ORIGINAL PAPER

# Conservation status of Asian elephants: the influence of habitat and governance

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**Abstract** Understanding the drivers of Asian elephant (*Elephas maximus*) abundance and distribution is critical for effective elephant conservation, yet no such analysis exists despite decades of assessments and planning. We explored the influence of habitat- and governance-related drivers on elephant abundance across the 13 Asian elephant range countries. We tested competing statistical models by integrating a binary index of elephant abundance (IEA) derived from expert knowledge with different predictor variables including habitat, human population, socioeconomics, and governance data. We employed logistic regression and model-averaging techniques based on Akaike's Information Criterion to identify the best-performing subset among our 12 candidate models and used the model-averaged results to predict IEA in other areas in Asia where elephant population status is currently unknown. Forest area was our strongest single predictor variable. The best performing model, however, featured a combination of habitat and governance variables including forest area, level of corruption, proportional mix of forest and agriculture, and total agricultural area. Our predictive model identified five areas with medium–high to high probability to have populations with >150 elephants, which we believe should be surveyed to assess their status. Asian elephants persist in areas that are dominated by forest

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but also seem to benefit from a mix of agricultural activities. A relatively low level of corruption is also important and we conclude that effective governance is essential for maintaining Asian elephant populations. Asian elephant populations cannot be maintained solely in protected areas but need well-managed, mixed-use landscapes where people and elephants coexist.

## Introduction

Broad-scale conservation assessments are essential tools for conservation planning and priority setting. Well-known examples include Tiger Conservation Landscapes (Dinerstein et al. 2006; Sanderson et al. 2010), Biodiversity Hotspots (Myers 1990; Myers et al. 2000), and Global Ecoregions (Olsen and Dinerstein 1998; Olsen et al. 2001; Sanderson et al. 2002). Many of these assessments are based on qualitative analysis and expert knowledge, and lack strong quantitative and statistical foundations (e.g., Leimgruber et al. 2003; Dinerstein et al. 2006; Sanderson et al. 2010). For example, data collection efforts for Asian elephants are sparse or non-existent across many areas of interest and are poorly standardized among regions (Blake and Hedges 2004; Hedges et al. 2009), and therefore efforts to fill these gaps are urgently needed. Despite these realities, conservation biologists need to extract as much useful information as possible from existing data sources to identify conservation priorities, while carefully acknowledging data limitations and their implications. Statistical and empirical analyses of drivers impacting species and ecosystems, such as regression modeling coupled with model selection techniques, can help make the most of available data, as has been done for African elephants (Burn et al. 2011; Maisels et al. 2014; Wittemyer et al. 2014).

Asian elephant (*Elephas maximus*) conservation is a key example of the need for developing a solid statistical and empirical framework for identifying conservation priorities (Blake and Hedges 2004; Leimgruber et al. 2003). For roughly the last 30 years, a total population estimate of 30,000–50,000 elephants continues to be restated (Blake and Hedges 2004) despite Asia having undergone dramatic human population growth and significant landscape transformations, including vast deforestation (Koh and Wilcove 2008; Sodhi et al. 2004) and the expansion of palm oil plantations in, especially, Indonesia and Malaysia (Fitzherbert et al. 2008; Koh and Wilcove 2008; Koh et al. 2011; Pirker et al. 2016; Vijay et al. 2016) during this time. Although rigorous quantitative estimates of wild Asian elephant population size are not available for most of the range [but for examples from Cambodia, the Lao PDR, Malaysia, and Sumatra (Indonesia) see Hedges et al. 2005, 2008, 2013; Pollard et al. 2007; Samsudin et al. in review], populations have likely declined given habitat loss (Leimgruber et al. 2003; Hedges et al. 2005), illegal killing (Campos-Arceiz et al. 2009; CITES 2016), capture of live elephants for the timber industry and other purposes (Hedges et al. 2006; Leimgruber et al. 2008; Leimgruber et al. 2011a), and the consequences of severe human-elephant conflict (hereafter HEC; Sukumar 1989; Zhang and Wang 2003; Blake and Hedges 2004; Choudhury 2003; Rood et al. 2008; Campos-Arceiz et al. 2009; Doyle et al. 2010; Choudhury et al. 2008; Fernando and Leimgruber 2011).

The best available information on Asian elephant status stems from an October 2008 expert workshop funded by IUCN, U.S. Fish and Wildlife Service, WCS, and WWF (Hedges et al. 2009). This dataset, when combined with other existing data sources, could facilitate quantitative assessment of geographic variation in the distribution of elephants, remaining elephant habitat, and threats to elephants and their habitat. However, patterns in Asian elephant distribution often seem counter-intuitive and perhaps inconsistent. For example, relatively small and fragmented habitat areas in India and Sri Lanka with some of the highest human population densities, habitat loss, and HEC appear to support the vast majority of remaining wild elephant populations (Leimgruber et al. 2003). These areas lost nearly 80% of their elephant habitat within the last 100 years (Fernando and Leimgruber 2011). In contrast, expansive and relatively intact forest areas in Myanmar with much lower human densities support relatively few elephants (Leimgruber et al. 2003).

These contrasting patterns suggest that simple proxies such as forest cover loss may not fully account for elephant decline, and that these habitat-related explanatory variables need to be combined with predictors quantifying the degree of corruption and quality of governance, as has been noted for elephants in Africa (Burn et al. 2011; Maisels et al. 2014; Bennett 2015; CITES 2016). A more comprehensive analysis that can weigh the contributions of other potential drivers, including socio-economic, governance, political, and cultural factors (for examples see Smith et al. 2003a; Trebilco et al. 2011; De Boer et al. 2013; Wittemyer et al. 2014) is therefore needed for Asian elephants. Here, we present such a quantitative framework and demonstrate how habitat and governance factors are related to Asian elephant abundance across their geographic range.

## Methods

### Analytical framework

We based our analyses on a binary "low/high" index of elephant abundance (IEA) derived from recent expert assessments (Hedges et al. 2009) of confirmed ranges believed to have at least some elephants (thus there is no absence category in the IEA). We then used logistic regression to model the relationship between IEA and habitat- and governance predictor variables. We built our set of 12 candidate models via a mix of a priori considerations and exploratory analysis, and then employed model selection and model averaging techniques based on Akaike's Information Criterion (AIC) to identify the subset of these models with the best balance of explanatory power and parsimony. We arrived at a final model by performing an AIC-weighted average across this subset (Burnham and Anderson 2002), and then used the averaged model to predict the status of the unconfirmed ranges based on their covariate values.

### Study species and study area

Asian elephants are found in 13 countries of South Asia and Southeast Asia, i.e. Nepal, India, Sri Lanka, Bangladesh, Bhutan, Myanmar, Thailand, Cambodia, Lao PDR, Vietnam, China, Malaysia (Peninsular and Sabah), and Indonesia (Sumatra and Kalimantan) (Choudhury et al. 2008). A report on a WCS, U.S. Fish and Wildlife Service, WWF, and IUCN funded assessment of Asian elephant status (hereafter Asian elephant report) provides the most recent distribution map together with some data on population sizes, both

based on expert knowledge (Hedges et al. 2009; available from the USFWS website at this URL: https://www.fws.gov/international/pdf/report-asian-elephant-range-wide-mapping-workshop-2008.pdf).

The 2008 Asian elephant report delineates 410 discrete range areas dispersed across the 13 range countries and covering a total area of 878,639 km$^2$. Elephant ranges were categorized into *confirmed*, *possible* and *recoverable* classes (see Appendix S1 of the Asian elephant report). Our main analysis focused on the 237 *confirmed ranges* (526,174 km$^2$) as these are areas in which wild Asian elephants occur with certainty. We combined adjoining ranges within a country that are separated by less than 30 km into elephant landscapes, resulting in 90 confirmed elephant landscapes (EL). This aggregation rule is justified because Asian elephants move on average 9.05 ± 0.61 km/day in zoos (Rowell 2014), with similar daily distances observed in the wild (Fernando and Pastorini, pers. Com.). Furthermore, data from elephant translocations indicate that elephants are capable of traversing substantially larger distances (Fernando et al. 2012). We then summed the minimum population values given by the Asian elephant report across the ranges comprising each EL to obtain a total population estimate for each EL (Appendix S1). Because population estimates from expert knowledge are relatively rough, we simplified the raw data into our IEA. We summed the population sizes of ranges within each EL to assign "low" (1–150 elephants; IEA = 1) or "high" (>150 elephants; IEA = 2) index values to each EL (Fig. 1). Our qualitative results were robust to the choice of threshold population for values between 150 and 450 (results not shown). We chose a threshold at the lower end of this range to ensure reliable analysis, as the number of ELs in the IEA = 2 category becomes very small for larger threshold values.
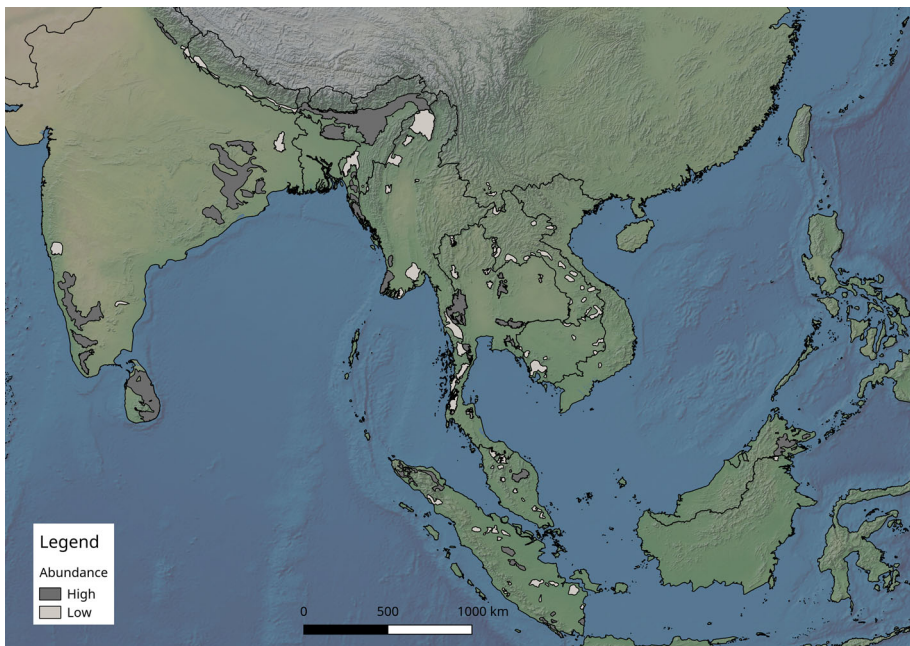


**Fig. 1** Elephant landscapes supporting low (1–150 elephants) and high (>150 elephants) abundance populations based on confirmed range data and population estimates taken from the Asian elephant report

As a target for our predictive models, we combined *possible* and *recoverable* ranges into an *unconfirmed* category, and then applied the same aggregation rules as for the confirmed ranges to produce unconfirmed ELs. We then used our averaged model to calculate the predicted probability (with 95% prediction intervals) that each of these unconfirmed ELs supports high (IEA = 2) elephant abundance.

## Predictor variables and candidate models

We compiled existing data sets on habitat- and governance-related drivers from the literature, online databases, and published GIS datasets (Appendix II). Habitat variables are compiled at the individual EL-level, while governance variables were typically available only at the country level. The EL-level variables are calculated based on the spatial definition of ELs, and country level predictors are calculated based on the country borders from the Database of Global Administrative Areas (GADM vers. 1.0, http://www.gadm.org/version1).

Our habitat variables are derived from the tiger land cover data, based on high resolution regional land cover data set integrated and simplified to develop a standardized data set for mapping Tiger Conservation Landscapes (Dinerstein et al. 2006; Sanderson et al. 2010; Songer et al. 2012). We aggregated the tiger land cover data forest types into a forest category and used the existing tiger land cover data agriculture category (Appendix S2). Together, these two land cover categories account for roughly 90% of the EL areas on average. Due to the extremely large range of EL areas, we first divided EL area (km$^2$) by 1000 to help stabilize model fits (Gelman and Hill 2007). Furthermore, as we expected proportional changes in area to have the same effect on abundance regardless of the initial area, we added 1 to each forest area and agricultural area (because each had several 0 observations) and then natural log transformed them (ln forest = *LnFor*; ln agriculture = *LnAg*).

Some authors (Sukumar 2003; Fernando and Leimgruber 2011; Fernando 2006) have argued that Asian elephants benefit from a mixture of forest and agricultural habitat, with individuals using forest for cover and browsing opportunities, and agricultural areas for easy and abundant grazing. We therefore included a mixture index, *Mix*, which is defined as the proportion of forested area times the proportion of agricultural area within each EL. This index is larger for ELs that feature a balanced (i.e., closer to 50:50) mixture of both habitat types, and smaller for those that are dominated by either forest or agriculture.

High human population densities are frequently seen as a root cause for HEC which ultimately results in elephant population declines and local extinctions (Choudhury et al. 2008; Leimgruber et al. 2003; Sukumar 2003; Hedges et al. 2005). We therefore used 1-km resolution LandScan data (LandScan 2008) to estimate human population densities for each EL (*Pop*, Appendix S2). The data utilized for governance predictors included Gross Domestic Product (*GDP*, Central Intelligence Agency 2009), Corruption Perceptions Index (*CPI*, Transparency International 2010), and Environmental Performance Index (*EPI,* Yale Center for Environmental Law and Policy, Yale University, Center for International Earth Science Information Network, Columbia University, World Economic Forum, and Joint Research Centre-European Commission 2010), all of which were only available at the country level (i.e., all ELs within a country have the same value for each index). The *GDP* is an index of a country's relative level of development, while *CPI* and *EPI* are aggregated indices derived from a suite of different metrics that reflect a country's level of corruption (*CPI*), and rank on environmental concerns in the areas of protection of human health and protection of ecosystems (*EPI*). Somewhat counter intuitively, *CPI* values range from zero

to 10, with zero being most corrupt and 10 being least corrupt, while *EPI* values range from zero to 100, with 100 being the best performance.

We considered seven predictor variables, of which three were related to range-level habitat (*LnFor*, *LnAg*, and *Mix*), and four pertained to social or governance factors (*GDP*, *CPI*, *EPI*, and *Pop*). Rather than blindly searching through the 127 possible models that can be built from these variables, we restricted the candidate set of models based on a mix of a priori considerations and exploratory analysis. Based on previous research, we expect that the habitat level predictors we obtained will all have a reasonable degree of explanatory power (Leimgruber et al. 2003; Choudhury et al. 2008). Even though elephants are regarded as habitat generalists, forest area is widely recognized as a key factor in determining elephant abundance (Choudhury et al. 2008), and so on a priori grounds we considered *LnFor* to be a basal variable for all models considering habitat factors. Additionally, some studies have shown evidence of the relationship of elephant status to social and governance variables (Burn et al. 2011; de Boer et al. 2013, Maisels et al. 2014), but these relationships are less clear. We therefore first performed a small exploratory analysis to eliminate social and governance variables that are not strongly related to IEA.

Our exploratory analysis consisted of logistic regression models that included each of the social and governance variables (*GDP*, *CPI*, *EPI*, and *Pop*) either singly or paired with *LnFor*, our a priori basal variable for the habitat-related models. This resulted in a total of eight exploratory models. We retained only variables whose coefficient estimate either when alone or when paired with *LnFor* was at least 1 standard error away from zero, which corresponds to $p < 0.32$. The goal of this analysis was not to determine which of these variables were "significant", but rather to eliminate those that clearly had little explanatory power, and therefore we set a relatively permissive threshold. Only *CPI* emerged from this analysis as potentially important, as none of the others had coefficient estimates farther than one standard error from zero (corresponding to $p > 0.32$ for all others).

## Model selection, averaging, and cross validation

We thus considered four variables in our final analysis: *LnFor*, *LnAg*, *Mix*, and *CPI*. We first verified that none of these predictors were problematically correlated (i.e., $r < 0.7$ for all pair-wise combinations of predictors, and variance inflation factors for all predictors <2; Dormann et al. 2013). We then defined a candidate set of 12 models (Table 1), divided into three groups, habitat + governance models, habitat only models, and governance models. The habitat + governance models (m1–m4) all featured both *LnFor* and *CPI*. The habitat models (m5–m8) all included *LnFor*. Finally, the governance models (m9–m12) all shared *CPI* as a common predictor. We used Akaike's Information Criterion corrected for small sample sizes (AICc) to rank all candidate models, and model-averaging techniques to make inferences based on all models ≤2 AICc units from the best model, which we refer to as the confidence set (Burnham and Anderson 2002). We report both the raw coefficient estimates for models in the confidence set as well as standardized coefficients, where each coefficient is multiplied by the standard deviation of the predictor variable to which it corresponds (Menard 2004). Standardized coefficients allow ranking the relative importance of predictor variables with different scales (Menard 2004). All analyses were performed in R 3.3.2 (R core team 2017) using the *glm()* function for fitting the models, and the multi-model inference package (Bartoń 2016) for model selection.

We then used Akaike weights to calculate a weighted average of the predictions of the models in the confidence set, which we hereafter refer to as the averaged model. An Akaike weight is a measure of relative support in the data for a particular model in the candidate

**Table 1** List of 12 candidate models in our model selection analysis, divided into three groups: habitat + governance, habitat, and governance. Additionally, explained deviance, AICc differences (relative to the best model) and Akaike weights are shown. Models in bold are in the confidence set and are used to construct the average model for prediction

| Model | Variables | Expl. dev. | ΔAICc | AICc weight |
|-------|-----------|-----------|-------|-------------|
| **m1** | **LnFor, LnAg, Mix, CPI** | **0.48** | **0** | **0.42** |
| **m2** | **LnFor, Mix, CPI** | **0.45** | **0.68** | **0.30** |
| **m3** | **LnFor, LnAg, CPI** | **0.45** | **1.03** | **0.25** |
| m4 | LnFor, CPI | 0.35 | 7.79 | 0.01 |
| m5 | LnFor, LnAg, Mix | 0.38 | 7.36 | 0.01 |
| m6 | LnFor, LnAg | 0.36 | 7.48 | 0.01 |
| m7 | LnFor, Mix | 0.35 | 8.28 | 0.01 |
| m8 | LnFor | 0.27 | 13.61 | 0 |
| m9 | CPI, LnAg, Mix | 0.31 | 14.33 | 0 |
| m10 | CPI, LnAg | 0.30 | 13.46 | 0 |
| m11 | CPI, Mix | 0.15 | 28.00 | 0 |
| m12 | CPI | 0.06 | 34.19 | 0 |

*LnFor* natural log of 1 + forest area (km$^2$/1000); *LnAg* natural log of 1 + agricultural area (km$^2$/1000); *Mix* proportion of agricultural area x proportion of forest area; *CPI* corruption perceptions index

set and can be calculated from the corresponding ΔAICc values (Burnham and Anderson 2002). We validated the predictive ability of the averaged model via leave-one-out cross validation. Specifically, we removed a single observation from the dataset, refit the models without that observation, determined which models fell in the confidence set, and then averaged models in confidence set to predict the holdout observation. We repeated this procedure once for each observation in the dataset and calculated the percentage of correctly predicted holdout observations across the entire dataset. We then used the validated averaged model to predict the probability of high abundance (IEA = 2) for the 64 unconfirmed ELs based on the values of the predictor variables for each EL. Finally, we placed 95% prediction intervals on the point predictions by combining the prediction variances and Akaike weights of each model in the confidence set via the unconditional variance estimator (Burnham and Anderson 2002, p. 162). The unconditional variance accounts for the non-independence among predictions of models in the confidence set, which arises because these models are structurally similar and are fit to the same data (Burnham and Anderson 2002).

## Results

The confidence set consisted of three models, all of which were habitat + governance models (Table 1). While *m*1 was the AICc-best model, models *m*2 and *m*3 were both <2 AICc units from *m*1 (Table 1), which suggests a model-averaging approach focusing on *m*1, *m*2, and *m*3 is warranted. All other models were >7 AICc units from *m*1 (Table 1). The proportion of deviance explained (a rough analog of $R^2$ for generalized linear models) for *m*1 was 0.48. As the AICc-best model was the full model, all variables considered had some effect on the IEA. Our cross-validation analysis of the averaged model showed that it

correctly predicted the holdout observation 83% of the time, confirming that the AIC-weighted average of *m*1, *m*2, and *m*3 has good predictive ability.

Ranking variable importance in the top three models via standardized coefficient estimates revealed that *LnFor* consistently had the largest impact on the IEA (Table 2). In the full model, *CPI* was the second most important predictor, while *Mix* and *LnAg* were the second most important predictors in *m*2 and *m*3, respectively (Table 2). We therefore conclude that *LnFor* is the main driver of elephant abundance considered in our analaysis, with *CPI*, *LnAg*, and *Mix* all having substantial but secondary effects. The model-averaged relationship of each predictor variable with *Prob(*IEA = 2*)* is displayed graphically (Fig. 2), with all other variables but the focal variable held at their means.

Using our validated, averaged model to predict IEA for unconfirmed ELs (Fig. 3), we found that most of these ELs (N = 59; 92.2%) had low or medium low probabilities of having high elephant abundance (blue and green areas in Fig. 3; Appendix S3), and thus are likely of poor quality for elephants. However, a few unconfirmed ELs (n = 5; 7.8%) had high or medium high probabilities of high elephant abundance (red and cyan ELs in Fig. 3; Appendix S3), including all remaining ELs in Myanmar, a Northern Thailand EL comprised of dense cluster of small elephant ranges, parts of Assam in India, and a small area of Bangladesh.

## Discussion

Asian elephant habitat needs are complex and our results reaffirm that elephants can persist in reasonable numbers in human-modified landscapes where substantial forest cover is maintained alongside agricultural activities and where there is relatively good governance. We found that our combined habitat and governance models performed best, with our full and most complex model being most effective in explaining current IEA patterns. This best performing model integrates forest area, level of corruption, habitat mix, and agricultural area. This suggests that the probability that an EL will have a higher IEA is highest in ELs featuring larger forest areas in countries that have relatively low corruption, e.g., India, Sri Lanka, Thailand, and Malaysia.

**Table 2** Standardized model coefficient estimates, raw (non-standarized) coefficient estimates, and standard errors associated with the raw coefficient estimates for the three models in the confidence set. Within each model, predictors are listed in order of decreasing variable importance, as ranked by the magnitudes of the standardized coefficient estimates

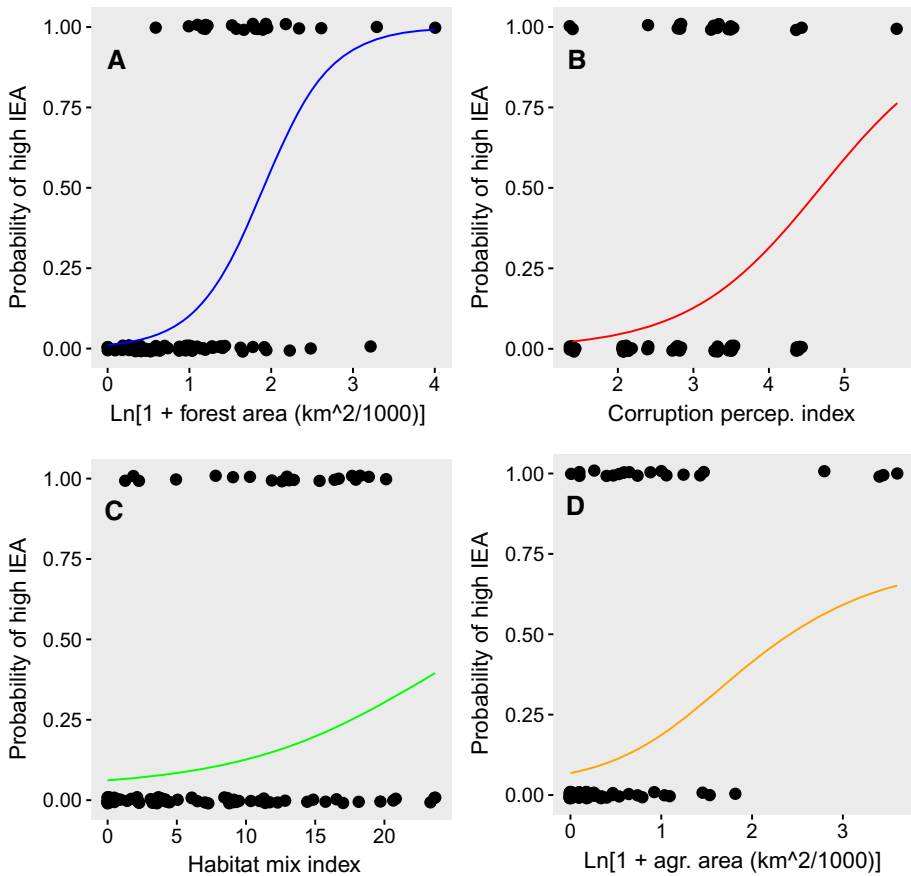| Model | Parameter | Standardized estimate | Estimate | SE |
|-------|-----------|-----------------------|----------|------|
| m1 | Intercept | NA | −9.58 | 2.49 |
| | *LnFor* | 1.92 | 2.40 | 0.74 |
| | *CPI* | 1.06 | 1.20 | 0.43 |
| | *LnAg* | 0.95 | 1.26 | 0.90 |
| | *Mix* | 0.82 | 0.12 | 0.07 |
| m2 | Intercept | NA | −9.90 | 2.50 |
| | *LnFor* | 2.24 | 2.80 | 0.74 |
| | *Mix* | 1.20 | 0.17 | 0.06 |
| | *CPI* | 1.03 | 1.17 | 0.41 |
| m3 | Intercept | NA | −7.80 | 1.89 |
| | *LnFor* | 1.58 | 1.98 | 0.59 |
| | *LnAg* | 1.47 | 1.96 | 0.75 |
| | *CPI* | 0.95 | 1.07 | 0.40 |

**Fig. 2** Influence of individual predictor variables on the probability that an EL has high abundance (IEA = 2). The data are shown as jittered black points at the bottom (EL's with IEA = 1) and top (EL's with IEA = 2) of each plot. The curves are the model-averaged (over the confidence set) response functions versus individual predictors, with all other predictors fixed at their means. Higher corruption index value means lower corruption

While we expected forest area to be important, the similarly high importance of corruption in explaining the IEA is a novel result for Asian elephants. CPI was a predictor in the three most highly ranked models. Low levels of corruption were consistently associated with increases in the probability of high IEA. It may be that countries where governments have developed land use and natural resource policies, and have the capacity and resources to implement and enforce such policies, have been able to maintain larger elephant populations. Such policies reduce illegal logging and land conversion, retaliatory killings resulting from HEC, and poaching. Recent research also support the ideas that governance factors may affect wildlife populations through a variety of mechanisms (Gore et al. 2013) and may help explain country-level variation in abundance of large herbivores (Smith et al. 2003b, 2015; Burn et al. 2011; De Boer et al. 2013). For example, high corruption has been shown to exacerbate threats to African elephants and black rhinos in Africa (Smith et al. 2003b; Martin et al. 2010; Rosen and Smith 2010). Additionally, Burn et al. (2011) analyzed poaching data on African and Asian elephants using a rigorous quantitative
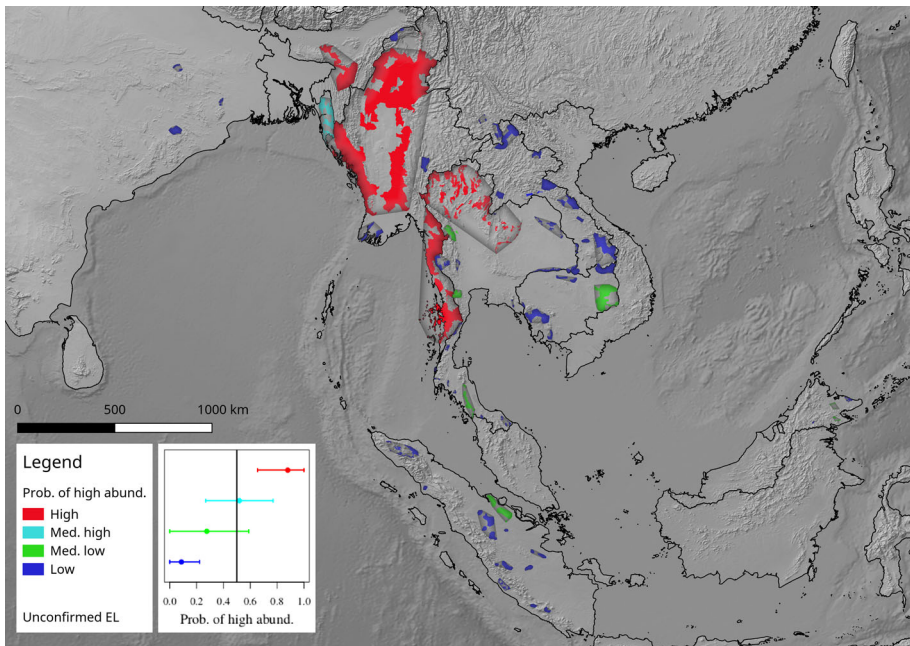
**Fig. 3** Map of model-averaged predictions for unconfirmed ELs. Based on the combination of point prediction (PP) for *Prob*(IEA = 2) and the associated 95% prediction interval (PI), we define the following prediction categories from highest to lowest chance of supporting high abundance (>150) elephant populations: (1) PP > 0.5 and entire PI > 0.5 (*red*); (2) PP > 0.5 but lower PI limit ≤0.5 (*cyan*); (3) PP ≤ 0.5 but upper PI limit >0.5 (*green*); and (4) PP ≤ 0.5 and entire PI ≤ 0.5 (*blue*). The *inset* figure shows examples of these four cases and their corresponding *colors*

analysis and provided strong evidence that corruption is a major driver of illegal killing of elephants (see also Maisels et al. 2014 and CITES 2016).

Habitat mix and agricultural area, which were each in two of the three best models, contributed additional predictive power. Our results suggest that a more equal proportion of forest to agriculture (i.e., closer to 50:50) supports an increased probability of high elephant abundance. This is likely due to forest supplying a combination of cover and browsing opportunities, and agricultural land providing an abundant growth of early successional plants with ample grazing and browsing opportunities. Such habitat mixtures have previously been recognized as being beneficial for elephants by allowing them to opportunistically switch between grazing and browsing depending on seasonal and phenological patterns in availability (Sukumar 2003; Fernando 2006; Fernando and Leimgruber 2011). On the other hand, agricultural forest mosaics could also sometimes represent ecological traps for elephants and other wildlife (Schlaepfer et al. 2002; Kristan 2003; Battin 2004). The abundant food and water resources attract elephants and potentially even increase reproduction (Fernando 2006; Fernando and Leimgruber 2011), but the ensuing HEC results in significant economic losses, often resulting in negative conservation attitudes and sometimes retaliatory killings or removal of elephants. Therefore, the nutritional benefits that may come from access to edges and agriculture may be counteracted, at least to some extent, by the HEC that often ensues in agricultural forest mosaics, leading to negative consequences for both humans and elephants. Relatively good

governance and lower corruption may help suppress this vicious cycle through implementation of good HEC management, including reduction of illegal land conversions, education campaigns, elephant-aware land use planning including use of buffer zones, well-maintained electric fencing, and involvement of local people in HEC prevention.

Our model-averaged predictive analysis identified four unconfirmed ELs with high probability (red areas in Fig. 3) and one with medium–high probability (cyan area in Fig. 3) of high elephant abundance (>150), which we believe should urgently be surveyed to confirm and document their status. Not surprisingly, two of the four high probability ELs are in Myanmar, a country considered to be a stronghold for Asian elephants (Sukumar 1989, 2003; Santiapillai and Jackson 1990) until relatively recently (Leimgruber et al. 2011a). Though these ranges were categorized as not confirmed in the Asian elephant report, some of these ranges have since been reported by experts as supporting populations of probably >150 elephants (Songer et al. 2016; Islam et al. 2011; Leimgruber et al. 2011a). Similarly, India's Ministry of Environment and Forests also estimates large elephant populations in Assam (http://envfor.nic.in/division/introduction-4). It is important to note that this newer information was not, in any way, used in the predictive model. More difficult to evaluate is the red cluster of small elephant ranges in Northern Thailand that form a complex EL, as well as the cyan area in Bangladesh (Fig. 3). It is possible that these ELs support relatively large populations (by Asian elephant standards) but surveys are urgently needed to assess the areas and take the necessary steps to secure any significant elephant populations remaining.

Most of the remaining blue and green ELs are likely to have already lost most of their elephants and habitat, and so the model predictions are quite plausible. For example, Sumatra has undergone serious declines in elephant populations in recent decades, which led to the reclassification of Sumatran elephants from Endangered to Critically Endangered in the IUCN Red List of Threatened Species in 2011 (Gopala et al. 2011). The only EL for which model predictions seem potentially at odds with newer data is the green area representing the Eastern Plains of Cambodia. This area has been surveyed more recently and preliminary results suggest that there are >150 elephants (Pollard et al. 2007, WCS and WWF unpublished data). On the other hand, the upper limit of the 95% prediction interval for this EL is >0.5, suggesting the possibility of high abundance despite the point prediction being <0.5. Partly, this potential misclassification may result from inadequate data on forest cover. Dry deciduous forests in eastern Cambodia are characterized by an open, savanna-like structure that often results in an underestimation of the actual forest cover by broad-scale land cover mapping (Leimgruber et al. 2011b, Wittemyer et al. 2014).

We thus conclude that our predictive model was very effective in identifying areas that would likely support high elephant abundance. The lack of evidence prior to the Asian elephant report highlights the difficulty in getting reliable current elephant population estimates. We therefore recommend that limited resources be allocated to the most promising areas, and suggest that each of the currently unconfirmed ELs with high predicted IEA (red and cyan areas in Fig. 3) be prioritized for surveys and conservation-relevant research.

It is important to recognize the limits of our approach to properly interpret the predictions it produces. First, the abundance data to which our models are fit are largely derived from expert opinion, so any systematic biases in the underlying abundance assessments would be reflected in predictions made with the fitted models. We specifically chose a relatively coarse binary representation of abundance to guard against biases of this nature. Second, a large number of factors likely affect Asian elephant abundance, but we have only been able to consider a small number of predictors. It is therefore possible that

our analysis misses some important driving relationships. On the other hand, the risk of identifying spurious relationships increases with the number of predictors considered. We have tried to balance these competing risks through a careful combination of a priori reasoning, an initial screening of predictors with poorly understood effects, and formal model selection among models that passed these first two filters. Finally, key driving relationships might change considerably over space. Resolving such differences would, however, likely require both more precise abundance data as well as finer-scale covariate information, particularly for predictors like CPI that are only available at the country level.

In the future, most regions in Asia will face even higher human population densities and there will be need for even more agricultural area. Clearly, the challenge is to balance the habitat needs of a wide-ranging mega-herbivore against human land use. Many argue that conservation is most effective where the widest range of biodiversity can be preserved with minimized conservation conflict potential, i.e. areas that have the least human influence (Sanderson et al. 2002). However, for elephants, especially Asian elephants, such a strategy is not likely to work. Existing protected area networks are too small, and significant numbers of wild elephants still live outside these networks. Our results further suggest that elephants can survive in human modified landscapes and, at least to some extent, benefit from landscape modifications due to agriculture. Consequently, successful Asian elephant conservation will require landscape-level management that allows for co-existence of elephants and people. However, the key role protected areas play in maintaining vital core populations of elephants within larger landscapes should not be minimized (Walston et al. 2016). The idea that elephants require space beyond the boundaries of protected areas in places that are compatible with human activities, but where priority is given to elephant needs has been referred to as the Managed Elephant Ranges concept (Santiapillai and Jackson 1990). Such landscape planning may include buffer zone areas (DeFries et al. 2010) where low-level agricultural activities such as shifting cultivation may be allowed and may provide ecosystem services by increasing graze availability for elephants.

Good governance and low levels of corruption are critical for successful conservation, not only for elephants, but for biodiversity in general, forest ecosystems, and for other megavertebrates such as rhinos (Smith, J. et al. 2003a; Smith, R.J. et al. 2003b). Despite this importance, little systematic research currently exists to better assess how governance and corruption act at the local level of an elephant range or protected area. What constitutes good governance at this level, how it should best be measured, and how local communities can be empowered to improve governance are all open questions for Asian elephant conservation that should be addressed in future research and policy initiatives.

## Supporting Information

Descriptions of confirmed ELs (Appendix S1), the predictor variables and sources thereof (Appendix S2), and unconfirmed ELs and corresponding abundance predictions (Appendix S3) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

# References

Bartoń K (2016) MuMIn: multi-model inference. R package version 1.15.6. http://CRAN.R-project.org/package=MuMIn. Accessed July 2016

Battin J (2004) When good animals love bad habitats: ecological traps and the conservation of animal populations. Conserv Biol 18:1482–1491

Bennett EL (2015) Legal ivory trade in a corrupt world and its impact on African elephant populations. Conserv Biol 29:54–60

Blake S, Hedges S (2004) Sinking the flagship: the case of forest elephants in Asia and Africa. Conserv Biol 18:1191–1202

Burn RW, Underwood FM, Blanc J (2011) Global trends and factors associated with the illegal killing of elephants: a hierarchical Bayesian analysis of carcass encounter data. PLoS ONE 6:e24165

Burnham KP, Anderson DR (2002) Multimodel inference, understanding AIC and BIC in model selection. Sociol Methods Res 33:261–304. doi:10.1177/0049124104268644

Campos-Arceiz A, Takatsuki S, Ekanayaka SKK, Hasegawa T (2009) The human-elephant conflict in southeastern Sri Lanka: type of damage, seasonal patterns, and sexual differences in the raiding behavior of elephants. Gajah 31:5–14

Central Intelligence Agency (2009) Gross Domestic Product (GDP). https://www.cia.gov/library/publications/the-world-factbook/index.html. Accessed July 2016

Choudhury A (2003) Human-elephant conflicts in Northeast India. Hum Dimens Wildl 9:261–270

Choudhury A, Lahiri Choudhury DK, Desai A, Duckworth JW, Easa PS, Johnsingh AJT, Fernando P, Hedges S, Gunawardena M, Kurt F, Karanth U, Lister A, Menon V, Riddle H, Rübel A, Wikramanayake E (IUCN SSC Asian Elephant Specialist Group) (2008) *Elephas maximus*. In: IUCN 2013. IUCN red list of threatened species. Version 2013.2. www.iucnredlist.org. Accessed July 2016

CITES (2016) Monitoring the illegal killing of elephants. Report presented at the Seventeenth Meeting of the Conference of the Parties, Johannesburg (South Africa), 24 September–04 October 2016, CoP17 Doc. 57.5, CITES Secretariat, Geneva, Switzerland. https://cites.org/sites/default/files/eng/cop/17/WorkingDocs/E-CoP17-57-05.pdf and https://cites.org/sites/default/files/eng/cop/17/WorkingDocs/E-CoP17-57-05-Add.pdf. Accessed Jan 2017

De Boer WF, van Langevelde F, Prins HHT, de Ruiter PC, Blanc J, Vis MJP, Gaston KJ, Hamilton ID (2013) Understanding spatial differences in African elephant densities and occurrence, a continent-wide analysis. Biol Conserv 159:468–476

DeFries R, Karanth KK, Pareeth S (2010) Interactions between protected areas and their surroundings in human-dominated tropical landscapes. Biol Conserv 143:2870–2880

Dinerstein E, Loucks C, Heydlauff A, Wikramanayake E, Bryja G, Forrest J, Ginsberg J, Klenzendorf S, Leimgruber P, O'Brien T, Sanderson E, Seidensticker J, Songer M (2006) Setting priorities for the conservation and recovery of wild tigers: 2005–2015. A user's guide. WWF, WCS, Smithsonian, and NFWF-STF, Washington, DC—New York

Dormann CF, Elith J, Bacher S et al (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36:27–46

Doyle S, Groo M, Sampson C, Songer M, Jones M, Leimgruber P (2010) Human-elephant conflict—what can we learn from the news? Gajah 32:14–20

Fernando P (2006) Elephant conservation in Sri Lanka: integrating scientific information to guide policy. In: Groom MJ, Meffe GK, Carroll CR (eds) Principles of conservation biology. Sinauer Associates, Sunderland, pp 649–652

Fernando P, Leimgruber P (2011) Asian elephants and seasonally dry forests. In: McShea WJ, Davis SJ, Bhumpakphan N (eds) The ecology and conservation of seasonally dry forests in Asia. Smithsonian Institution Scholarly Press, Washington, DC, pp 151–164

Fernando P, Leimgruber P, Prasad T, Pastorini J (2012) Problem-elephant translocation: translocating the problem and the elephant? PLOS ONE 12:e50917

Fitzherbert EB, Struebig MJ, Morel A, Danielsen F, Brühl CA, Donald PF, Phalan B (2008) How will oil palm expansion affect biodiversity? Trends Ecol Evol 23:538–545. doi:10.1016/j.tree.2008.06.012

GADM. Geographic database of global administrative areas (boundaries. GADM version 1.0, March 2009. http://www.gadm.org/version1. Accessed July 2016

Gelman A, Hill J (2007) Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, Cambridge. ISBN 978-0-521-68689

Gopala A, Hadian O, Sunarto, Sitompul A, Williams A, Leimgruber P, Chambliss SE, Gunaryadi D (2011) *Elephas maximus* ssp. *sumatranus*. In: IUCN 2011. IUCN Red List of Threatened Species. Version 2011.2

Gore ML, Ratsimbazafy J, Lute ML (2013) Rethinking corruption in conservation crime: insights from Madagascar. Conserv Lett 6:430–438

Hedges S, Gunaryadi D (2010) Reducing human–elephant conflict: do chillies help deter elephants from entering crop fields? Oryx 44:139–146

Hedges S, Tyson MJ, Sitompul AF, Kinnaird MF, Gunaryadi D (2005) Distribution, status, and conservation of Asian Elephants (*Elephas maximus*) in Lampung Province, Sumatra, Indonesia. Biol Conserv 124:35–48

Hedges S, Tyson MJ, Sitompul AF, Hammatt H (2006) Why inter-country loans will not help Sumatra's elephants. Zoo Biol 25:235–246

Hedges S, Gumal M, Ng S (2008) WCS/GoM West Malaysian Elephant Project: Year 1, Elephant surveys and training in Taman Negara National Park, Malaysia: Final Report to the U.S. Fish and Wildlife Service. Wildlife Conservation Society, Bronx

Hedges S, Fisher K, Rose R (2009) Range-wide mapping workshop for Asian elephants (*Elephas maximus*), Cambodia, October 2008. A report to the U.S. Fish and Wildlife Service on Assistance Award No: 98210-6-G232. Wildlife Conservation Society, Bronx

Hedges S, Johnson A, Ahlering M, Tyson M, Eggert LS (2013) Accuracy, precision, and cost-effectiveness of conventional dung density and fecal DNA based survey methods to estimate Asian elephant (*Elephas maximus*) population size and structure. Biol Conserv 159:101–108

Islam MA, Mohsanin S, Chowdhury GW, Chowdhury SU, Aziz MA, Uddin M, Saif S, Chakma S, Akter R, Jahan I, Azam I (2011) Current status of Asian elephants in Bangladesh. Gajah 35:21–24

Koh LP, Miettinen J, Liew SC, Ghazoul J (2011) Remotely sensed evidence of tropical peatland conversion to oil palm. Proc Natl Acad Sci USA 108:5127–5132

Koh LP, Wilcove DS (2008) Is oil palm agriculture really destroying tropical biodiversity? Conserv Lett 1:60–64. doi:10.1111/j.1755-263X.2008.00011.x

Kristan WB (2003) The role of habitat selection behavior in population dynamics: source–sink systems and ecological traps. Oikos 103:457–468

LandScan. LandScan Global Population Database (2008) Population counts at 30 arc second resolution. Oak Ridge National Laboratory; Bright EA, Coleman PR, Rose AN, June 2009. https://share.ornl.gov/sites/landscan/2008. Accessed July 2016

Leimgruber P, Gagnon JB, Wemmer C, Kelly DS, Songer MA, Selig ER (2003) Fragmentation of Asia's remaining wildlands: implications for Asian elephant conservation. Anim Conserv 6:347–359

Leimgruber P, Senior B, Aung M, Songer MA, Mueller T, Wemmer C, Ballou JD (2008) Modeling population viability of captive elephants in Myanmar (Burma): implications for wild populations. Anim Conserv 11(3):198–205

Leimgruber P, Oo ZM, Aung M, Kelly DS, Wemmer C, Senior B, Songer M (2011a) Current status of Asian Elephants in Myanmar. Gajah 35:76–86

Leimgruber P, Delion M, Songer M (2011b) Uncertainty of mapping tropical dry forests in Asia. In: McShea WJ, Davies SJ, Phumpakphan N, Pattanavibool A (eds) The ecology and conservation of seasonally dry forests in Asia. Smithsonian Institution Scholarly Press, New York, pp 59–74

Maisels F, Strindberg S, Blake S et al (2014) Devastating decline of forest elephants in central Africa. PLoS ONE 8:1–13

Martin J, Chamaillé-Jammes S, Nichols JD, Fritz H, Hines JE, Fonnesbeck CJ, MacKenzie DI, Bailey LL (2010) Simultaneous modeling of habitat suitability, occupancy, and relative abundance: African elephants in Zimbabwe. Ecol Appl 20(4):1173–1182

Menard S (2004) Six approaches to calculating standardized logistic regression coefficients. Am Stat 58(3):218–223

Myers N (1990) The biodiversity challenge: expanded hot-spots analysis. Environmentalist 10:234–256

Myers N, Mittermeier RA, Mittermeier CG, da Fonseca GAB, Kent J (2000) Biodiversity hotspots for conservation priorities. Nature 403:853–858

Olsen DM, Dinerstein E (1998) The global 200: a representation approach to conserving the earth's most biologically valuable ecoregions. Conserv Biol 12:502–515

Olsen DM, Dinerstein E, Wikramanayake ED et al (2001) Terrestrial ecoregions of the world: a new map of life on earth. BioScience 51:933–938

Pirker J, Mosnier A, Kraxner F, Havlík P, Obersteiner M (2016) What are the limits to oil palm expansion? Glob Environ Chang 40:73–81

Pollard E, Hedges S, Gately M (2007) Elephant conservation and capacity-building in Seima Biodiversity Conservation Area, Cambodia. Final Report to the U.S. Fish and Wildlife Service, November 2007. Wildlife Conservation Society, Bronx

R Core Team (2017) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Rood EJJ, 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

Rosen GE, Smith KF (2010) Summarizing the evidence on the international trade in illegal wildlife. EcoHealth 7:24–32

Rowell Z (2014) Locomotion in captive Asian elephants (*Elephas maximus*). J Zoo Aquar Res 2:130–135

Samsudin AR, Yasak MH, Gumal M, Saaban S, Oziar A, Cheong F, Shaari Z, Tyson M, Hedges S (In review) Viability and management of the Asian elephant population in the Endau Rompin landscape, Malaysia. PLoS ONE

Sanderson EW, Malanding E, Levy M, Redford K, Wannebro A, Woolmer G (2002) The human footprint and the last of the wild. BioScience 52:891–904

Sanderson EW, Forrest J, Loucks C, Dinerstein E, Seidensticker J, Leimgruber P, Songer M, Heydlauff A, O'Brien T, Bryja G, Klenzendorf S, Wikramanayake E (2010) Setting priorities for tiger conservation: 2005–2015. In: Tilson R, Nyhus P (eds) Tigers of the world. The science, politics, and conservation of *Panthera tigris*, 2nd edn. Academic Press, New York, pp 143–161

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

Schlaepfer MA, Runge MC, Sherman PW (2002) Ecological and evolutionary traps. Trends Ecol Evol 17:474–480

Smith J, Obidzinski K, Subarudi S, Suramenggala I (2003a) Illegal logging, collusive corruption and fragmented governments in Kalimantan, Indonesia. Int For Rev 5:293–302

Smith RJ, Muir RDJ, Walpole MJ, Balmford A, Leader-Williams N (2003b) Governance and the loss of biodiversity. Nature 426:67–70

Smith RJ, Biggs D, St John FA, Sas-Rolfes M, Barrington R (2015) Elephant conservation and corruption beyond the ivory trade. Conserv Biol 29:953–956

Sodhi NS, Koh LP, Brook BW, Ng PKL (2004) Southeast Asian biodiversity: an impending disaster. Trends Ecol Evol 19:654–660

Songer M, Aung M, Allendorf TD, Calabrese JM, Leimgruber P (2016) Drivers of change in Myanmar's wild elephant distribution. Trop Conserv Sci 9(4):1–10

Songer M, Sampson C, Williams C, Forrest J, Gyeltshen K, Huy K, Sharma A, Gopala A, Budiman A, Sadikin H, Yulianto K, Viengkhamhak A, Ayub EA, Anthony D, Alfred R, Pandav B, Dachyosdee U, Tri ODB, Raj M, Delion M, Thapa GJ, Leimgruber P (2012) Mapping habitat loss and human-elephant-conflict (HEC) in WWF priority landscapes. Gajah 36:3–10

Sukumar R (1989) The Asian elephant. Ecology and management. Cambridge University Press, Cambridge

Sukumar R (2003) The living elephants evolutionary ecology, behavior, and conservation. Oxford University Press, Oxford

Transparency International (2010) Corruption perceptions index (CPI). http://www.transparency.org/cpi2010/results. Accessed July 2016

Trebilco R, Halpern BS, Mills Flemming J, Field C, Blanchard W, Worm B (2011) Mapping species richness and human impact drivers to inform global pelagic conservation prioritization. Biol Conserv 144:1758–1766

Vijay V, Pimm SL, Jenkins CN, Smith SJ (2016) The impacts of oil palm on recent deforestation and biodiversity loss. PLoS ONE 11:e0159668

Walston J, Stokes E, Hedges S (2016) The importance of Asia's protected areas for safeguarding commercially high value species. In: Joppa LN, Baillie JEM, Robinson JG (eds) Protected areas: are they safeguarding biodiversity. Wiley, London, pp 190–207

Wittemyer G, Northrup JM, Blanc J, Douglas-Hamilton I, Omondi P, Burnham KP (2014) Illegal killing for ivory drives global decline in African elephants. Proc Natl Acad Sci USA 111:13117–13121

Yale Center for Environmental Law and Policy—YCELP—Yale University, Center for International Earth Science Information Network—CIESIN—Columbia University, World Economic Forum—WEF, and Joint Research Centre—JRC—European Commission. 2010. 2010 Environmental Performance Index (EPI). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). http://dx.doi.org/10.7927/H4D21VHT. Accessed July 2016

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. Biol Conserv 112:453–459