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Spatial variation in the response of tiger gene flow to landscape features and limiting factors

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Abstract

Integrated landscape management of key population areas along with the corridors linking them is important for tiger conservation in the Indian subcontinent. Relationships between gene flow and landscape patterns, however, cannot be generalized given that different limiting factors influence movement in different spatial contexts**.** Here, we study the landscape features affecting tiger gene flow in the Western Ghats, and examine how and why limiting landscape features differ between Central India and the Western Ghats. We also assess whether these landscape features have been altered by land use changes in the last five decades. Our study area covers 30 000 km^2 from Bhadra Tiger Reserve to the Nilgiri Biosphere Reserve in India. We used genetic data of 115 tigers and landscape resistance model optimization to create a resistance surface to gene flow in the Western Ghats. Tiger gene flow, both in Central India and the Western Ghats, is primarily related to topographic roughness and secondarily to diffuse disturbance, however these relations are inverted in the two landscapes - in Central India, gene flow correlates with rough terrain, whereas in the Western Ghats, it correlates with smooth, forested terrain with minimal human disturbance. Topographic complexity is an important factor affecting tiger dispersal, but tiger's response to topography seems to be dependent upon interactions with human-related disturbance. Tigers in Central India favor rough terrain for dispersal primarily because it is the only part of the landscape without heavy human footprint and the last refuge for natural vegetation, whereas in the Western Ghats, forest cover is more extensive in flatter terrain and human footprint is generally lower.

Introduction

In order to draw meaningful inferences from landscape genetics it is essential to conduct multiple studies in different landscapes and on different spatial scales (Balkenhol *et al.*, 2016). Research findings on the influence of landscape patterns and processes on gene flow in one landscape often cannot be generalized and applied across multiple landscapes due to differences in limiting factors that influence movement in different spatial contexts (Cushman, Shirk & Landguth, 2013). This is especially true when landscape features vary considerably between areas, and extrapolations can lead to incorrect inferences about barriers to movement and functional corridors (Short Bull *et al.*, 2011; Vergara *et al.*, 2017). McGarigal & Cushman (2002) argued that strong inferences about the effects of habitat fragmentation require a meta-replicated approach where multiple independent landscapes are studied, and recently this has been applied in studies of habitat suitability (Shirk, Raphael & Cushman, 2014), and landscape genetics (Short Bull *et al.*, 2011; Vergara *et al.*, 2017). Understanding how and why differences are found in the factors that affect gene flow in different study areas has been identified as a priority area of landscape genetics research (Balkenhol *et al.*, 2016). Currently, there are only a few examples of meta-replicated studies in landscape genetics, but these have shown substantial variations in landscape factors affecting gene flow between study areas with different limiting factors (Short Bull *et al.*, 2011; Vergara *et al.*, 2017). Understanding the causes of these observed variations is critical to be able to produce clear insights into species biology and applications of the results to conservation planning.

The global wild tiger population is now approximately 4000 individuals, and is scattered across many small, fragmented subpopulations (Goodrich *et al.*, 2015). Effective conservation and recovery of the species will require a landscape management approach to protect core population areas and maintain connectivity between them to allow gene flow and prevent inbreeding depression (Johnson *et al.*, 2010). Landscape level planning to identify and prioritize core areas and

critical linkages requires an understanding of the animal's ability to respond and adapt to rapidly changing landscapes (Cushman *et al.*, 2013). Given the large home range size, low density and highly fragmented distribution of tiger, any attempt to understand its movement and population connectivity across a landscape requires investigations over several thousand square kilometers. Empirical data-based analysis of gene flow across such large landscapes can be challenging for rare species such as the tiger. However, recent research has demonstrated that multi-model optimization using landscape genetic methods produces more reliable predictions of the factors affecting population connectivity than expert opinion (Mateo-Sánchez, Cushman & Saura, 2014) or habitat-quality surrogates (Shirk *et al.*, 2015; Zeller *et al.*, 2018).

The tiger is a habitat generalist capable of persisting in different habitat types with a wide range of temperature and rainfall regimes (Sunquist, Karanth & Sunquist, 1999). However, the last few decades have witnessed dramatic changes and declines in natural ecosystems across the tiger's range, challenging the species' resilience and viability (Wikramanayake *et al.*, 2011). In India, forests with tiger presence occur largely in six landscape complexes – Shivalik Hills and the Gangetic plains, Central India, Eastern Ghats, Western Ghats, North-eastern Hills and Brahmaputra plains, and Sundarbans, each with its unique habitat characteristics and conservation issues (Wikramanayake *et al.*, 1999). These meta-populations consist of networks of subpopulations, which individually are usually too small for long-term viability in isolation, and which depend on broad-scale connectivity to support demographic rescue and gene flow.

To improve understanding about the effects of landscape structure on tiger dispersal, Reddy *et al.* (2017) optimized a resistance surface to gene flow across Central India by correlating individual genetic distance to landscape variables in a reciprocal causal modelling framework. They noted that after partialling out geographic distance, gene flow in Central India is primarily related to topographic roughness and slope position, and secondarily to human footprint and forest cover. Their study found that gene flow is facilitated by areas of rough topography and ridge tops which have relatively high forest cover and low human footprint. These findings, however, may not apply to all tiger landscapes within India, since landscape features which influence gene flow may not be detected until they are limiting, and different landscapes may limit dispersal and gene flow in different ways (Short Bull *et al.*, 2011; Cushman *et al.*, 2013; Vergara *et al.*, 2017).

We conducted a meta-replication of the study carried out in Central India (Reddy *et al.*, 2017) to identify the relationship between landscape features and tiger population connectivity in the northern parts of the Western Ghats. The Western Ghats are not only remarkable for their tropical biodiversity and high levels of endemism, but also host the largest contiguous tiger population in the world (Jhala, Qureshi & Gopal, 2015). Over centuries the land use and resultant landscape patterns in this region have differed dramatically from those in Central India. The aim of this study was to identify landscape features affecting gene flow of tigers in the Western Ghats and to assess how and why the limiting landscape features differ between Central India and the Western Ghats. A secondary objective is to assess whether landscape features in the Western Ghats have been altered by land use changes in the last five decades. Identifying differences in observed drivers of gene flow and explaining them based on differences in limiting factors is essential to generalize the understanding of the relationships between gene flow and landscape conditions (Short Bull *et al.*, 2011; Cushman *et al.*, 2013). Given the critical need for proactive landscape-level conservation to protect declining tiger populations, meta-replicated landscape genetics studies are particularly important for this species, and may provide clarity about what features drive genetic differentiation and under what conditions they become limiting to gene flow.

Materials and methods

Study area, sample details and DNA analyses

Our study area covers approximately 30 000 km^2 from Bhadra Tiger Reserve in the north to the Nilgiri Biosphere Reserve spanning Karnataka and parts of Tamil Nadu and Kerala (Fig. 1). We analyzed samples from Bhadra, Nagarhole, Bandipur, Mudumalai, Wayanad, Satyamangalam and Biligiri Rangaswamy Temple protected areas (Fig. 1), which include tiger faecal samples collected from 2008 to 2012, and forensics samples which came to the CCMB for species and individual identification from 2011 to 2015. We surveyed and collected large carnivore faecal samples along forest roads, pathways and near water bodies in core protected areas, in zip-lock covers with silica beads or in ethanol, and with all collection details duly noted. Details on study area and DNA analyses are given in Data S1.

Thematic layers

All thematic layers were projected in UTM and coarsened to 100 m spatial resolution. Details on layer preparation are given in Data S2.

Recent land use (median 2004-2005)

Land cover and land use categories were taken from the Roy *et al.* (2015) vegetation map of India (http://bis.iirs.gov.in). This map however focuses on natural vegetation, and underrepresents human-dominated areas. The NRSC (2014) 1:50 000 land use maps for the year 2012 (http://bhuvan5.nrsc.gov.in/bhuvan/wms) provided high resolution delineation of urban, rural and mining areas. Since tigers react to human presence, we added the NRSC (2014) developed areas to the Roy *et al.* (2015) map and this almost doubled the predicted developed area (to 2076 km^2). Relevant classes from the Roy *et al.* (2015) map were merged into (1) closed canopy forest/vegetation providing concealment, (2) scrub forest and open vegetation, (3) agriculture-village mosaic, (4) urban areas, and (5) water bodies.

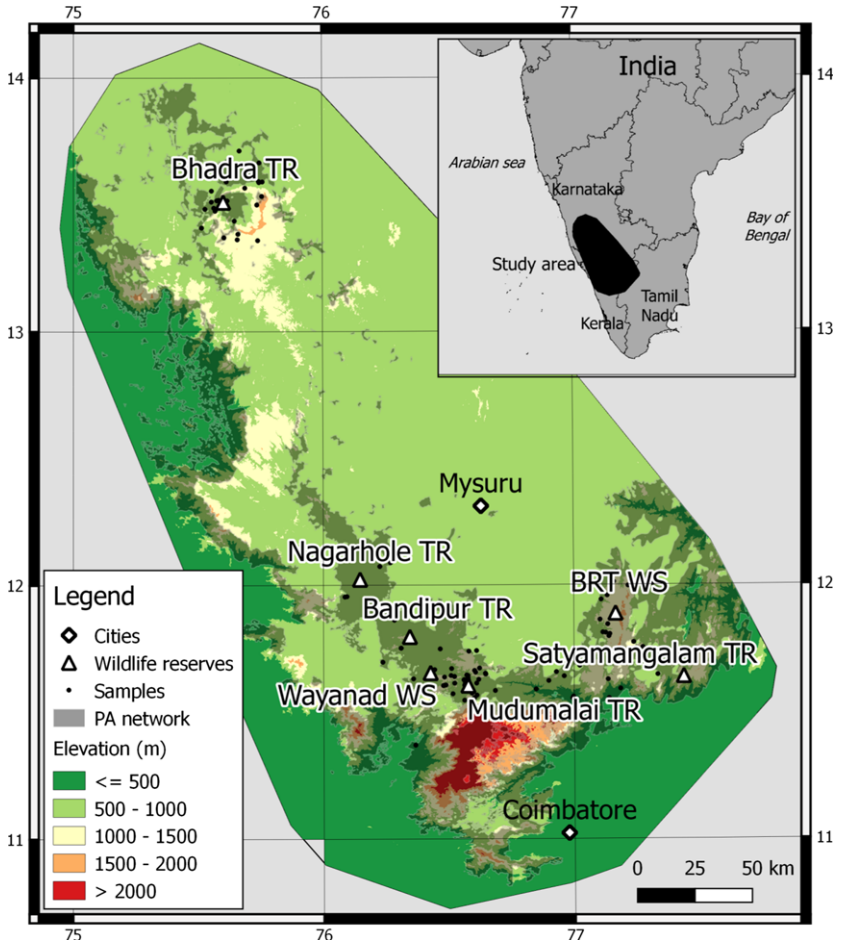

Figure 1 Extent of study area and geographical locations of tiger samples in the Western Ghats.

Land use in the 1960s

There are often time lags in the response of gene flow patterns to landscape changes (Landguth *et al.*, 2010; Reding *et al.*, 2013), and so it is important to evaluate whether past landscape patterns improve prediction of current genetic structure. To accomplish this, two 1:1.000.000 land use maps from the 1960s (Gaussen *et al.*, 1961, 1964) were digitized to provide historical vegetation cover.

Roads

The original road map was downloaded from OpenStreetMaps (http://openstreetmap.in/#5/22.150/79.081). Roads were coded as: ordinary roads (1), state highways (2), and national highways (3).

Roughness and slope

For terrain elevation, we used the ASTER global digital elevation model from the Shuttle Radar Topography Mission (SRTM) (Jarvis *et al.*, 2006; ASTER GDEM Validation Team, 2009). We derived topographical roughness and relative slope position from the DEM and these were calculated using Geomorphometry and Gradient Metrics Toolbox (Evans *et al.*, 2014) in ArcGIS 10.0 at a focal radius of 450 m.

Univariate resistance model functions

We evaluated the hypotheses that gene flow in tigers is influenced by present and past land use, roads, topographical roughness, relative slope position and human disturbance. To make the results directly comparable to the previous study of tiger gene flow in Central India (Reddy *et al.*, 2017) we used comparable data sets, and an identical modeling approach. The methods used in this study and Reddy *et al.* (2017) have been shown through extensive evaluation with simulation modeling to have high power and are among the best methods currently available to predict landscape resistance to dispersal using genetic data (Shirk, Landguth & Cushman, 2017). As in Reddy *et al.* (2017), we evaluated five levels of maximum resistance (R_{Max} = 5, 10, 20, 40, 80) for each variable, in which resistance was scaled from 1 to R_{Max}. In addition, we evaluated a range of power functions

(Shirk *et al.*, 2010) that control the shape of the functional response between the landscape variable and resistance to gene flow, ranging from concave downward (power p = 0.1) to concave upward (power p = 4). Landscape resistance was calibrated between 1 and Rmax for each raster with the formula:

$$R = 1 + (R_{\max} - 1)\left[\frac{x - \min}{\max - \min}\right]^{p},$$

where "min" was the minimum value of a layer, and "max" the maximum value. Further details are given in Data S2.

Resistance model optimization

Following the method of Shirk *et al.* (2010), we evaluated the strength of support for each landscape variable (present land use, past land use, roads, topographical roughness, inverted topographical roughness, relative slope position, inverted relative slope position and human-related disturbance) across the full suite of thematic resolutions. We used the costmat function in sGD (Shirk, Cushman & Landguth, 2012) to model isolation by resistance and construct a pair-wise resistance matrix for each landscape resistance surface. We assessed correlation between matrices using Mantel tests with the ECODIST package in R (R Core Team, 2016). We evaluated the partial Mantel correlation after 'partialling out' Euclidian distance to detect the influence of variables without the isolation by distance (IBD) effect. For each landscape variable, we identified the top candidate model by its significance based on the lowest p-value. A total of 22 roughness resistance layers and 5 diffuse disturbance layers had p-values less than 0.15. Each roughness resistance layer was added to each diffuse disturbance layer, giving a total of 110 composite resistance layers that allowed us to identify the most significant bivariate model.

FRAGSTATS

In order to compare differences in limiting factors between the two meta-replicated study areas, Western Ghats and Central India (Reddy *et al.*, 2017), we calculated a number of landscape metrics with FRAGSTATS (McGarigal, Cushman & Ene, 2012), including aggregation index (AI, an index that increases when patches are clumped and compact), edge density (ED), number of patches (NP) and percentage of the landscape occupied by a particular path type or class (PLAND). The four metrics were measured in circular moving windows of radii 250, 500, 1000, 2000 and 4000 m. FRAGSTATS produced 80 maps, given the two regions, four metrics, two land use categories and five scales. The rasters were imported in R and we extracted values at 100 000 random locations, from which histograms were produced. For each combination of metric, land use category and scale, two histograms were obtained, one from Western Ghats and one from Central India. The two histograms were superimposed using the R package ggplot (Wickham, 2009; Data S3), and the metric distributions from Western Ghats and Central India were compared with Kolmogorov-Smirnov tests.

We further examined the correlations between topographical roughness and PLAND for tiger habitat and agriculture at 500 m scale. We produced 10 000 sampling points in each study area (Western Ghats and Central India). We removed the sampling points with no data. As the PLAND statistics could not be normalized, we examined correlations between the FRAGSTATS metrics and roughness with the Spearman rank correlation, rho.

Results

We collected 680 carnivore faecal samples from protected areas in the Western Ghats from 2008 to 2012, out of which 379 samples were found to be tiger-positive. Tiger-positive samples were genotyped at eight to thirteen microsatellite loci and we identified 102 individuals. We received and analyzed 13 forensic cases from our study area from 2011 to 2015, pertaining to tiger deaths where carcasses were found in respective forest areas, resulting in a total of 115 individual tiger genotypes for landscape genetic analysis.

Partial Mantel correlation, after partialling out the IBD model, was significant for topographic roughness and marginally significant for diffuse disturbance (Table 1). The other variables (present land use, past land use, roads, inverted topographical roughness, relative slope position and inverted relative slope position) were not significantly related to the tigers' genetic distance independent of geographical distance. Topographical roughness had optimal univariate thematic resolution with RMax value of 80 and power exponent of 0.1, indicating a high effect of roughness resistance, with a resistance increase that was concave downwards (resistance increased rapidly with high roughness). Diffuse disturbance had a univariate RMax value of 5, with much weaker effects on genetic distance than topography. The power exponent of 0.1 signified that the negative effects of diffuse disturbance were acting even at low densities of disturbance (strongly concave resistance curve).

The most supported bivariate model after partialling out the IBD model included topographic roughness together with diffuse disturbance (Table 1). The partial Mantel r also increased compared to the univariate models. In the bivariate

Table 1 Comparison of thematic resolution and model support for univariate and bivariate optimization of the relationship between genetic distance and land cover variables (topographical roughness and diffuse disturbance)

Scheme	Layer	*P*-value	*r*	R_{max}	Power
Univariate	Topographical roughness	0.023	0.08	80	0.1
	Diffuse disturbance	0.07	0.05	5	0.1
Bivariate	Topographical roughness	0.0041	0.11	10	0.5
	Diffuse disturbance			20	0.1

Univariate optimization reports thematic resolution (power exponent and R_{Max}) as well as partial Mantel *r* (controlling for distance) and *P*-value of the partial correlation with genetic distance for each variable. Bivariate optimization reports thematic resolution for each variable after multivariate optimization.

analysis, however, resistance due to roughness diminished from Rmax = 80 to Rmax = 10. Conversely, the resistance induced by human disturbance increased from Rmax = 5 to Rmax = 20. In both cases, the form of the function remained concave downwards, with a marked affect at low values.

Distributions of all FRAGSTATS metrics (Data S3) differed significantly between Western Ghats and Central India, except in one instance (NP at the scale of 250 m for agriculture). In the case of vegetation, (1) aggregation index (AI) was systematically higher at all scales in the Western Ghats compared to Central India, indicating a more compact distribution and lower fragmentation of tiger habitat in the Western Ghats, (2) edge density (ED) was lower at all scales in Western Ghats, also indicating lower fragmentation and higher habitat homogeneity, (3) the number of patches in the landscape (NP) was substantially lower in Western Ghats, again indicating lower subdivision and fragmentation and (4) the proportion of landscape (PLAND) in forest cover was systematically higher in the Western Ghats. The Kolmogorov-Smirnov statistic was maximum or approaching a plateau at the scale of 500 m for AI, ED and PLAND (Data S4). For NP, the difference between Western Ghats and Central India continuously increased with increasing scale. However, the strongest increase occurred between the scale of 250 m and 500 m. The 500 m scale consequently was the scale at which differences were most marked between the two regions for the metrics examined.

For agriculture, the Kolmogorov-Smirnov statistic was generally low, below 0.1. Even though FRAGSTATS metrics for the agriculture class were distributed differently, the difference was not marked, except for AI at the scale of 500 m and to a lesser extent at the scale of 1000 m, where agricultural patches tended to be more aggregated at these scales.

In the Western Ghats, PLAND was significantly and positively correlated to roughness (rho = 0.41, $n = 4692$, $P \ll 0.001$) for natural vegetation, and was significantly and negatively correlated to roughness (rho = −0.39, $n = 7706$, $P \ll 0.001$) for agriculture. In Central India PLAND was significantly but weakly correlated to roughness (rho = 0.03, $n = 4707$, $P = 0.02$) for natural vegetation, but was not correlated to roughness (rho = −0.02, n = 9054, $P = 0.08$) in the case of agriculture.

Discussion

Habitat selection by large mobile predators reveals a preference for extensive, undisturbed habitat, and sensitivity to ecosystem types and quality at various scales (Elliot *et al.*, 2014; Mateo-Sánchez *et al.*, 2014; Zeller *et al.*, 2016). The narrow range of conditions that are required to provide highly suitable home-range habitat however, do not seem to apply so strictly during dispersal (Wasserman *et al.*, 2012; Elliot *et al.*, 2014; Mateo-Sánchez *et al.*, 2015). For example, a study on brown bears (Mateo-Sánchez *et al.*, 2015) found that certain land cover types and transport infrastructure were restrictive factors for species occurrence, but did not appear to impede brown bear movements that determined observed genetic structure. Similarly, Elliot *et al.* (2014) observed that anthropogenic disturbance had much higher resistance to movement by territorial adult lions than juvenile dispersing lions, and Wasserman *et al.* (2010) found that American marten gene flow was much less restricted than habitat suitability. Given the fragmented nature of most conservation networks, establishing a species' requirement for dispersal in human-dominated landscapes will help design effective corridors among reserves. This is particularly true for tigers which have vast area requirements, and live in low density and extremely fragmented subpopulations in highly human-dominated landscapes.

It is now well established, however, that one must be careful in generalizing observations on population connectivity. What is true in one region may be modulated differently in another, hence the need for meta-replication (McGarigal & Cushman, 2002; Short Bull *et al.*, 2011; Cushman, Lewis & Landguth, 2014). Shirk *et al.* (2014) found that the American marten (*Martes americana*) depends on riparian forests in mesic habitats, and on canopy cover and avoidance of forest clearings in xeric habitats. In the context of landscape genetics, Short Bull *et al.* (2011) observed that forest cover was limiting to gene flow in American black bear when forest was highly fragmented, and roads were limiting when there were a large number of roads traversing a landscape. Similarly, Vergara *et al.* (2017) found that topography limited gene flow in stone marten in landscapes with high heterogeneity in elevation, and cover was limiting when there was high heterogeneity in the pattern of land cover. When an ecological characteristic such as forest cover becomes a limiting factor in a landscape, it alters the relationship a species forms with its habitat. Therefore, it is important for landscape genetics research to investigate limiting factors and how they differ in different regional contexts (Cushman *et al.*, 2014; Balkenhol *et al.*, 2016).

Reddy *et al.* (2017) observed that tiger gene flow in Central India was related to topographic roughness and slope position, and secondarily, to human footprint and land cover, independently of Euclidean distance. Another study by Krishnamurthy *et al.* (2016) also found that landscape resistance to tiger movement in Central India was primarily related to topographical roughness, forest cover and human footprint. Given the different ecological and human histories of Central India and the Western Ghats, we expected *a priori* that there would be differences in terms of which variables would be related to gene flow and tiger movement. Specifically, the Central Indian landscape is much more fragmented, with lower forest cover, higher forest fragmentation, and higher human population density. As a result we expected that there would be much stronger association of gene flow and tiger movement with rough topography where human presence is lower in Central India, and more association with flatter topography in the Western Ghats, given the lower human footprint in that part of India.

In the Western Ghats, topographic roughness was significantly and positively correlated to genetic distance, after partialling out Euclidean distance, whereas diffuse disturbance was positively and marginally significantly correlated to

genetic distance (Table 1). Distance, topographic roughness and human-related disturbance were consequently the main correlates to genetic structure in both the landscapes. However, several differences became apparent between the Western Ghats and Central India. Firstly, fewer explanatory variables were detected in the Western Ghats and secondly, the relation between gene flow and topographic roughness was inverted.

The reason why fewer variables were detected as explanatory variables in the Western Ghats may be related to sample size: we used genetic data of 115 tigers in the Western Ghats compared to 309 tigers in Central India (Reddy *et al.*, 2017). Our sample size may have been insufficient to detect the effects of more explanatory variables. However, as shown by Landguth *et al.* (2012), the power to detect landscape genetic relationships is relatively robust when sample sizes are greater than 100 and is primarily related to the number of markers and genetic diversity of the samples. Given that genetic diversity was as high in the Western Ghats as in Central India, and the number of markers was similar, we do not believe the difference in results can be explained by sample size, genetic diversity or number of markers. Therefore, we believe differences in variables and number of variables reflect ecological differences between the two regions. Specifically, the lower number of variables indicates that fewer landscape features are limiting to tiger dispersal in the Western Ghats landscape. In particular, land use and natural vegetation are not sufficiently fragmenting to alter patterns of genetic differentiation in the Western Ghats, whereas they do structure population connectivity in Central India.

We also found an inverted relationship between topographic roughness and gene flow in the two landscapes. In Central India, gene flow correlated with rough terrain, whereas in the Western Ghats, it correlated with smooth terrain. As noted above, *a priori* we expected a difference of this kind, since human footprint and deforestation in Central India have resulted in a landscape where the only places with natural vegetation and low human impacts are rough ridges and other steep topography. Conversely, higher forest cover and lower habitat fragmentation in the Western Ghats do not limit tiger dispersal to rough terrain, which provides a refuge from human disturbance in Central India. In the absence of a strong anthropogenic driver, we would expect tiger movement and dispersal to be higher in flatter topography given the energetic and mechanical difficulty of moving through rough terrain, and this is indeed our finding in the Western Ghats. In most other species where topography was evaluated as a predictor of connectivity, connectivity was seen to be higher in areas with flatter topography (Puyravaud *et al.*, 2016; Vergara *et al.*, 2017).

An additional difference that may explain the inverse relationship with topographical roughness has to do with the topographical structure in the two areas. Specifically, in the Western Ghats there are a number of very steep escarpments that might act as physical barriers to animal movement. Puyravaud *et al.* (2016) found that the very steep cliffs surrounding the Nilgiri Plateau form an impassable barrier for elephant movement. Tigers are much more mobile and agile than elephants, but the negative correlation between gene flow and topographical roughness in the Western Ghats may

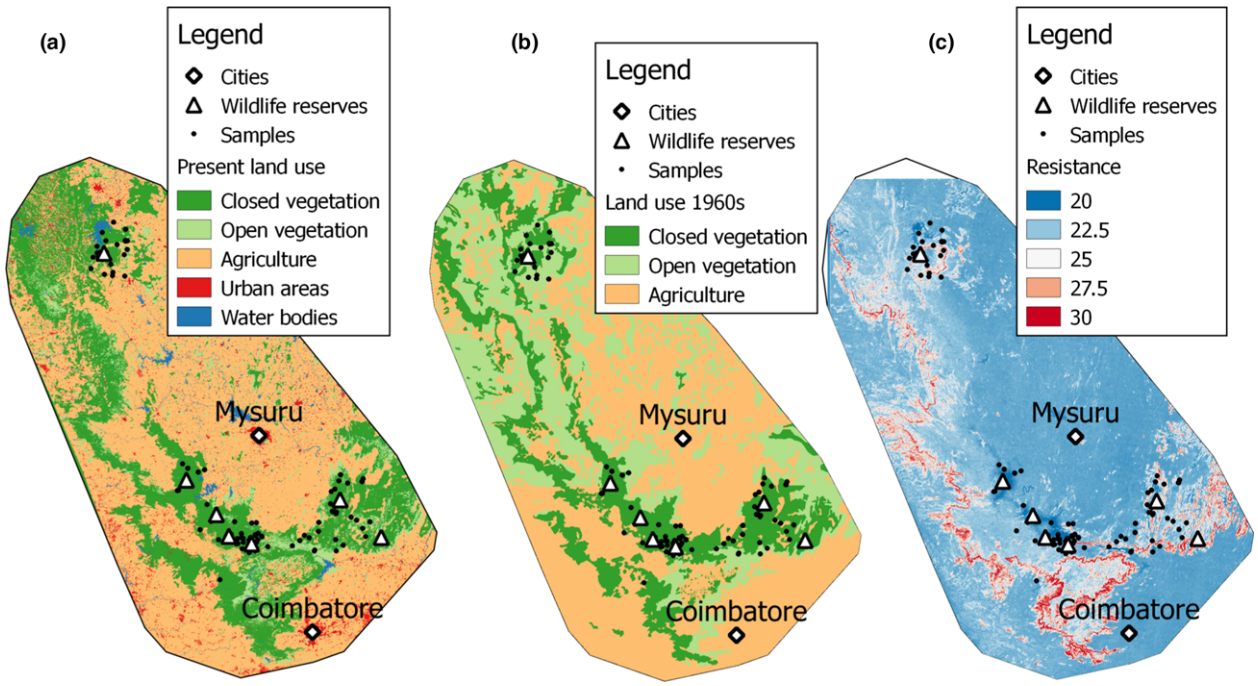

Figure 2 (a) Present land use, (b) land use in the 1960s, and (c) the best resistance model to tiger gene flow in the Western Ghats.

also reflect the higher barrier effect of these steep escarpment features for tigers, as compared to the less extreme topography in Central India. Furthermore, in the Western Ghats landscape, tiger reserves are distributed along the Western Ghats escarpment and Nilgiris Mountains. Connectivity among these patches of remnant tiger habitat seems to be limited by the steep cliffs of these escarpments and is concentrated in areas of lower topographical roughness that also have relatively low human footprint and high cover of natural vegetation.

The difference in the fragmentation of tiger habitat and tiger population may be another factor that can explain the different results between Central India and the Western Ghats. Specifically, FRAGSTATS metrics calculated on tiger habitat displayed significantly different distributions between the Western Ghats and Central India. The largest differences were observed at a 500 m radius. At this scale, tiger habitat was more extensive, more aggregated, more compact and less fragmented in the Western Ghats. Cushman *et al.* (2013) found that when habitat is highly extensive and aggregated its pattern does not strongly affect gene flow and its influence on population connectivity is often undetectable, which was seen empirically by Short Bull *et al.* (2011) and Vergara *et al.* (2017) as well.

Another focus of this study was the effect of landscape change and time lags on detected landscape genetic relationships. It is well known that there is a substantial time lag following landscape change until genetic structure equilibrates with landscape features (Landguth *et al.*, 2010). Landguth *et al.* (2010) found that it takes dozens to several hundred generations for genetic signals to equilibrate following landscape change, but also found that, using the individual-based approaches we utilized, the correlations between landscape features and genetic structure emerge relatively quickly and can often be detected within 10–20 generations. In the Western Ghats landscape, human population has increased greatly, with simultaneous development of agriculture, and progressive loss and fragmentation of natural vegetation and tiger habitat. In the 1960s, wildlife reserves near the future Bhadra Tiger Reserve, were still strongly connected to the southern set of reserves by mostly private forests (Fig. 2). Tigers had large tracks of the Deccan Plateau available for dispersal, which may explain why smooth terrain facilitates gene flow in this region. This situation is changing as habitat connectivity seems to now be severed (Fig. 2) between Bhadra Tiger Reserve and the Nilgiris Biosphere Reserve. In Central India, human population increase and development of agriculture seem to have been more randomly distributed as far as the landscape topology is concerned. This would naturally follow from the fact that there is no equivalent to the continental escarpment and climate gradient formed by the Western Ghats. As a consequence, avoidance of human settlements (since human footprint or human-related disturbance are always adversary to tiger gene flow) can be possible in Central India only in rough terrain. In the Western Ghats however, remnants of natural vegetation and reserves on the plains seem to facilitate gene flow. While this landscape history partly explains the inverse relationship with topography, we did not find stronger correlations between current genetic structure and past landscape conditions, suggesting the time lag between landscape change and genetic differentiation may not be strongly affecting observed landscape genetic relationships (Reding *et al.*, 2013).

Conclusions

It emerges from this study and from Reddy *et al.* (2017) that tiger dispersal is affected by landscape features. Topographical roughness is an important factor affecting tiger dispersal but the nature of that effect seems to be dependent upon limiting factors related to human disturbance. In the highly human-altered Central Indian landscape, tigers select rough terrain for dispersal, while in the Western Ghats landscape gene flow is correlated with flatter terrain. This difference is likely due to the relatively more extensive and less fragmented distribution of tiger habitat in the Western Ghats where conditions suitable for dispersal are not exclusively limited to the roughest ridgelines. Empirical data and connectivity models generated from this study will help in landscape level planning and management. In particular, this study demonstrates that factors affecting population connectivity of tigers differ depending on the extent and fragmentation of remaining tiger habitat and its distribution in the landscape. Our results suggest tiger dispersal is facilitated by areas of the landscape with natural vegetation and low human disturbance, and its relationship with topography can be variable depending on the pattern and character of these factors across the landscape. Differences in observed relationships between genetic differentiation and landscape features in these two regions of India provide a clear example of differing limiting factors, and these differences are important to understand the ecology and conservation of tiger, and to tailor conservation actions to most effectively incorporate the biology of the species.

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Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Data S1. Detailed description of study area and DNA analyses.
Data S2. Thematic layers and description of landscape variables used in univariate and bivariate resistance models.
Data S3. Histograms comparing FRAGSTATS metrics (AI, ED, NP and PLAND) distributions relative to vegetation (left histograms) and agriculture (right histograms) in the Western Ghats (blue histograms) and Central India (red histograms) at five scales (250, 500, 1000, 2000 and 4000 m radii). Axes labels indicate in order: the scale, the metric and the land use. D is the Kolmogorov-Smirnov statistic, and p is the probability of observing the value of D at random.
Data S4. Comparison of Kolmogorov-Smirnov D statistic (all non-zero values are very highly significant) between Fragstats metrics distributions in Western Ghats and Central India for tiger habitat (a) and agriculture (b).