest slope in degrees	Yes	Yes
Terrain ruggedness 250 m	Standard deviation of elevation in a 250 m circular surrounding	Yes	Yes
Terrain ruggedness 500 m	Standard deviation of elevation in a 500 m circular surrounding	Yes	No: correlated to ruggedness 250
Terrain ruggedness 5000 m	Standard deviation of elevation in a 5 km circular surrounding	Yes	No: correlated to ruggedness 250
Curvature 500 m	Curvature: relative elevation in relation to a 500 m circular surrounding	Yes	Yes
Curvature 2000 m	Curvature: relative elevation in relation to a 2000 m circular surrounding	Yes	No: correlated to curvature 500 m
Curvature 5000 m	Curvature: relative elevation in relation to a 5 km circular surrounding	Yes	Yes
Resource			
Forest cover	Proportion forest cover in a 5 km surrounding	No	Yes
Productivity	Normalized difference vegetation index	Yes	Yes
Disturbance			
Road density 1000 m	Road length in a 1 km circular surrounding	Yes	Yes
Road distance	Euclidian distance to the nearest road	Yes	No: correlated to road density

respectively). A forest encroachment map was derived by overlaying the two subsequent forest cover maps. Vegetation productivity was measured as the relative greenness of a pixel which was calculated as the normalized difference vegetation index (NDVI, cf. Hansen *et al.*, 2009a).

A 90 × 90 m digital elevation model was downloaded from the internet (http://srtm.csi.cgiar.org) from which additional descriptors were generated within the GIS. Terrain ruggedness was calculated using the standard deviation of elevation within a 1 km distance of each cell. High terrain ruggedness will considerable limit elephant movement and pose an energetic constraint to elephants moving through the landscape. Landscape curvature was calculated as the difference in elevation between the focal cell and the average of a 500/2000/5000 m circular surrounding, respectively. High curvature values relate to elevated or exposed areas, whereas low curvature values relate to landscape depressions and valley bottoms. Hence, landscape curvature relates to the amount of solar irradiation, local hydrology and exposure of an area shaping local microhabitats.

Comparing the ecological variation of survey sites ($N = 60$) with that of a random sample of background cells ($N = 160$) did not show any significant differences, indicating a good coverage of the ecological variation present in the area (Mann–Whitney U-test: all variables $Z > -1.61$; $P > 0.107$).

Data analysis

To enable the model to discriminate between correlated variables which explain elephant habitat use patterns, collinearity of environmental variables was corrected for by removing variable that showed more than 50% correlation with other variables (Table 1). HS maps were calculated using the geometric mean algorithm (Hirzel & Arlettaz, 2003). The ENFA algorithm was implemented using Biomapper 3.1 software (Hirzel *et al.*, 2002).

Validation

The HS model was validated using a continuous Boyce validation technique available within Biomapper software (Hirzel *et al.*, 2006; Pearce & Boyce, 2006). The validation statistic was calculated using ratio between the number of observed presences and the number expected based on a random distribution (Hirzel *et al.*, 2006). Good model performance is indicated by a high correlation between the HS score and the ratio of observed and expected values. Additionally, to estimate model predictive power, pseudo-area under the curve (AUC) scores were calculated using a sample of 160 random pseudo-absences from the background environment (Pearce & Boyce, 2006).

Core areas

To identify core areas of elephant habitat, a second habitat model was calculated excluding presence records that were found to deviate strongly from the average condition in which elephants were found. We followed the method outlined by Titeux *et al.* (2007), who defined spatial outliers as those presence records located at the outermost 10% of the marginality axis, focusing however on the 90% percentile interval of the marginality *and* specialization scores (Fig. 2). As such, 88 (of an initial 112) independent presence records were included to model core areas. Employing Boyce continuous validation (Hirzel *et al.*, 2006) plots, areas of high suitability were defined as those that were used disproportionally (i.e. HS > 50%) and

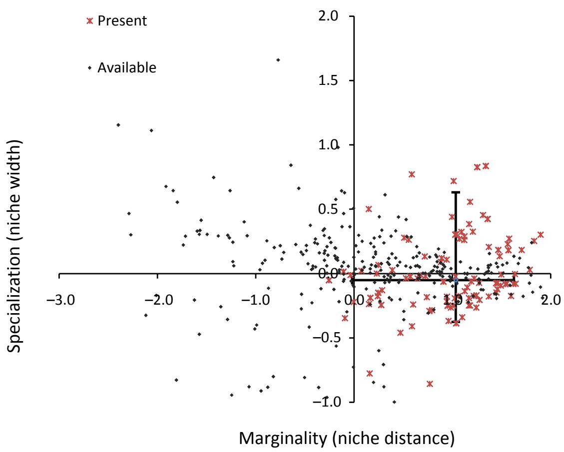

Figure 2 Distribution of elephant presence records (crosses, $n = 112$) and a random sample of background records (representing available habitat; small black dots, $n = 200$) along the marginality and specialization scores. Core elephant presence records ($n = 88$) are those presences located within the 90% percentile interval.

highly unsuitable areas were defined as those that the model indicated as being avoided (in this case HS < 10%).

Encroachment

The relative impact of forest encroachment on elephant habitat destruction was assessed by comparing the forest encroachment map, as revealed by the forest cover analysis, to the spatially explicit habitat model. Moreover, to investigate the relative threat of forest encroachment to elephants' habitat, the proportion of the elephant's niche subjected to encroachment was determined. Hence, a random sample of 150 points was taken from the encroachment map and its distribution was compared to the distribution of elephant presence records along the first two factors computed by the ENFA analysis. Elephant niche width and ecological range of encroachment were calculated by means of Hurlbert's index B' (Hurlbert 1978). To analyse how much of the elephants niche has been subjected to encroached, the Pianka's overlap index (Pianka, 1974) was computed.

RESULTS

Habitat analysis

During the initial training surveys, the presence of elephants was found at each of the 12 study sites, either through direct observations or indirectly by their sign (dung, vocalizations, tracks, etc.) confirming their presence throughout the northern forest. Within the survey plots, elephant presence was established on 35% (1.6 ± 0.09 95% confidence interval transects per plot) of transects surveyed. Trails were most abundant on flat areas, but narrow trails were present across a large altitudinal range from fresh water swamp forest at sea level to ridges up to 1600 m a.s.l.

The ENFA analysis showed that elephants occupied areas that deviate substantially from the average available habitat (Marginality; $M = 0.49$). Elephant signs were found to be more frequent in forested areas of relatively high productivity and in mountain valleys. The first niche factor, the marginality score, was weakly and negatively correlated to slopes (Table 2), indicating that elephants did not show a strong preference for flat areas. Similarly, elephant marginality was negatively related to the road density (Table 2), which implies an avoidance of areas with a dense road network. Within the total range of potentially occupied habitats, elephants appeared to be restricted to a narrow range of specialized habitats (Total Specialization; $S = 2.87$, Tolerance = 0.348), suggesting that elephants tend to occupy a relatively small ecological range when compared to habitat conditions available on a landscape scale. The first factor of the ENFA analysis (marginality), which maximizes the distance between the average conditions present and the average conditions at which elephant were found,

Table 2 Scores of the ecological niche factor analysis. The marginality scores indicate the average distance between the ecological conditions at which elephants were found present and the average conditions present in the study area. High values (> 0.500) indicate higher use by elephants than expected on availability. Specialization scores indicate the proportion of ecological conditions present in the study area which were found to be occupied by elephants.

	Factors all presences			Factors core presences		
Variable	Marginality	Specilization-1	Specialization-2	Marginality	Specilization-1	Specialization-2
Forest cover	0.379	−0.298	0.538	0.366	−0.271	0.547
Curvature 500 m	−0.136	−0.022	0.119	−0.142	−0.103	0.050
Curvature 5000 m	−0.571	−0.338	0.007	−0.570	−0.358	0.047
Elevation	−0.363	0.035	−0.264	−0.365	0.091	−0.185
Productivity	0.463	0.232	−0.761	0.431	0.221	−0.762
Road density	−0.296	0.809	−0.072	−0.316	0.799	−0.049
Slope	−0.177	0.012	−0.037	−0.188	0.035	−0.038
Terrain ruggedness 250 m	−0.218	−0.295	−0.203	−0.258	−0.302	−0.277
Variance explained	48%	24%	10%	40%	36%	10%
Total variance explained	82%			86%		

accounted for 48% of the total variation described by the presence records. Hence, the environmental factors describing the distance between the elephants' optimal niche and the available habitat are the same factors describing the actual width of the species' niche width. Overall model predictability was good with an average Boyce statistic of 0.71 and a receiver operating characteristic (ROC)-AUC score of 0.80 ± 0.013.

Core areas

Plotting all elephant presence records against the calculated marginality and specialization showed that the distribution of elephant presence records is highly skewed towards the positive end of the marginality factor (Fig. 2), which corresponds to forested habitat types located within landscape depressions. After excluding outlier presence records, a second habitat model was calculated (Table 2). The core area ENFA analysis factor scores are similar to the general habitat model, but showed a higher marginality score ($M = 0.501$ core-model vs. $M = 0.493$ model including all records), indicating that core presences deviate more from the average available conditions compared to the total range of ecological conditions used by elephants.

The marginality factor and two specialization factors were used to produce a final HS map (Fig. 3). The Boyce continuous validation statistic showed that the proposed core habitat model preformed well at distinguishing areas of highly suitable elephant habitat (Boyce = 0.75, AUC = 0.85 ± 0.014). These results can therefore be used to identify areas of critical elephant habitat. HS values at which the model predicted elephant presences at higher rates than expected based on random occurrence (e.g. 90% of the presence observations) were classified as intermediate habitat. Likewise, HS values at which < 50% of the presence observations were correctly classified by the ENFA model were classified as suitable habitat (Fig. 3).

Deforestation

Between 2005 and 2006, 351 km^2 (2.41%) of the total forest cover present in the study area was converted to agriculture resulting from encroachment. As such, deforestation within the study area accounted for a loss of 69 km^2 (4%) of suitable elephant habitat and 112 km^2 (3%) of intermediate habitat. Analysis of the ecological conditions at which forest encroachment occurred showed that forest encroachment poses a serious threat to elephant habitat. Firstly, forest encroachment

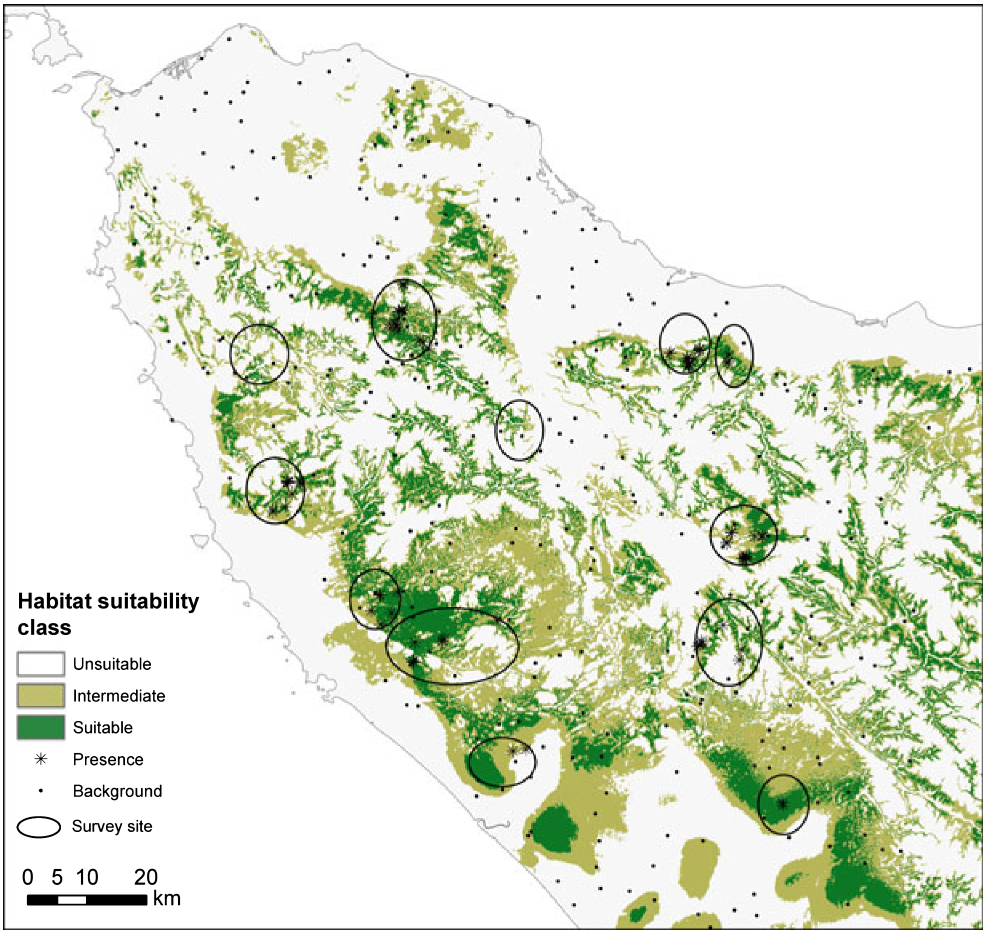

Figure 3 Elephant habitat suitability map based on ecological niche factor analysis indicating areas of high and marginal suitability. Recorded elephant presences are indicated (asterisks), as well as the location of survey sites (ellipses).

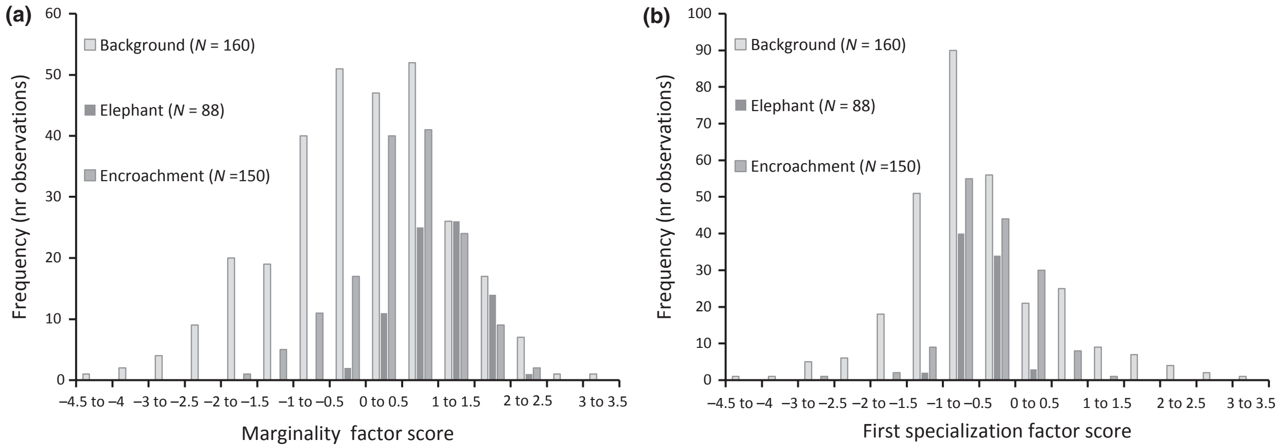

Figure 4 Frequency distribution of elephant presences (dark grey bars), forest encroachment localities (intermediate grey bars) and background environment (light grey bars) across the marginality factor (a) and first specialization factor (b) of the elephant core niche model. Considerable overlap exists between the preferred ecological conditions at which elephants were found and where forest encroachment has taken place.

occurred along a wider range of ecological conditions when compared to the elephants' niche as indicated by the Hurlbert's niche breadth index (marginality: $B' = 0.734$ vs. $B' = 0.334$, respectively; first specialization: $B' = 0.678$ vs. $B' = 0.380$, respectively). Moreover, forest encroachment occurred almost across the complete ecological range of covered by the elephants' niche (Fig. 4, Pianca's *L* statistic marginality: $O = 0.785$ first specialization $O = 0.882$), presenting a serious threat to elephant habitat prevalence if forest conversion continues in the area.

DISCUSSION

From our study, it is clear that elephants have a strong preference for forests with a high productivity located within valleys. This pattern is believed to be a result of the fact that landscape depressions are also natural waterways providing a main source of water and natural routes crossing through rugged terrain (Pan *et al.*, 2009; Shannon *et al.*, 2009). The spatially explicit habitat model (Fig. 3) showed that elephant habitat was mainly concentrated along the forest edges that were generally less rugged and often subjected to intermediate levels of human disturbance. As secondary regrowth is abundant in these areas, forest edges are generally rich in elephant foliage, which in return could benefit elephants living on the forest–non-forest interface (Sukumar, 1989, 1990; Zhang & Wang, 2003).

Previous studies have found that elephants prefer lowland forest habitats (Kinnaird *et al.*, 2003; Hedges *et al.*, 2005; Azad, 2006; Pradhan & Wegge, 2007) where nutritious foliage is abundant. Our finding that the elephants' optimal niche is depicted by areas of high forest cover as well as of high productivity support this conclusion (Fig. 3, Table 2). However, our finding that elephant occurrence is concentrated at forest edges does not agree with the results published by Kinnaird *et al.* (2003) who conclude that elephants avoid forest edges. Yet, incongruent forest definitions as well as diverging in ecological conditions encountered in the field could have led to these observed differences. Moreover, the study presented here does relate elephant abundance to habitat characteristics at small scales (cf. Kinnaird *et al.*, 2003), but rather reflects elephant habitat use at larger landscape scales.

Steep slopes have been mentioned to constrain elephant movements (Feng *et al.*, 2008; Pan *et al.*, 2009). (Sukumar, 1989). We found elephant to use areas up to 1600 m a.s.l., and, concurrently to our study, fresh signs have been observed at 2200 m a.s.l. in the north-central part of our study area (M. Kamsi, pers. comm. Nov 2007). Our analysis found no marked relationship between slopes and the predicted distribution of elephants. Thus, whilst elephants might prefer flatter, lowland area, this does not imply that elephants are absent from mountainous areas with steep slopes that could limit their movements. The low correlation between slopes and the principal factors describing the elephants' niche suggest that elephants are well capable to move through mountainous areas. Terrain ruggedness, however, seems to constrain elephant niches to some extent, with lower frequencies of elephant occurrence in highly rugged terrain and elephant presences occurring over a relatively narrow range of relative ruggedness (Table 2).

The avoidance of areas with high road densities relating to high human population pressure implies elephant avoidance of human encroachment. Consequently, elephants are believed to move away from human-dominated areas and move into more forested areas available within mountain areas. We acknowledge the fact that other parameters describing anthropogenic influences, such as human population density, would enable a more thorough analysis of the effect of human presence on elephant habitat selection. Such data, however, is scantly available and often is outdated or unreliable, making comparisons hard to accomplish. Still, as road density (or distance) denotes a well-established parameter that has often been used as an indirect measure of human disturbance throughout conservation literature (Brooks *et al.*, 1999; Linkie *et al.*, 2004; Fuentes-Montemayor *et al.*, 2009; Linkie *et al.*, 2010), it comprises a valuable and consistent parameter for such purposes.

One of the most prominent opinions amongst conservation biologists studying the effect of anthropogenic influences on wildlife distributions is that habitat alterations is the biggest threat to the survival of wildlife today (Laurance, 1999; Achard *et al.*, 2002; Brook *et al.*, 2003). As elephant habitat increasingly becomes encroached, the competition between humans and elephants for suitable living is likely to in finish in favour of humans. We found that 4% of suitable elephant habitat was lost in a single year, which is two times higher than the annual deforestation rate in the study area. Apparently, forest encroachment and elephant habitat destruction accordingly is more common in areas of high HS. Conditions at which deforestation is likely to occur also comprises more than 80% of the elephant's ecological niche space. Hence, if forest encroachment continues at its current rate, elephants are deemed to prevail within suboptimal habitat conditions at the margins of their niche.

From the results presented here, it becomes clear that not all areas that are occupied by elephants are indeed rated as suitable habitat by the ENFA analysis. We believe that the occurrence of elephants within marginal habitats reflects the occurrence the conversion of previously suitable habitat. In some cases, past habitat destruction has left elephants ranging within agricultural landscapes completely dominated by humans (Rood *et al.*, 2008, 2009). Oppositely, it is not yet clear whether all areas suitable for elephants are indeed occupied and if not for what reasons. Future work should therefore aim to identify whether the total extent of elephant habitat is sufficient to support a viable elephant population and whether different subpopulations are still connected.

Implications for conservation

The changing landscape across northern Aceh and the use of elephants of this area presents a conservation dilemma. Whilst elephants did indeed reside at forested edges rather than at the primary forest interior, it is unclear how deforestation will affect elephants in the long term. In Aceh, elephant habitat use is limited by the total area of lowland forest, congruent to the work of Kinnaird *et al.* (2003) in southern Sumatra. Further clearance of these areas could therefore lead to further deterioration of available habitat and may ultimately lead to the escalation of human elephant conflict in the area and a decline of conservation moral amongst local stakeholders (Rood *et al.*, 2008; Uryu *et al.*, 2008). As land use planning for conservation landscapes within and outside established conservation areas is becoming a new standard in large mammal conservation practices (Nyhus & Tilson, 2004; Linkie *et al.*, 2006), the effects of land use configuration, elephant behaviour and human response are amongst the most important issues to account for when setting long-term elephant conservation priorities. This study has provided an initial step to identify and prioritize core areas for elephant conservation. Hence, local authorities have been provided with the foremost tools to incorporate species conservation priorities to be built on when future spatial plans for the region are developed.

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REFERENCES

Achard, F., DeFries, R., Eva, H., Hansen, M., Mayaux, P. & Stibig, H.J. (2007) Pan-tropical monitoring of deforestation. *Environmental Research Letters*, **2**, 045022.

Achard, F., Eva, H.D., Stibig, H.J., Mayaux, P., Gallego, J., Richards, T. & Malingreau, J.P. (2002) Determination of deforestation rates of the world's humid tropical forests. *Science*, **297**, 999–1002.

Azad, M. (2006) Mammal diversity and conservation in a secondary forest in Peninsular Malaysia. *Biodiversity and Conservation*, **15**, 1013–1025.

Beaumont, L.J., Hughes, L. & Poulsen, M. (2005) Predicting species distributions: use of climatic parameters in BIOCLIM and its impact on predictions of species' current and future distributions. *Ecological Modelling*, **186**, 250–269.

Bellehumeur, C. & Legendre, P. (1998) Multiscale sources of variation in ecological variables: modeling spatial dispersion, elaborating sampling designs. *Landscape Ecology*, **13**, 15–25.

Braunisch, V., Bollmann, K., Graf, R.F. & Hirzel, A.H. (2008) Living on the edge – modelling habitat suitability for species at the edge of their fundamental niche. *Ecological Modelling*, **214**, 153–167.

Brook, B.W., Sodhi, N.S. & Ng, P.K.L. (2003) Catastrophic extinctions follow deforestation in Singapore. *Nature*, **424**, 420–423.

Brooks, T.M., Pimm, S.L., Kapos, V. & Ravilious, C. (1999) Threat from deforestation to montane and lowland birds and mammals in insular South-east Asia. *Journal of Animal Ecology*, **68**, 1061–1078.

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**, 555–566.

Canney, S. & Jepson, P. (2002) *Current status of knowledge on elephants in Aceh Province*. FFI, Banda Aceh.

Chefaoui, R.M. & Lobo, J.M. (2008) Assessing the effects of pseudo-absences on predictive distribution model performance. *Ecological Modelling*, **210**, 478–486.

Choudhury, A. (1999) Status and conservation of the Asian Elephant *Elephas maximus* in north-eastern India. *Mammal Review*, **29**, 141–173.

Cianfrani, C., Le Lay, G., Hirzel, A.H. & Loy, A. (2010) Do habitat suitability models reliably predict the recovery areas of threatened species? *Journal of Applied Ecology*, **47**, 421–430.

Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kuhn, I., Ohlemuller, R., Peres-Neto, P.R., Reineking, B., Schroder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.

Elith, J., Graham, C.H., Anderson, R.P. *et al.* (2006) Novel methods improve prediction of species' distributions from occurrence data. *Ecography*, **29**, 129–151.

Feng, Limin., Pan, W., Guo, X., Zhao, J., Luo, A. & Zhang, L. (2008) Habitat selection and the change in distribution of Asian elephants in Mengyang Protected Area, Yunnan, China. *Acta Theriologica*, **53**, 365–374.

Gaucherel, C., Balasubramanian, M., Karunakaran, P.V., Ramesh, B.R., Muthusankar, G., Hely, C. & Couteron, P. (2010) At which scales does landscape structure influence the spatial distribution of elephants in the Western Ghats (India)? *Journal of Zoology*, **280**, 185–194.

Hansen, B.B., Herfindal, I., Aanes, R., Saether, B.E. & Henriksen, S. (2009a) Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore. *Oikos*, **118**, 859–872.

Hansen, M.C., Stehman, S.V., Potapov, P.V., Arunarwati, B., Stolle, F. & Pittman, K. (2009b) Quantifying changes in the rates of forest clearing in Indonesia from 1990 to 2005 using remotely sensed data sets. *Environmental Research Letters*, **4**, 1–12.

Hedges, S., Tyson, M.J., Sitompul, A.F., Kinnaird, M.F., Gunaryadi, D. & Aslan (2005) Distribution, status, and conservation needs of Asian elephants (*Elephas maximus*) in Lampung Province, Sumatra, Indonesia. *Biological Conservation*, **124**, 35–48.

Hirzel, A.H. & Arlettaz, R. (2003) Modeling habitat suitability for complex species distributions by environmental-distance geometric mean. *Environmental Management*, **32**, 614–623.

Hirzel, A. & Guisan, A. (2002) Which is the optimal sampling strategy for habitat suitability modelling. *Ecological Modelling*, **157**, 331–341.

Hirzel, A.H., Helfer, V. & Metral, F. (2001) Assessing habitat-suitability models with a virtual species. *Ecological Modelling*, **145**, 111–121.

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**, 2027–2036.

Hirzel, A.H., Le Lay, G., Helfer, V., Randin, C. & Guisan, A. (2006) Evaluating the ability of habitat suitability models to predict species presences. *Ecological Modelling*, **199**, 142–152.

Hurlbert, S.H. (1978) Measurement of niche overlap and some relatives. *Ecology*, **59**, 67–77.

Hutchinson, G. (1957) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.

Kinnaird, M.F., Sanderson, E.W., O'Brien, T.G., Wibisono, H.T. & Woolmer, G. (2003) Deforestation trends in a tropical landscape and implications for endangered large mammals. *Conservation Biology*, **17**, 245–257.

Laurance, W.F. (1999) Reflections on the tropical deforestation crisis. *Biological Conservation*, **91**, 109–117.

Lawrence, R.L. & Wright, A. (2001) Rule-based classification systems using classification and regression tree (CART) analysis. *Photogrammetric Engineering and Remote Sensing*, **67**, 1137–1142.

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. *Animal Conservation*, **6**, 347–359.

Lichstein, J.W., Simons, T.R., Shriner, S.A. & Franzreb, K.E. (2002) Spatial autocorrelation and autoregressive models in ecology. *Ecological Monographs*, **72**, 445–463.

Linkie, M., Chapron, G., Martyr, D.J., Holden, J. & Leader-Williams, N. (2006) Assessing the viability of tiger subpopulations in a fragmented landscape. *Journal of Applied Ecology*, **43**, 576–586.

Linkie, M., Rood, E.J.J. & Smith, R.J. (2010) Modelling the effectiveness of enforcement strategies for avoiding tropical deforestation in Kerinci Seblat National Park, Sumatra. *Biodiversity and Conservation*, **19**, 973–984.

Moisen, G.G. & Frescino, T.S. (2002) Comparing five modelling techniques for predicting forest characteristics. *Ecological Modelling*, **157**, 209–225.

Nyhus, P. & Tilson, R. (2004) Agroforestry, elephants, and tigers: balancing conservation theory and practice in human-dominated landscapes of Southeast Asia. *Agriculture Ecosystems & Environment*, **104**, 87–97.

Pan, W., Lin, L., Luo, A. & Zhang, L. (2009) Corridor use by Asian elephants. *Integrative Zoology*, **4**, 220–231.

Pearce, J.L. & Boyce, M.S. (2006) Modelling distribution and abundance with presence-only data. *Journal of Applied Ecology*, **43**, 405–412.

Phillips, S.J., Anderson, R.P. & Schapire, R.E. (2006) Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, **190**, 231–259.

Pianka, E.R. (1974) Niche Overlap and Diffuse Competition. *Proceedings of the National Academy of Sciences USA*, **71**, 2141–2145.

Pradhan, N.M.B. & Wegge, P. (2007) Dry season habitat selection by a recolonizing population of Asian elephants *Elephas maximus* in lowland Nepal. *Acta Theriologica*, **52**, 205–214.

Ripley, B.D. (1977a) Modeling spatial patterns. *Journal of the Royal Statistical Society. Series B, Statistical Methodology*, **39**, 172–212.

Rood, E.J.J. (2006) *The status and distribution of the Sumatran elephant in Aceh, Indonesia*. WWF Netherlands, Zeist.

Rood, E.J.J., Azmi, W. & Linkie, M. (2008) Elephant crop raiding in a disturbed environment: the Effect of landscape clearing on elephant distribution and crop raiding patterns in the north of Aceh, Indonesia. *Gajah*, **29**, 17–23.

Rood, E.J.J., Linkie, M. & Azmi, W. (2009) *Protection and sustainable management of forest in Aceh*. FFI Indonesia, Banda Aceh.

Santiapillai, C. & Jackson, P. (1990) *The Asian elephant: an action plan for its conservation*. IUCN/SSC Asian Elephant Specialist Group, Gland.

Shannon, G., Matthews, W.S., Page, B.R., Parker, G.E. & Smith, R.J. (2009) The affects of artificial water availability on large herbivore ranging patterns in savanna habitats: a new approach based on modelling elephant path distributions. *Diversity and Distributions*, **15**, 776–783.

Stockwell, D. & Peters, D. (1999) The GARP modelling system: problems and solutions to automated spatial prediction. *International Journal of Geographical Information Science*, **13**, 143–158.

Sukumar, R. (1989) Ecology of the Asian elephant in southern India 1 Movement and habitat utilization patterns. *Journal of Tropical Ecology*, **5**, 1–18.

Sukumar, R. (1990) Ecology of the Asian elephant in southern India 2 Feeding-habits and crop raiding patterns. *Journal of Tropical Ecology*, **6**, 33–53.

Titeux, N., Dufrene, M., Radoux, J., Hirzel, A.H. & Defourny, P. (2007) Fitness-related parameters improve presence-only distribution modelling for conservation practice: the case of the red-backed shrike. *Biological Conservation*, **138**, 207–223.

Tsoar, A., Allouche, O., Steinitz, O., Rotem, D. & Kadmon, R. (2007) A comparative evaluation of presence-only methods for modelling species distribution. *Diversity and Distributions*, **13**, 397–405.

Uryu, Y., Mott, C. & Fouad, N. (2008) *Deforestation, forest degradadtion, biodiversity loss and CO2 emissions in Riau, Sumatra, Indonesia*. WWF Indonesia, Jakarta.

Walsh, P.D., White, L.J.T., Mbina, C., Idiata, D., Mihindou, Y., Maisels, F. & Thibault, M. (2001) Estimates of forest elephant abundance: projecting the relationship between precision and effort. *Journal of Applied Ecology*, **38**, 217–228.

Wiegand, T. & Moloney, K.A. (2004) Rings, circles, and null-models for point pattern analysis in ecology. *Oikos*, **104**, 209–229.

Zhang, L. & Wang, N. (2003) An initial study on habitat conservation of Asian elephant (*Elephas maximus*), with a focus on human elephant conflict in Simao, China. *Biological Conservation*, **112**, 453–459.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Addressing Spatial Autocorrelation.

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