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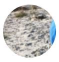

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Energetics-based connectivity mapping reveals new conservation opportunities for the endangered tiger in Nepal

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Abstract

Enhancing habitat connectivity is a key strategy for conserving endangered species in anthropogenic landscapes. However, connectivity planning often overlooks the crucial energetic costs to animals of traversing complex terrains. We applied a novel approach for estimating energy costs of movement for tigers – a globally endangered species. We used those estimates to calculate landscape connectivity for these animals across the extreme altitudinal gradient of Nepal, where recent sightings of tigers at higher elevations (~3200 m) suggest an upward range expansion from the tiger-rich lowlands. To evaluate our estimates, we simulated tiger routes to higher-elevation locations and compared modeled energy costs of those ascents to those derived from a previous model calibrated with data from GPS-collared tigers in Russia. In areas below 3200 m, we found about 7.5 times greater land areas with high connectivity outside protected areas (~51 000 km^2) than inside (~6800 km^2). However, most of the highly connected areas below 3200 m consist of croplands (56%). Importantly, community-managed forests, which spanned the altitudinal gradient, tended to include areas with moderate levels of connectivity. Our estimates of energy costs and those from Russia showed a strong consensus ($\rho = 0.70$, $P < 0.05$), with ours better capturing the higher energy costs of traversing mountains and of very large total ascents. Our results show that while barriers to tiger movement across Nepal are ubiquitous, other effective area-based conservation measures (OECMs), like community-managed forests, can play prominent roles in promoting tiger habitat connectivity while minimizing human–tiger conflict across anthropogenic landscapes. Our results also underscore the utility of integrating first principles of energy efficiency into connectivity analyses and planning.

Introduction

Habitat connectivity is crucial for facilitating animal dispersal, gene flow, demographic rescue and movement in response to climate change (Crooks & Sanjayan, 2006). Furthermore, improving habitat connectivity can reduce the likelihood of negative encounters between people and wildlife, which is a leading cause of wildlife declines in anthropogenic landscapes (Nyhus, 2016). Studies that model connectivity characterize features of the landscape that facilitate or impede animal movement (Crooks & Sanjayan, 2006). These features typically include attributes of the landscape, such as land-cover type and elevation, and those of the focal species, such as dispersal distances (Crooks & Sanjayan, 2006). Implicit to many of these studies are the energetic costs of movement, for example, mountainous terrain is more 'resistant' to animal movement than flatter terrain (Sawyer, Epps, & Brashares, 2011). The energetic costs of movement are important for animals in deciding where to move (Wall, Douglas-Hamilton, & Vollrath, 2006; Wilson, Quintana, & Hobson, 2012). Explicitly incorporating these energetic costs is an important next step in connectivity modeling, as it better reflects the energetic landscape that animals navigate. Doing so also reveals the physiological constraints to movements that animals experience and provides more realistic expectations of how wildlife respond to changing resource availability and distribution.

Connectivity studies often infer energy costs of movement based on distance (Sawyer, Epps, & Brashares, 2011). Other studies include the additional costs of moving along an elevation gradient, recognizing that moving uphill is energetically costly compared to moving over flat ground (Shirk *et al.*, 2010; Green *et al.*, 2020). For example, a study of chimpanzees (*Pan troglodytes*) found that their observed travel routes were closely aligned with predicted least-cost routes based on energetic costs of moving over uneven terrain (Green *et al.*, 2020). However, these studies do not explicitly translate these distances to energetic costs of locomotion, such as kilocalories, that account for body mass. Research in locomotion shows that the energetic cost of movement varies with an organism's mass due to mass-specific efficiencies and terrain topography due to gravity (Full, 1989; Snyder & Carello, 2008). Recent work shows that wildlife, including large carnivores such as grizzly bears (*Ursus arctos horribilis*), mountain lions (*Puma concolor*) and jaguars (*Panthera onca*), preferentially select habitat in order to reduce energetic costs (Dunford *et al.*, 2020; Carnahan *et al.*, 2021; Chambers *et al.*, 2022a, 2022b). Indeed, the energy landscape is central to general frameworks of animal movement research (Shepard *et al.*, 2013; Gallagher *et al.*, 2017). Furthermore, as many species' distributions are shifting to different elevations in response to climate change (Lenoir & Svenning, 2015), a better understanding of the associated energetic costs of doing so will help predict species' future viability.

Knowledge of the energy landscape is especially important for conservation planning of the endangered tiger (*Panthera tigris*) in Nepal – a country with complex and extreme topography. For decades, tigers have remained confined to national parks at lower elevations (<1000 m) along the base of the Himalayan mountains (referred to as the Terai lowlands), taking advantage of the high densities of prey that utilize the forage-rich valleys and grasslands (Seidensticker *et al.*, 2010). However, in recent years, there has been increasing, albeit sporadic, camera trap evidence of tigers occupying forests at higher elevations (<3200 m) in multiple sites across the country (Shrestha *et al.*, 2021). It is unclear whether these higher-elevation sightings are caused by tiger population growth, increasing human disturbance, climate change, or the interactions among those three factors. Or if they are simply exceptional cases and not indicative of tiger range expansion. Nevertheless, these sightings beg the important question: what is the landscape connectivity between the tiger-rich lowlands and higher-elevation forests? Delineating areas of high connectivity can help guide future conservation actions by prioritizing new areas for tiger habitat restoration and protection and identifying the various threats to tigers as they traverse the altitudinal gradient.

For the first time, we mapped the energy costs of movement for tigers in Nepal and used them to estimate landscape connectivity across the country. We estimated energy costs of movement for tigers based on a general locomotory model for terrestrial animals that accounts for animal mass and elevation changes. We compare the modeled energetic costs to other estimates of tiger energy expenditures from the literature, validating our predictions while also revealing the utility of accounting for terrain. We then used our modeled energy costs as a resistance surface in a circuit theory approach for estimating landscape connectivity (McRae & Beier, 2007). Here, we focus only on travel costs due to limited available data for including other factors, such as prey availability and anthropogenic disturbance, that may influence tigers' space use (Carter *et al.*, 2012, 2023). Nevertheless, energy expenditures strongly determine animal movement behavior (Wilson, Quintana, & Hobson, 2012), especially for large mammals (Wall, Douglas-Hamilton, & Vollrath, 2006; Dunford *et al.*, 2020) and provide an effective framework to quantify a simple, yet informative, measure of landscape connectivity. In lieu of empirical data on how tigers respond to habitat characteristics and anthropogenic pressures in higher elevations of Nepal, we consider our maps of landscape connectivity as a null, theoretically derived model of where we expect tigers to travel – based solely on minimizing energy costs – as they leave protected areas in the lowlands.

We used our connectivity maps to address three objectives germane to tiger conservation planning: (1) identify likely movement paths between protected areas in both the Terai lowlands and higher-elevation Himalayas where tiger dispersal faces various obstacles; (2) examine the overlay of connectivity with different human land-uses that can differentially impact tiger recovery and human–tiger interactions; and (3) investigate connectivity levels in existing community-managed forests to understand their potential in aiding future tiger conservation in regions without protected national parks. Mapping tiger habitat connectivity as a function of energy provides spatial insights on the barriers and opportunities to future tiger recovery in Nepal and other tiger range countries. Our approach also allows for constructing baseline connectivity maps for other species moving across complex energetic landscapes.

Materials and methods

Tiger energy landscapes and connectivity in Nepal

We computed landscape connectivity for tigers with the assumption that they follow favorable energy landscapes. Energy landscapes are spatially explicit projections that map energetic costs of travel onto the landscape (Shepard *et al.*, 2013). Energy landscapes were computed using the R package *enerscape* (Berti *et al.*, 2022), which models the energy cost of transport following Pontzer (2016), using the digital elevation model of Nepal at 26 × 26 m^2 from NASADEM (Jpl, 2020). We calculated energy landscapes assuming a body mass of 150 kg, typical of females (Hunter, 2015). We modeled only females because they are the reproductive unit of the population and necessary to long-term range expansion. In addition, we checked that the results did not change significantly when using 200 kg, the average body mass of males (Figure S1). As there were minimal differences between the two, we retained the female-only results in the main text.

Energy landscapes were then used as resistance matrices to calculate landscape connectivity using Omniscape (Landau *et al.*, 2021). Omniscape is a circuit theory approach that calculates connectivity based on all possible pathways across a landscape simultaneously. We specified a ‘search’ radius of 260 m, which assumes tigers chose optimal travel routes to minimize energy expenditures at a small/intermediate local scale, that is, without taking decisions based on distant areas, while minimizing computational costs. The connectivity maps are also available online in a Google Earth Engine app: https://emilioberti90.users.earthengine.app/view/connectivity-tigers-nepal.

To assess how connectivity was distributed across different land-use types, we divided the connectivity values into 10 ordered classes, from class 1 having lowest connectivity to class 10 having the highest. We then calculated the total area covered by land-cover types per connectivity class. We obtained land cover from the ESA WorldCover database (Zanaga *et al.*, 2021). We repeated this after excluding cells above 3200 m (the highest elevation at which a tiger was recently observed in Nepal, (Shrestha *et al.*, 2021)) and additionally after excluding areas outside (a) the current network of protected areas and (b) outside the current network of community-managed forested areas. We compiled existing geographic boundaries of community forests in Nepal from the Nepal Department of Forests (Nepal Department of Forests, 2020) and ICIMOD (ICIMOD, 2020). To our knowledge, these are best available data, though as many community forests do not provide spatially explicit boundary data, our data underestimate the number and geographic extent of community forests.

Longitudinal dispersal along the Terai lowlands

We then assessed the connectivity in areas of the Terai lowlands – an area harboring almost all the tigers in Nepal. We focused on three forest corridors that are of particular interest for longitudinal (west–east) dispersal of tigers: the Lamahi and Dovan areas, which create a bridge between the western protected areas and the Chitwan-Parsa protected area complex located in the center of Nepal; and the Brahmadev area, which connects the Indian population of tigers to Nepal and near which long-dispersing tigers have recently been observed (DNPWC & DOFSC, 2022). For these three forest corridors, we calculated the connectivity that a tiger would experience when moving across the whole landscape. Specifically, we identified the two locations that the tigers are *more likely* to use as entry points, namely forest locations located at the edge of the area and that lie on the direction of dispersal between protected areas.

Comparison with other estimates of energy expenditures

To assess the reliability of our predictions, we compared the predicted energy costs obtained using *enerscape* with another energetic model (Taylor *et al.*, 1970) calibrated on field data from Amur tigers (Miller *et al.*, 2014). This model provides the total daily energy requirements of an adult tiger as the sum of the costs from basal metabolism, traveling, predation and reproduction. Importantly, total costs depend on the sex of the individual and seasonality. As we are interested only in the overall costs due to locomotion, we extracted from the model the traveling component and averaged the reported distance traveled per day across the whole year. The travel component of the model predicted the energy costs (C) for a general animal of mass W as $C = 5.8 \times W^{0.75} \times t + 2.6 \times W^{0.60} \times d$ (Taylor *et al.*, 1970), where t are the hours spent moving and d the total distance in km. Given an average distance traveled per day of 5.50 km and an average proportion of day spent moving of 0.33 (Miller *et al.*, 2014), we derived $t = d \times 0.33/5.5 \times 24 = 1.44 \times d$, that is, an average moving time of ~1 h and 26 min km^{-1}. We then calculated the predicted costs of locomotion for tigers in Nepal using *enerscape*, which also includes topography, and compared this estimate to the model from (Taylor *et al.*, 1970) calibrated with the data from (Miller *et al.*, 2014). Specifically, we sampled 500 random paths and calculated the energy costs of locomotion using both *enerscape* and the Amur tiger model. For the latter, we multiplied the time that tigers would need to travel the whole distance (hours) by the cost of traveling per unit of time (kcal h^{-1}), resulting in the total energetic costs of travel (kcal). The distance for this comparison spanned 0.51–24.44 km, with an average of 10.19 km and a standard deviation of 4.94 km. As a measure of consensus between the two models, we calculated the Pearson’s correlation coefficient, with high values of correlation indicating strong consensus among models.

Results

Tiger energy landscapes and connectivity in Nepal

There are extensive connected habitats across Nepal, many of which are not currently occupied by tigers (Fig. 1a). Similarly, areas in Nepal below 3200 m where tigers have recently been sighted encompass a great deal of connected habitats (Fig. 1b). Many of these areas are outside protected area networks. For example, areas of high connectivity (>=6) below 3200 m comprise ~58 123 km^2, which is about 8.5 times greater than that of high connectivity only inside protected areas below 3200 m (~6800 km^2). Further, the highest connectivity areas (>=9) below 3200 m are shared with many croplands (56%). Likewise, even in protected areas (including buffer zones), high connectivity intersects with croplands (14% of areas with connectivity >=6 and 25% of areas with connectivity >=9). Moderate to high levels of connectivity exist in community forests, with limited exposure to dense croplands (Fig. 1d). However, these areas are relatively small (Fig. 1d) compared to protected areas (Fig. 1c), with an extent of only 338 km^2.

Longitudinal and latitudinal dispersal

The median costs of travel for tigers were 0.03 kcal m^{-1} in the Terai (lowlands) area, 0.16 kcal m^{-1} in the mid-hills region and 0.21 kcal m^{-1} in the Himalayan area (Fig. 2). Despite the clear energetic burden of moving to higher elevations, we found that energetically efficient corridors exist that connect tiger source populations in the Terai lowlands to higher-elevation protected areas where tigers do not currently occupy (Fig. 3). For example, there are potential pathways for connecting tigers in the lowlands to protected areas farther north, such as from Suklaphanta National Park to Khaptad National Park (Fig. 3a) or from Chitwan National Park to the Annapurna Conservation Area (Fig. 3b). These pathways often intersect community forests and river networks and are interspersed with larger tracts of connected habitats that are not under any form of formal protection. These maps suggest that there are energetically efficient movement corridors across the country that could potentially expand the available habitat for tigers and facilitate their range shift under future climate changes.

We also examined connectivity across three key forest corridors in the Terai lowlands – corridors that can connect isolated tiger populations – and found that habitat connectivity, while relatively high, intersects with low-lying croplands and is constrained by higher elevations (Fig. 4). These maps suggest that, despite being forested, the hills just north of the Terai lowlands constitute an energetic barrier that might push tigers to move near or within croplands that prevail in these areas.

Comparison with other model of energy expenditures

Overall, the two models showed a high level of consensus (Fig. 5), despite large deviations for travel paths that had large elevation gradients. In addition to these overpredictions, *enerscape* also underpredicted the costs for paths that lied predominantly in flat terrains compared to the model from (Taylor *et al.*, 1970) and Miller *et al.* (2014). An important distinction between the two models is that the model for Amur tigers was tailored to estimate travel costs for

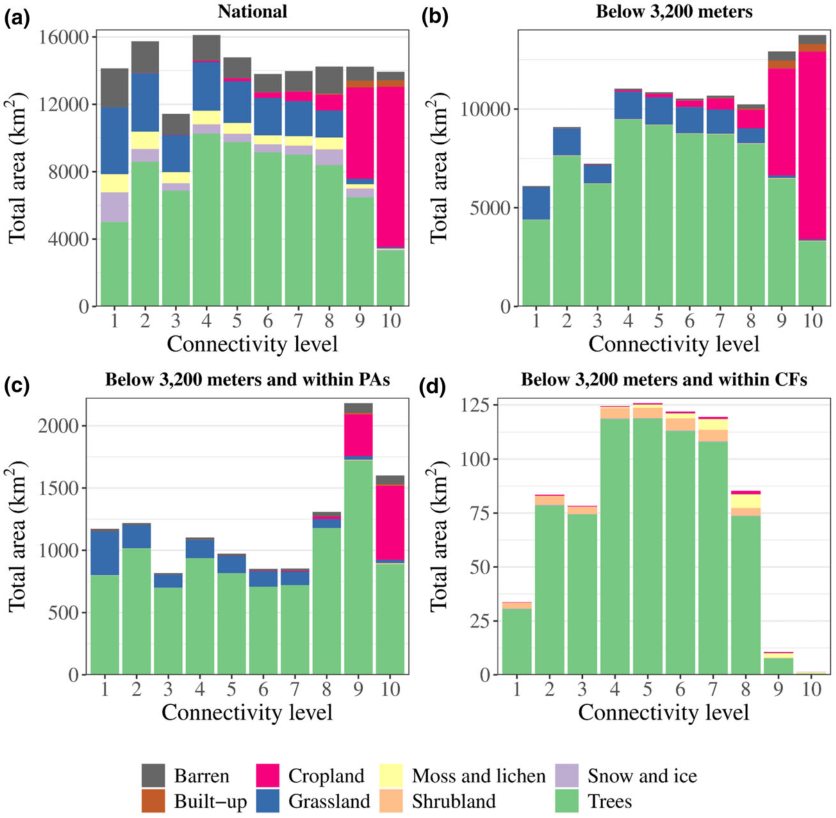

Figure 1 Land-cover zonal statistics grouped by connectivity levels for a female tiger of 150 kg. Stacked bars show the area covered by land-cover types for each connectivity level. Connectivity levels were obtained as binned ranges of the landscape connectivity estimated using *omniscape*, with higher levels having higher connectivity based on energetic costs of movement for a female tiger of 150 kg. Zonal statistics were calculated: (a) for the whole Nepal; (b) only for areas with elevation below 3200 m; (c) only for areas below 3200 m and within the network of protected areas (PAs), including buffer zones and game reserves; and (d) below 3200 m and within the network of community forests (CF).

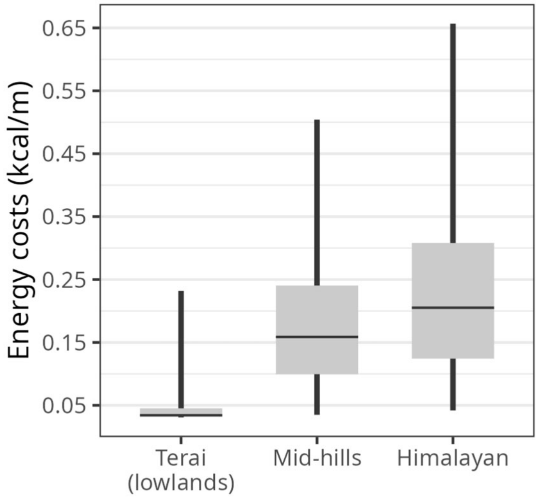

Figure 2 Boxplots of estimated energetic costs of travel for a female tiger of 150 kg across the three main geographic regions of Nepal. Boxplots represent the 25th and 75th percentiles, whiskers represent the 95% confidence intervals, and black lines within boxes represent medians.

'average' conditions, that is, assuming an average energetic cost over the whole landscape and at large time scales. Moreover, the model for Amur tigers did not account explicitly for elevation in the calculations of travel costs. As such the discrepancies between the two models can be explained by their different aim and by *enerscape* including increasing, non-linear costs for steeper terrains were not incorporated by (Taylor *et al.*, 1970) and (Miller *et al.*, 2014). Nevertheless, the two models were highly correlated (Pearson's correlation = 0.70) and showed qualitatively comparable trends (Fig. 5).

Discussion

Our energetics-informed map of tiger habitat connectivity in Nepal indicated the presence of numerous areas of moderate to high habitat connectivity across the country's altitudinal gradient. Many moderately connected habitats intersect with existing community-managed forests or other areas outside of the existing protected area network. Much of the country's highest connectivity levels were covered by croplands, especially in the Terai lowlands. Using our model, we found that

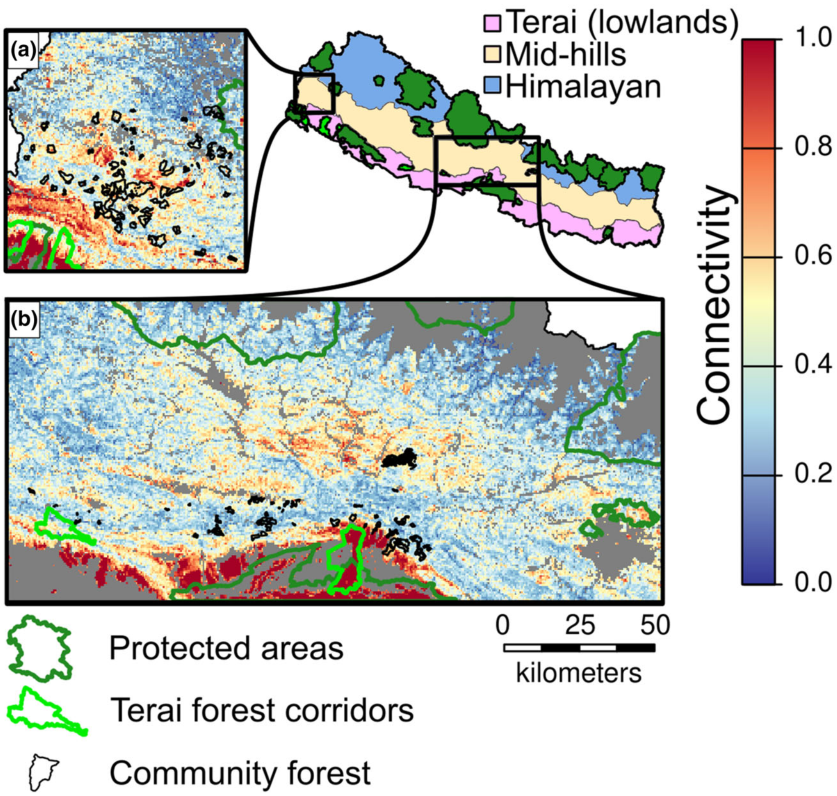

Figure 3 Landscape connectivity based on energy costs of travel for a female tiger of 150 kg. Connectivity in western Nepal (a) showing pathways between Suklaphanta National Park in the Terai lowlands to Khaptad National Park in the Himalayas; connectivity in central Nepal (b) showing pathways between Chitwan National Park in the Terai to the Annapurna Conservation Area in the Himalayas (leftmost protected area in far north of inset). Connectivity values were standardized from zero, indicating low connectivity (blue), to one, indicating high connectivity (red). Areas that were covered by human land-uses, such as croplands and settlements, are shown in gray. The major geographic regions – Terai lowlands, mid-hills and Himalayan – are indicated in the map of Nepal.

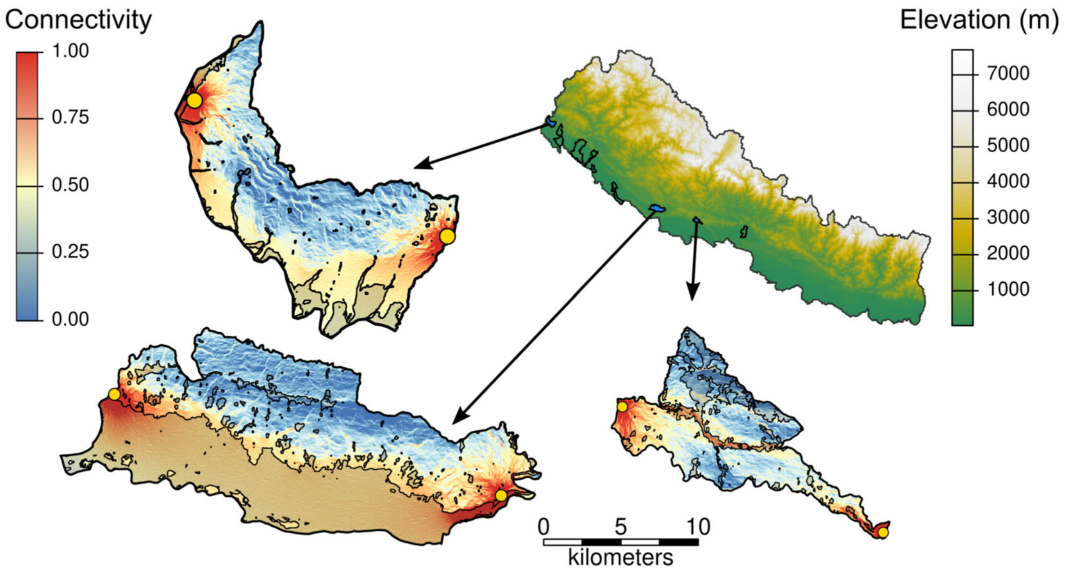

Figure 4 Landscape connectivity for a tiger (female of 150 kg) traveling through three forest corridors that link protected areas in the Terai lowlands. The forest corridors are from top-left to bottom-right: Brahmadev, Lamahi and Dovan. Connectivity was calculated using as resistance matrix the energy costs of traveling across the landscape. Connectivity values were standardized from zero, indicating low connectivity (blue), to one, indicating high connectivity (red). The yellow circles show the travel origin and destination for a hypothetical tiger that crosses the corridor area. Gray shade shows areas of human land-use, such as croplands and settlements.

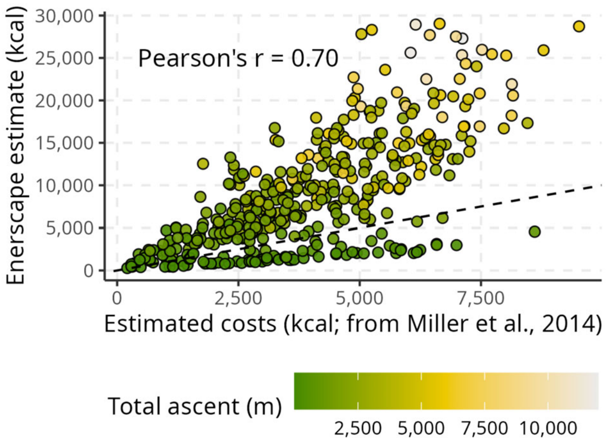

Figure 5 Comparison between field-informed estimates of locomotion cost for Amur tigers in Russia from Miller *et al.* (2014) and our predictions for a female of 150 kg using *enerscape*. Points show the estimated energy costs for both models for 500 random paths across Nepal. The distance of the random paths spanned 0.51–24.44 km, with an average of 10.19 km and a standard deviation of 4.94 km. Colors show the total ascent of the paths and the dashed line the 1:1 identity line. The two models had a good degree of consensus (Pearson's $r = 0.70$, $P < 0.05$), except for terrains with steep inclines, not accounted for in Miller's model, but included in *enerscape*.

tiger energy usage grows exponentially when traversing high altitudinal gradients, far surpassing previous empirical estimates of tiger energetics from flatter areas. Combined, these insights underscore the need to integrate energetics in tiger habitat and connectivity assessments, especially in topographically complex landscapes such as the Himalayas.

While tiger populations in Nepal are currently concentrated in the Terai lowlands, our results show that the mid-hills region at elevations upwards of 3000 m will be critical for connecting tiger populations across these source populations and for enabling tiger expansion to other forested areas. In the last decade, tigers have been observed using unexpectedly high-elevation, mountainous habitat in Nepal, India and Bhutan (Adhikarimayum & Gopi, 2018; Tempa *et al.*, 2019; Shrestha *et al.*, 2021). The range expansion by tigers into higher elevations might increase as their numbers saturate the lowlands and they respond to changing climate patterns, such as lower water availability or increased temperatures. Although more research is needed to determine the causes for this expansion, the more frequent sightings in different parts of the Himalayan range suggest a growing trend of more tigers entering the mid-hills region.

Therefore, more protections are needed for tigers that are moving into higher elevations. However, the mid-hills region, despite being almost 30% of Nepal's area, has the lowest protected area coverage of any region in Nepal (Fig. 3). Although much of the mid-hills are used extensively by humans, in recent years human population densities in the region have declined with people migrating to cities or other countries to find employment (Shrestha *et al.*, 2010; Nepal, Tripathi, & Adhikari, 2021). Moreover, community forestry has helped significantly increase forest cover in the mid-hills (Oldekop *et al.*, 2019). It is possible that greater intact forest area and fewer people in the mid-hills are enabling conditions for tigers and other species to increase their numbers (Shrestha *et al*., 2021). Nevertheless, if tigers expand to the mid-hills, considerable effort will be needed to mitigate conflict events between tigers and people, such as livestock depredation, especially as communities will not have prior experience living with tigers.

The mid-hills are an ideal location to implement an integrated system of conservation approaches, such as combining protected areas that restrict human access with other effective area-based conservation measures (OECMs) that are more permissive of human activities. OECMs were introduced in Aichi Target 11 of the 2010 Convention on Biological Diversity and defined in 2018 as 'a geographically defined area other than a Protected Area (PA), which is governed and managed in ways that achieve positive and sustained long-term outcomes for the *in situ* conservation of biodiversity, with associated ecosystem functions and services and where applicable, cultural, spiritual, socio–economic and other locally relevant values' (IUCN, 2019). OECMs can provide habitat protection for wildlife, like tigers and their prey, while communities manage its sustainable use (Alves-Pinto *et al*., 2021). Currently, zero OECMs are officially recognized in Nepal by the Convention on Biological Diversity. However, Nepal's existing community forests are candidates to be recognized as aligning with the OECM goals based on World Commission on Protected Area's criteria, which could bring international support (IUCN, 2019). Regardless of official status, international and national investment into community forests in the mid-hills of Nepal will be crucial for maintaining connectivity for tigers while facilitating coexistence with people.

In the lowlands where the current tiger population is concentrated and growing, coexistence between people and tigers is an ongoing challenge. Recent reports indicate the tigers are frequently venturing outside protected areas and coming into conflict with adjacent human communities, a pattern that is increasing in intensity (Fitzmaurice *et al*., 2021). Our results suggest that this pattern might, in part, be due to the relative energetic ease with which tigers can traverse these low-lying croplands that abut natural forests and grasslands in protected areas (Fig. 4). Tigers might therefore be more likely to encounter people or their livestock while traversing these energetically efficient routes. Future research could examine whether our energetics-based connectivity maps are also predictive of human–tiger conflict. Restoring habitats to facilitate dispersal between protected areas in the lowlands will require a suite of conservation actions, with community-based conservation initiatives as a central piece given the prominent presence of human settlements and land-uses. Intensifying conflict with tigers in the lowlands underscores the conservation opportunity to provide and restore viable paths for tigers to move to higher altitudes and avoid extensive croplands. However, restoring viable paths for tigers to the mid-hills should be paired with robust strategies for reducing any conflict with tigers that may arise from their new and increasing presence. Otherwise, increasing conflict may jeopardize tiger conservation in this region and deleteriously affect human wellbeing.

Our simulations indicated that tigers in the Himalayas would experience dramatically greater energetic demands while traveling across mountainous terrain than in flatter terrain. For example, our model indicates that a tiger would require 2–3 times more kcal for the energetic costs of traveling from the lowlands to 3000 m (~12 400 kcal) compared to empirical estimates of energy usage from flatter terrains in Russia (~5100 kcal). This is a large difference, one that tigers would have to compensate for by changing their hunting strategies or movement behaviors. For example, to meet these increased energetic demands, a tiger would have to kill a greater amount of prey. Although systematic assessments of tiger prey abundances in the mid-hills are lacking, the general consensus is that the mid-hills region has fewer prey animals than the lowlands (Paudel & Kindlmann, 2012; Paudel, Sipos, & Brodie, 2018). To meet higher energetic demands, tigers may need to expand their territories to find sufficient prey resources. The relative lack of prey in the mid-hills might thus push tigers to kill and eat livestock or come into greater contact with human settlements, underscoring the importance of maintaining or restoring wild prey populations in the mid-hills as well as implementing effective conflict mitigation strategies.

To guide future tiger action plans, we need systematic assessments of tiger presence and prey abundances in the mid-hills, especially as tigers expand into higher elevations. We recommend using our model results to target the locations of those assessments, assuming that areas of high connectivity are the most likely routes on which to find tigers venturing uphill. We also recommend future research to build on these models to include other barriers to movement, such as transportation infrastructure, thereby providing increasingly detailed assessments of connectivity across anthropogenic landscapes. Future research could also combine energy benefits, based on spatially explicit estimates of prey biomass, with the energetic costs of movement measured here. By integrating first principles of energy efficiency into connectivity analyses, we demonstrate that both geography and resource distributions influence tiger dispersal and coexistence with humans in shared spaces.

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Author contributions

NHC and EB conceived the ideas and designed methodology; NHC and EB collected the data; EB analyzed the data; NHC led the writing of the manuscript. All authors contributed to the drafts and gave final approval for publication.

References

Adhikarimayum, A.S. & Gopi, G.V. (2018). First photographic record of tiger presence at higher elevations of the Mishmi Hills in the Eastern Himalayan Biodiversity Hotspot, Arunachal Pradesh, India. *J. Threat. Taxa* **10**, 12833–12836.

Alves-Pinto, H., Geldmann, J., Jonas, H., Maioli, V., Balmford, A., Ewa Latawiec, A., Crouzeilles, R. & Strassburg, B. (2021). Opportunities and challenges of other effective area-based conservation measures (OECMs) for biodiversity conservation. *Perspect. Ecol. Conserv.* **19**, 115–120.

Berti, E., Davoli, M., Buitenwerf, R., Dyer, A., Hansen, O.L.P., Hirt, M., Svenning, J.-C., Terlau, J.F., Brose, U. & Vollrath, F. (2022). The R package enerscape: a general energy landscape framework for terrestrial movement ecology. *Methods Ecol. Evol.* **13**, 60–67.

Carnahan, A.M., van Manen, F.T., Haroldson, M.A., Stenhouse, G.B. & Robbins, C.T. (2021). Quantifying energetic costs and defining energy landscapes experienced by grizzly bears. *J. Exp. Biol.* **224**, jeb241083.

Carter, N.H., Shrestha, B.K., Karki, J.B., Pradhan, N.M.B. & Liu, J. (2012). Coexistence between wildlife and humans at fine spatial scales. *Proc. Natl. Acad. Sci. USA* **109**, 15360–15365.

Carter, N.H., Zuckerwise, A., Pradhan, N.M.B., Subedi, N., Lamichhane, B.R., Hengaju, K.D., Acharya, H.B. & Kandel, R.C. (2023). Rapid behavioral responses of endangered tigers to major roads during COVID-19 lockdown. *Glob. Ecol. Conserv.* **42**, e02388.

Chambers, S., Villarreal, M.L., Duane, O., Munson, S.M., Stuber, E., Tyree, G., Waller, E.K. & Duniway, M.C. (2022*b*). Conflict of energies: spatially modeling mule deer caloric expenditure in response to oil and gas development. *Landsc. Ecol.* **37**, 2947–2961.

Chambers, S.N., Villarreal, M.L., Norman, L.M., Bravo, J.C. & Traphagen, M.B. (2022*a*). Spatial models of jaguar energy expenditure in response to border wall construction and remediation. *Front. Conserv. Sci.* **3**, 1012010.

Crooks, K.R. & Sanjayan, M. (2006). *Connectivity conservation*. Cambridge: Cambridge University Press.

DNPWC, & DOFSC. (2022). *Status of tigers and prey in Nepal 2022*. Kathmandu: Nepal Department of National Parks and Wildlife Conservation and Department of Forests and Soil Conservation.

Dunford, C.E., Marks, N.J., Wilmers, C.C., Bryce, C.M., Nickel, B., Wolfe, L.L., Scantlebury, D.M. & Williams, T.M. (2020). Surviving in steep terrain: a lab-to-field assessment of locomotor costs for wild mountain lions (*Puma concolor*). *Mov. Ecol.* **8**, 34.

Fitzmaurice, A., Poudel, P., Offord-Woolley, S., Macdonald, D., Thapa, S., Lamichhane, B.R., Baral, A. & Yadav, B.P. (2021). Complex consequences of conservation success: emerging human-tiger conflicts in Nepal. *CatNews* **72**, 23–27.

Full, R.J. (1989). Mechanics and energetics of terrestrial locomotion: from bipeds to polypeds. In *Energy transformations in cells and organisms*: 175–182. Gnaiger, W.W. (Ed.). New York: Georg Thieme Verlag.

Gallagher, A.J., Creel, S., Wilson, R.P. & Cooke, S.J. (2017). Energy landscapes and the landscape of fear. *Trends Ecol. Evol.* **32**, 88–96.

Green, S.J., Boruff, B.J., Bonnell, T.R. & Grueter, C.C. (2020). Chimpanzees use least-cost routes to out-of-sight goals. *Curr. Biol.* **30**, 4528–4533.e5.

Hunter, L. (2015). *Wild cats of the world*. New York: Bloomsbury Publishing.

ICIMOD. (2020). *Community Forest Boundary of Kayar Khola Watershed, Chitwan Nepal*. Lalitpur: ICIMOD. http://rds.icimod.org/home/datadetail?metadataid=7999&searchlist=true.

IUCN. (2019). *Recognising and reporting other effective area-based conservation measures*. Switzerland: IUCN Gland.

Jpl, N. (2020). Nasadem Merged dem global 1 arc Second v001 [data set]. nasa eosdis Land Processes daac.

Landau, V., Shah, V., Anantharaman, R. & Hall, K. (2021). Omniscape.jl: software to compute omnidirectional landscape connectivity. *J. Open Source Softw.* **6**, 2829.

Lenoir, J. & Svenning, J.-C. (2015). Climate-related range shifts – a global multidimensional synthesis and new research directions. *Ecography* **38**, 15–28.

McRae, B.H. & Beier, P. (2007). Circuit theory predicts gene flow in plant and animal populations. *Proc. Natl. Acad. Sci. USA* **104**, 19885–19890.

Miller, C.S., Hebblewhite, M., Petrunenko, Y.K., Seryodkin, I.V., Goodrich, J.M. & Miquelle, D.G. (2014). Amur tiger (*Panthera tigris* altaica) energetic requirements: implications for conserving wild tigers. *Biol. Conserv.* **170**, 120–129.

Nepal Department of Forests. (2020). Community forests web map. https://www.google.com/maps/d/u/0/viewer?mid=1azvsij8fpwzjmxqfaxdu3ylt4rkz9wuy&ll=28.554136387572974%2c84.73547225000003&z=7

Nepal, S., Tripathi, S. & Adhikari, H. (2021). Geospatial approach to the risk assessment of climate-induced disasters (drought and erosion) and impacts on out-migration in Nepal. *Int. J. Disaster Risk Reduct.* **59**, 102241.

Nyhus, P.J. (2016). Human–wildlife conflict and coexistence. *Annu. Rev. Environ. Resour.* **41**, 143–171.

Oldekop, J.A., Sims, K.R.E., Karna, B.K., Whittingham, M.J. & Agrawal, A. (2019). Reductions in deforestation and poverty from decentralized forest management in Nepal. *Nat. Sustain.* **2**, 421–428.

Paudel, P.K. & Kindlmann, P. (2012). Human disturbance is a major determinant of wildlife distribution in Himalayan midhill landscapes of Nepal. *Anim. Conserv.* **15**, 283–293.

Paudel, P.K., Sipos, J. & Brodie, J.F. (2018). Threatened species richness along a Himalayan elevational gradient: quantifying the influences of human population density, range size, and geometric constraints. *BMC Ecol.* **18**, 6.

Pontzer, H. (2016). A unified theory for the energy cost of legged locomotion. *Biol. Lett.* **12**, 20150935.

Sawyer, S.C., Epps, C.W. & Brashares, J.S. (2011). Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? *J. Appl. Ecol.* **48**, 668–678.

Seidensticker, J., Dinerstein, E., Goyal, S.P., Gurung, B., Harihar, A., Johnsingh, A.J.T., Manandhar, A., McDougal, C.W., Pandav, B., Shrestha, M., David Smith, J.L., Sunquist, M. & Wikramanayake, E. (2010). Tiger range collapse and recovery at the base of the Himalayas. In *Biology and conservation of wild felids*: 305–324. Macdonald, D.W. & Loveridge, A.J. (Eds.) Oxford, UK: Oxford University Press.

Shepard, E.L.C., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A. & Vosper, S.B. (2013). Energy landscapes shape animal movement ecology. *Am. Nat.* **182**, 298–312.

Shirk, A.J., Wallin, D.O., Cushman, S.A., Rice, C.G. & Warheit, K.I. (2010). Inferring landscape effects on gene flow: a new model selection framework. *Mol. Ecol.* **19**, 3603–3619.

Shrestha, S., Sherpa, A.P., Lama, S., Tamang, M. & Paudel, P.K. (2021). Tigers at higher elevations outside their range: what does it mean for conservation? *Eco Mont* **14**, 43–46.

Shrestha, U.B., Shrestha, S., Chaudhary, P. & Chaudhary, R.P. (2010). How representative is the protected areas system of Nepal? *Mt. Res. Dev.* **30**, 282–294.

Snyder, G.K. & Carello, C.A. (2008). Body mass and the energy efficiency of locomotion: lessons from incline running. *Comp. Biochem. Physiol. A Mol. Integr. Physiol.* **150**, 144–150.

Taylor, C. R., Schmidt-Nielsen K., and Raab J. L. (1970). Scaling of energetic cost of running to body size in mammals. *Am. J. Physiol.* **219**, 1104–1107.

Tempa, T., Hebblewhite, M., Goldberg, J.F., Norbu, N., Wangchuk, T.R., Xiao, W. & Mills, L.S. (2019). The spatial distribution and population density of tigers in mountainous terrain of Bhutan. *Biol. Conserv.* **238**, 108192.

Wall, J., Douglas-Hamilton, I. & Vollrath, F. (2006). Elephants avoid costly mountaineering. *Curr. Biol.* **16**, R527–R529.

Wilson, R.P., Quintana, F. & Hobson, V.J. (2012). Construction of energy landscapes can clarify the movement and distribution of foraging animals. *Proc. Biol. Sci.* **279**, 975–980.

Zanaga, D., Van De Kerchove, R., De Keersmaecker, W., Souverijns, N., Brockmann, C., Quast, R., Wevers, J., Grosu, A., Paccini, A., Vergnaud, S., Cartus, O., Santoro, M., Fritz, S., Georgieva, I., Lesiv, M., Carter, S., Herold, M., Li, L., Tsendbazar, N.-E., Ramoino, F. & Arino, O. (2021). *ESA WorldCover 10 m 2020 v100*. Zenodo.

Supporting information

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

Figure S1. Land-cover zonal statistics grouped by connectivity levels for both female (150 kg) and male (200 kg) tigers. Stacked bars show the area covered by land-cover types for each connectivity level. Connectivity levels were obtained as binned ranges of the landscape connectivity estimated using *omniscape*, with higher levels having higher connectivity based on energetic costs of movement for a female tiger of 150 kg or a male tiger of 200 kg. Zonal statistics were calculated: (a) for the whole Nepal; (b) only for areas with elevation below 3200 m; (c) only for areas below 3200 m and within the network of protected areas (PAs), including buffer zones and game reserves; and (d) below 3200 m and within the network of community forests (CF).