Title

Protected corridors preserve tiger genetic diversity and minimize extinction into the next century

Authors

Prachi Thatte[1*], Aditya Joshi[2], SrinivasVaidyanathan[3]and Uma Ramakrishnan[1*]

Affiliations

1-National Center for Biological Sciences

2-Wildlife Conservation Trust

3-Foundation for Ecological Research, Advocacy and Learning

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*** *Corresponding authors:*** prachi.thatte@gmail.com; uramakri@gmail.com

Abstract

Maintaining connectivity among tiger populations is critical for their long-term survival in the wild. Population genetic data at 12 microsatellite loci from 116 individuals in Central India reveals connectivity is negatively impacted by dense human settlements and high-traffic roads, features likely to increase in the future with population growth and economic development. In order to investigate how populations, connectivity and genetic variation can be maintained, we simulated the impacts of future development scenarios over the next century. Unplanned development results in significant loss of genetic variation (35% lower) and an average extinction probability of 56% across protected areas. Persistence of populations will require increasing the number of tigers along with careful land-use planning to establish corridors between populations. Our approach allows quantitative evaluation of the effect of different land-use policies on connectivity and extinction, linking basic science to policy decisions.

Introduction

The current rate and magnitude of species decline and extinction are higher than ever before (Barnosky et al. 2011; Dirzo et al. 2014). Most mammalian species have lost more than 50% of their range over the last two centuries leading to substantial population decline and fragmentation of their habitat (Morrison et al. 2007; Dirzo et al. 2014). Substantial conservation efforts like monitoring populations, legal protection, reintroductions and translocations have allowed some species to recover (e.g. grey wolf in North America (Ripple & Beschta 2012) and brown bears in northern Europe (Hagen et al. 2015)). Much conservation attention is focused on tiger recovery, with less than 4000 individuals left in the wild.

Tigers have lost four subspecies and 93% of their historical range and what remains is highly fragmented. Tiger range countries spend around US $50 million annually on conservation, most of which is contributed by and spent in India (Walston et al. 2010). With about 65% of the world's tigers (Jhala, Y. V.;Qureshi, Q.;Gopal 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, Y. V.;Qureshi, Q.;Gopal 2015). However, the median number of tigers in any protected area (PA) in India is low (median: 19, range: 2-215)(Wikramanayake et al. 2010; Jhala, Y. V.;Qureshi, Q.;Gopal 2015). Most populations by themselves may not be viable, and continued tiger survival may be contingent on the maintenance of connectivity between PAs.

Several independent genetic studies in Central India, a high priority tiger conservation landscape, confirm that PAs here exchange migrants and are fairly well connected (Joshi et al. 2013; Sharma et al. 2013; Yumnam et al. 2014). About 35% of India's tigers are estimated to live outside PAs (Jhala, Y. V.;Qureshi, Q.;Gopal 2015) and may play a critical role in maintaining connectivity. Most PAs are too small to harbor demographically and genetically viable populations of tigers over the long-term (Dinerstein et al. 2007) and conserving areas outside the current PA network maybe important for continued connectivity.

Correlating genetic connectivity with landscape elements revealed that tiger connectivity is negatively impacted by human footprint on the landscape (Joshi et al. 2013). With increase in human population size and anthropogenic development in the future (United Nations 2014), linear infrastructure and urban areas are projected to increase (Planning Commission 2013; United Nations 2014) and will negatively impact tiger connectivity. Fragmentation can lead to creation of small isolated populations, which may have a high probability of local extinction due to environmental, genetic and stochastic reasons (Hanski, Ilkka A.; Gaggiotti 2004). However, these are general predictions: we do not know how land use change in the future will specifically impact connectivity between populations.

We examine genetic connectivity among tiger populations in the central Indian landscape including samples from within and outside PAs. We use these data to infer the effect of different landscape features on dispersal and connectivity. We then model how area under these lands-use classes may change in the future. Finally, we 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 tiger inside and inside/outside PAs. We also test the effect of increase in tiger numbers and effect of assumptions about dispersal, modeling a total of 70 scenarios.

Methods

Study area and sampling

The central Indian landscape has several PAs 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 non PAs) in the state of Maharashtra, Madhya Pradesh and Chhattisgarh (Figure 1). See S1 for details

Genotyping and population genetic analysis

Standardized methods were used to extract DNA and identify individuals(Mukherjee et al. 2007; Mondol et al. 2009b). Heterozygosity based differentiation statistics were calculated using packages PopGenReport (Adamack & Gruber 2014), MMOD (Winter 2012) and HIERFSTAT (GOUDET 2005) in R (Ihaka & Gentleman 2012). We used STRUCTURE v. 2.3.4(Pritchard et al. 2000) for an assessment of population structure. See S2 for details.

Landscape genetics analysis

Following layers were used to build resistance models- land-cover, human settlements, roads, railway-lines and density of linear features. Refer S3 for details.

Previous studies carried out on tigers in the same landscape have found the genetic distance to be a function of isolation-by-resistance (as opposed to isolation-by-distance) (Joshi et al. 2013; Yumnam et al. 2014). However, unlike these past studies (Joshi et al. 2013; Yumnam et al. 2014), we used genetic data (inter-population D_{PS}) to infer resistance values using multi-model optimization approach described in Shirk et al (2010). Each landscape variable was related to landscape resistance using a simple 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 highest significant correlation with genetic data, after controlling for the effect of geographic distance. Variables with a significant correlation in such a partial Mantel's test (Smouse et al. 1986) were retained for further analysis. The univariate models 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 inferred landscape resistance data to see how changing landscapes changes the resistance surface (and therefore, connectivity) as described below.

Landscape genetic simulations

We explored the effects of future landscape change on tiger connectivity. Land Change Modeler in IDRISI (Selva, http://www.clarklabs.org) was used for assessment and projection of land-cover change based on the change in land cover, road width and nightlight from 2001 to 2012. Future landscape predictions were generated for every 20 years for the next 100 years. See S5 for details.

Simulations were carried out for nine landscape change scenarios (see Table 1 for the scenario description and rationale). Simulations for each of the first eight scenarios were carried out under 4 sub-scenarios. Sub-scenario a) with tigers restricted to PAs (current numbers constant), b) with tigers inside and outside PAs (outside individuals distributed randomly), c) with tigers inside and outside PAs (outside individuals clustered in space) d) with tigers restricted to PAs (numbers increase). See S5 for details. Table S4 provides information on current population sizes, PA areas and increase in population sizes. Each simulation was repeated at two different dispersal thresholds (300km and 500km) to understand the effect of scale on connectivity (see S5 for details).

The simulations included nine other PAs (see S5 for details). These areas were not included in the previous part of the study since some of them have no tigers currently and we did not have permits to sample in the others.

Forward time simulations were carried out based on the current genetic variation and inferred effect of landscape variables using CDPOP (Landguth & Cushman 2010) (see Table S1 for simulation parameters). We simulated 20 generations (=100 years for tigers) of mating and dispersal, the probabilities of which were governed by matrices of pairwise cost distances between individuals. At the end of each simulation, we calculated genetic diversity indices (heterozygosity, inbreeding estimate and allelic richness) and differentiation indices (Global and pairwise Fst and G'st) using R package PopGenReport and adegenet (Jombart 2008; Adamack & Gruber 2014). Probability of extinction of each population was estimated, based on the number of times a population goes extinct among the 100 replicate runs for each simulation.

Results

Population Genetic Analysis

Out of the 289 samples that were identified as tigers, data for more than 8 microsatellite loci could be generated from 127 samples, 116 out of which were identified as unique individuals. Probability of misidentifying individuals and genotyping error rates were low (see S6 for details).

We found two major genetic clusters (K=2, STRUCTURE, Figure S4)- a northern and a southern cluster. Individuals from TATR, BPR, UK, TIP, CHA and BOR formed the southern cluster. The northern cluster consisting of PTR, KTR, NGZ, ATR, BAL and BTR showed further sub-structuring, with BTR separating out as distinct cluster (at K=3).

Landscape Genetic Analysis

Human settlement layer was the most important (highest magnitude of correlation) landscape variable explaining genetic distance between populations. Land use and traffic intensity on roads also explained significant variation, even after accounting for geographic distance. These three variables- traffic intensity on roads, human settlements and land use were retained for multivariate optimization (Table 2).

Shape parameter (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 interaction between these variables. Non-linear transformations (shape parameter >1) suggest, that roads with low to moderate traffic offer negligible resistance to movement. However, the resistance increases steeply with very high traffic intensity. Final estimated parameters are presented in Table 3. Correlation between the pairwise cost distance among populations (estimated from the combined resistance surface) and genetic distance was high (0.7857, geographic distance controlled, 0.8166 geographic distance not controlled). Isolation by distance model (geographical distance alone) had poorer explanatory power (r=0.624).

Future change in connectivity

Genetic diversity reduces over time in all simulation scenarios. Restoring and protecting corridors between PAs results in minimal decline in genetic variation. Heterozygosity decreased faster and was lower at 100 years for lower dispersal threshold (300km) scenarios. Within both the dispersal categories, the loss of genetic diversity was greater when forest cover loss was higher (Figure S5). Figure 2 summarizes the implications of different management decisions on genetic variation 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. Small PAs that are currently well connected (UK, CHH, NGZ and NAW) had a 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 and S-U) also had high extinction probability except in the sub-scenarios where tiger numbers increase. Large isolated PAs (RAT and NOR) which currently have a low number of tigers had high extinction probabilities in all the scenarios, except in scenario 8 where forest is restored to establish corridors between PAs.

Change in connectivity: specific infrastructure projects

Increase in mined area and associated increase in built-up area lead to ~18 times higher extinction probability of even large PAs (BTR, SAN, TAM and TATR) which are near coal fields. Presence of NH7 as a barrier without any gaps(scenario 6) increased the F_{ST} between KTR and PTR ~4 times compared to scenario 1 and scenario 7 (Figure S8). NH7 bisects the corridor between these two PAs. NH6 bisects the corridor between NGZ and NAW and scenario with NH6 as a barrier (scenario 6) leads to ~42 times higher probability of extinction. Within a scenario, sub-scenarios c (tigers inside and clustered outside) and d (increase in tiger numbers) lead to overall lower extinction probabilities and a lower reduction in heterozygosity.

Discussion

Current connectivity

Our population genetic data is more extensive in spatial coverage than any study so far (1,22,217 km^2 (Sharma et al. 2012; Joshi et al. 2013; Yumnam et al. 2014)). The Central Indian landscape is differentiated into two major clusters, with sub-structuring within one of them, suggesting ongoing genetic differentiation. The two major clusters have structural connectivity are not completely isolated. The intervening PAs (NGZ, NAW and UK) that may act as connecting links (as suggested by centrality analysis (Dutta et al. 2015) and movement reports (Times News Network 2013; Pinjarkar 2014)), but are among the smallest in the landscape. Our simulations suggest that they have high extinction probability in the future, making them weak links unless corridors are established.

What impacts current connectivity?

Dense human settlements and roads with high traffic were found to offer highest resistance to movement. Degraded forests and agriculture-village matrix offer negligible and low resistance respectively. Our results are supported by empirical data on tiger movement. Recent data from GPS radio-collared tigers reveals that long distance dispersing tigers do use agriculture-village matrix and cross low traffic roads (Athreya et al. 2014; Krishnamurthy et al. 2016). India has the second largest road network in the world, yet only 54% of the roads are surfaced (Planning Commission 2013) and very few segments are fenced. As a result, even national highways connecting major centers may not act as complete barriers since all segments of the highways do not have equally heavy traffic. This may change in the future with increase in intensity of traffic and highways being widened.

Future change in diversity, connectivity and extinction

Genetic diversity reduces over time in all the simulation scenarios. Even establishing corridors along with restoration of habitat is insufficient to maintain current genetic variability. Our results support suggestions of Bay et al (2013) where simulations of mitochondrial diversity revealed that even with connectivity, a very large number of tigers are essential to maintain current level of diversity (Bay et al. 2013). Put simply we suggest that both increase in the number of tigers and maintaining connectivity are essential to prevent drastic reduction of genetic variation.

Stepping-stone corridors preserve connectivity

Our simulations show that loss of forest cover due to diversion of land for agriculture, infrastructure, etc leads to high genetic differentiation. However, increasing the number of tigers and having individuals in clusters outside PAs decreased the observed genetic differentiation and inbreeding estimate. Presence of breeding clusters of tigers outside PAs also reduced the probability of extinction dramatically. These intervening clusters aid in dispersal between the larger, more robust populations, thus forming 'stepping-stone corridors'.

Habitat restoration and protection are critical

Dinerstein et al (2006) had recommended restoring habitat to increase population connectivity between tiger conservation landscapes(Dinerstein et al. 2006). Our results (Scenario 8, Figure

3a and 3b) demonstrate that such habitat restoration to establish corridors between PAs would be critical for persistence of populations in the future. Such landscape restoration will require careful selection of areas so as to benefit both people and wildlife.

Our results show that increasing tiger numbers decreases the extinction probability of tigers in PAs that have a large area but currently have low tiger numbers, suggesting the importance of better PA management with greater protection for future persistence of these populations. In the case of small PAs, an increase in tiger numbers can act as a buffer against demographic stochasticity decreasing the overall extinction probability, but even this may fail in the case of already isolated populations except when connectivity is restored. Such extinction debt poses a significant challenge for conservation while these populations still persist.

Low levels of inbreeding

Our results suggest that inbreeding does not increase appreciably over the next 100 years ($F < 0.25$ in all scenarios). Levels of inbreeding appear lower than are known to impact fitness in mammals based on studies in the wild and in captivity (Ralls & Ballou 1982; Keller 2002). Hence, we have not simulated the effect of inbreeding depression. However, further increase in the inbreeding co-efficient over time may lead to inbreeding depression and increase the extinction risk of even large populations (Kenney et al. 2014).

Implications for Conservation Planning

Our results have significant implications for regional land-use management and planning. Nearly 50% of India's population is projected to live in cities by 2030 (World Bank Group 2015).

Coal requirement for electricity generation is projected to increase ~2.5 times by 2031-32 (Greenpeace 2012). Road traffic is estimated to grow at about 13% per year over the next 20 years although the road transport system is already facing capacity constraints. To meet these demands, massive infrastructure development projects are being undertaken (Planning Commission 2013). Prevention of new infrastructure projects inside PAs and realignment of new roads to avoid critical tiger habitat should be prioritized while planning development (as recommended by (Raman 2011)). Overpasses and underpasses of various sizes and types are being built worldwide, to mitigate the negative effects of existing roads on wildlife (Lesbarrères & Fahrig 2012). Our results suggest that having such structures is essential to maintaining genetic connectivity. Research shows that planning and installing structures for wildlife passage before roads are built or widened is more economical than retrofitting existing roads and should be considered during the environment impact assessment of the infrastructure projects (Glista et al. 2009). Currently, such planning is in its infancy in India. Our results should provide impetus to such efforts.

Diversion of forest-land for mining is another major cause for loss of structural connectivity within the landscape. Coal mining alone accounted for 65% of the total land diverted for mining between 2007 and 2011 (Centre for Science and Environment 2012). Our simulations show that increase in mining area and associated increase in built-up area would isolate certain PAs and steeply increase their extinction risk. There is an urgent need to delimit corridors to preserve vital connections between populations. Our approach can be used to create a software module to test connectivity/extinction impacts of alternate development scenarios and made accessible to park managers, local stakeholders and policy makers.

The St. Petersburg declaration on tiger conservation of 2010 envisaged doubling tiger numbers by 2022. Our simulations demonstrate that maintaining and/ or establishing connectivity and ensuring protection will be critical to achieve and sustain such increase in numbers. Along with corridors, designing, notifying and maintaining stepping stone populations within corridors between PAs is critical. Land-use planning should focus on concentrating people in well-planned, restricted areas and planning infrastructure projects in areas that do not hinder connectivity. Our results highlight the urgent need to plan development in the context of its impact on biodiversity and connectivity outcomes for endangered species. Such approaches will allow both development and conservation of tigers into the future.

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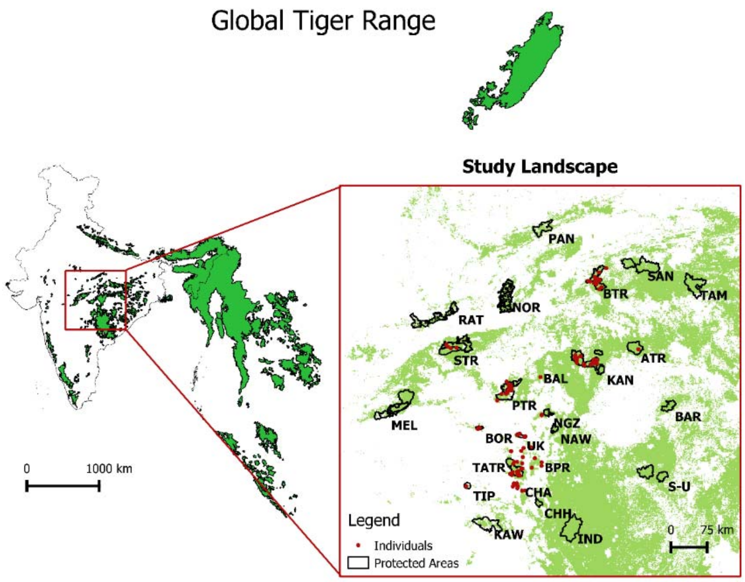
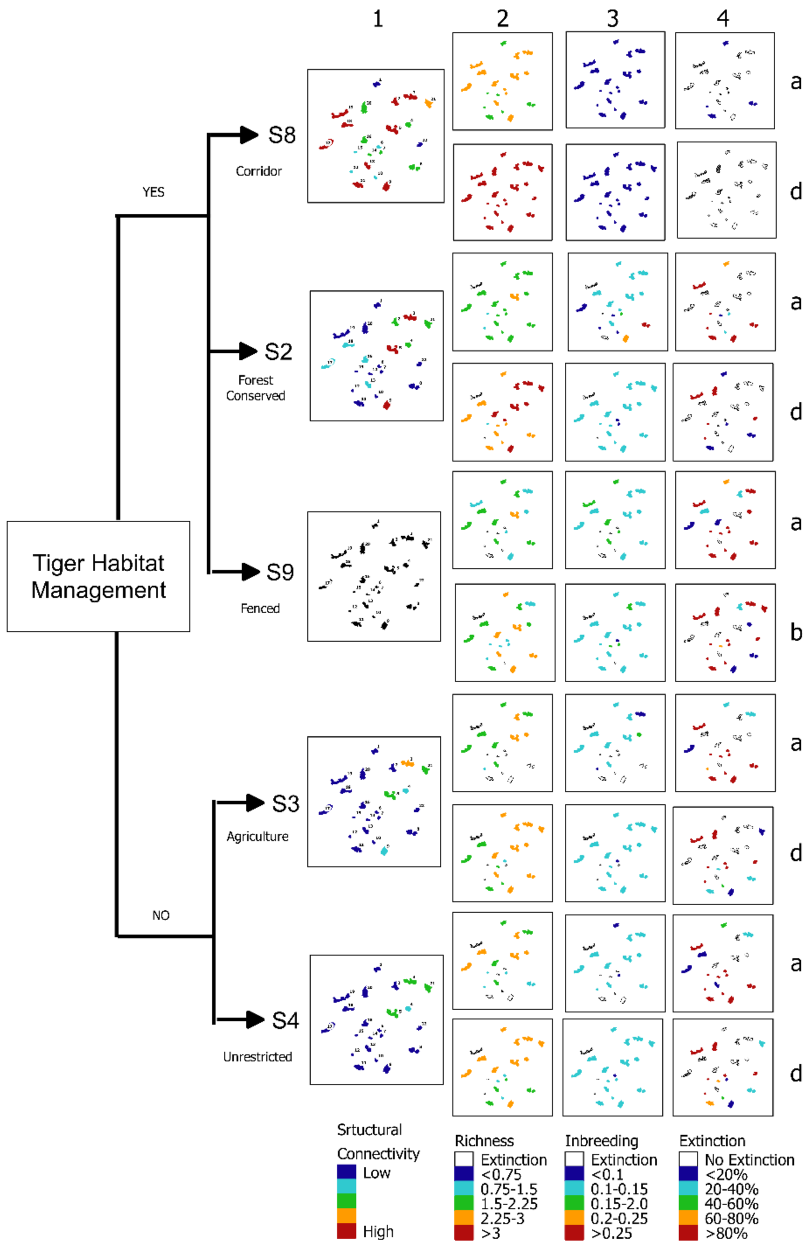
Figures and Tables

Figure 1. Global tiger range map with study area as inset



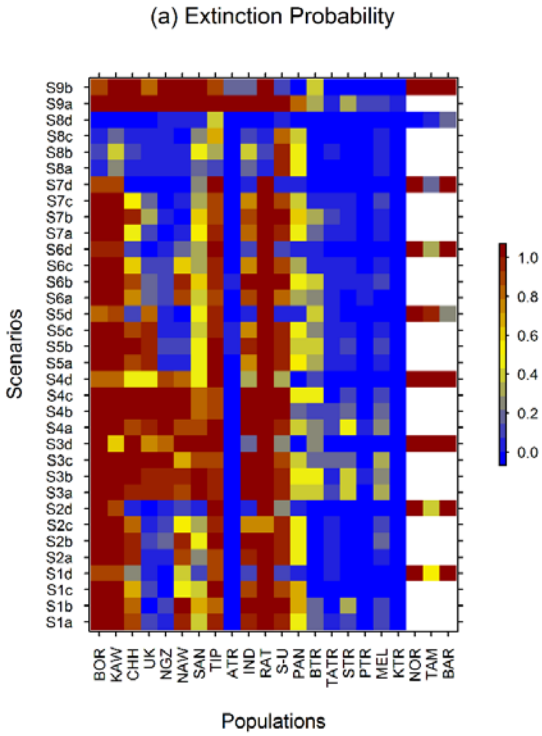
The map represents the global tiger range with the study landscape as an inset. In the inset, protected areas are marked by black outline and sampling locations as red dots.

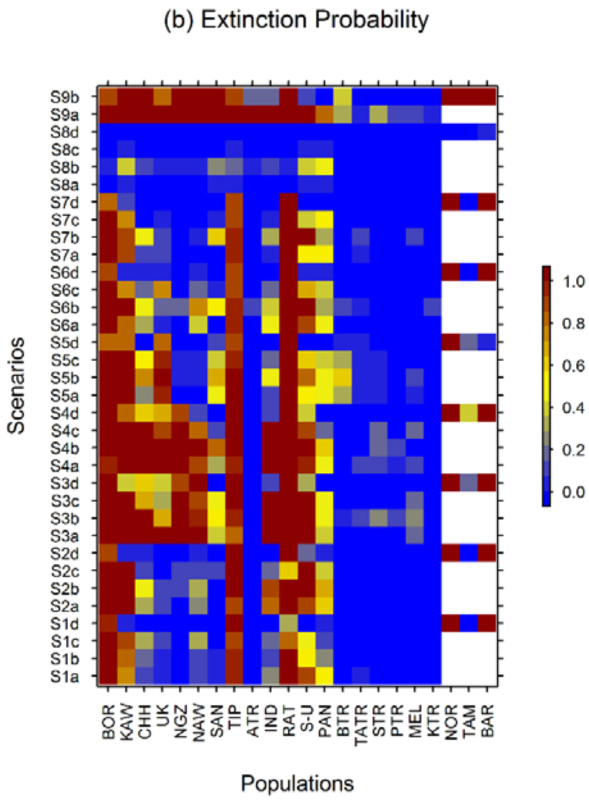
Figure 2.Structural connectivity, allelic richness, inbreeding and extinction after 100 years under selected management scenarios



The 5 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. Plots in the panels from L to R: connectivity index, allelic richness, inbreeding estimate, and extinction probability.

Figure 3. Extinction Probability




(b) Extinction Probability
Scenarios
S9b
S9a
S8d
S8c
S8b
S8a
S7d
S7c
S7b
S7a
S6d
S6c
S6b
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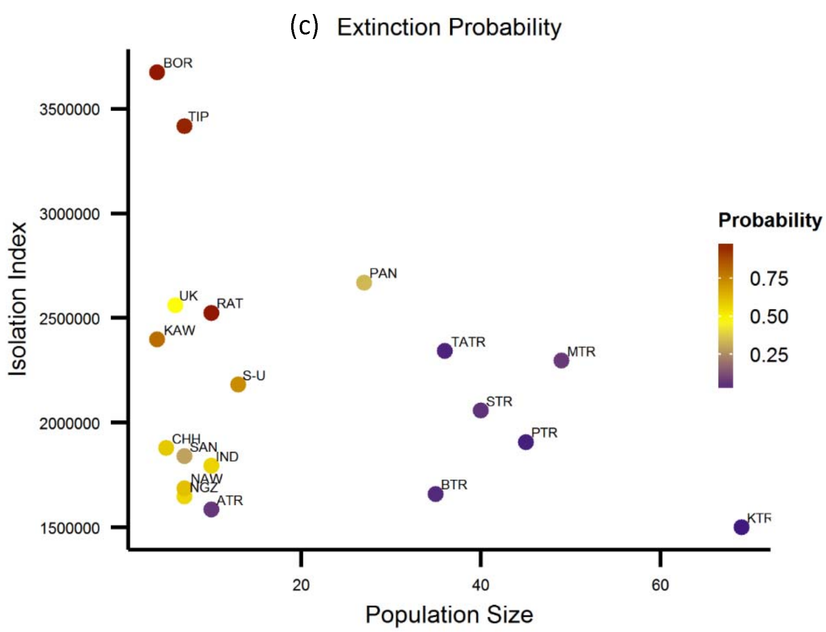
S1a
BOR KAW CHH UK NGZ NAW SAN TIP ATR IND RAT S-U PAN BTR TATR STR PTR MEL KTR NOR TAM BAR
Populations
1.0
0.8
0.6
0.4
0.2
0.0

414


(c) Extinction Probability
Isolation Index
3500000
3000000
2500000
2000000
1500000
BOR
TIP
PAN
UK
RAT
KAW
S-U
TATR
MTR
STR
PTR
CHH
SAN
IND
NAW
NGZ
ATR
BTR
Probability
0.75
0.50
0.25
20
40
60
Population Size

415

(a) Matrix representing extinction probability for each population for each of the scenarios after 100 years- dispersal threshold 300km (b) Matrix representing extinction probability for each population for each of the scenarios after 100 years- dispersal threshold 500km. x-axis represents the PAs and y axis represents the scenarios and sub-scenarios (c) Scatterplot of population size vs. isolation index calculated as the average cost distance between populations. Each point represents a population and the colour represents it's extinction probability.

Scenarios: S1-No change in landscape, S2- Forest cover constant, S3- Area under agriculture constant, S4- Unconstrained landscape change, S5- Mines,S6- NH6 and NH7 as barriers, S7- NH6 and NH7 as barriers with gaps, S8- Corridors, S9- 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.

Table 1. Landscape change scenarios for forward time simulations

Scenario	Description	Rationale
S1- No landscape change	Status quo	Null scenario
S2- Forest cover constant	Landscape change modeled while keeping the forest cover constant	The Green India mission under the National Action Plan on Climate Change (*66*) advocates achieving a forest cover of 33%. Current forest cover is 21% (*67*). In 1996, the supreme court of India redefined the scope of Forest Conservation Act 1980 and banned tree felling inside forests across India (*68*).
S3- 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(*53*)
S4- Unrestricted change	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 2001-2011. Although this rate reduced after 2011, the recent government's development driven policies are likely to increase the economic growth rate (*69*). The rate of granting forest clearances has also been highest from 2002- 2011 within the last three decades. 387952 hectare of forest land was diverted during this decade for defense, mining, irrigation, power projects, industries and infrastructure projects (*49*)
S5- 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 S1) 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 (*70*)	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 (*71*). 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 (*70*, *72*) and the setting up of DMF will only increase the rate of this conversion.
S6- 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 (*37*). 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) (*73*), 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.
S7- 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	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

S8- Habitat restoration to establish corridors between all PAs	The corridors were designated based on the least cost paths (generated using the gdistance package(*74*) in R(*59*)) 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 (*33*, *39*). We test how beneficial establishing these corridors would be.
S9- 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.

Table 2. Univariate optimization results

Landscape Variable	Maximum Resistance	Shape Parameter	Mantel's r	Partial Mantel's r	Significance (partial)
Nightlight (continuous)	10	0.1	0.823	0.689	0.002
Nightlight (Categorical)	10	0.1	0.816	0.683	0.001
Landuse	10000	10	0.806	0.678	0.001
Linear density	10	0.01	0.683	0.383	0.027
Roads (traffic)	10000	10	0.776	0.603	0.003

Table 3. Multivariate optimization results

Landscape Variable	Maximum Resistance	Shape Parameter
Human Settlement	1000	5
Landcover	100	50
Roads (traffic)	1000	10