

Community-managed forests and wildlife-friendly agriculture play a subsidiary but not substitutive role to protected areas for the endangered Asian elephant



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ABSTRACT

Global conservation policy is increasingly debating the feasibility of reconciling wildlife conservation and human resource requirements in land uses outside protected areas (PAs). However, there are few quantitative assessments of whether or to what extent these ‘wildlife-friendly’ land uses fulfill a fundamental function of PAs—to separate biodiversity from anthropogenic threats. We distinguish the role of wildlife-friendly land uses as being (a) subsidiary, whereby they augment PAs with secondary habitat, or (b) substitutive, wherein they provide comparable habitat to PAs. We tested our hypotheses by investigating the influence of land use and human presence on space-use intensity of the endangered Asian elephant (*Elephas maximus*) in a fragmented landscape comprising PAs and wildlife-friendly land uses. We applied multistate occupancy models to spatial data on elephant occurrence to estimate and model the overall probability of elephants using a site, and the conditional probability of high-intensity use given that elephants use a site. The probability of elephants using a site regardless of intensity did not vary between PAs and wildlife-friendly land uses. However, high-intensity use declined with distance to PAs, and this effect was accentuated by an increase in village density. Therefore, while wildlife-friendly land uses did play a subsidiary conservation role, their potential to substitute for PAs was offset by a strong human presence. Our findings demonstrate the need to evaluate the role of wildlife-friendly land uses in landscape-scale conservation; for species that have conflicting resource requirements with people, PAs are likely to provide crucial refuge from growing anthropogenic threats.

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1. Introduction

The conservation value of land uses that have the potential to reconcile biodiversity conservation and human livelihood needs (hereafter, ‘wildlife-friendly land uses’), is receiving increasing scientific attention (Daily et al., 2001; Norris, 2008; Kinnaird and O’Brien, 2012). This emergent trend largely stems from the urgent

need for strategies that can minimize threats to wildlife species in the face of growing human demands on the land (Fischer et al., 2008; Koh, 2008), and two key concerns associated with conservation in traditional, government-managed protected areas (PAs). First, notwithstanding their demonstrated success in conserving wildlife habitat worldwide (Bruner et al., 2001; Geldmann et al., 2013), PAs are often limited in size (Woodroffe and Ginsberg, 1998), and are becoming increasingly insular due to expansion and intensification of human land use around them (Hansen and DeFries, 2007). Secondly, the exclusionary policy of strictly inviolate PAs is often in conflict with livelihoods of local communities

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(Adams et al., 2004). Wildlife-friendly land uses, including community-managed forests (CMFs) and certain agricultural systems (Daily et al., 2001), can address livelihood concerns through mechanisms such as sustainable natural resource extraction, crop harvest, local enterprise and payments for conservation (Ferraro, 2001; Salafsky et al., 2001; Berkes, 2007). The integration of wildlife-friendly land uses into conservation plans, however, hinges on the effectiveness with which they fulfill their purported conservation role.

Protected areas have long been a cornerstone for conservation policy (Margules and Pressey, 2000; Hansen and DeFries, 2007). Therefore, a valuable benchmark for the conservation role of wildlife-friendly land uses would be to determine whether or to what extent these land uses fulfill a fundamental function of PAs—to separate elements of biodiversity from processes that threaten their persistence (Margules and Pressey, 2000). From such a standpoint, wildlife-friendly land uses can be conceptualized to perform two distinct conservation roles relative to PAs. (1) *Subsidiarity*: wildlife-friendly land uses perform a subsidiary function to PAs by serving as secondary wildlife habitat, thereby augmenting overall habitat availability and supplementing the conservation potential of PAs. Under this scenario, wildlife conservation at the landscape scale is largely facilitated by PAs. (2) *Substitution*: wildlife-friendly land uses provide alternative habitats that are comparable in quality to those offered by PAs (e.g., Western et al., 2009). Although several studies have documented the biodiversity in wildlife-friendly land uses (e.g., Daily et al., 2001; Raman, 2001), the subsidiary and substitutive roles of these land uses relative to PAs have not been formally evaluated in landscape-scale conservation programs. Distinguishing these roles can provide a mechanistic basis to evaluate the conservation value of various wildlife-friendly land uses. This can facilitate realistic assessments of the extent to which visualized conservation goals may be achieved over time. For instance, if wildlife-friendly land uses (e.g., certain agricultural practices) play a subsidiary role in achieving specific conservation objectives in heterogeneous landscapes, PAs (or areas under a similar protective regime) would represent unique and critical components vis-à-vis the realization of these objectives. In such landscapes, wildlife-friendly agriculture may not be expected to play a substitutive role relative to PAs (Ehrlich and Pringle, 2008); however, the degree of subsidiarity of such agricultural practices (Raman, 2001; Balmford et al., 2012) still offers valuable insight into the conservation utility of these land uses. Furthermore, understanding the conservation role of wildlife-friendly land uses compared to PAs directly speaks to the conservation debate of land sparing versus land sharing (Green et al., 2005; Fischer et al., 2008), providing a potential approach to evaluate the viability of these contrasting strategies in different contexts.

The pervasive influence of a growing human footprint is driving much of the decline in wildlife populations across the world (Sanderson et al., 2002a; Karanth et al., 2010). Large-bodied mammals are particularly affected because they are intrinsically extinction-prone (Cardillo et al., 2005), and share a long history of competition with people over limited space and resources (Woodroffe et al., 2005). Given the growth of human populations in conservation landscapes (Wittemyer et al., 2008), and the likely negative influence of this trend on large mammal populations (Brashares et al., 2001; Cardillo et al., 2004), anthropogenic factors can potentially modulate the subsidiary or substitutive roles of wildlife-friendly land uses (e.g., Stokes et al., 2010). The substitution of PAs by wildlife-friendly land uses would necessitate interventions that minimize threats such as poaching (Blake et al., 2007) and human-wildlife conflict (Woodroffe et al., 2005) in wildlife-friendly land uses. In the absence of such regulations, hunted or conflict-prone species might avoid frequent and high-density use (henceforth ‘high-intensity use’) of areas outside PAs due to a

strong human presence (Ciuti et al., 2012). High-intensity use thus could be indicative of areas that serve as refuges from anthropogenic threats while meeting species resource requirements (Charnov, 1976; Lima and Bednekoff, 1999), and in doing so, have high conservation potential. While species occurrence in wildlife-friendly land uses might indicate that they at least perform a subsidiary role, the use of the same land uses with high-intensity would therefore affirm their potential for PA substitution (e.g., Daily et al., 2001; Kinnaird and O’Brien, 2012).

We evaluate the subsidiary and substitutive roles of CMFs and wildlife-friendly agriculture in the context of habitat needs of the endangered Asian elephant (*Elephas maximus*), a conflict-prone large mammal species. We apply multistate occupancy models (Nichols et al., 2007) to spatial data on elephant occurrence to differentiate between the overall probability of elephants using a given site (Ψ^1), and the conditional probability of high-intensity use given that a site is used by the species (Ψ^2). Under the subsidiarity hypothesis, we predicted that elephants would not differentiate between wildlife-friendly land uses and PAs in their overall space-use patterns but high-intensity use would be restricted to PAs. Under the substitution hypothesis, however, elephant space-use intensity would be comparable between wildlife-friendly land uses and PAs. Finally, we investigate if human presence modulates the conservation potential of wildlife-friendly land uses by precluding either their subsidiary or their substitutive roles.

2. Methods

2.1. Study system

We used the Asian elephant (*Elephas maximus*) as an example species based on the following: (a) its expansive space and resource requirements (Sukumar, 2003; Fernando et al., 2008) necessitates a potential dependency on areas outside PAs for persistence; (b) the susceptibility of the species to threats from poaching (Blake and Hedges, 2004) and human-elephant conflict (Williams et al., 2001) can potentially limit its occurrence in human-dominated areas. These factors, combined with its significant influence on ecosystem structure and function (Sukumar, 2003), contributes to the recognition of the Asian elephant as a landscape species, whose conservation can benefit other species and the landscape as a whole (Sanderson et al., 2002b).

We conducted the study in a heterogeneous landscape in Garo Hills (25°08′–25°23′N; 90°37′–90°58′E) located in the state of Meghalaya, northeastern India, that comprises a mosaic of PAs, CMFs, areas under slash-and-burn shifting cultivation (locally known as *jhum*), monoculture plantations of cashew (*Anacardium occidentale*), rubber (*Hevea brasiliensis*) and areca palm (*Areca catechu*), and human habitation (Fig. 1). PAs in the landscape approximately occupy 276 km² and include Balphakram National Park (220 km²), Siju Wildlife Sanctuary (6 km²), Baghmara Reserve Forest (44 km²) and Rewak Reserve Forest (6 km²); CMFs encompass an area of about 60 km². Our study site provided an ideal opportunity to: (a) compare forests under two management regimes (i.e., CMFs and PAs) and test if CMFs can substitute for PAs; (b) evaluate if the conservation roles of wildlife-friendly land uses vary by land use type; and (c) contrast the degree of subsidiarity of *jhum* fallows undergoing regeneration of native vegetation to areas of more intensive agriculture (i.e., monoculture plantations).

2.2. Sampling

We used a grid-based sampling approach to collect data on signs of elephant presence (e.g., dung piles, tracks and feeding signs). Occupancy studies make a distinction between ‘occupancy’

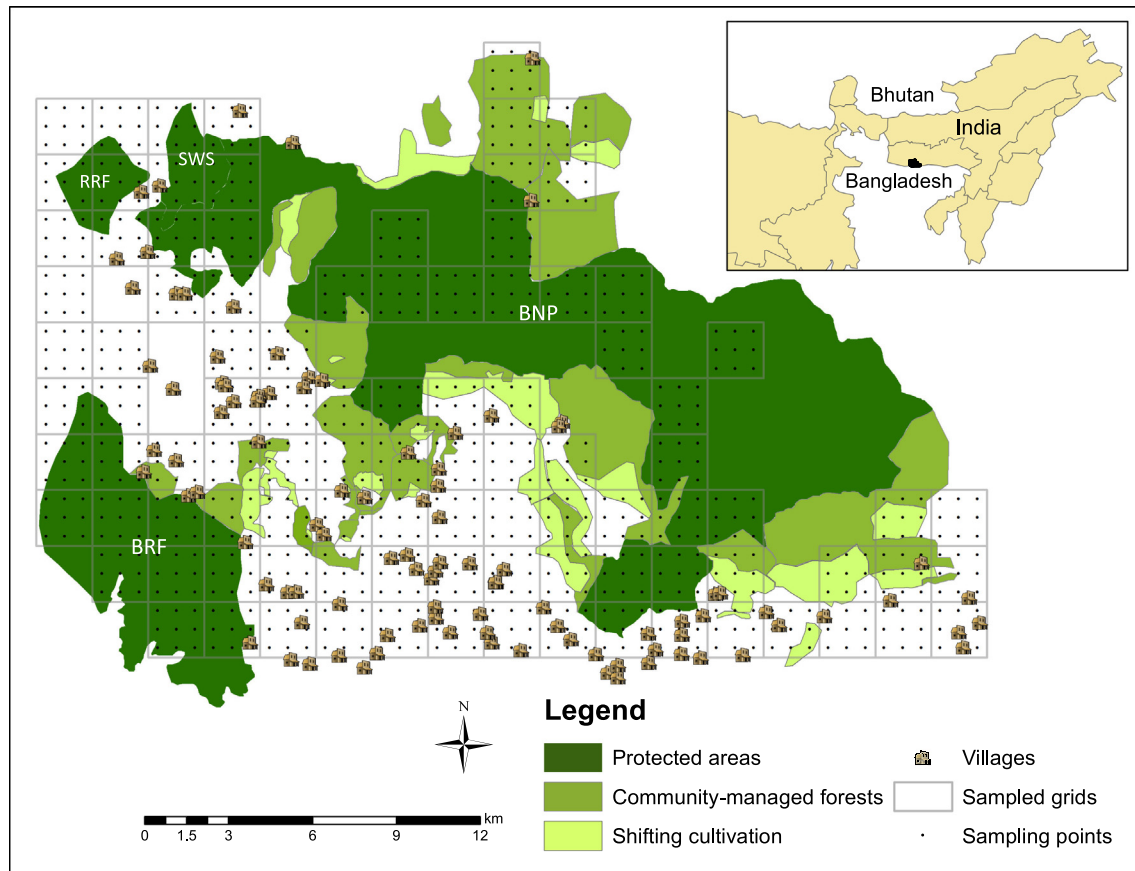


Fig. 1. Study area in Garo Hills, India (black polygon in the inset) comprising four protected areas (PAs)—Balphakram National Park (BNP), Baghmara Reserve Forest (BRF), Siju Wildlife Sanctuary (SWS) and Rewak Reserve Forest (RRF)—and community-managed forests (CMFs) interspersed within a human-dominated, agricultural landscape. Sampled sites included 99 grid cells of size 4 km² distributed across the landscape. Within each grid cell, there were nine uniformly distributed sampling points, and a walk between two adjacent points represented a spatial replicate. Land use in grid cells outside PAs and CMFs largely included fallows of slash-and-burn shifting cultivation or jhum, plantations of cashew, rubber and areca palm, and human habitation.

and ‘use’ as different parameters of interest—a landscape unit is ‘occupied’ if a species is physically present somewhere in the unit during the survey period; use on the other hand may be defined as the species being present within the unit at random points in time (Mackenzie, 2005). Since the objective of the study was to measure intensity of use by elephants rather than true occupancy, we defined each study site as a 4 km² grid cell such that it is smaller than the minimum expected home range size of Asian elephants (Fernando et al., 2008). Typically, occupancy studies account for detection probability through repeated assessments of sampling units assuming that the occupancy state at each unit is static during these assessments (i.e., the system is closed to changes in occupancy) (Kendall and White, 2009). Repeated surveys within a site may be executed over time (temporal replication), or across space (spatial replication; i.e., different locations within a site) (Mackenzie et al., 2006). Given the remoteness of a large proportion of our study site, we opted for spatial replication (Kendall and White, 2009) to meet the assumption of closure (Mackenzie et al., 2006). Therefore, each grid cell encompassed a set of nine uniformly distributed sampling points (Fig. 1), and the approximate Euclidean path between two consecutive points represented one spatial replicate. Following this design, we sequentially sampled eight spatial replicates per site, starting at the most accessible sampling point, and walking in a predetermined direction to all other points within the site. Replicates within a site that were not sampled were incorporated into the detection history as missing values (see Mackenzie et al., 2006).

We sampled a total of 80 sites encompassing 320 km² between January and May 2011, and an additional 19 sites covering 76 km²

in January and early February 2012. During this period, we invested approximately 990 person hours of effort walking a distance of 540.8 km. We encountered and recorded 2225 elephant signs along sampled spatial replicates within the 99 sites. We also documented land use at each of the nine sampling points and at the mid-point of each spatial replicate. Thus, we obtained 17 within-site records of observed land use for sites where all eight spatial replicates were sampled. We classified land use as forest, jhum fallow (i.e., areas undergoing varying stages of successional regeneration following the abandonment of cultivation), monoculture plantation and human habitation. Percentage land use (averaged across sampled sites) was: (a) forest = 52% ($N = 668$ observed points); (b) jhum fallow = 21% ($N = 261$); (c) monoculture plantation = 18% ($N = 215$); and human habitation = 9% ($N = 98$). Modal land use in a given site accounted for 70% of observed within-site land use records on average. We used a global positioning system and available GIS information to map the locations of PAs, CMFs, jhum fallows, monoculture plantations and villages within the study area.

2.3. Occupancy models and data analysis

We used a multistate occupancy model (Nichols et al., 2007) to evaluate the subsidiary and substitutive roles of lands outside PAs for the Asian elephant. Occupancy studies generally record the detection or non-detection of species presence as binary data (Mackenzie et al., 2006). Multistate models are an extension of the standard occupancy models, and they allow the classification of sites by different categories of occupancy (Nichols et al., 2007).

Therefore, these models were ideally suited for differentiating between low- and high-intensity elephant use of sites (e.g., Martin et al., 2010). We defined the two states of use (low- and high-intensity use), based on median counts of elephant signs per replicate across all sites (5 signs per replicate). Thus, elephant sign detection along replicate r in site s was assigned state 1 (low-intensity use) when signs encountered along r were >0 and <5 , and state 2 (high-intensity use) when encountered signs along r were ≥ 5 . Using these data, we were able to estimate the following model parameters: (a) the probability of detecting elephant presence along replicate r conditional on low-intensity use of site s (p_{sr}^1); (b) the probability of detecting elephant presence along replicate r conditional on high-intensity use of site s (p_{sr}^2); (c) the overall probability that site s is used, regardless of intensity (Ψ_s^1); (d) the probability of high-intensity use of site s conditional on elephant use of the site (Ψ_s^2); and (e) the probability that high-intensity use was observed along replicate r given detection of elephant presence and that site s was used with high-intensity (δ_{sr}).

We estimated the five parameters of interest using Program MARK (White and Burnham, 1999) implemented in R (R Development Core Team, 2013) with the help of the 'MSOccupancy' model in the RMark library (Laake and Rexstad, 2007). We first identified the most appropriate model structure for the detection probability parameters (p^1 , p^2 and δ) based on Akaike's information criterion corrected for small sample sizes (AIC_c). Sample size was the number of surveyed sites. We modeled p^1 , p^2 and δ using the independent, additive and two-way interactive effects of modal land use, and mean ruggedness, a measure of variation in elevation within a sampling site. We considered the following land uses: forest (including both PAs and CMFs), jhum fallow and plantation; we did not have *a priori* reasons to expect variation in detection probabilities between PAs and CMFs as they were both largely comprised of moist deciduous and tropical evergreen forests in our study landscape. During this analysis we allowed the intensity of use parameters (Ψ^1 and Ψ^2) to vary as a function of (a) distance to forest (in m), that is, distance of site s to the closest forest irrespective of whether it is community-managed or within a PA, (b) distance of site s to PAs (in m), (c) mean village density (per km²) within site s , and (d) modal land use within s . Our intention was to use the most general model for Ψ^1 and Ψ^2 while identifying the best model structure for p^1 , p^2 and δ .

Next, we fixed p^1 , p^2 and δ to the best-supported model structure from the previous analysis, and evaluated the relative

influence of the independent, additive and pair-wise interactive effects of the aforementioned site-specific covariates (a–d) on Ψ^1 and Ψ^2 . We also compared all models to an intercept-only model whereby parameters of interest were constant. Since there were three model structures for p^1 , p^2 and δ that had comparable support ($\Delta AIC_c < 2$) (Appendix A: Table A1) (Burnham and Anderson, 2002), we carried out three sets of analyses whereby p^1 , p^2 and δ were fixed to one structure per analysis set. Model comparisons were made on the basis of their AIC_c scores and Akaike weights (w_i). Top models for Ψ^1 and Ψ^2 were identical in all three sets (Appendix A: Tables A1 and A2). We largely used the top model in Table A1 to make inferences on parameters of interest as the model was well supported (ΔAIC_c between this model and the next best model >3 ; w_i for the model >0.5).

We used ArcGIS v.9.3 to create a distance map for forests (including both PAs and CMFs), and thereafter extract the minimum Euclidean distance of the centroid of each sampled site from the nearest forest, irrespective of PA or CMF. We similarly extracted the Euclidean distance of each site from PAs. We used ArcGIS to create a density map of village locations within the study area, and obtained the average number of villages per km² within each site. Finally, we used Quantum GIS v.1.6 to estimate mean ruggedness for each site—an index of terrain heterogeneity defined as the average elevation change between any point in a sampled site and its immediate neighborhood (Riley et al., 1999)—from a digital elevation model of the area.

3. Results

3.1. Detection of elephant presence

The probability of detecting elephant presence when a given site was used by the species with low-intensity (p^1) depended on the additive effect of land use and ruggedness within the site (Table A1). Land use also influenced detection probability in sites used with high-intensity (p^2). Detection probability for both states of site use intensity was higher in forests ($p^1 = 0.57$, 95% CI = 0.41–0.72; $p^2 = 0.83$, 95% CI = 0.78–0.86), declining progressively as the land use transitioned to jhum fallows ($p^1 = 0.14$, 95% CI = 0.05–0.34; $p^2 = 0.74$, 95% CI = 0.64–0.82) and monoculture plantations ($p^1 = 0.08$, 95% CI = 0.03–0.20; $p^2 = 0.41$, 95% CI = 0.27–0.58) (Fig. 2a). The dense growth of herbaceous weeds such as

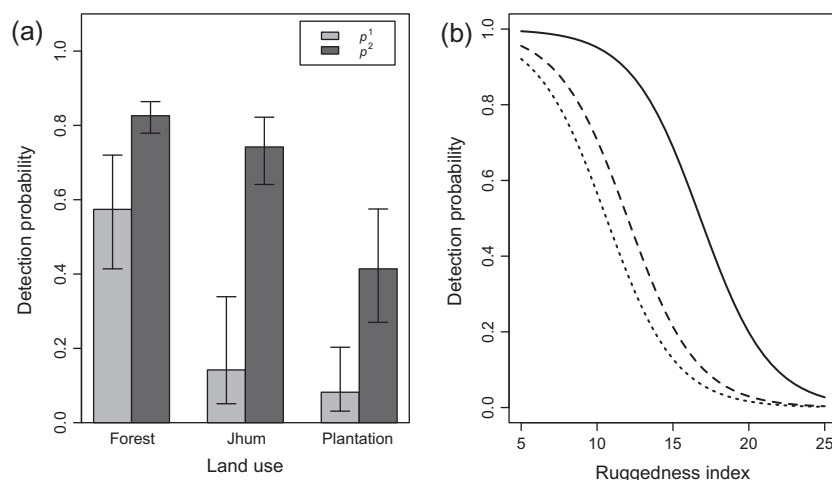


Fig. 2. (a) Probability of detecting elephant presence conditional on low-intensity and high-intensity use of a site by elephants (p^1 and p^2 , respectively) as a function of land use within the site. Shaded bars represent detection probability estimates and the error bars are 95% confidence intervals. Ruggedness for p^1 was the average value across sites. (b) The influence of ruggedness within a site on p^1 when land use was forest (solid line), jhum fallow (dashed line) and monoculture plantation (dotted line). Shaded circles represent observed elephant detections or non-detections in sampled sites.

Eupatorium adenophorum and *Mikania micrantha* in jhum fallows, and the combination of a hard and dry soil structure and thick layer of leaf litter in plantations, likely had a negative influence on detection probabilities in these land uses. Site ruggedness had a negative effect on p^1 for all land uses (Table A1; Fig. 2b). The probability that high-intensity use was observed given detection of elephant presence and that a site was in fact used with high-intensity (δ) was estimated to be 0.57 (95% CI = 0.52–0.62).

3.2. Role of community-managed forests and the importance of human presence

Asian elephants have been shown to prefer forest fragments and riparian habitats in heterogeneous landscapes (Kumar et al., 2010). Our results support this observation whereby distance to forests, including both PAs and CMFs, was the overwhelming driver of the probability of elephants using a site regardless of intensity (Ψ^1) (Table A1). The relationship between Ψ^1 and distance to forest was strongly negative ($\beta = -0.004$, 95% CI = -0.008 to -0.0005). Thus, while the probability of elephants using a site was high within a distance of 1.5 km from forests ($\Psi^1 > 0.9$), it declined sharply to nearly zero ($\Psi^1 = 0.02$) at a distance of just 3 km from the forest edge (Appendix A: Fig. A1).

The probability of high-intensity use conditional on elephant use of a site (Ψ^2), however, was best explained by the interactive effect of distance to PAs and village density (Table A1). For a given distance of a site to PAs, Ψ^2 declined with an increment in village density (Fig. 3a). While Ψ^2 remained relatively unchanged (mean $\Psi^2 = 0.84$, SE = 0.12) within a maximum distance of 5.7 km from PAs in the study system when there were no villages (Fig. 3b), it rapidly declined to near zero as village density increased (Fig. 3c–e). For example, at a mean density of 1.33 villages per km^2 , which was the maximum among sampled sites, the probability of high-intensity use dropped to negligible levels ($\Psi^2 < 0.01$) when distance to PAs exceeded 2.7 km (Fig. 3e). The strong negative influence of village density notwithstanding, Ψ^2 remained

high at approximately 0.9 within a distance of 1.5 km from the edge of PAs even with increasing village density (Fig. 3a).

Thus, our results suggest that elephants do not differentiate between PAs and CMFs in their overall space-use patterns but restrict high-intensity use to PAs. This lends support to the subsidiarity hypothesis with respect to CMFs and contradicts the hypothesis that CMFs or other wildlife-friendly land uses can substitute for PAs in the context of elephant habitat requirements. The finding that village density influenced Ψ^2 but not Ψ^1 (Table A1) suggests that although human presence does not detract from the subsidiary role of wildlife-friendly land uses, it precludes PA substitution.

3.3. Degree of subsidiarity of wildlife-friendly agriculture

We further investigated the degree of subsidiarity of other wildlife-friendly land uses in our study area using models where Ψ^1 varied with land use. Unfortunately, the models failed to converge when other parameters (i.e., p^1 , p^2 , Ψ^2) were a function of site-specific covariates. Therefore, we used a simpler model where Ψ^1 varied with land use while all other parameters were fixed to the intercept (i.e., Ψ^2 , p^1 , p^2 and δ were constant). Estimates of Ψ^1 for different land uses as per this model were: $\Psi^1_{\text{FOREST}} > 0.99$; $\Psi^1_{\text{JHUM}} = 0.94$, 95% CI = 0.52–0.99; and $\Psi^1_{\text{PLANTATION}} = 0.65$, 95% CI = 0.40–0.84. We did not separate forests into PAs and CMFs because our top model (Table A1) suggested that forests, irrespective of whether they were within PAs or CMFs, were associated with $\Psi^1 = 0.99$ (95% CI = 0.78–0.99).

The best-supported model that included land use as a covariate for Ψ^2 (Table A1: model 3) suggested an additive effect of distance to PAs and within-site land use on high-intensity use. This model further supports the finding that wildlife-friendly land uses do not substitute for PAs. As per this model, there was a strong likelihood of high-intensity use inside PAs ($\Psi^2_{\text{PA}} = 0.93$, 95% CI = 0.82–0.98) (Fig. 4a). At an average distance of 1.5 km from the outer edge of PAs, CMFs and jhum fallows were also fairly likely to support

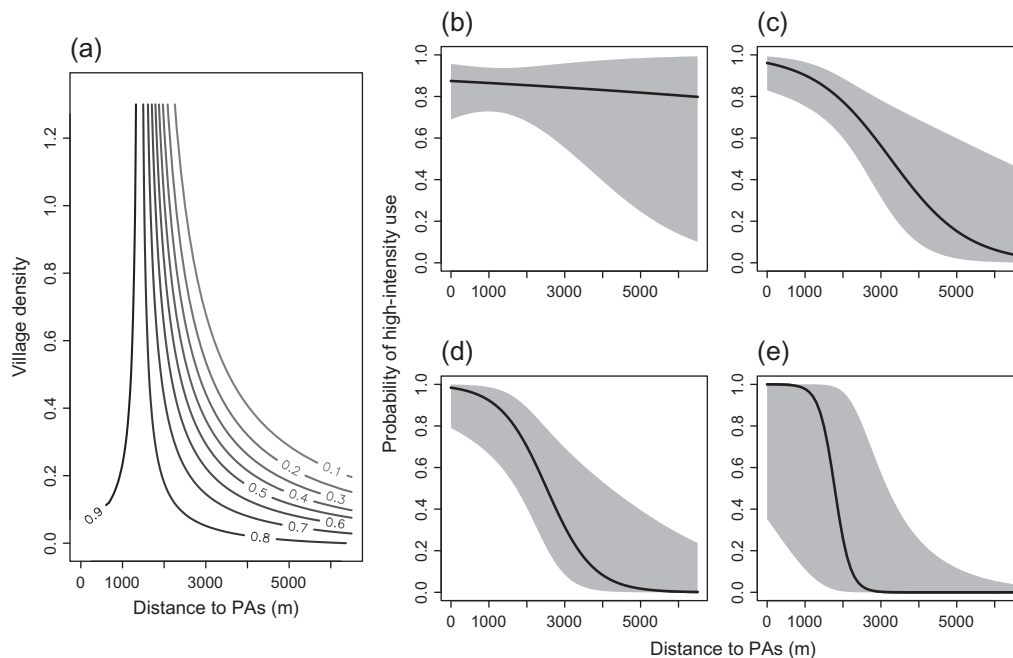


Fig. 3. Interactive effects of distance to protected areas (PAs) and village density (VD) on the probability of high-intensity use of a site conditional on elephant use of the site (Ψ^2). (a) Contour lines represent Ψ^2 estimates across the range of distance to PAs and mean village densities associated with sampled sites within the study area. Variation in estimates of Ψ^2 (solid lines) as a function of distance to PAs, are plotted for increasing village density ranging from (b) VD = 0 (first quartile), through (c) VD = 0.25 (mean), and (d) VD = 0.43 (third quartile) to (e) VD = 1.33 (maximum). VD was quantified as the number of villages per km^2 averaged across each 4 km^2 sampling site. Shaded polygons represent 95% confidence intervals.

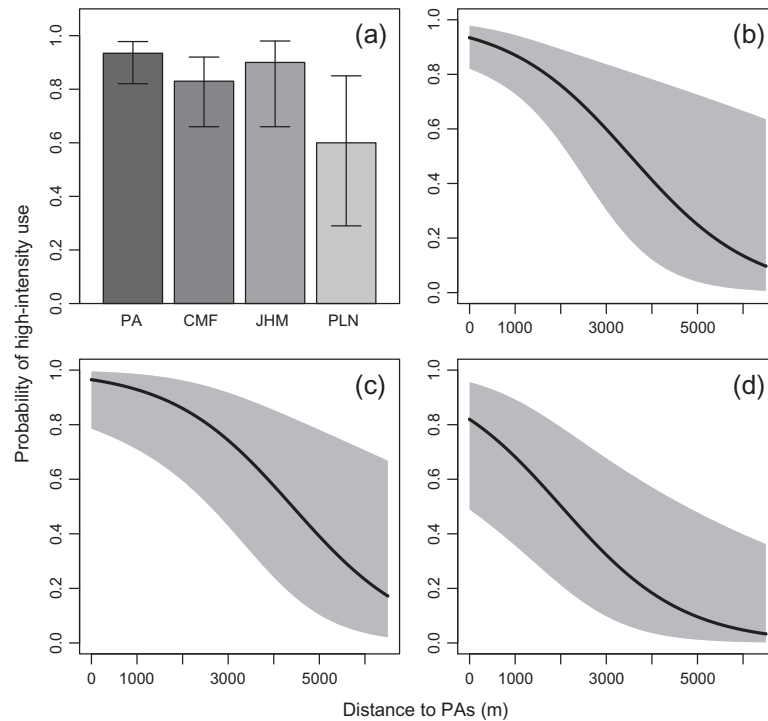


Fig. 4. Probability of high-intensity use of a site conditional on elephant use of the site (Ψ^2) as a function of land use and distance to protected areas (PAs). Estimates of Ψ^2 in community-managed forests (CMF), jhum fallows (JHM) and plantations (PLN) are presented for (a) sites at an average distance of 1.5 km from the edge of PAs (shaded bars), and with increasing distance to PAs (solid lines in b, c and d, respectively). Error bars and shaded polygons represent 95% confidence intervals.

high-intensity use by elephants conditional on elephants using these land uses ($\Psi_{\text{CMF}}^2 = 0.83$, 95% CI = 0.66–0.92; $\Psi_{\text{JHM}}^2 = 0.90$, 95% CI = 0.66–0.98) (Fig. 4a). The estimate of Ψ^2 in plantations at the same distance from PAs was lower and less precise ($\Psi^2 = 0.60$, 95% CI = 0.29–0.85). As distance to PAs increased, however, Ψ^2 decreased rapidly in all land use types (Fig. 4b–d), with the sharpest decline in plantations (Fig. 4d), and the shallowest in jhum fallows (Fig. 4c). Mean village densities per km² in CMFs, jhum and plantations were 0.20 (SE = 0.04), 0.17 (SE = 0.05) and 0.64 (SE = 0.06), respectively. Thus, it is conceivable that a ~200% higher village density in plantations compared to CMFs and jhum contributed to a considerably lower probability of high-intensity use of this land use.

4. Discussion

The purported failure of state-run exclusionary conservation is a key factor that contributed to the development of different community-based conservation approaches (Berkes, 2007). Thus, there is discussion on whether sustainable use in CMFs presents an alternative model to preservation in nationally mandated PAs (e.g., Bray et al., 2003; Ostrom and Nagendra, 2006). This view of community-based conservation, however, implicitly assumes that CMFs can substitute for PAs in terms of the benefits they offer to wildlife species of conservation concern. Our results suggest that this assumption may not be valid for species that compete with humans for resources—high-intensity space use by elephants was largely confined to PAs with CMFs playing a subsidiary conservation role. Wildlife-friendly land uses could potentially play a substitutive role for certain species or taxa (e.g., Daily et al., 2001; Ranganathan et al., 2008). But for conflict-prone species such as the Asian elephant, our results suggest that the inclusion of CMFs in conservation plans should perhaps be viewed as a strategy for augmenting habitat availability (e.g., buffer zones), while meeting sustainable livelihood needs of local communities. They could also serve as corridors or movement conduits between PAs. Further, our

results emphasize the need to evaluate the role of CMFs in landscape-scale conservation programs. Insights thus obtained can help clarify the importance of CMFs and other wildlife-friendly land uses in meeting current and future conservation targets, and can also inform global policy. For example, the Convention on Biological Diversity's Aichi Target 11 calls for at least 17% of terrestrial land to be conserved through various area-based conservation measures (Geldmann et al., 2013); the subsidiary versus substitutive roles of wildlife-friendly land uses could help determine the extent to which the expansion of these conservation lands would need to be within PAs.

We recognize that an experimental study would have provided stronger inference, and thus would have allowed us to better assess the conservation potential of land uses independent of their spatial location and context. Unfortunately, true experiments at moderate to large spatial scales are rarely possible in real-world systems, and observational studies such as ours do provide important insights. Inferences specific to our study system could also be strengthened by data collected from other seasons and over a longer time frame. Finally, we note that research focusing on quantifying demographic parameters in different land uses over time could provide useful insight into the dynamics and viability of wildlife populations. Nevertheless, our observational study permitted inferences about the hypotheses of interest, and we believe that it makes an important contribution to our overall understanding of the conservation potential of wildlife-friendly land uses in heterogeneous, human-dominated landscapes.

Land sharing through wildlife-friendly farming can be a suitable conservation strategy for adaptable species that can persist in a 'soft-matrix' landscape (Green et al., 2005; Fischer et al., 2008). For generalist species such as the Asian elephant, (Sukumar, 2003), wildlife-friendly farming therefore has the potential to play a subsidiary role to PAs, providing secondary habitat to the species. We tested this hypothesis in the context of jhum, a wildlife-friendly farming technique, and evaluated its conservation value

relative to intensive agriculture in monoculture plantations. Both Ψ^1 and Ψ^2 were $\sim 30\%$ greater in jhum fallows than plantations, suggesting that the former is the more elephant-friendly land use. Jhum fallows are often characterized by grasses, that at a later stage of succession, are replaced by dense bamboo culms (Raman et al., 1998). Both grasses and bamboo are valuable resources for elephants (Sukumar, 2003), and their prevalence likely attracts elephants to these fallows. It is important to note, however, that high-intensity use of these agricultural areas was contingent on elephant presence, which was strongly dependent on proximity to forests within PAs or CMFs (Table A1 and Fig. A1). The importance of neighboring forests has been highlighted by other studies investigating the conservation value of wildlife-friendly farming (Raman, 2001; Bali et al., 2007), and their maintenance will likely hold the key to successful elephant conservation within heterogeneous landscapes.

Human-wildlife coexistence, particularly in the context of conflict-prone megafauna, has been the subject of much research (Woodroffe et al., 2005; Carter et al., 2012) and recent debate (Goswami et al., 2013; Harihar et al., 2013; Karanth et al., 2013). Coexistence is generally difficult to achieve because of competing, and often conflicting, resource needs of large mammals and people (Woodroffe et al., 2005), and the resultant decline in large mammal populations in the face of a burgeoning human footprint (Brashares et al., 2001; Cardillo et al., 2004). Our results clearly demonstrate this contention, whereby the substitutive role of wildlife-friendly land uses was mediated by human presence. Thus, even though CMFs and wildlife-friendly farming might 'soften' the matrix between PAs in heterogeneous landscapes, threats imposed by prevalent human populations can substantially limit species like the Asian elephant from using the matrix. This apparent avoidance response to a human-dominated "landscape of fear" is analogous to observed species behavioral responses to human disturbance (Ciuti et al., 2012). Therefore, the mitigation of anthropogenic threats outside PAs can substantially contribute to realizing the conservation potential of wildlife-friendly land uses. For example, the adoption of conflict mitigation measures (reviewed in Treves et al., 2009) would likely be important in scenarios such as ours, where regular human–elephant conflicts outside PAs (Datta-Roy et al., 2009) potentially limits the conservation effectiveness of existing wildlife-friendly land uses.

The currency for conservation is increasingly transitioning towards multiple-use, heterogeneous landscapes to meet the habitat requirements of wide-ranging species (Sanderson et al., 2002b). Conservation investment and planning in lands outside PAs clearly need to be based on empirical evidence vis-à-vis their conservation value (Sutherland et al., 2004; Ferraro and Pattanayak, 2006). Here, we highlight the potential for CMFs and wildlife-friendly agriculture to strengthen the conservation benefits offered by PAs to wide-ranging species like the Asian elephant. However, our results emphasize that these wildlife-friendly land uses do not substitute for PAs in their ability to support viable elephant populations. We show that the strong presence of humans outside PAs has an overriding negative influence on the conservation potential of CMFs and wildlife-friendly farming. Therefore, global conservation policy not only needs to recognize the multiple roles that wildlife-friendly land uses can fulfill, but also their conservation limitations. This holds the key to effecting successful conservation initiatives in human-dominated landscapes.

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Appendix A. Supplementary material

Top-ranked models used to assess probabilities of elephant detection and site use; and probability of elephants using a site regardless of intensity (Ψ^1) as a function of distance to forests. Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.biocon.2014.06.013>.

References

- Adams, W.M., Aveling, R., Brockington, D., Dickson, B., Elliott, J., Hutton, J., Roe, D., Vira, B., Wolmer, W., 2004. Biodiversity conservation and the eradication of poverty. *Science* 306, 1146–1149.
- Bali, A., Kumar, A., Krishnaswamy, J., 2007. The mammalian communities in coffee plantations around a protected area in the Western Ghats, India. *Biol. Conserv.* 139, 93–102.
- Balmford, A., Green, R., Phalan, B., 2012. What conservationists need to know about farming. *Proc. R. Soc. B* 279, 2714–2724.
- Berkes, F., 2007. Community-based conservation in a globalized world. *Proc. Natl. Acad. Sci. U.S.A.* 104, 15188–15193.
- Blake, S., Hedges, S., 2004. Sinking the flagship: the case of forest elephants in Asia and Africa. *Conserv. Biol.* 18, 1191–1202.
- Blake, S., Strindberg, S., Boudjan, P., Makombo, C., Bila-Isia, I., Ilambu, O., Grossmann, F., Bene-Bene, L., de Semboli, B., Mbenzo, V., S'hwá, D., Bayogo, R., Williamson, L., Fay, M., Hart, J., Maisels, F., 2007. Forest elephant crisis in the Congo Basin. *PLoS Biol.* 5, e111.
- Brashares, J.S., Arcece, P., Sam, M.K., 2001. Human demography and reserve size predict wildlife extinction in West Africa. *Proc. R. Soc. B* 268, 2473–2478.
- Bray, D.B., Merino-Pérez, L., Negreros-Castillo, P., Segura-Warnholtz, G., Torres-Rojo, J.M., Vester, H.F.M., 2003. Mexico's community-managed forests as a global model for sustainable landscapes. *Conserv. Biol.* 17, 672–677.
- Bruner, A.G., Gullison, R.E., Rice, R.E., da Fonseca, G.A.B., 2001. Effectiveness of parks in protecting tropical biodiversity. *Science* 291, 125–128.
- Burnham, K.P., Anderson, D.R., 2002. *Model Selection and Inference: A Practical Information-Theoretic Approach*. 2nd ed. Springer-Verlag, New York, NY, USA.
- Cardillo, M., Mace, G.M., Jones, K.E., Bielby, J., Bininda-Emonds, O.R.P., Sechrest, W., Orme, C.D.L., Purvis, A., 2005. Multiple causes of high extinction risk in large mammal species. *Science* 309, 1239–1241.
- Cardillo, M., Purvis, A., Sechrest, W., Gittleman, J.L., Bielby, J., Mace, G.M., 2004. Human population density and extinction risk in the world's carnivores. *PLoS Biol.* 2, e197.
- Carter, N.H., Shrestha, B.K., Karki, J.B., Pradhan, N.M.B., Liu, J., 2012. Coexistence between wildlife and humans at fine spatial scales. *Proc. Natl. Acad. Sci. U.S.A.* 109, 15360–15365.
- Charnov, E.L., 1976. Optimal foraging, the marginal value theorem. *Theor. Popul. Biol.* 9, 129–136.
- Ciuti, S., Northrup, J.M., Muhly, T.B., Simi, S., Musiani, M., Pitt, J.A., Boyce, M.S., 2012. Effects of humans on behaviour of wildlife exceed those of natural predators in a landscape of fear. *PLoS ONE* 7, e50611.
- Daily, G.C., Ehrlich, P.R., Sanchez-Azofeifa, G.A., 2001. Countryside biogeography: use of human-dominated habitats by the avifauna of southern Costa Rica. *Ecol. Appl.* 11, 1–13.
- Datta-Roy, A., Ved, N., Williams, A.C., 2009. Participatory elephant monitoring in South Garo Hills: efficacy and utility in a human-animal conflict scenario. *Trop. Ecol.* 50, 163–171.
- Ehrlich, P.R., Pringle, R.M., 2008. Where does biodiversity go here? A grim business-as-usual forecast and a hopeful portfolio of partial solutions. *Proc. Natl. Acad. Sci. U.S.A.* 105, 11579–11586.
- Fernando, P., Wikramanayake, E.D., Janaka, H.K., Jayasinghe, L.K.A., Gunawardena, M., Kotagama, S.W., Weerakoon, D., Pastorini, J., 2008. Ranging behavior of the Asian elephant in Sri Lanka. *Mamm. Biol.* 73, 2–13.
- Ferraro, P.J., 2001. Global habitat protection: limitations of development interventions and a role for conservation performance payments. *Conserv. Biol.* 15, 990–1000.
- Ferraro, P.J., Pattanayak, S.K., 2006. Money for nothing? A call for empirical evaluation of biodiversity conservation investments. *PLoS Biol.* 4, 482–488.

- Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J., Lindenmayer, D.B., Manning, A.D., Mooney, H.A., Pejchar, L., Ranganathan, J., Tallis, H., 2008. Should agricultural policies encourage land sparing or wildlife-friendly farming? *Front. Ecol. Environ.* 6, 380–385.
- Geldmann, J., Barnes, M., Coad, L., Craigie, I.D., Hockings, M., Burgess, N.D., 2013. Effectiveness of terrestrial protected areas in reducing habitat loss and population declines. *Biol. Conserv.* 161, 230–238.
- Goswami, V.R., Vasudev, D., Karnad, D., Krishna, Y.C., Krishnadas, M., Pariwakam, M., Nair, T., Andheria, A., Sridhara, S., Siddiqui, I., 2013. Conflict of human-wildlife coexistence. *Proc. Natl. Acad. Sci. U.S.A.* 110, E108.
- Green, R.E., Cornell, S.J., Scharlemann, J.P.W., Balmford, A., 2005. Farming and the fate of wild nature. *Science* 307, 550–555.
- Hansen, A., DeFries, R., 2007. Ecological mechanisms linking protected areas to surrounding lands. *Ecol. Appl.* 17, 974–988.
- Harihar, A., Chanchani, P., Sharma, R.K., Vattakaven, J., Gubbi, S., Pandav, B., Noon, B., 2013. Conflating “co-occurrence” with “coexistence”. *Proc. Natl. Acad. Sci. U.S.A.* 110, E109.
- Karanth, K.K., Nichols, J.D., Karanth, K.U., Hines, J.E., Christensen Jr., N.L., 2010. The shrinking ark: patterns of large mammal extinctions in India. *Proc. R. Soc. B* 277, 1971–1979.
- Karanth, K.U., Gopalaswamy, A.M., Karanth, K.K., Goodrich, J., Seidensticker, J., Robinson, J.G., 2013. Sinks as saviors: Why flawed inference cannot assist tiger recovery. *Proc. Natl. Acad. Sci. U.S.A.* 110, E110.
- Kendall, W.L., White, G.C., 2009. A cautionary note on substituting spatial subunits for repeated temporal sampling in studies of site occupancy. *J. Appl. Ecol.* 46, 1182–1188.
- Kinnaird, M.F., O'Brien, T.G., 2012. Effects of private-land use, livestock management, and human tolerance on diversity, distribution, and abundance of large African mammals. *Conserv. Biol.* 26, 1026–1039.
- Koh, L.P., 2008. Can oil palm plantations be made more hospitable for forest butterflies and birds? *J. Appl. Ecol.* 45, 1002–1009.
- Kumar, M.A., Mudappa, D., Raman, T.R.S., 2010. Asian elephant *Elephas maximus* habitat use and ranging in fragmented rainforest and plantations in the Anamalai Hills, India. *Trop. Conserv. Sc.* 3, 143–158.
- Laake, J.L., Rexstad, E.A., 2007. RMark. In Program MARK: a gentle introduction. In: Cooch, E.G., White, G.C. (Eds.), <<http://www.phidot.org/software/mark/docs/book>>.
- Lima, S.L., Bednekoff, P.A., 1999. Temporal variation in danger drives antipredator behavior: the predation risk allocation hypothesis. *Am. Nat.* 153, 649–659.
- MacKenzie, D.I., 2005. What are the issues with presence-absence data for wildlife managers? *J. Wildl. Manage.* 69, 849–860.
- Mackenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L.L., Hines, J.E., 2006. *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence* Elsevier San Diego.
- Margules, C., Pressey, R., 2000. Systematic conservation planning. *Nature* 405, 243–253.
- Martin, J., Chamaillé-James, S., Nichols, J.D., Fritz, H., Hines, J.E., Fonnesbeck, C.J., MacKenzie, D., Bailey, L.L., 2010. Simultaneous modeling of habitat suitability, occupancy, and relative abundance: African elephants in Zimbabwe. *Ecol. Appl.* 20, 1173–1182.
- Nichols, J.D., Hines, J.E., MacKenzie, D.I., Seamans, M.E., Gutierrez, R.J., 2007. Occupancy estimation and modeling with multiple states and state uncertainty. *Ecology* 88, 1395–1400.
- Norris, K., 2008. Agriculture and biodiversity conservation: opportunity knocks. *Conserv. Lett.* 1, 2–11.
- Ostrom, E., Nagendra, H., 2006. Insights on linking forests, trees, and people from the air, on the ground, and in the laboratory. *Proc. Natl. Acad. Sci. U.S.A.* 103, 19224–19231.
- R Development Core Team, 2013. *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raman, T.R.S., 2001. Effect of slash-and-burn shifting cultivation on rainforest birds in Mizoram, northeast India. *Conserv. Biol.* 15, 685–698.
- Raman, T.R.S., Rawat, G.S., Johnsingh, A.J.T., 1998. Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *J. Appl. Ecol.* 35, 214–231.
- Ranganathan, J., Daniels, R.J.R., Chandran, M.D.S., Ehrlich, P.R., Daily, G.C., 2008. Sustaining biodiversity in ancient tropical countryside. *Proc. Natl. Acad. Sci. U.S.A.* 105, 17852–17854.
- Riley, S.J., DeGloria, S.D., Elliot, R., 1999. A terrain ruggedness index that quantifies topographic heterogeneity. *Intermt. J. Sci.* 5, 23–27.
- Salafsky, N., Cauley, H., Balachander, G., Cordes, B., Parks, J., Margoluis, C., Bhatt, S., Encarnacion, C., Russel, D., Margoluis, R., 2001. A systematic test of an enterprise strategy for community-based biodiversity conservation. *Conserv. Biol.* 15, 1585–1595.
- Sanderson, E.W., Jaiteh, M., Levy, M.A., Redford, K.H., Wannebo, A.V., Woolmer, G., 2002a. The human footprint and the last of the wild. *Bioscience* 52, 891–904.
- Sanderson, E.W., Redford, K.H., Vedder, A., Coppolillo, P.B., Ward, S.E., 2002b. A conceptual model for conservation planning based on landscape species requirements. *Landscape Urban Plann.* 58, 41–56.
- Stokes, E.J., Strindberg, S., Bakabana, P.C., Elkan, P.W., Iyenguet, F.C., Madzoké, B., Malanda, G.A.F., Mowawa, B.S., Moukoumbou, C., Ouakabadio, F.K., Rainey, H.J., 2010. Monitoring great ape and elephant abundance at large spatial scales: measuring effectiveness of a conservation landscape. *PLoS ONE* 5, e10294.
- Sukumar, R., 2003. *The Living Elephants: Evolutionary Ecology, Behavior and Conservation*. Oxford University Press, New York.
- Sutherland, W.J., Pullin, A.S., Dolman, P.M., Knight, T.M., 2004. The need for evidence-based conservation. *Trends Ecol. Evol.* 19, 305–308.
- Treves, A., Wallace, R.B., White, S., 2009. Participatory planning of interventions to mitigate human-wildlife conflicts. *Conserv. Biol.* 23, 1577–1587.
- Western, D., Russel, S., Cuthill, I., 2009. The status of wildlife in protected areas compared to non-protected areas of Kenya. *PLoS ONE* 4, e6140.
- White, G.C., Burnham, K.P., 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Supplement), 120–138.
- Williams, A.C., Johnsingh, A.J.T., Krausman, P.R., 2001. Elephant-human conflicts in Rajaji National Park, northwestern India. *Wild. Soc. Bull.* 29, 1097–1104.
- Wittemyer, G., Elsen, P., Bean, W.T., Burton, A.C.O., Brashares, J.S., 2008. Accelerated human population growth at protected area edges. *Science* 321, 123–126.
- Woodroffe, R., Ginsberg, J.R., 1998. Edge effects and the extinction of populations inside protected areas. *Science* 280, 2126–2128.
- Woodroffe, R., Thirgood, S., Rabinowitz, A., 2005. *People and Wildlife: Conflict or Coexistence?* Cambridge University Press, Cambridge, UK.

Appendix A. Supplementary material

Table A1. Top-ranked models used to assess probabilities of elephant detection and site use

Model	K	AIC _c	ΔAIC _c	w _i
<i>Detection Probability</i>				
$\Psi^1(\text{FD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\cdot)$	12	1184.76	0.00	0.30
$\Psi^1(\text{FD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU} + \text{RG}) \delta(\cdot)$	13	1186.30	1.54	0.14
$\Psi^1(\text{FD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\text{RG})$	13	1186.59	1.83	0.12
$\Psi^1(\text{FD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\text{LU})$	14	1186.96	2.20	0.10
$\Psi^1(\text{FD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\text{LU} \times \text{RG})$	17	1187.55	2.80	0.07
$\Psi^1(\text{FD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU} + \text{RG}) \delta(\text{RG})$	14	1188.20	3.44	0.05
<i>Site Use Probability</i>				
$\Psi^1(\text{FD}) \Psi^2(\text{PAD} \times \text{VD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\cdot)$	14	1181.61	0.00	0.53
$\Psi^1(\text{FD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\cdot)$	12	1184.76	3.15	0.11
$\Psi^1(\text{FD}) \Psi^2(\text{LU} + \text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\cdot)$	13	1184.97	3.36	0.10
$\Psi^1(\text{FD}) \Psi^2(\text{PAD} + \text{VD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\cdot)$	13	1185.85	4.24	0.06
$\Psi^1(\text{FD} + \text{VD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\cdot)$	13	1186.21	4.60	0.05
$\Psi^1(\text{FD} \times \text{VD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\cdot)$	14	1186.97	5.36	0.04

Probabilities of detecting low and high intensity use (p^1 and p^2 , respectively), and the probability of observing high intensity use given elephant detection and actual high intensity use of a site (δ), were modeled to vary with land use (LU), ruggedness (RG) and spatial replicate. Covariates for the probability of site use (Ψ^1) and the probability of high intensity

site use (Ψ^2) included distance to forests (FD), distance to PAs (PAD), village density (VD) and land use. Covariate structure for p^1 , p^2 and δ were fixed to the top detection probability model to estimate site use probability; Ψ^1 and Ψ^2 were modeled as a function of the same covariates as for detection probability, as well as their additive and interactive effects. The table includes the top six models from the two respective analyses. AIC_c represents Akaike's information criterion corrected for small sample size; differences in AIC_c between each model and the most parsimonious model are denoted by ΔAIC_c . K is the number of parameters and w_i is the AIC_c model weight. Model notation follows that of linear models: $a \times b$ includes additive and interactive effects of a and b , whereas $a + b$ includes additive effects only. A model where parameter a was held constant is represented by $a(.)$. AIC_c of intercept-only models in (A) i.e., $p^1(.) p^2(.) \delta(.)$ and (B) i.e., $\Psi^1(.) \Psi^2(.)$ were 1233.61 and 1217.1, respectively.

Table A2. Top-ranked multistate occupancy models used to evaluate elephant site use

Model	K	AIC _c	ΔAIC _c	w _i
<i>Analysis Set 2</i>				
$\Psi^1(\text{FD}) \Psi^2(\text{PAD} \times \text{VD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU} + \text{RG}) \delta(\cdot)$	15	1183.25	0.00	0.53
$\Psi^1(\text{FD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU} + \text{RG}) \delta(\cdot)$	13	1186.30	3.05	0.11
$\Psi^1(\text{FD}) \Psi^2(\text{LU} + \text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU} + \text{RG}) \delta(\cdot)$	14	1186.64	3.39	0.10
$\Psi^1(\text{FD}) \Psi^2(\text{PAD} + \text{VD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU} + \text{RG}) \delta(\cdot)$	14	1187.46	4.21	0.06
$\Psi^1(\text{FD} + \text{VD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU} + \text{RG}) \delta(\cdot)$	14	1187.81	4.56	0.05
$\Psi^1(\text{FD} \times \text{VD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU} + \text{RG}) \delta(\cdot)$	15	1188.63	5.38	0.04
<i>Analysis Set 3</i>				
$\Psi^1(\text{FD}) \Psi^2(\text{PAD} \times \text{VD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\text{RG})$	15	1183.61	0.00	0.52
$\Psi^1(\text{FD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\text{RG})$	13	1186.59	2.98	0.12
$\Psi^1(\text{FD}) \Psi^2(\text{LU} + \text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\text{RG})$	14	1186.90	3.29	0.10
$\Psi^1(\text{FD}) \Psi^2(\text{PAD} + \text{VD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\text{RG})$	14	1187.75	4.14	0.07
$\Psi^1(\text{FD} + \text{VD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\text{RG})$	14	1188.11	4.50	0.05
$\Psi^1(\text{FD} \times \text{VD}) \Psi^2(\text{PAD}) p^1(\text{LU} + \text{RG}) p^2(\text{LU}) \delta(\text{RG})$	15	1188.92	5.31	0.04

Probabilities of detecting low and high intensity use (p^1 and p^2 , respectively), and the probability of observing high intensity use given elephant detection and actual high intensity use of a site (δ), were fixed to the second model in Table A1 (Analysis Set 2) and the third model in Table A1 (Analysis Set 3), respectively. Covariates for the probability of site use (Ψ^1) and the probability of high intensity site use (Ψ^2) included the independent, as well as additive and interactive effects of distance to forests (FD), distance to PAs (PAD), village

density (VD) and land use (LU). Both sets include the top six models from the two respective analyses. AIC_c represents Akaike's information criterion corrected for small sample size; differences in AIC_c between each model and the most parsimonious model are denoted by ΔAIC_c . K is the number of parameters and w_i is the AIC_c model weight. Model notation follows that of linear models: $a \times b$ includes additive and interactive effects of a and b , whereas $a + b$ includes additive effects only. A model where parameter a was held constant is represented by $a(.)$.

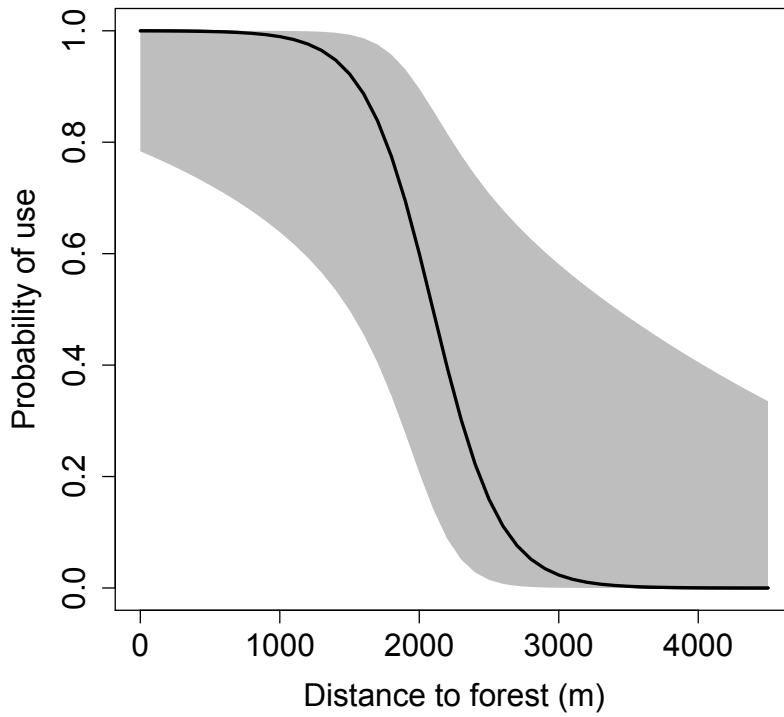


Fig. A1. Overall probability of elephants using a site, regardless of intensity (Ψ^1), as distance to forests (within protected areas or community-managed forests) increases. The solid line represents Ψ^1 estimates, and shaded polygon, the 95% confidence interval around these estimates. Shaded circles represent observed elephant detections or non-detections in sampled sites.