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# Identifying realistic recovery targets and conservation actions for tigers in a human-dominated landscape using spatially explicit densities of wild prey and their determinants

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## ABSTRACT

**Aim** Setting realistic population targets and identifying actions for site and landscape-level recovery plans are critical for achieving the global target of doubling wild tiger numbers by 2022. Here, we estimate the spatially explicit densities of wild ungulate prey across a gradient of disturbances in two disjunct tiger habitat blocks (THBs) covering 5212 km$^2$, to evaluate landscape-wide conditions for tigers and identify opportunities and specific actions for recovery.

**Location** Western Terai Arc Landscape, India.

**Methods** Data generated from 96 line transects in 15 systematically selected geographical cells (166.5 km$^2$) were used to estimate spatially explicit densities of six wild ungulate prey species at a fine scale (1 km$^2$). Employing distance-based density surface models, we derived species-specific estimates within three major forest land management categories (inviolate protected areas (PA), PAs with settlements and multiple-use forests). By scaling estimated prey densities using an established relationship, we predicted the carrying capacity for tigers within each THB.

**Results** Species-specific responses of the six wild ungulates to natural-habitat and anthropogenic covariates indicated the need for targeted prey recovery strategies. Inviolate PAs supported the highest prey densities compared with PAs with settlements and multiple-use forests, and specifically benefited the principal tiger prey species (chital *Axis axis* and sambar *Rusa unicolor*). The estimated mean prey density of 35.16 ($\pm$5.67) individuals per km$^2$ can potentially support 82 (62–106) and 299 (225–377) tigers across THB I and THB II, which currently support 2 (2–7) and 225 (199–256) tigers, respectively. This suggests a potential *c.* 68% increase in population size given existing prey abundances. Finally, while THB I represents a potential tiger recovery site given adequate prey, PAs where resettlement of pastoralists is underway represent potential prey recovery sites in THB II.

**Main conclusions** This systematic approach of setting realistic population targets and prioritizing spatially explicit recovery strategies should aid in developing effective landscape conservation plans towards achieving global tiger conservation targets.

**Keywords**
Anthropogenic disturbance, carrying capacity, density surface modelling, inviolate, multiple-use forests, protected areas.

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## INTRODUCTION

Wild tiger *Panthera tigris* populations have reduced to < 3600 and occupy a mere 7% of their historic range (Dinerstein *et al.*, 2007). Recognizing this decline, heads of the 13 range countries convened at the Tiger Summit in 2010 and set an aspirational goal of doubling the population of wild tigers by the year 2022 (GTRP, 2010). While large-scale initiatives such as this are among the most effective responses to guide conservation investment, they do not identify targets and actions for site-level conservation (Eken *et al.*, 2004). Strategies to recover wild tiger populations (Walston *et al.*, 2010; Wikramanayake *et al.*, 2011), call for securing existing source sites through enhanced protection, maintaining landscape-level connectivity between these source sites and identifying opportunities to expand existing breeding populations within the identified tiger conservation landscapes (TCLs; Sanderson *et al.*, 2006). However, prioritizing investments towards initiating such recoveries should be evidence-based, requiring site-specific assessments of the population size each TCL is capable of supporting (O'Kelly *et al.*, 2012).

Current recovery targets (e.g. Wikramanayake *et al.*, 2011) are set by estimates of potential tiger densities assigned to biomes/major habitat types and do not account for heterogeneity in habitat features and management regimes within landscapes. However, with prey availability being a key determinant of carnivore densities (Fuller & Sievert, 2001; Carbone & Gittleman, 2002; Karanth *et al.*, 2004; Hayward *et al.*, 2007), estimating prey abundances across a landscape of multiple uses constitutes a critical first step in evaluating the recovery potential of TCLs, identifying potential source sites and suggesting appropriate interventions such as enhanced protection, prey augmentation or translocation of tigers to meet conservation targets (Dinerstein *et al.*, 2006).

Wild ungulates, which constitute the principal prey of tigers, are becoming increasingly threatened by habitat destruction and degradation (Macdonald, 2001; Ceballos *et al.*, 2005). Threats to these prey populations are exacerbated by being prized for meat for human consumption (Corlett, 2007) and their conflict with agriculturalists due to crop raiding (Madhusudan & Mishra, 2003; Cardillo *et al.*, 2005). Through most of the tiger's range in the tropics of South Asia population dynamics of these species remain understudied, with most studies presenting site-specific [primarily within protected areas (PAs)] estimates of wild ungulate densities and/or biomass to assess conditions for mammalian carnivores (e.g. Harihar *et al.*, 2009a; Wegge & Storaas, 2009; Gray *et al.*, 2012; O'Kelly *et al.*, 2012). While analyses using site-specific density estimates from within inviolate reserves can inform us about how prey densities vary across ecoclimatic gradients or major habitat types, which are excluded from disturbances (e.g. Karanth *et al.*, 2004), these estimates are not very useful at the scale of individual TCLs, which require managing ungulate populations across a gradient of protection, habitats and anthropogenic

disturbances. Furthermore, with prey assemblages consisting of species ranging across a wide spectrum of body sizes and habits, these species-specific traits are expected to interact with habitat and anthropogenic factors to determine their spatially explicit densities (Cromsigt *et al.*, 2009; Pettorelli *et al.*, 2009; Ogutu *et al.*, 2010; Bhola *et al.*, 2012). Hence, understanding how prey densities vary across a landscape in response to environmental and anthropogenic factors and existing land management types is essential for effectively managing prey populations to meet global conservation targets for tigers.

In this study, we estimate the spatially explicit densities of an assemblage of wild ungulates across protected and multiple-use forests in two disjunct tiger conservation units (Tiger Habitat Blocks; THB I & II) within the western Terai Arc Landscape (TAL), to evaluate landscape-wide conditions for tigers and identify opportunities for recovery, consistent with global conservation targets. To achieve this objective, we (1) estimate the spatially explicit densities of six wild ungulates at a fine spatial scale (1 km$^2$), while accounting for imperfect detection and modelling factors influencing their distribution and abundance; (2) derive well-stratified estimates of prey within three major forest land management categories (inviolate PAs, PAs with settlements and multiple-use forests) across the two THBs; and (3) predict the density and number of tigers that could be supported within each of the THBs by scaling the estimated prey densities using existing empirical models (Karanth *et al.*, 2004).

## METHODS

### Study area

The western TAL, ranging in elevation from 200 to 2500 m, is primarily rugged and the natural forests can be categorized as northern Indian moist-deciduous and northern tropical dry-deciduous forests (Champion & Seth, 1968). Fringed by terrace fields in the hills and extensive agriculture and horticulture along the plains, this linear forested landscape is characterized by multiple resource-use pressures. In addition to facing disturbances such as resource extraction and hunting from rural and semi-urban settlements along the forest edges, 82% of the forested landscape, including parts of the two designated PAs (Rajaji National Park; RNP and Corbett Tiger Reserve; CTR), are inhabited by Gujjars. This pastoralist community resides within these forests and traditionally graze their livestock, cut grass and lop branches off trees for leaves to provide fodder to their livestock holdings (Harihar & Pandav, 2012; Harihar *et al.*, 2014). Administratively, the landscape is managed under 10 multiple-use forest divisions and two PAs (see Figure S1 in Appendix S1 in Supporting Information).

### Wild ungulate prey assemblage

In this study, we investigate patterns of density distribution of six wild ungulates; the red muntjac *Muntiacus muntjak*,

Himalayan goral *Naemorhedus goral*, wild pig *Sus scrofa*, chital *Axis axis*, sambar *Rusa unicolor* and nilgai *Boselaphus tragocamelus*. As this assemblage represents a range of body size and dietary groups (Table S1), it is expected that the interaction between these critical biological traits and the distribution of biotic and abiotic factors would influence species-specific distribution and abundances (Cromsigt *et al.*, 2009; Pettorelli *et al.*, 2009). In human-impacted systems, such as the western TAL, the realized distribution and abundance of these ungulates are expected to be altered owing to the effects of anthropogenic influences on habitats or populations (Ogutu *et al.*, 2010; Bhola *et al.*, 2012). In particular, resource limitation (mediated through edge effects or livestock competition) is expected to negatively affect species associated with forested habitats (chital, sambar, red muntjac and goral), while wild pig (adaptable to human modified environments) and nilgai (being culturally tolerated) are capable of persisting in human-dominated landscapes (Karanth *et al.*, 2010). Furthermore, illegal hunting is expected to primarily affect larger species (sambar and chital), whereas smaller or more resilient species (red muntjac and wild pig) can often persist but at lower densities (Steinmetz *et al.*, 2010). Drawing on these generalities, we estimate spatially explicit densities from distance-based detection data collected using a robust survey design and modelled in relation to species-specific habitat affinities and anthropogenic effects on populations.

## Study design and field methods

The 57 geographical grid cells (166.5 km² each) initially demarcated to estimate the occupancy of tigers in the western TAL (Harihar & Pandav, 2012) were used as the basis for sampling. Using a multicriteria approach, a subsample of these grids was selected to conduct field surveys. Cells with < 25% forest cover (11 cells) were excluded and *c.* 33% (15 cells) were chosen to represent the entire gradient of wild prey and disturbance indices previously identified (Harihar & Pandav, 2012). The selected cells were further divided into 16, ten km² subcells of which eight were chosen in a checker-board fashion and one line transect of *c.* 2 km each was laid within each of the 96 selected subcells (Fig. S2). For the purpose of analyses, line transects were subdivided into equal segments of 250 m.

All field surveys were conducted during the 'cool dry season' (November 2010 to March 2011) by four experienced surveyors. Two teams of two observers each carried out surveys simultaneously in the mornings (between 06:15 and 09:30 hours) in a 'single-observer' mode. Each line transect was walked twice. Species, group size, sighting angle (measured using a hand-held compass) and sighting distance (measured by a laser range-finder) were recorded and detections assigned to spatially referenced segments during the field surveys.

## Estimating spatially explicit prey densities

To generate reliable design-based extrapolations of densities, species counts (obtained along segmented transects) were modelled as a function of spatially explicit habitat covariates using generalized additive models (GAMs) (Hastie & Tibshirani, 1990; Miller *et al.*, 2013), incorporating the effective area of the segment (derived from modelling the distance-based detection function) as an offset term in a joint modelling process (density surface modelling; DSM) executed in R (version 3.0.1: http://www.r-project.org) using package *dsm* (Miller *et al.*, 2013).

To account for variations in body sizes and grouping behaviour of the target species (Table S1), we modelled the smooth function of perpendicular distances from line transects specific to each species, using uniform key with cosine adjustments, half-normal key with cosine or Hermite polynomial adjustments and hazard-rate key with simple polynomial adjustments as candidate forms of detection function. Data were examined for signs of evasive movement and peaking at great distance from the transect and the need for truncation was tested by examining the effect of removing 5–10% farthest sightings on estimates of the probability density function evaluated on the line of sighting [$f(0)$]. Following this, distance data were reclassed so as to ensure a reliable fit of detection functions using Akaike Information Criterion (AIC) and goodness-of-fit (GOF-p) tests to judge the fit of the model (Buckland *et al.*, 2001).

For the spatial modelling process, we used the 'count method' (Hedley & Buckland, 2004) and incorporated the segment area derived from the modelling procedure detailed above, as the offset term. Counts of individuals (per species) obtained along segmented transects were modelled as a function of segment-specific covariates indexing habitat variables. As our modelling aim was to predict density over space by identifying factors influencing abundance, we chose covariates based on their potential predictive capability and availability across the entire survey (Table 1). The geographical covariates consisted of two terrain parameters (elevation; *Elev* and Topographic Ruggedness Index; *TRI*), two variables indexing vegetation characteristics (Normalized Difference Vegetation Index; *NDVI* and seasonality in NDVI; *NDVI-CV*) and two anthropogenic factors (distance from forest settlements; *ForSettDist* and distance from forest edge; *ForEdgeDist*). In addition to using these covariates as additive influencers of density, selected two-way interactions between covariates were also considered. The interactions of interest were (1) *NDVI*: *ForSettDist*, (2) *NDVI*: *ForEdgeDist* and (3) *ForSettDist*: *ForEdgeDist*, which primarily indexed the interactive effects of anthropogenic variables on vegetation (1 & 2) or the combined effects of anthropogenic influences on species (3). Models were fit using forward–backward covariate selection, in which each forward step was followed by a backward step to remove any variables in the model that were no longer significant (Pearce & Ferrier, 2000). Variables were retained in the model if their removal caused a

**Table 1** Predictor variables used in the generalized additive models to estimate spatially explicit densities of ungulates

| Variable | Description |
| --- | --- |
| Elevation (*Elev*) | Derived from ground elevation data at 90-m resolution from the Shuttle Radar Topographic Mission dataset (SRTM; Jarvis *et al.*, 2008) |
| Topographic Ruggedness Index (*TRI*) | Computed using the SRTM digital elevation model (Riley *et al.*, 1999) |
| Normalized Difference Vegetation Index (*NDVI*) | Derived from Landsat 4–5 Thematic Mapper imagery (30 m × 30 m resolution) of the study area during the 'cool dry season' (January 2011). Used as a measure of vegetation productivity (Pettorelli *et al.*, 2009) |
| Seasonal variation in vegetation productivity (*NDVI-CV*) | Calculated as the coefficient of variation in NDVI using 3 seasons (October 2010, January 2011 and May 2011) Landsat 4–5 TM imagery. Used as a measure of vegetation deciduousness |
| Distance from forest settlement (*ForSettDist*) | Generated a surface by calculating the Euclidean distance from forest settlement using field-collected data on the location of forest settlements across the landscape gathered both during this study and prior surveys (Harihar & Pandav, 2012). As forest settlements in this landscape are Gujjar settlements with livestock holdings, this covariate serves as a surrogate for livestock densities following Ogutu *et al.* (2010) |
| Distance from forest edge (*ForEdgeDist*) | Calculated as the Euclidean distance from the non-forest interface to forest interior. As forest edge presents an interface with settlements, this covariate serves as a measure of access to forest resources/hunting. Also as agricultural fields fringe the forests, this measure also indexes the distance to crops for habitual raiders |

significant increase in model deviance based on *F*-tests at $P = 0.05$ (Crawley, 2007). Species-specific model sets were compared using generalized cross validation (GCV) scores and percentage deviance explained. As segment counts displayed some degree of overdispersion under a Poisson distribution, we used a Tweedie distribution assuming negligible residual autocorrelation. For these data, we specified the θ parameter as 1.6 based on the visual comparison of residual fits (Williams *et al.*, 2011).

Finally, a prediction grid was developed by gridding the study region into 5212 cells of 1 km² each using Arc GIS 10 (ESRI, 2010). The geographical covariates were rescaled to a resolution of 1 km² from their original resolutions and the final GAM per species used to generate a surface of density. Thereby, maps of species densities were produced, and uncertainties in model prediction were estimated using the variance propagation method of Williams *et al.* (2011).

### Assessing prey densities across management categories

To derive species-specific stratified estimates within the three major forest land management categories (inviolate PAs, PAs with settlements and multiple-use forests) across the two THB's, we subdivided areas of differing management regimes using an overlay function in a GIS environment and derived mean estimates of density and tested for differences using one-way analysis of variance (Crawley, 2007). In THB I (1266 km²), 747 km² (59%) is administered under four multiple-use forests, while 179 km² (14%) and 340 km² (27%) of western RNP are managed as PAs with settlements and inviolate PAs, respectively. Across 3946 km² of THB II, 2581 km² (65%) is administered under six multiple-use forest divisions, 774 km² (20%) encompassing regions within eastern RNP and CTR as PAs with settlements and 591 km² (15%) comprising parts of eastern RNP and Corbett National Park (CNP) as inviolate PAs.

### Estimating potential tiger densities

We scaled tiger densities based on the density of all potential prey species at a site (e.g. O'Kelly *et al.*, 2012). Although it has been suggested that predictions based on preferred prey could yield more accurate estimates of carrying capacity (Hayward *et al.*, 2007, 2012), prey preferences within this landscape and across the tiger's range are known only from within PAs, which contain largely intact assemblages of prey species (Harihar *et al.*, 2011; Hayward *et al.*, 2012). However, as is typical of most TCLs, no information on tiger diets is available from outside reserves with greater disturbances, where populations of specific prey species may be considerably depressed (Dinerstein *et al.*, 2006). Hence, we estimate potential tiger densities for this landscape spanning varied land management types based on all potential prey species using the scaling relationship established by Karanth *et al.* (2004) specific to tigers, where $T_j$ is the density of tigers at a site *j*, based on prey density $U_j$:

$$T_j = \frac{0.10}{50} U_j \ddot{a}_j$$

and, $\ddot{a}_j$ is a mean one random variable.

With Harihar & Pandav (2012) having identified that tiger occupancy in the western TAL was severely affected by the lack of connectivity across two Tiger Habitat Blocks (THB I & II), we predicted potential tiger densities and numbers that could be supported specific to 1266 km² of THB I and 3946 km² of THB II.

## RESULTS

### Spatially explicit species-specific prey densities

The total survey effort comprised 422.5 km of walk along 96 spatial replicates. The six target species were detected on 517 independent occasions along 325 of 845 segments. Chital were the most commonly sighted ungulate species (40.8% of detections), followed by sambar (28.22%). Although red muntjac, Himalayan goral, wild pig and nilgai had fewer than the recommended 60–80 detections, the data conformed to the underlying assumptions of model fit (Buckland et al., 2001). Most detection data (chital, goral, nilgai and sambar) were best described by a hazard-rate detection function, while for red muntjac and wild pig, half-normal key functions were the best fit (Table 2).

The final GAMs accounted for 51.2–71.3% of the deviance in species data (Table 2). The models indicated that the relative importance of each variable was different for each species, with a few similarities. In all the final models, at least one terrain variable (Elev or TRI) and one covariate characterizing the vegetation (NDVI or NDVI-CV) had a significant effect on species densities (Table 2, Fig. 1, see Text S1 in Appendix S2 in Supporting Information). With the exception of the Himalayan goral, anthropogenic influences on habitats displayed significant effects on all species densities (Fig. 1a–f). The distance to forest settlements (ForSettDist) affected red muntjac densities in combination with edge effects (ForSettDist: ForEdgeDist) resulting in higher densities at greater distances from both the forest edge as well as forest settlements (Fig. 1a). Chital densities were influenced by livestock-mediated disturbance on vegetation characteristics (NDVI: ForSettDist), with the two-way interaction indicating

higher densities at intermediate levels of NDVI furthest from forest settlements (Fig. 1d). As expected, for forest-associated species (chital and sambar), nonlinear relationships indicated lower densities closer to the forest edge (Fig. 1d,e). In the case of nilgai (Fig. 1f), this trend was reversed, and for wild pig, the shape of the relationship was inconspicuous (Fig. 1c). Using the final models, extrapolations of species-specific densities were made across the landscape (Fig. 2) and mean overall densities (individuals per km²) estimated (Table 2).

### Prey densities across management categories

Overall, wild ungulate densities (individuals per km² ± SE) were higher in inviolate PAs (THB I; 51.16 ± 4.49 and THB II; 59.03 ± 3.65) than in either PAs with settlements (THB I; 23.87 ± 3.28 and THB II; 30.6 ± 1.92) or multiple-use forests (THB I; 22.25 ± 1.28 and THB II; 24.06 ± 0.91), although species-specific densities across these three forest land management categories differed (Fig. 4). Chital was the most numerous prey across the landscape (Fig. 4) with significant differences in densities being recorded across the three management categories in both habitat blocks (THB I; $F_{2,1574} = 76.6$, $P < 0.0001$, THB II; $F_{2,3943} = 117.1$, $P < 0.0001$). Sambar, the second most dominant prey (Fig. 4), also displayed significant differences in densities across the management categories (THB I; $F_{2,1574} = 35.8$, $P < 0.0001$, THB II; $F_{2,3943} = 80.1$, $P < 0.0001$). No significant differences in red muntjac densities were observed in THB I ($F_{2,1574} = 0.66$, $P = 0.517$), while in THB II, densities were higher in PAs (both categories) than in multiple-use forests ($F_{2,3943} = 12.9$, $P < 0.0001$). In the case of Himalayan goral, densities were comparable across all management categories

Table 2 The best-supported model for each species. Presented per species are the number of detections (n), the best-fit detection model with goodness-of-fit statistics [GOF-p (d.f.)], the significant smooth functions (with estimated degrees of freedom) included in the final generalized additive model, percentage deviance explained by the final model and landscape-level density (individuals per km²) with associated standard errors (SE) of each species

| Species (n) | Red Muntjac (51) | Himalayan Goral (30) | Wild Pig (30) | Chital (211) | Sambar (146) | Nilgai (49) |
|---|---|---|---|---|---|---|
| Detection model | Half-normal | Hazard-rate | Half-normal | Hazard-rate | Hazard-rate | Hazard-rate |
| GOF-p [d.f.] | 0.7462 [6] | 0.8671 [5] | 0.9561 [5] | 0.8171 [9] | 0.8881 [11] | 0.9282 [6] |
| Generalized additive models | | | | | | |
| Intercept | −25.46* | −11.83* | −12.98* | −15.55* | −18.92* | −9.89* |
| s(Elev) | 7.89* | – | 7.49* | 7.85* | – | – |
| s(TRI) | – | 7.17* | – | – | 2.45* | 7.95* |
| s(NDVI) | – | 7.27* | 5.14* | – | – | – |
| s(NDVI-CV) | 3.11* | – | – | – | 5.49* | 7.43* |
| s(ForSettDist) | – | – | – | – | – | – |
| s(ForEdgeDist) | – | – | 2.39* | 2.74* | 2.88* | 7.02* |
| s (NDVI: ForSettDist) | – | – | – | 3.01* | – | – |
| s (NDVI: ForEdgeDist) | – | – | – | – | – | – |
| s (ForSettDist: ForEdgeDist) | 2.12* | – | – | – | – | – |
| Deviance explained (%) | 66.9 | 69.4 | 51.2 | 54.6 | 61.6 | 71.3 |
| Overall density ± SE (individuals per km²) | 2.27 ± 0.32 | 1.61 ± 0.22 | 4.82 ± 0.91 | 16.32 ± 1.43 | 8.85 ± 0.61 | 1.33 ± 0.19 |

*$P < 0.05$.
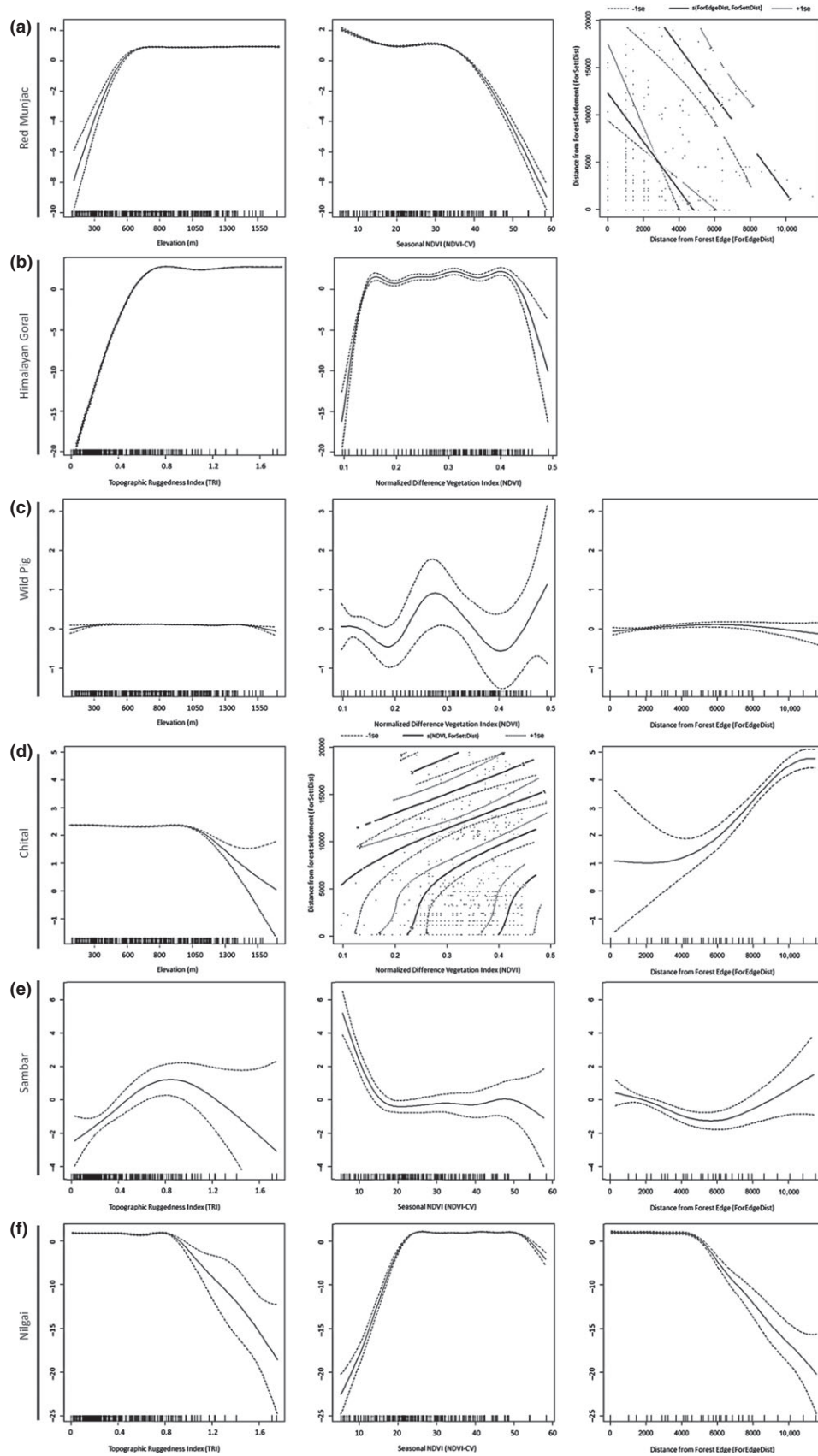
**Figure 1** Generalized additive model response curves (solid lines) with 95% confidence intervals (dashed lines) presented for each of the covariates in the linear predictor scale from the best-fit models for each of the six wild ungulate species.
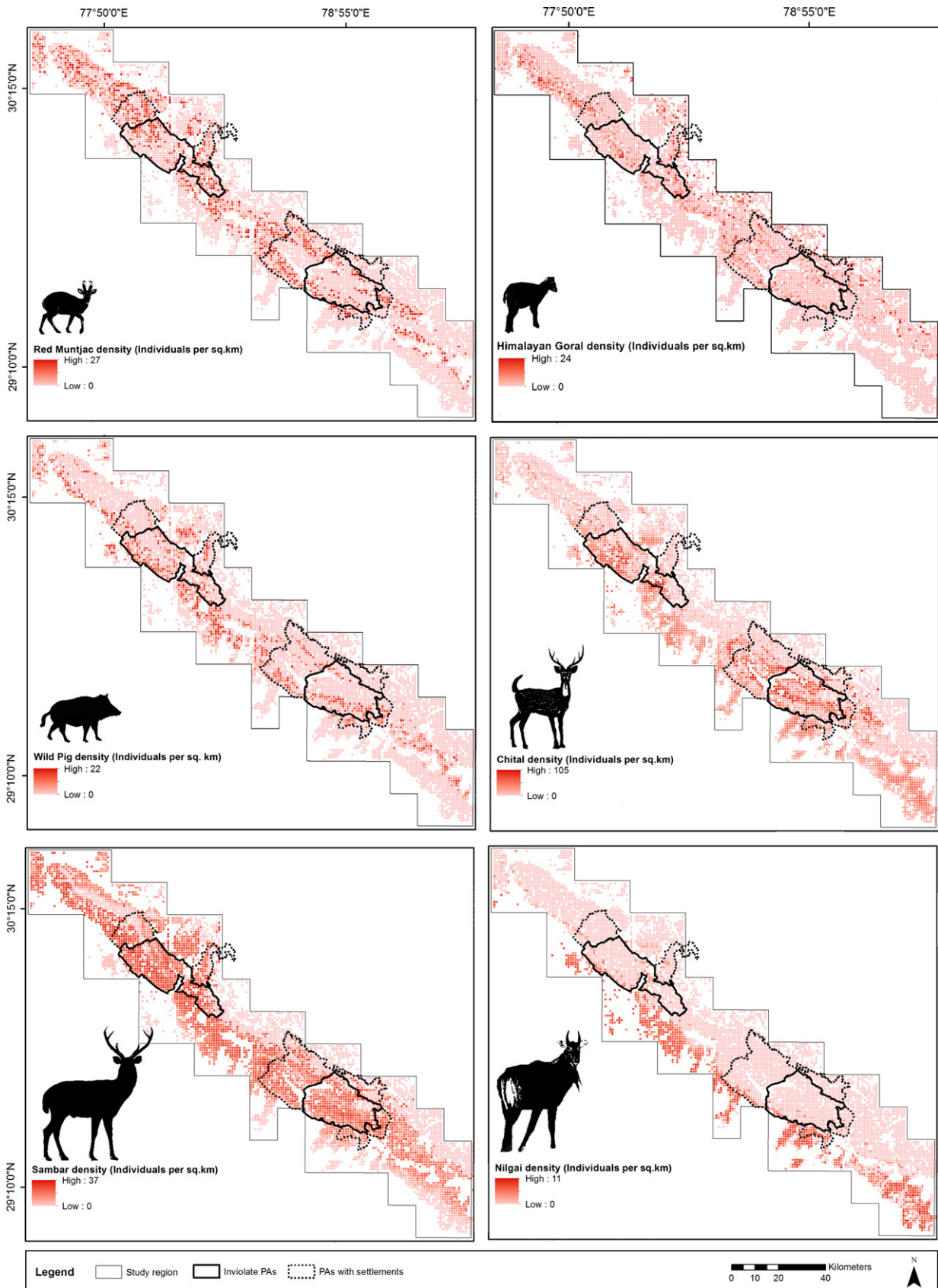


**Figure 2** Distribution of individual density over 1-km² grid cells across the western Terai Arc Landscape (TAL) for the six ungulate species. Species silhouettes are scaled to body size and the three forest management categories are indicated.

in THB I ($F_{2,1574} = 0.72$, $P = 0.484$), while in THB II, differences in densities were observed primarily owing to the non-availability of suitable habitat within multiple-use forests ($F_{2,3943} = 7.2$, $P < 0.0001$). As expected, wild pig densities were comparable across the three forest land management categories in both habitat blocks (THB I; $F_{2,1574} = 35.8$, $P < 0.0001$, THB II; $F_{2,3943} = 80.1$, $P < 0.0001$). Nilgai densities were significantly higher in the multiple-use forests of THB I and THB II (THB I; $F_{2,1574} = 5.48$, $P < 0.001$, THB II; $F_{2,3943} = 47.39$, $P < 0.0001$).

## Potential tiger densities

Our study estimates an average wild ungulate density of 35.16 (SE 5.67) individuals per km$^2$, capable of supporting 7.03 tigers per 100 km$^2$ (SE 1.6) in the western TAL. Corresponding to a population of 381 individual tigers (95% CI 313–480) across 5212 km$^2$, these results suggest that a *c.* 68% increase in tiger numbers is possible given existing prey abundances as current tiger numbers total 227 (199–256) (Table 3). While predicted tiger densities and numbers differed across THB I and THB II primarily owing to variations in available habitat area, our results highlight that THB I represents a promising recovery site, whereas the tiger population in THB II is near saturation (Table 3).

## DISCUSSION

In this study, we set a realistic population target and develop spatially explicit conservation strategies for tigers in the western TAL based on reliable estimates of landscape-wide prey densities and its determinants. By estimating a carrying capacity of *c.* 381 individual tigers for this human-dominated landscape based on current densities of prey, we highlight the need for divergent strategies across this disjunct landscape, which can help increase the tiger population by *c.* 68% as current tiger numbers total 227 (199–256) (Table 3). Additionally, by identifying species-specific determinants of prey densities, we recommend specific interventions for the three management categories towards managing prey and further enhancing the predicted carrying capacity.

The forested habitats of the western TAL are managed under 10 multiple-use forest divisions and two PAs. With only 18% of the landscape being categorized as inviolate PAs, the majority of the land area is subjected to multiple resource-use pressures. Comprising suitable habitats for all species (with the relative exception of nilgai) and offering protection against direct persecution and livestock-mediated competition, we clearly demonstrate that inviolate PAs harbour the highest densities of ungulates across this landscape (Fig. 3). In particular, chital and sambar attain their highest densities within these forests. Constituting the most numerically dominant ungulates (79.9%), these results assume significance as the two species occur most commonly (70–78%) in diet of tiger (Harihar *et al.*, 2009b, 2011). Given that both species are vulnerable to poaching (Madhusudan & Karanth, 2002; Karanth *et al.*, 2010) and the observed negative influence of forest edge on densities, enforcement of antipoaching measures met out in these parts of RNP and CTR appear to positively influence species densities. Additionally, chital densities in inviolate PAs (devoid of Gujjar settlements) are at their highest as livestock-mediated competition is excluded from within these forests.

Protected areas with settlements, constituting 18% of the land area, are administered under the unified control of protected area managers and offer protection against direct killing through enactment of antipoaching measures. Differing from inviolate PAs in that they still permit Gujjars and/or village enclaves residing within to extract required natural resources, these regions offer suboptimal habitat conditions for species negatively influenced by the presence of forest settlements (a surrogate to livestock densities). Through this study, we confirm that chital densities are significantly lower in PAs with settlements in comparison with inviolate PAs across this landscape. Despite the availability of suitable low-lying, mixed forest habitats in these regions (e.g. parts of western RNP-THB I; western CTR-THB II), the interactive effect of the presence of forest settlements on vegetation

Table 3 Predicted tiger density and numbers that can be supported in the two disjunct habitat blocks of the western Terai Arc Landscape (TAL) based on available individual prey density using the scaling relationship developed Karanth *et al.* (2004). Also presented are the current estimated tiger population sizes estimated from camera trap based studies in the western TAL

| Tiger habitat block | Available habitat area in km$^2$ | Estimated overall prey density as individuals per km$^2$ (SE) | Predicted tiger density as individuals per 100 km$^2$ (SE) | Predicted number of tigers[‡] (95% CI) | Estimated number of tigers (95% CI) |
|---|---|---|---|---|---|
| THB I | 1266 | 32.43 (3.93) | 6.48 (1.54) | 82 (62–106) | 2* (2–7) |
| THB II | 3946 | 37.90 (4.09) | 7.58 (1.87) | 299 (225–377) | 225[†] (199–256) |
| Entire western TAL | 5212 | 35.16 (5.67) | 7.03 (1.6) | 381 (313–480) | 227 (199–256) |

*Harihar & Pandav (2012).
[†]Jhala *et al.* (2011).
[‡]Estimates based on preferred, non-avoided, principal prey derived using the scaling relationship in Karanth *et al.* (2004) is provided in Table S2.
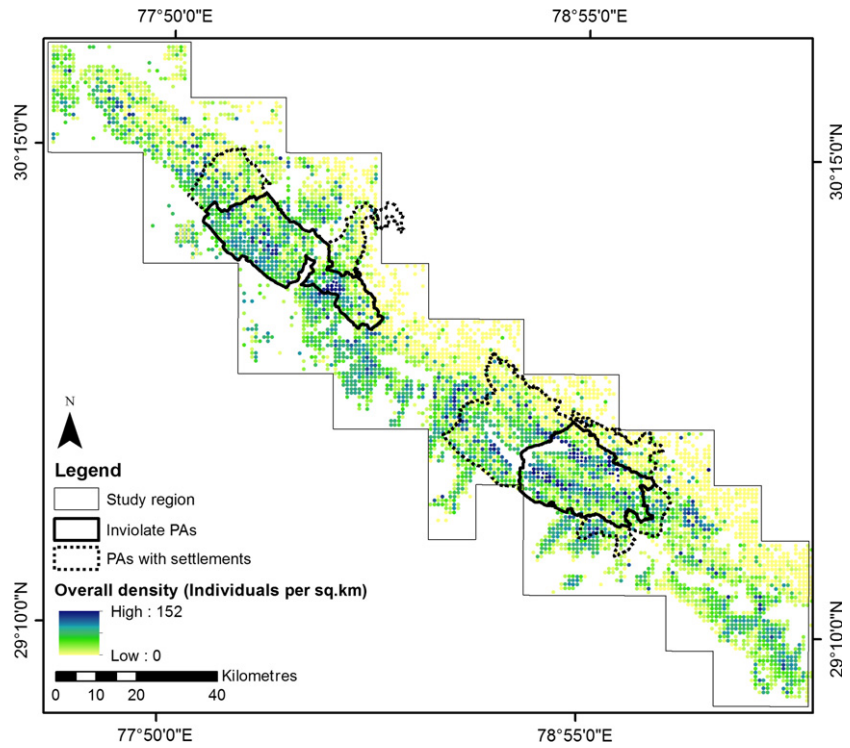
Figure 3 Distribution of combined wild prey density (individuals per km$^2$) at the scale of 1 km$^2$ across the western Terai Arc Landscape (TAL). Also indicated are the three forest management categories.
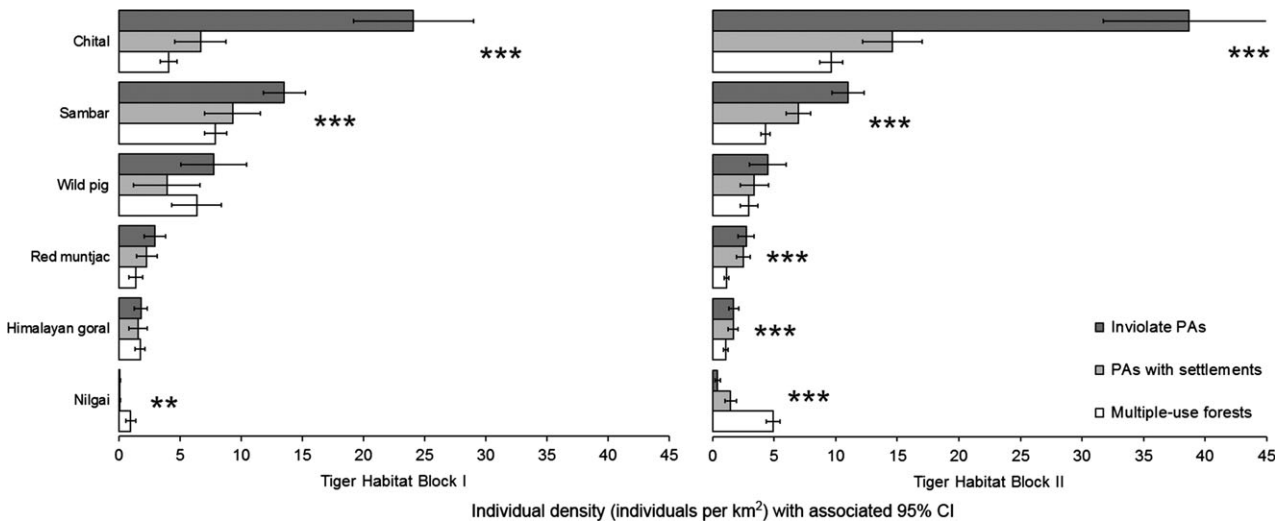


Figure 4 Comparison of species-specific individual densities (with 95% CI) across inviolate protected areas (dark grey bars), protected areas (PAs) with settlements (light grey bars) and multiple-use forests (open bars) in the western Terai Arc Landscape. Significance levels – ***$P < 0.0001$, **$P < 0.001$.

productivity appears to be depressing chital densities. Conforming to earlier findings that show that livestock-mediated competition for resources depress densities and population performance of chital (Madhusudan, 2004; Harihar et al., 2009a), our results also highlight the role of PAs with settlements in presenting potential recovery habitat for the species. In the case of Red muntjac, for which densities are lowest in proximity to Gujjar resettlements near the forest edge, removal of Gujjar-mediated disturbances from within the

forests may not lead to significant increase in densities. However, resettlement process is currently underway from all these areas, and the resulting availability of disturbance-free habitat and enhanced enforcement is expected to additionally benefit red muntjac and sambar, which are vulnerable to poaching (Madhusudan & Karanth, 2002; Johnsingh et al., 2004; Steinmetz et al., 2010).

Managing wild prey populations is particularly challenging in the multiple-use forests (64%) as they face intense pressures of

timber-extraction, resource extraction by local communities, the presence of Gujjar settlements and illegal hunting (Johnsingh *et al.*, 2004). Present management of these forests is geared to meet diverse silvicultural and regulated community livelihood objectives, and is not aligned or equipped towards protecting wildlife (Harihar & Pandav, 2012). Consequently, the three species vulnerable to poaching (barking deer, chital and sambar) are particularly depressed in these forests given minimal protection (Fig. 4). In contrast, being culturally tolerated (Karanth *et al.*, 2010), nilgai densities peak in multiple-use forests closer to the southern edge although they raid crops in the adjacent agricultural fields. Wild pigs, being generalists, and gorals, being confined to very rugged and steep hillsides which are relatively inaccessible, are able to persist in comparable densities across all three categories (Fig. 4). Chronic disturbances related to various extraction pressures are not expected to abate unless these areas are redesignated for wildlife conservation. However, given the conservation significance of these forests as 'critical tiger habitats' (THB II, Harihar & Pandav, 2012), important corridors (Johnsingh *et al.*, 2004), and areas of recovery (in THB I, Table 3), the removal of tiger/prey individuals through illegal hunting/conflict needs to be urgently arrested through enhanced antipoaching measures. Therefore, investments to procure adequate financial and infrastructural support for training, equipping and deploying staff for law enforcement could potentially enhance the conservation value of these forests.

While it is well recognized that prior knowledge of predator carrying capacity is essential to make informed conservation decisions (Fuller & Sievert, 2001; Hayward *et al.*, 2007), such an exercise is yet to become part of the tiger conservation strategies across range countries. Our study shows that, although prey densities varied across the three land management categories, densities are comparable across the two habitat blocks and that differences in carrying capacities arise largely as an artefact of available habitat area (Table 3). This also confirms that the drastically lower occupancy of tigers in THB I in comparison with THB II is not a result of poorer prey base, but is instead a consequence of a break in habitat connectivity (Harihar & Pandav, 2012). In THB I, tigers face almost imminent extinction, as the small, non-viable population (at their north-western range limit) is disjunct from the existing source in THB II. With our results clearly highlighting that the current prey base is capable of supporting *c.* 82 individual tigers and studies showing that a remnant population of only two females inhabit these forests (Harihar & Pandav, 2012), this habitat block presents an opportunity to significantly enhance the population. Unlike other sites assessed in Cambodia (Gray *et al.*, 2012; O'Kelly *et al.*, 2012), recovering tigers in THB I is not contingent on recovery prey and would only require the supplementation of individuals from a nearby source (THB II).

In THB II, recent studies reveal that an estimated population of 225 (199–256) individuals occupy 88.5% of available habitat (Jhala *et al.*, 2011; Harihar & Pandav, 2012). With numbers having reached the predicted carrying capacity, recovery of populations in THB II is contingent upon recovering prey. This

could, for example, be achieved by resettling Gujjars from western CTR and parts of RNP, in addition to areas of high tiger occupancy (Harihar & Pandav, 2012), where community members have expressed their willingness to resettle (Harihar *et al.*, 2014). However, in the current scenario, management strategies need to be developed to actively manage the population, which could also include translocating individuals to THB I. As THB II also experiences high conflict, in the form of livestock depredation by tigers, which are rarely and inadequately compensated and often result in retaliatory killing of tigers (Harihar *et al.*, 2014), effective conflict mitigation is essential to ensure support for tiger conservation among the local communities (Karanth & Gopal, 2005; Goodrich, 2010).

## Conservation implications

In conclusion, our results have critical implications for assessing the feasibility of conservation programmes targeting to double tiger numbers by 2022. We present the first estimates of landscape-wide, spatially explicit carrying capacity for tigers and suggest interventions tailored to local land management. Lack of pre-project evaluation of this nature has resulted in allocation of conservation funds in sites, where it has been discovered that the prey populations are inadequate to support a viable tiger population upon project initiation (Gray *et al.*, 2012). Hence, we suggest that such an evaluation is indispensable to set realistic conservation targets and should ideally precede pledging investments to recover tiger populations.

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## SUPPORTING INFORMATION

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

**Appendix S1** Potential tiger habitat (Figure S1) and location of line transects in the western Terai Arc Landscape (Figure S2); description of the six wild ungulate prey species (Table S1).

**Appendix S2** Estimated prey densities and carrying capacity for tigers across THB I and THB II (Table S2); additional GAM results (Text S1).

## BIOSKETCHES

**Abishek Harihar** has interests in large carnivore conservation, population ecology and conservation prioritization. His current research involves integrating ecological, social and economic concerns into conserving tigers in the western Terai Arc Landscape, India.

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