Biological Conservation 218 (2018) 181–191

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Maintaining tiger connectivity and minimizing extinction into the next century: Insights from landscape genetics and spatially-explicit simulations

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ABSTRACT

Habitat loss is the greatest threat to large carnivores around the world. Maintenance of functional connectivity in fragmented landscapes is important for long-term species persistence. Here, we merge landscape genetics analyses and spatially-explicit simulations to understand future persistence and extinction of tigers (*Panthera tigris*) in Central India. Tigers in this landscape are restricted to Protected Areas (PAs) and forest fragments embedded within a mosaic of agricultural fields and human settlements. We examined current population connectivity of tigers across nine reserves (using 116 non-invasively sampled individuals and 12 microsatellites). Genetic data was used to infer resistance-to-movement. Our results suggest that dense human settlements and roads with high traffic are detrimental to tiger movement. We used landscape genetic simulations to model 86 different scenarios that incorporated impacts of future land-use change on inferred population connectivity and extinction. Our results confirm that genetic variability (heterozygosity) will decrease in the future and small and/or isolated PAs will have a high risk of local extinction. The average extinction risk of small PAs will reduce by 23–70% if a 5 km buffer is added around existing boundaries. Unplanned development will result in 35% lower heterozygosity and 56% higher average extinction probability for tigers within protected areas. Increasing tiger numbers in such a scenario will decrease extinction probability just by 12% (from 56% to 44%). Scenarios where habitat connectivity was enhanced and maintained, stepping-stone populations were introduced/maintained, and tiger numbers were increased, led to low overall extinction probability (between 3 and 21%). Our simulations provide a means to quantitatively evaluate the effects of different land-use change scenarios on connectivity and extinction, linking basic science to land-use change policy and planned infrastructure development.

1. Introduction

The current rates and magnitude of species decline and extinction are higher than ever before (Barnosky et al., 2011; Dirzo et al., 2014). Most mammals retain less than half of their historical range, resulting in substantial population decline and habitat fragmentation (Dirzo et al., 2014; Morrison et al., 2007). Due to their large area requirements, slower life histories and low densities, large carnivores are especially vulnerable to habitat fragmentation and isolation. A majority (77%) of large carnivores continue to undergo worldwide decline, with populations at risk of local extirpation due to habitat loss (Ripple et al., 2014).

Conservation efforts, including population monitoring, legal protection, creation of protected areas, reintroductions and translocations, have ensured recovery of species, such as the grey wolf (*Canis lupus*) in North America and brown bears (*Ursus arctos*) in northern Europe, among others (Hagen et al., 2015; Ripple and Beschta, 2012). Long-term persistence of such threatened populations requires identifying and maintaining connectivity among habitat patches (Jackson et al., 2016). Among large carnivores, significant attention and resources are invested in recovery and conservation of the tiger, an iconic species with < 4000 individuals left in the wild.

Tigers have lost four subspecies and 93% of their historical range, and what remains of their existing range is highly fragmented. With nearly 65% of the world's wild tigers (Jhala et al., 2015) and substantial genetic variation (Mondol et al., 2009a), India is a stronghold for tiger survival. Recent reports suggest that conservation and management efforts in India over the last three decades have led to a 30% increase in tiger numbers (Jhala et al., 2015). Reintroduction of tigers in Panna Tiger Reserve and Sariska Tiger Reserve, where they had gone extinct in the recent past, have resulted in recovery of populations in these two

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https://doi.org/10.1016/j.biocon.2017.12.022
Received 27 April 2017; Received in revised form 24 November 2017; Accepted 14 December 2017

protected areas (PA) (Sankar et al., 2010; Sarkar et al., 2016). Despite what appears to be a demographic recovery, the median number of tigers within individual PAs in India is low (median: 19, range: 2–215; (Jhala et al., 2015; Wikramanayake et al., 2010)). Most populations by themselves may not be viable, and the continued survival of tigers could be contingent on maintaining connectivity between PAs.

Several independent genetic studies in the high priority tiger conservation landscape of Central India confirm that PAs exchange dispersing individuals and are fairly well connected (Joshi et al., 2013; Reddy et al., 2017; Sharma et al., 2013b; Yumnam et al., 2014). About 35% of India's tigers are estimated to live outside PAs (Jhala et al., 2015) and may play a critical role in maintaining connectivity. However, India is a country with over a billion people, an economy growing at 7% annually, poised for rapid urbanization and the ensuing increase in associated infrastructure. Among the planned infrastructure, existing highways in the landscape are being widened to meet the demands of increasing traffic (e.g., National Highway 7 which bisects a critical corridor is being widened after a prolonged legal battle owing to the conflict between tiger conservation and development activities (Srivastava and Tyagi, 2016)), further fracturing an already highly fragmented landscape. Landscapes outside PAs (~95% of India's area) are about to change dramatically, and tiger management and conservation is currently only focused on protected areas.

Earlier studies correlating genetic connectivity with landscape elements have revealed that tiger movement is negatively impacted by human settlements within the Central Indian landscape (CIL) (Joshi et al., 2013). Urban populations in India are projected to double from 410 million in 2014 to 814 million in 2050 (United Nations, Department of Economic and Social Affairs, Population Division, 2014). Additionally, built-up areas have been increasing almost 3 times faster than the population in nearly all large Indian cities (Sudhira, 2011). Along with the urbanization, demands for better road and railway connectivity between cities are also projected to increase (National Transport Policy Development Committee, 2013). Such landscape transitions will negatively impact tiger connectivity. Small, isolated populations have known genetic consequences, including low variation (Boersen et al., 2003; Frankham, 1996), increased inbreeding and increased disease susceptibility (Spielman et al., 2004; Trinkel et al., 2011), and heightened extinction risk (Saccheri et al., 1998). However, these are general predictions, and we do not know how future land-use change will specifically impact connectivity and persistence of tigers in the landscape.

Few studies (Tian et al., 2011, 2014) have attempted to understand how future climate and landscape change might affect persistence of tigers. Tian et al. (2014) used population viability analysis (PVA) to simulate the effect of climate change and habitat fragmentation on future persistence of Amur tigers by incorporating factors affecting species distribution, but not dispersal. Persistence of tigers in complex and changing landscapes such as CIL requires modeling population persistence based on empirical genetic data, factors affecting dispersal, predicted landscape/climate change and interactions of these factors with demography. Globally, very few such intensive modeling exercises have been conducted to predict future persistence of endangered species (Benson et al., 2016; Brown et al., 2016; Landguth et al., 2014).

In this paper, we examine genetic connectivity among tiger populations in the CIL, including individuals within and outside PAs. We use this data on gene flow to infer the effect of different landscape features on dispersal and connectivity. We then carry out forward- time, spatially-explicit, individual-based simulations to understand how genetic diversity, connectivity and extinction probability will change under nine different development scenarios. We examine these scenarios while accounting for tigers inside and outside PAs. We also test the effect of increasing tiger numbers and the effects of assumptions about dispersal, modeling a total of 86 scenarios.

2. Materials and methods

In this study, we collected genetic samples from wild populations (*Study area and sampling*), generated genetic data and conducted population genetic analyses (*Genotyping and population genetic analysis*). Landscape genetic analyses allowed us to infer landscape elements impacting connectivity (*Landscape genetic analyses*). Future scenarios were simulated assuming various criteria for landscape change, including specific management relevant scenarios, and tiger demography (*Landscape genetic simulations*). All simulations inferred genetic variability, inbreeding, connectivity and extinction probability in 2100. A flow chart of the methods is presented in Fig. S1 and more detail is described as follows.

2.1. Study area and sampling

The CIL is a global priority tiger conservation landscape. With ~34% forest cover and an estimated 688 (596–780) tigers (Jhala et al., 2015), it is a stronghold for tiger conservation. The PAs in the landscape are embedded in a heterogeneous matrix of multiple land-use types.

Non-invasive (scat) samples (n = 580) were collected between October 2012 and April 2014 from potential areas (PAs and forested areas outside PAs which are a part of territorial forest divisions and forest development corporations) in the state of Maharashtra, Madhya Pradesh and Chhattisgarh. We sampled eleven PAs: (1) Kanha Tiger Reserve (KTR), (2) Pench Tiger reserve (PTR), (3) Bandhavgarh Tiger Reserve (BTR), (4) Achanakmar Tiger Reserve (ATR), (5) Nagzira (NGZ) and (6) Nawegaon (NAW) (which together comprise a Tiger Reserve) (7) Satpura Tiger Reserve (STR), (8) Tadoba-Andhari Tiger Reserve (TATR), (9) Bor Tiger Reserve (BOR), (10) Umred-Karhandla Wildlife Sanctuary (UK) and (11) Tipeshwar Wildlife Sanctuary (TIP). We also sampled in three territorial forest divisions outside PAs: (1) Balaghat Forest Division (BAL), (2) Central-Chanda Forest Division (CHA) and (3) Bramhapuri Forest Division (BPR) (Fig. 1). Sampling was also carried out in Sitanadi-Udanti Tiger Reserve (S-U) and Panna Tiger Reserve (PAN). We did not find any tiger scat samples in S-U and samples from PAN were not used to optimize the resistance layers since tigers in PAN have been reintroduced from KTR and PTR after they went extinct locally in 2006. However, we included PAN in the forward-time simulations. See Supplementary material S1 for more details.

2.2. Genotyping and population genetic analysis

In order to quantify genetic connectivity between different PAs, we first extracted DNA using standardized methods and identified individuals (Mondol et al., 2009b; Mukherjee et al., 2007). We then calculated heterozygosity based differentiation statistics (PopGenReport (Adamack and Gruber, 2014), MMOD (Winter, 2012), and HIERFSTAT (Goudet, 2005) in R (R Core Team, 2017)). For further details about genetic analysis, refer to the Supplementary material S2.

2.3. Landscape genetics analysis

We calculated inter-PA genetic distances based on the proportion of shared alleles (D_{PS}; (Bowcock et al., 1994)) using Microsatellite Analyzer (MSA, version 4.05; (Dieringer and Schlotterer, 2003)). The relationship between the observed genetic structure and the landscape variables likely to affect tiger dispersal was systematically evaluated using a multi-model inference and optimization approach (Shirk et al., 2010) described next.

We selected landscape variables known to affect tiger dispersal based on Joshi et al. (2013) (i.e., land cover, human settlement layer, roads and railway lines along with the density of linear features) to build resistance models. We did not use topography related variables (as used in Krishnamurthy et al., 2016; Reddy et al., 2017). Tigers are habitat generalists (ranging from 0 to 3000 m above sea level), their

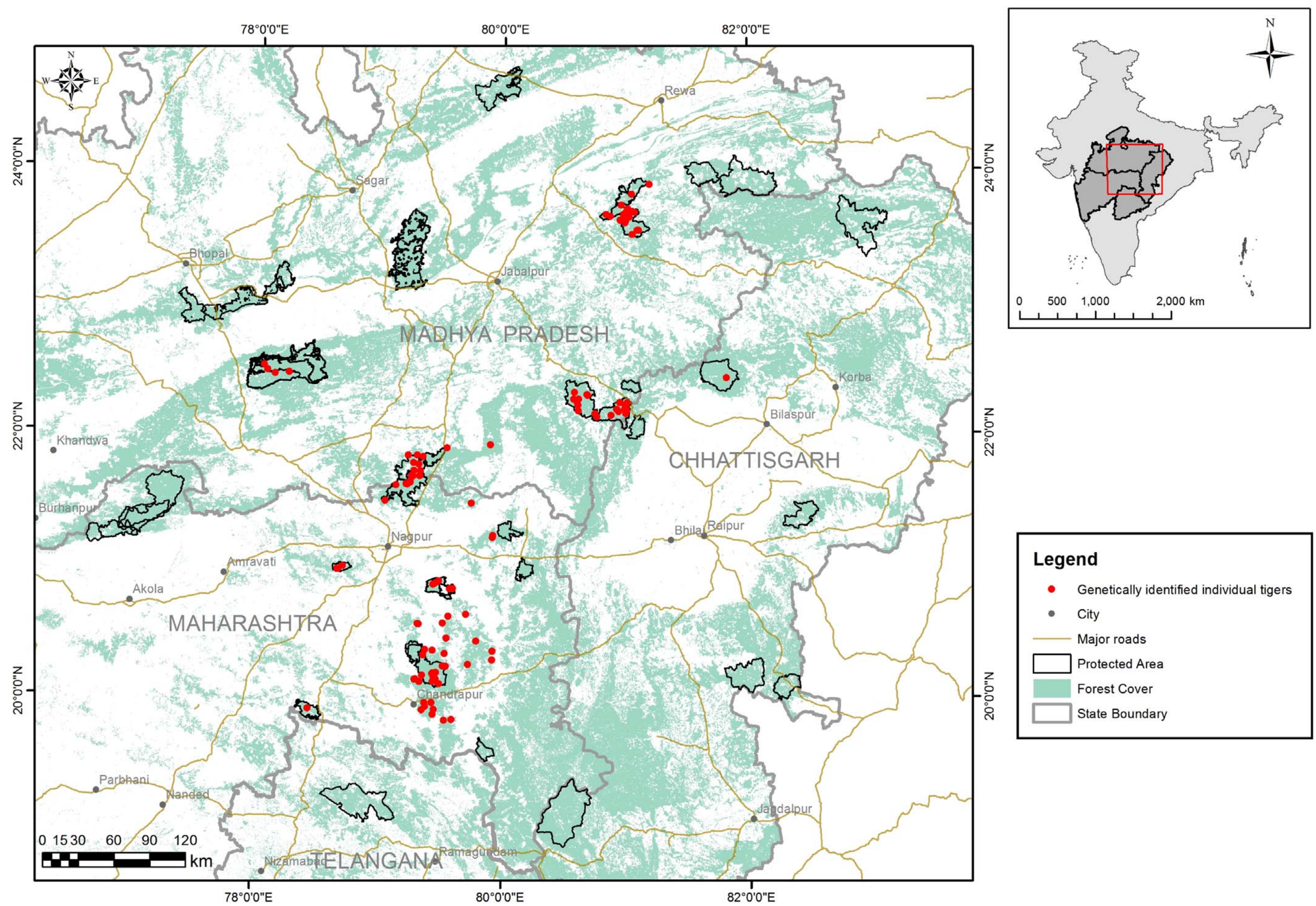


Fig. 1. Study area. The figure contains a map of India with the study landscape highlighted and enlarged. In the enlarged study area, protected areas are marked by black outline and genetically identified individual tigers as red dots. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

occurrence is associated with forests in the CIL and they have been reported to avoid desserts and short grasslands (Kitchener and Dugmore, 2000; Yumnam et al., 2014). Athreya et al. (2014) revealed that tigers disperse through and use less rugged areas in Central India. Additionally, over the last 300 years, most forest cover loss has been in the low elevation and less rugged areas (Sharma et al., 2013a). As a result, the current forest cover is concentrated in highly rugged and relatively high-slope areas (Supplementary fig. S3). We used MODIS land-cover data (MCD12Q1, https://lpdaac.usgs.gov/dataset_discovery/modis/modis_products_table/mcd12q1) and reclassified it into five broad land-cover types which we ranked in order of increasing resistance: (i) forest, (ii) degraded and scrub forest, (iii) agriculture (including fallow/ wasteland) and (iv) built-up (developed with buildings and non-building structures) areas. After reclassification, we resampled the layer using the Nearest Neighbor method to get a layer with 1 km resolution. We developed a layer of human settlements by merging urban and peri-urban areas derived from nightlight data (available at National Geophysical Data Centre) and rural areas from population density data (available at http://www.worldpop.org.uk/data/get_data/). Since all villages in the study landscape are not electrified, using nightlights alone would have underrepresented human settlements within the landscape (see Supplementary material S3 for more details). A vector layer of national highways, state highways and major public roads was reclassified into 5 categories based on the intensity of traffic on the road (based on Passenger Car Unit (PCU) data for 2006 from the Ministry of Road Transport and Highways). PCU represents the number of vehicles in terms of passenger cars and accounts for all types of vehicles. See Supplementary material S3 for more details. Railway lines and roads were used to generate a layer representing the density of linear features.

Landscape resistance values were inferred from the genetic data using multi-model optimization approach described in Shirk et al. (2010). Each landscape variable was related to landscape resistance using a mathematical model (Supplementary material S4). Using genetic data as the response variable and systematically varying the model parameters (maximum resistance and a shape parameter to account for the relationship of the variable with resistance), we identified the best fitting model parameters for each variable. The best-fitting model was identified as the one with the most significant correlation with genetic data, after controlling for the effect of geographic distance using partial Mantel tests (Smouse et al., 1986). The landscape variables that explained significant variation after controlling for geographic distance in univariate models were retained for further analysis. The retained variables were combined (additively) and optimized again in a multivariate context to account for interactions between different landscape variables (Shirk et al., 2010). We then used the estimated landscape resistance data to understand how future landscape change may alter the resistance surface (and therefore, connectivity) as described below.

2.4. Landscape genetic simulations

We used CDPOP (Landguth and Cushman, 2010) to simulate 20 non-overlapping generations (~100 years for tigers) of mating and dispersal among individuals for each scenario (scenarios described in next section). CDPOP is a spatially-explicit, individual-based simulator of population genetic processes. It simulates mating and dispersal in a finite population assigned to fixed locations, recording alleles of all individuals every generation. We initialized individuals in the simulations as being characterized by 12 loci with at most 11 alleles per locus. For the PAs with genetic data, individuals were assigned alleles based on the allele frequency distribution for that PA. For PAs without genetic data, we assigned allele frequencies based on STRUCTURE results (Fig. S5) or using other information (see S5 (a) for details). Individuals were initially seeded on the landscape based on the current tiger estimates (Table S4). In each generation, females gave birth to offspring (number based on a normal distribution with mean 3 ± 2) with an equal sex ratio at birth. Adults died, and the vacant locations were occupied by dispersing individuals. Probability governing mating and dispersal related movement was based on proximity of individual locations specified by the pairwise cost-distance matrices between individuals (calculated using 'gdistance' in R), which were scenario-specific (see next section). A negative exponential function (Sutherland et al., 2000) with median dispersal distance of 85 km (Bowman et al., 2002) and two different maximum dispersal distances of 300 km (Patil et al., 2011) and 500 km (Bowman et al., 2002; Natesh et al., 2017) was used to model natal dispersal. If all locations were occupied, any remaining offspring not assigned to a location were eliminated (Balloux, 2001).The probabilistic functions governing birth rate, mating and dispersal introduced demographic stochasticity in the model. See Table S1 for more details on simulation parameters. At the end of each simulation, we calculated genetic diversity indices (heterozygosity, inbreeding and allelic richness) and differentiation indices (Global and pairwise Fst, G'st, Jost D) (Adamack and Gruber, 2014; Jombart, 2008). The probability of tiger extinction for each PA was the number of times the tiger population within the PA went extinct out of 100 replicate simulation runs. We calculated sex ratio skew and fluctuations in population size across generations.

2.5. Simulation scenarios

In order to explore how future landscape change may affect dispersal and connectivity of tiger populations, we carried out spatially-explicit genetic simulations under different landscape change scenarios. All scenarios we present are plausible and derived from covariates which are known to influence land-use land-cover change. The objective of these scenarios was to identify the kind of landscape-wide, land-use changes that will facilitate or impede tiger connectivity, and not to identify where land-use change will occur in the future. Scenarios of landscape change were developed using Land Change Modeler (LCM) in IDRISI (SELVA, http://www.clarklabs.org) based on the change in land-use land-cover (LULC) from a combination of land cover (MODIS) and human settlements data and road expansion from 2001 to 2012. Future LULC maps were generated for 2020, 2040, 2060and 2080. See Supplementary S3a for details.

Simulations to assess change in genetic connectivity in the future were carried out for nine landscape change scenarios (labelled F1-F9, see Table 1 for the scenario description and rationale). For each of these scenarios, the landscape was parameterized using optimized resistance values based on the landscape genetic analysis described in the previous section. Cost-distance matrices were calculated for all the future maps that were generated. During simulations, the distance matrices changed after every 4 generations (~20 years) to account for the changing landscape except for scenario F1 (no landscape change) and F9 (PAs were fenced at the 1st time step of 20 years and remained fenced after that). Along with scenarios F1 to F9, we carried out additional simulations for scenarios F1 and F4 where we added a 5 km buffer around the smaller PAs in the landscape (< 400 km^2). We evaluated the effect of increased PA size on connectivity and extinction estimates. Simulations for the first eight scenarios were carried out under 4 sub-scenarios: (a) with tigers restricted to PAs (current numbers constant), (b) with tigers inside and outside PAs (outside individuals distributed randomly within existing forest patches), (c) with tigers inside and outside PAs (outside individuals clustered in space to form 'stepping-stone' populations between PAs), and (d) with tigers restricted to PAs (numbers increase). See Supplementary material S5b for details.

The simulations included eleven additional unsampled PAs: PAN, S-U, Indravati Tiger Reserve (IND), Melghat Tiger Reserve (MEL), Ratapani Wildlife Sanctuary (RAT), Kawal Tiger Reserve (KAW), Tamorpingla Wildlife Sanctuary (TAM), Sanjay Tiger Reserve (SAN), Noradehi Wildlife Sanctuary (NOR), Barnawapara Wildlife Sanctuary (BAR)and Chaprala Wildlife Sanctuary (CHH). These areas were included in future scenario simulations as some have tigers, while others have a high probability of tiger occupancy, or are protected reserves.

3. Results

3.1. Population genetic analysis

Out of 289 samples identified as tigers, data for at least 8 out of 12 microsatellite loci could be generated from 127 samples, 116 of which were identified as unique individuals. The P(ID) (the probability of two different individuals having the same genotype) was 1.48×10^{-11} and the more conservative measure Sib P(ID) (PID when all individuals in the population are assumed to be siblings) was 5.1×10^{-5}, indicating that even related individuals would have a very low probability of having identical genotypes. The estimated allelic dropout across loci was 0.062 and the frequency of false alleles was 0.013 (comparable to other studies in the landscape; (Caragiulo et al., 2015)). Six out of the 12 loci showed significant deviation from Hardy- Weinberg equilibrium, suggesting the presence of genetic structure. The mean number of alleles per locus was 8.7 and expected heterozygosity was 0.723 (Supplementary Table S2). Global F_{ST} was estimated to be 0.169, with highest pairwise differentiation between BTR and BPR (Tables S2 and S3). Table 2 presents D_{PS}, a measure of contemporary genetic differentiation.

3.2. Functional connectivity

Human settlements were the most important (highest magnitude of correlation) landscape variable explaining genetic distance between PAs. Land-use and traffic intensity on roads also explained significant variation, even after accounting for geographic distance (Table 3). These three variables (traffic intensity on roads, human settlements and land-use) were retained for multivariate optimization. The parameter estimates for each landscape variable are presented in Table 3.

Shape parameter (the parameter that determines the shape of the relationship between the landscape variable and resistance) and maximum resistance of the optimum models of all the three landscape variables changed on combining, suggesting an interaction between these variables. The non-linear transformations (x > 1) indicate that low resistance is offered by smaller and middle values assigned to the variable and the resistance increases steeply with very high values. For example, roads with low and moderate traffic offer negligible resistance to movement, however, the resistance increases steeply with very high traffic. Correlation between the pairwise cost distance among populations (estimated from the combined resistance surface) and genetic distance was high (0.7857 after controlling for the geographic distance, 0.8166 without controlling for geographic distance). The correlation value for isolation by distance model (geographical distance alone) was 0.624.

3.3. Future connectivity

Overall, genetic diversity reduced over time in all the simulation scenarios (Fig. S6). However, restoring and protecting corridors between PAs lead to the least decline in genetic variation (~20%). Heterozygosity decreased faster and reduced to a lower final value at

Table 1
Landscape change scenarios for forward time simulations.

Scenario	Description	Rationale
F1-No landscape change[a]	Status quo	Null scenario
F2-Forest cover constant	Landscape change modeled while keeping the forest cover constant	The Green India mission under the National Action Plan on Climate Change (Ministry of Environment and Forests, 2008) advocates achieving a forest cover of 33%. Current forest cover is 21% (Forest Survey of India, 2015). In 1996, the supreme court of India redefined the scope of Forest Conservation Act 1980 and banned tree felling inside forests across India (Lele and Rosencranz, 2008).
F3-Agriculture area constant	Landscape change modeled while keeping the area under agriculture constant	Global food demand is projected to double by 2050. Even if use of technology to intensify agriculture increases yield, area under agriculture is not expected to reduce in the future (Laurance and Balmford, 2013)
F4-Unrestricted change[a]	Landscape change modeled based on change from 2000 to 2012	India's Gross Domestic Product (GDP) growth rate was higher than ever before in the decade from 2001 to 2011. Although this rate reduced after 2011, the recent government's development driven policies are likely to increase the economic growth rate (Dooley et al., 2014). The rate of granting forest clearances has also been highest from 2002 to 2011 within the last three decades. 387,952 ha of forest land was diverted during this decade for defense, mining, irrigation, power projects, industries and infrastructure projects (Centre for Science and Environment, 2012)
F5-Effect of mines and associated landuse change	In order to evaluate the effect of mines, we let the rest of the landscape remain constant (like in F1) except for the increase in area of mines and associated built-up area over the next 100 years. The mining area (mine + built-up) increased 3.6 times every 20 years based on a study in central India (Areendran et al., 2013)	The central Indian region is rich in mineral deposits. The mining sector currently contributes ~2% to India's GDP and the Ministry of Mines, Government of India has targeted to increase this share to 5% of GDP (Ministry of Mines, 2011). The Government of India amended the Mines and Minerals (Development and Regulation) Act in 2015 in order to expedite environmental clearances and issuance of licenses. This amendment also provides for the creation of District Mineral Foundations (DMF) to work towards developing mining affected areas. Research in Central India has shown that mining leads to landuse change and an increase in built-up areas around mines (Areendran et al., 2013; Prakash and Gupta, 2016) and the setting up of DMF will only increase the rate of this conversion. Data on mines were obtained from the Ministry of Mines database (http://mcas.nic.in/Mining_plan_web_Query.asp) and Greenpeace India (Fernandes, 2012). The data from Ministry of Mines were converted into a spatial layer based on their GPS locations and area of the mines. Data on coal mines described in (Fernandes, 2012) was obtained as shapefiles through personal communication.
F6-Highways as barriers	Landscape does not change except two national highways (NH6 and NH7) which cut across the landscape are converted into barriers to movement	Road traffic is estimated to grow at about 13% per annum over the next 20 years (National Transport Policy Development Committee, 2013). NH7, which runs north to south, bisects a critical corridor in the landscape and has recently been cleared to be widened from two to four lane capacity. NH6, which runs east to west and bisects another critical corridor, is also being considered for widening. Yadav et al. (2012) have observed agriculture and built-up area encroachment along NH6 in the forested area which connects two PAs (NGZ and NAW) (Yadav et al., 2012), thus potentially increasing the resistance to movement of tigers. This scenario is a case study to specifically look at the effects of these highways, if they were to become barriers in the future, on the corridors they bisect.
F7-Highways as barriers with wildlife crossings	Landscape does not change except two national highways (NH6 and NH7) which cut across the landscape are converted into barriers with provision for wildlife crossing at points where they bisect critical corridors. There was one gap in each highway. The gaps were 1 pixel wide and were placed near the locations where the NH6 and NH7 are currently narrow (2lanes wide, without a divider in between) and there is forest cover on the either side.	Guidelines to mitigate impacts of linear infrastructure on wildlife recommend a 100 m mitigation structure per 1 km length of infrastructure in critical tiger corridors (Wildlife institute of India, 2016). Although we cannot test the effectiveness of different kinds of structures which can provide connectivity across roads in this simulation, we investigate the effect of having a gap in the barrier which can potentially maintain connectivity.
F8-Habitat restoration to establish corridors between all PAs	The corridors were designated based on the least cost paths (generated using the gdistance package(van Etten, 2017) in R (R Core Team, 2017)) between PAs and the proposed corridor between Kanha and Pench.	Restoration of habitat and establishing corridors between PAs has been recommended to maintain and even increase the connectivity in the landscape (Dinerstein et al., 2006; Dutta et al., 2015). We generated least cost paths between PAs and we assigned a value of 1 to all the pixels in these paths (equivalent to forest). All non-forest pixels within the least cost paths were converted to forest to represent restoration of habitat. These paths overlap with the corridors delineated in previous studies (Dutta et al., 2015; Qureshi et al., 2014). We test how beneficial establishing these corridors would be.
F9-Fenced PAs	All the protected areas have fence around them in the future preventing dispersal	Extreme scenario to investigate the effect of fencing on genetic variation and extinctions in the future.

[a] We carried out additional simulations for scenarios F1 and F4 where we added a 5 km buffer around the smaller PAs in the landscape (< 400 km^2). We evaluated the effect of increased PA size on connectivity and extinction estimates.

Table 2
Genetic differentiation-DPS.

	BTR (n = 20)	BPR (n = 18)	BOR (n = 4)	KTR (n = 22)	CHA (n = 8)	PTR (n = 15)	STR (n = 4)	TATR (n = 26)	UK (n = 5)
BTR	0								
BPR	0.629	0							
BOR	0.669	0.456	0						
KTR	0.548	0.597	0.641	0					
CHA	0.621	0.286	0.359	0.592	0				
PTR	0.501	0.627	0.612	0.351	0.637	0			
STR	0.541	0.612	0.598	0.3541	0.592	0.416	0		
TATR	0.639	0.213	0.413	0.571	0.267	0.612	0.591	0	
UK	0.700	0.358	0.373	0.624	0.474	0.635	0.624	0.322	0

the end of 100 years in the scenarios with lower dispersal threshold (300 km). Within both the dispersal categories, the loss of genetic diversity was greater in the scenarios where the forest cover loss was higher (Fig. S6). Our results suggest that inbreeding did not increase appreciably over 100 years (F < 0.25 in all scenarios). Fig. 2 summarizes the implications of three different management decisions on structural connectivity, allelic richness, inbreeding and extinction in a subset of the simulated scenarios.

Irrespective of land-use change scenario, dispersal threshold and tiger demographic trajectory, small isolated PAs (TIP and BOR) had the highest risk of extinction. Reducing the dispersal threshold from 500 km to 300 km doubled the average extinction probability of some populations (BTR, PTR, MEL and STR, see Fig. 3a and b). Currently well connected, but small PAs (UK, CHH, NGZ and NAW) had high extinction probability only in the scenarios where forest cover around them was lost. Some large PAs that currently have a very low number of tigers (< 10 tigers, KAW, IND, RAT and S-U) also had high extinction probability except in the sub-scenarios where tiger numbers increased. Small population size was associated with high variance and highly skewed sex ratios (Figs. S7 and S8). The extinction probability of small PAs was also governed by their isolation and associated re-colonization probability (Fig. 3). Adding a buffer around the small PAs reduced their overall extinction probability. Among the isolated small PAs (TIP and BOR), the addition of buffer reduced the extinction probability by ~23%. Adding a buffer zone around the small, currently connected populations reduced the extinction probability to a large extent (~70%), but only in the simulations where the landscape around the buffers changed (F4). The benefit of having a buffer around the small PAs was the highest in the sub-scenario with stepping stone populations (sub-scenario c) between PAs.

3.4. Change in connectivity: specific infrastructure projects

Increase in mined area and the associated increase in built-up areas lead to ~15 times higher extinction probability in small and medium-sized PAs of BTR, SAN, UK and KAW due to their proximity to coal fields. TATR, another medium sized PA, also showed ~12 times increase in extinction probability due to mining, but only when the dispersal threshold was 500 km. When the dispersal threshold was low, the increase in extinction probability was also low (~1.8 times) because of the overall higher extinction probability of TATR in scenario F1 at this threshold. Presence of NH7 as a barrier without any mitigation structures (scenario F6) increased the F_{ST} between KTR and PTR ~4 times compared to scenario F1 and scenario F7 (Fig. S9). NH7 bisects the corridor between these two PAs. NH6 bisects the corridor between NGZ and NAW. The scenario with NH6 as a barrier (scenario F6) leads to ~19 times and ~65 times higher probability of extinction for dispersal threshold of 500 km and 300 km respectively. Higher increase in the genetic differentiation in the latter case (between NGZ-NAW, as compared to KTR-PTR) could be due to the smaller current population sizes of NGZ and NAW. Across land-use change scenarios, increasing tiger number (sub-scenario d) within and outside PAs (sub-scenarios c) lead to ~37% lower extinction probabilities overall and ~11% lower reduction in heterozygosity.

4. Discussion

The St. Petersburg declaration of 2010 envisaged doubling tiger numbers across all tiger nations by 2022 (Global Tiger Recovery Program, 2011). Our results from CIL demonstrate that maintaining or establishing connectivity and ensuring protection will be critical to meet such tiger conservation targets. Along with corridor conservation, designing, notifying and maintaining stepping-stone populations between PAs will be beneficial for maintaining future connectivity. To facilitate regional planning, spatially explicit analysis could help identify locations where infrastructure could be developed without affecting tiger connectivity. The current results are general prescriptions, but findings from this study provide evidence that can be translated into spatially explicit conservation planning exercises. Additionally, our framework can be applied globally to other landscapes and species (where genetic data are available) to improve connectivity in the context of development.

4.1. What impacts current tiger connectivity?

Human footprint on the landscape had the strongest impact on

Table 3
Univariate optimization results.

Landscape variable	Maximum resistance (R_{max})	Shape parameter (x)	Mantel's r	Partial Mantel's r	Significance (partial)
Univariate optimization					
Human settlement	10	0.001	0.859	0.778	0.001
Land-use	10,000	10	0.806	0.678	0.001
Linear density	10	0.01	0.683	0.383	0.027
Roads (traffic)	10,000	10	0.776	0.603	0.001
Multivariate optimization					
Human settlement	1000	5	0.8166	0.7857	0.001
Land-use	100	50			
Roads (traffic)	1000	10			

Non-linear exponential transformations were the best models for all these variables.

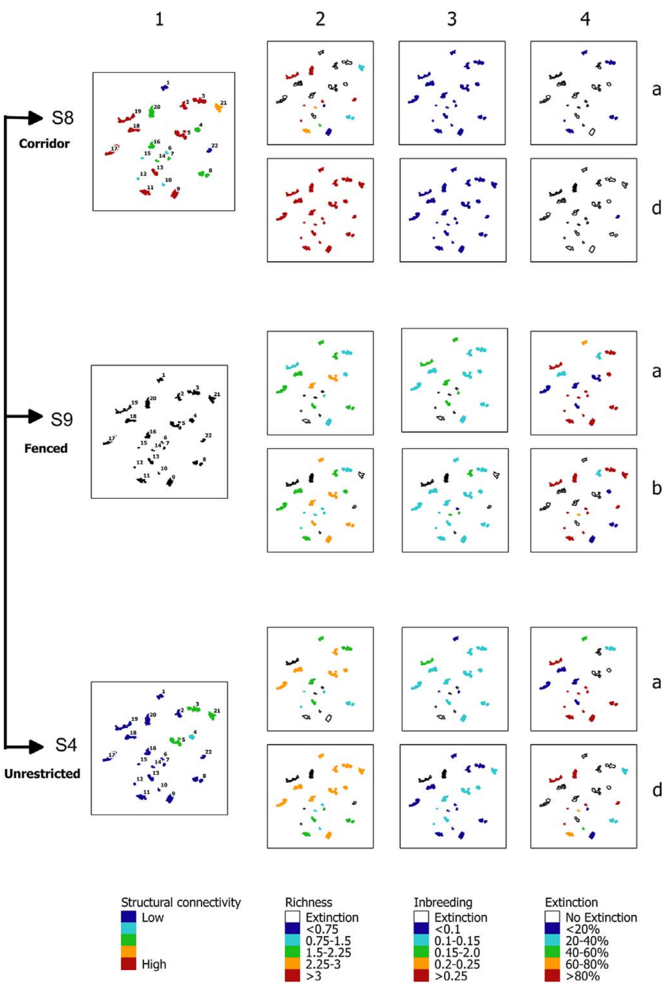
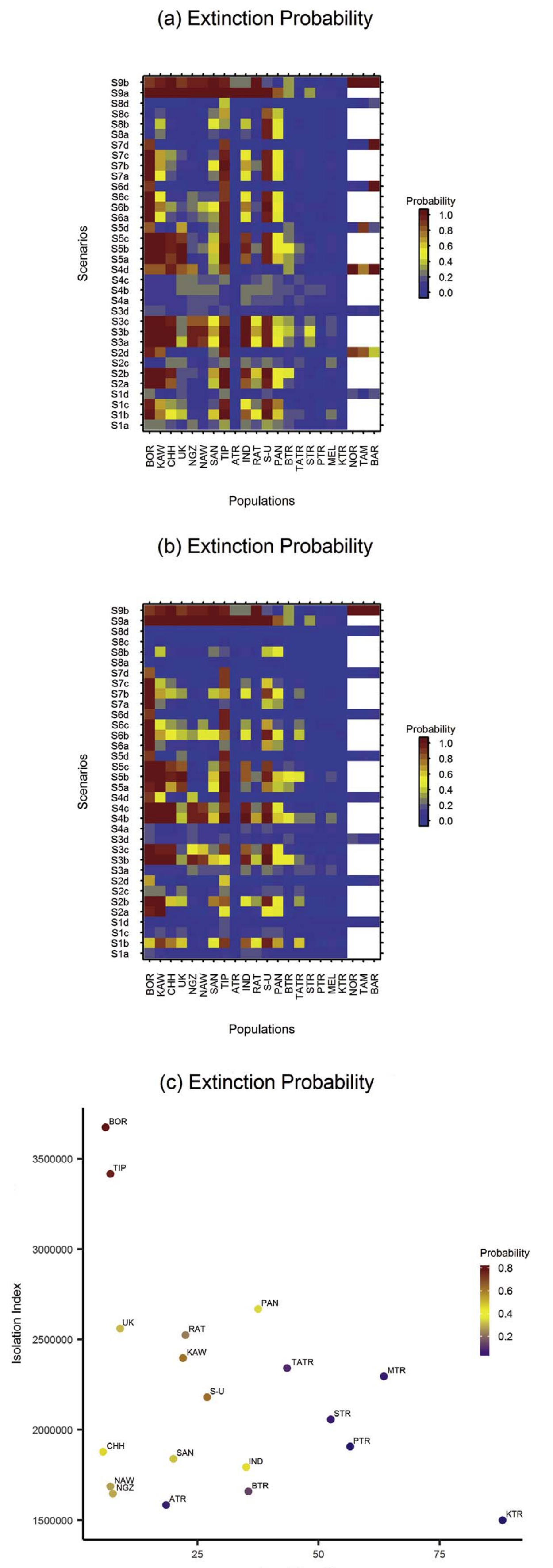


Fig. 2. Structural connectivity, allelic richness, inbreeding and extinction after 100 years under selected management scenarios. The 3 management scenarios in this figure have corresponding panels with two sub-scenarios (a- tiger number does not increase and d- increase in tiger number) and 4 plots each representing management outcomes for (L to R): 1-structural connectivity, 2-allelic richness, 3-inbreeding estimate, and 4-extinction probability. The structural connectivity is the same for sub-scenarios a and d. Hence there is a single structural connectivity plot for each of the management outcomes. Completely isolated PAs (scenario F9) are represented in black. The outcomes for different scenarios can be compared within a column. The coloured areas in each plot are the protected areas and their colour represents the scenario-specific outcome. The gradient from blue to red represents low to high (structural connectivity, allelic richness, inbreeding coefficient and extinction probability). Blank PAs in the plots within columns 2 and 3 are the PAs which go extinct by the year 2100. Blank PAs in column 4 (extinction probability plots) are the ones which do not show extinction in any of the 100 replicate simulation runs. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

connectivity. Dense human settlements and roads with high traffic offered highest resistance to movement. Degraded forests and plantations offered negligible resistance and agriculture-village matrix offered low resistance to tiger movement. However, long contiguous stretches of agriculture-village matrix could lead to accumulation of cost over space and impede movement. Our results are supported by empirical data on tiger movement. Recent data from radio-collared tigers reveals that long distance dispersing tigers do not avoid agriculture-village matrix and cross low traffic roads (Athreya et al., 2014; Krishnamurthy et al., 2016). Both, traffic intensity and dense human settlements have a non-linear relationship with resistance, suggesting that only very high-intensity traffic and high-density human settlements offered high resistance to movement (Table 3).

Roads are known to negatively impact genetic diversity and differentiation in animal species, especially for mammals and amphibians



(caption on next page)

Fig. 3. Extinction probability. (a) Matrix representing extinction probability for each population for each of the scenarios after 100 years-dispersal threshold 300 km (b) Matrix representing extinction probability for each population for each of the scenarios after 100 years-dispersal threshold 500 km. x-axis represents the PAs and y axis represents the scenarios and sub-scenarios (c) Scatterplot of population size (average of current size and size in sub-scenario d) vs. isolation index calculated as the average cost distance between populations. Each point represents a population and the colour represents it's average extinction probability across scenarios. NOR, TAM, BAR do not have any tigers currently and were only included in the simulation sub-scenario d where tiger numbers increase. Hence they do not have colour in panels (a) and (b) for scenarios a, b and c.
Scenarios: F1-No change in landscape, F2-Forest cover constant, F3-Area under agriculture constant, F4-Unconstrained landscape change, F5-Mines, F6-NH6 and NH7 as barriers, F7-NH6 and NH7 as barriers with gaps, F8-Corridors, F9-PAs fenced. Sub-scenarios: a-Tigers only inside protected areas, b-Tigers inside and outside (random), c-Tigers inside and outside (clustered), d-Tiger numbers increase. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

(Holderegger and Di Giulio, 2010; Shirk et al., 2010). However, most of these studies have been carried out in developed/industrialized countries where road density is high and many of the roads are fenced (Holderegger and Di Giulio, 2010). Although India has the second largest road network in the world, 46% of the roads are currently not surfaced (National Transport Policy Development Committee, 2013) and very few segments are fenced. As a result, even the existing national highways connecting major centers may be permeable to tiger movement on stretches with low traffic volumes and when other landscape features promote dispersal. However, this is bound to change in the future as roads will be widened to accommodate increasing traffic volumes.

4.2. Future change in diversity

Genetic diversity reduced over time in all simulated scenarios. Results suggest that even establishing corridors would not suffice to maintain the current level of heterozygosity. Our results are supported by Bay et al. (2013), where simulations of mitochondrial diversity revealed that even with geneflow, the number of tigers essential to maintain current heterozygosity would exceed the carrying capacity of PAs in peninsular India (Bay et al., 2013). Our simulations revealed that both increasing tiger numbers and maintaining connectivity were essential for preventing drastic reduction of heterozygosity.

4.3. Stepping-stone corridors preserve connectivity

Our simulations revealed that loss of forest cover due to the diversion of land for agriculture or infrastructure lead to high genetic differentiation. However, increasing number of tigers within existing PAs and allowing clusters of individuals to survive outside PAs decreased the observed genetic differentiation and inbreeding. Presence of breeding clusters of tigers outside PAs also reduced the probability of extinction. These intervening clusters aid in dispersal between the larger, more robust populations, thus forming ‘stepping-stone corridors’. Scenarios that incorporated stepping-stone corridors resulted in 10% higher genetic variation and 6–86% lower extinction probability compared to those without.

Habitat restoration and protection is critical.

Dinerstein et al. (2006) recommended restoring habitat to increase population connectivity between tiger conservation landscapes. Our results demonstrated that such habitat restoration to establish corridors reduced extinction probability by 68% (Scenario F8, Fig. 3a and b) and was critical for population persistence in the future. Such landscape restoration may require careful selection of areas so as to benefit both people and wildlife (Defries et al., 2007). This may be difficult to achieve between all pairs of PAs, especially those that have negligible structural connectivity between them. Our results revealed that increasing tiger numbers allowed large but currently degraded PAs (with few tigers) to achieve low extinction probability, underscoring the importance of better PA management and protection. Increased tiger numbers buffered against demographic stochasticity in small PAs and decreased the overall extinction probability. This was best demonstrated in the scenario where we added a buffer around the small PAs and extinction probability dropped by 23–70%. The government of India is taking steps to notify ‘Eco-sensitive Zones’ around PAs to regulate developmental activities (Mathur, 2012). However, our results suggest that unless connectivity is restored and stepping-stone populations protected (also suggested by Chundawat et al. (2016)), even such rescue effects would fail for small PAs when the landscape around them became unsuitable. Such extinction debt poses a significant challenge for conservation while these tiger populations still persist.

4.4. Low levels of inbreeding in Central Indian tigers of the future

Kenney et al. (2014) investigated the effect of inbreeding depression on population viability in tigers and found that even populations as large as (with 63–80 > 1 year old tigers) the big populations in our study have a high future risk of extinction due to inbreeding depression if connectivity was not maintained. Our results suggest that inbreeding did not increase appreciably over the next 100 years ($F < 0.25$ in all scenarios). Levels of inbreeding were lower than those known to impact fitness in mammals based on studies in the wild and captivity (Keller, 2002; Ralls and Ballou, 1982). Hence, we did not simulate the effect of inbreeding depression on survival and extinction. However, a further increase in the inbreeding coefficient over time may lead to inbreeding depression and increase extinction risk of even large populations. Our simulations suggest that inbreeding coefficient is likely to increase faster if tiger numbers do not increase in the future (Fig. S12).

4.5. Model assumptions and caveats

Overall, our framework provides the first snapshot of the potential to combine landscape genetics with spatially explicit simulations for tiger conservation. Future studies should investigate how different land-use change data and dispersal strategies would affect tiger connectivity in CIL. For example, future landscape change projection in our simulations was based on landscape change over one decade (2001 − 2012). Would longer decadal datasets help us better understand LULC change in the CIL? Additionally, our model does not allow for future land-use policy changes. For example, accelerated development could result in loss of connectivity in < 100 years. However, we do incorporate scenarios which demonstrate the impacts of specific infrastructure projects currently being undertaken or envisaged in the future (Scenarios F5–F7).

While modeling tiger dispersal, we did not consider the variation in behavioral response of individuals to land use change and the probability of locating a corridor. Modeling how individuals incorporate information about surrounding habitat while dispersing would improve the simulation results (Colbert et al., 2009). However, such data is currently not available. Future research should evaluate the influence of different dispersal strategies on tiger connectivity. Finally, our simulations investigating tiger connectivity assume a maximum dispersal distance, which is difficult to estimate in the wild. The two maximum dispersal distances of 300 and 500 km that we used were based on available data (Bowman et al., 2002; Natesh et al., 2017; Patil et al., 2011). A possibility of longer than 500 km dispersal cannot be ruled out, and hence we carried out simulations with a longer maximum dispersal distance (as suggested in Joshi et al. (2013)), results in the Supplementary material). This longer threshold led to lower genetic differentiation (in scenario F1) than currently observed, suggesting that this particular dispersal scenario may be overestimating the probability of long-distance dispersals. However, even with such enhanced dispersal distances, the key populations that needing management attention, the impact of infrastructure projects, and scenarios that lead to better outcomes did not change (Supplementary Figs. S6, S9–S12).

4.6. Implications for conservation planning

Our results reveal that multiple actions like delineating and maintaining corridors, with stepping-stone populations between PAs, along with increasing tiger numbers are necessary to maintain long-term viable tiger populations at a landscape scale. Our results highlight the immediate need for regional land-use management and planning exercises aimed at managing tiger populations as a network of PAs connected with corridors.

4.6.1. Land-use change

Currently, infrastructure development does not incorporate conservation goals while developing project plans, which could seriously undermine ongoing tiger conservation efforts within the landscape. Nearly 50% of India's population is projected to live in cities by 2030 (World Bank Group, 2015), and research has shown that built- up area increases faster than population increase in urban areas (Sudhira et al., 2004). Along with urbanization, coal requirement for electricity generation is projected to increase ~2.5 times by 2031–32 (Fernandes, 2012). To provide better connectivity between cities and to accommodate increasing road traffic (estimated to grow at about 13% per year over the next 20 years), massive infrastructure development projects are being undertaken (National Transport Policy Development Committee, 2013). Our simulations reveal the impacts of upcoming development on tiger connectivity. Ideally, expansion of the current road network should include realignment of new roads to avoid critical tiger habitat (see Raman (2011)). We show that widening national highways without installing crossing structures (NH6 and NH7, Scenario F6) in an area critical to tiger connectivity will increase genetic differentiation between populations on either side 19 to 65 fold. When alternative routes are not available, we strongly recommend planning and installing mitigation structures (under and over-passes) for wildlife passage before roads are built or widened. This is more economical than retrofitting existing roads and should be considered during the Environmental Impact Assessment (EIA) of new infrastructure projects (Glista et al., 2009). Our results (Fig. S9) highlight the importance of installing crossing structures for maintaining connectivity (F_{ST} increases by 80% from an average 0.025 to 0.13 in the absence of such structures). Currently, such regional level planning which aligns conservation goals with developmental plans is in its infancy in India. Our results provide impetus to such efforts by highlighting landscape variables that need to be considered while developing infrastructure plans.

4.6.2. Forest diversion and mining

Diversion of forest for mining is one of the major causes of loss of forest cover and structural connectivity within the CIL. Over the last 3 decades, 40% of the total forest land diverted has been for mining (Centre for Science and Environment, 2012). Coal mining alone accounted for 65% of the total land diverted for mining between 2007 and 2011 (Centre for Science and Environment, 2012). If along with other minerals being mined, all the coal blocks in the study landscape were opened for mining, the mined area and associated increase in built-up area would lead to ~22% higher extinction probability even for large PAs in proximity to these blocks. We emphasize the urgent need to protect the delineated corridors (as in Qureshi et al. (2014)) for preserving connectivity to prevent extinctions.

5. Conclusion

Several species globally face threats due to anthropogenic impacts, similar to the tigers in our study area. Landscapes with high conservation value, especially in the tropics, have been changing rapidly due to increasing human population and exploitation of natural resource leading to conversion and degradation of habitat (Crooks et al., 2011; Elmhagen et al., 2015; Newbold et al., 2015). Our results highlight the urgent need for informed development plans that consider biodiversity and connected wildlife populations in addition to human development goals. With habitats of most large mammals getting increasingly fragmented, our approach of combining landscape genetics with forward-time simulations to estimate extinction probability and loss of connectivity provides a valuable tool for conservation management. Such an approach can help identify populations vulnerable to landscape change, improving conservation and management of populations, species and landscapes to ensure long-term persistence.

Acknowledgements

We are thankful to the Maharashtra, Madhya Pradesh and Chhattisgarh Forest Departments for providing the necessary permissions and logistical support for this research. We sincerely thank the forest department staff, field assistants and volunteers for their help and support during the fieldwork. We thank the Indian Resource Center for Clark Labs at Ashoka Trust for Research in Ecology and the Environment for letting us use their facilities. We thank V. V. Robin, Meghana Natesh, Y. V. Jhala and an anonymous reviewer for helpful comments on the manuscript. We are grateful to the National Tiger Conservation Authority (NTCA) (Sanction Order No.15-30/2011-NTCA dated 14-March-2012) of India for partially funding this study. We thank the National Centre for Biological Sciences (NCBS) for institutional support. PT was supported by Council for Industrial and Scientific Research fellowship and NCBS. UR was supported by the DAE outstanding Scientist Award.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2017.12.022.

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