Biological Conservation 298 (2024) 110763

Contents lists available at ScienceDirect

Biological Conservation

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

Integrating high-resolution remote sensing and empirical wildlife detection data for climate-resilient corridors across tropical elevational gradients

Ian M. McCullough [a,b,*], Christopher Beirne [a,b], Carolina Soto-Navarro [a,b,c], Amy Eppert [d], Eleanor Flatt [a,b,e], Yvonne J.M. Kemp [a,b], Péter K. Molnár [f,g], Michael S. Mooring [d,h], Yana Nikolova [i], Erik R. Olson [j,k], Carolina Pinto [a,b], Junior Porras [l], María José Mata Quirós [a,b], Guido Saborío Rodriguez [a,b], Jan Schipper [m,n], Chelsey R. Tellez [m], Juan S. Vargas Soto [f], Andrew Whitworth [a,b,o,p]

[a] Osa Conservation, Washington, DC, USA
[b] Osa Conservation Campus, Puntarenas, Costa Rica
[c] Rewilding Europe, ED, Nijmegen, the Netherlands
[d] Point Loma Nazarene University, San Diego, CA, USA
[e] Deanery of Biomedical Sciences, College of Medicine and Veterinary Medicine, University of Edinburgh, Edinburgh, UK
[f] Department of Biological Sciences, University of Toronto Scarborough, Toronto, ON, Canada
[g] Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, ON, Canada
[h] Quetzal Education & Research Center (QERC), San Gerardo de Dota, Costa Rica
[i] Department of Geoinformatics - Z_GIS, Paris-Lodron University of Salzburg, Salzburg, Austria
[j] JaguarOsa, Ashland, WI, USA
[k] Northland College, Ashland, WI, USA
[l] Sistema Nacional de Areas de Conservación, Costa Rica
[m] Arizona State University, West Valley, Glendale, AZ, USA
[n] Fundacion ProCAT (Proyecto de Conservación de Aguas y Tierras), Coto Brus, Costa Rica
[o] Institute of Biodiversity, Animal Health and Comparative Medicine, College of Medical, Veterinary and Life Sciences, University of Glasgow, Glasgow, UK
[p] Department of Biology, Center for Energy, Environment, and Sustainability, Wake Forest University, Winston-Salem, NC, USA

A R T I C L E I N F O

Keywords:
Central America
Costa Rica
Connectivity
Corridor
Fragmentation
Spatial conservation planning

A B S T R A C T

Corridors are essential tools for promoting biodiversity resilience under climate change. However, corridor design studies are often conducted at spatial scales too coarse to guide implementation by local conservation practitioners. We mapped potential climate-resilient corridors linking lowland to highland protected areas within a highly biodiverse but fragmented landscape of southwestern Costa Rica (6311 km^2) using least cost path and circuit theory approaches at high spatial resolution (10 m). We then applied an extensive camera trap dataset of medium-large vertebrates to examine corridor functionality. Although least cost paths (n = 40) were predominantly forested (median = 76 %, range = 57–82 %) and somewhat protected (median = 31 %, range = 3–55 %), they were also highly fragmented. Least cost paths from lowland to highland protected areas traversed medians of 252 forest patches (range = 162–328), 11,186 agriculture patches (range = 822–1,771), and 106 roads (range = 50–252), translating to 2 forest patches, 11 agriculture patches, and 1 road crossed every kilometer. Circuit analyses identified many high-connectivity areas outside of protected areas, including but not limited to least cost paths, but these high-connectivity areas were mostly small forest fragments. Nonetheless, capture rates for medium-to-large mammals at camera traps indicated that many species are currently unlikely to use unprotected, fragmented areas thought to be important for connectivity. In other words, additional conservation and restoration are necessary to establish functional corridors within the landscape. More broadly, this study exemplifies an approach to bridging the gap between regional-scale connectivity analyses and the needs of local practitioners

* Corresponding author.
E-mail addresses: ianmccullough@osaconservation.org (I.M. McCullough), chrisbeirne@osaconservation.org (C. Beirne), eleanorflatt@osaconservation.org (E. Flatt), yvonnekemp@osaconservation.org (Y.J.M. Kemp), peter.molnar@utoronto.ca (P.K. Molnár), mmooring@pointloma.edu (M.S. Mooring), yana.nikolova@plus.ac.at (Y. Nikolova), eolson@northland.edu (E.R. Olson), carolinapinto@osaconservation.org (C. Pinto), junior.porras@sinac.go.cr (J. Porras), mariajosemata@osaconservation.org (M.J.M. Quirós), guidosaborio@osaconservation.org (G.S. Rodriguez), jan.schipper@asu.edu (J. Schipper), chelsey.tellez@wildlifeinmotion.org (C.R. Tellez), juan.vargassoto@mail.utoronto.ca (J.S. Vargas Soto), andywhitworth@osaconservation.org (A. Whitworth).

https://doi.org/10.1016/j.biocon.2024.110763
Received 7 May 2024; Received in revised form 11 July 2024; Accepted 12 August 2024
Available online 26 August 2024

by identifying locations that could be targeted for conservation or restoration within multi-use tropical landscapes.

1. Introduction

Corridors are an essential tool for biodiversity conservation for facilitating gene flow, retaining migration paths, and accommodating range shifts (Heller and Zavaleta, 2009, Krosby et al., 2018, Mohammadi et al., 2024, Pineda-Zapata et al., 2024). The importance of corridors for conservation in a climate change context is well established. The International Union for Conservation of Nature emphasizes that corridors can increase biodiversity resilience under climate change by facilitating range shifts, colonization of newly suitable habitat, and climate change adaptation, particularly across heterogeneous landscapes and elevational or other critical gradients (Hilty et al., 2020). However, "climate-resilient corridors" (landscape features designed to promote biodiversity persistence and recovery under future climate change) are urgently needed in the tropics. Tropical deforestation and habitat fragmentation are increasing, often due to logging or agriculture (e.g., cattle, oil palm), with limited forest land remaining for new protected areas (Lewis et al., 2015). Consequently, over 62 % of tropical forests have become disconnected from future climate analogues (areas with similar climate regimes), and this loss of connectivity exacerbates the vulnerability of many of the Earth's most biodiverse regions to climate change (Senior et al., 2019).

Whereas restoring connectivity in the tropics will require substantial investment and conservation efforts worldwide, elevational gradients may represent promising opportunities for climate-resilient corridors (Fung et al., 2017). Topographically heterogeneous tropical landscapes not only support exceptionally high biodiversity and rates of endemism, but their environmental variability can promote short-distance range shifts (because climate varies over short distances) the buffering the effects of climate change (Trew and Maclean, 2021). For example, variability in topography and vegetation structure can produce over 10 °C of variability in maximum daily temperatures, with intact forest canopies providing the greatest cooling effect (Jucker et al., 2018). Such thermal heterogeneity and buffering represents a nature-based solution to help support local persistence of biodiversity otherwise threatened by regional warming (Scheffers et al., 2017). However, tropical mountain landscapes are often insufficiently protected or connected to lowland habitats to function as climate change refugia (Sales and Pires, 2023). Thus, designing corridors that consider small-scale habitat heterogeneity will be essential for biodiversity conservation in tropical mountainous regions.

Previous studies have identified corridors by linking large protected areas at regional to continental scales (Jantz et al., 2014; Stralberg et al., 2020; Almasieh et al., 2023; Iannella et al., 2024). Although such analyses are an important step, they often produce coarse boundaries of corridors and therefore may provide incomplete guidance for local conservation action. The scale mismatch between regional conceptualization and local actions is a key reason why many corridor studies face implementation challenges (Correa Ayram et al., 2016; Keeley et al., 2018). Furthermore, coarse-scale corridors may overlook potential for relatively short-distance range shifts in heterogeneous landscapes where climate and elevational gradients span short geographic distances (Dobrowski, 2011; Trew and Maclean, 2021). Therefore, finer-scale approaches are required to help identify the most likely pathways for biodiversity at local to landscape scales to facilitate movements under future climatic conditions (Beier, 2012).

Fine-scale mapping of potential climate-resilient corridors offers a unique opportunity to inform local conservation planning or restoration strategies more effectively. However, a major assumption of corridor-mapping studies is that land cover or habitat suitability are indicators of connectivity (Zeller et al., 2012). While some previous studies have tested this assumption using biological data (e.g., movement tracking or camera trap data; LaPoint et al., 2013), few studies have examined biodiversity indicators along landscape permeability gradients to assess functional connectivity (i.e., to what extent organisms use corridors; Kindlmann and Burel, 2008), particularly across heterogeneous landscapes. Proposed corridors could be validated using biological data to help inform targeted conservation or restoration, but this is frequently not done due to data or resource limitations (Lalechère and Bergès, 2021). Nonetheless, such analyses may be critical for establishing functional connectivity within fragmented, multi-use landscapes, which often require additional on-the-ground efforts, such as wildlife road crossings or afforestation (Pinto et al., 2024).

In this study, we combined fine-scale landscape connectivity modeling and empirical wildlife detection data for characterization of climate-resilient corridors in a multi-use tropical landscape (mixture of protected areas and agriculture). By building upon a previous, regional-scale connectivity analysis in Central America (McCullough et al., 2024) and a developing regional camera trapping network (Vargas Soto et al., 2022), this work can help bridge the implementation gap that often exists between coarse-scale connectivity research and local conservation practitioners (Correa Ayram et al., 2016). We use a landscape in southwestern Costa Rica as a case study, one of the high-priority landscapes previously identified to support climate resilience across Central America (McCullough et al., 2024). Our objectives were to: 1) identify potential climate-resilient corridors using least cost path and circuit theory approaches, 2) analyze the ecological characteristics and conservation status of these corridors, and 3) validate use of these corridors by medium-large vertebrates using camera trap data.

2. Methods

2.1. Study area

The study landscape (6311 km^2) is located in southwestern Costa Rica and spans from the Osa Peninsula along the Pacific coast to the highlands of La Amistad International Park (hereafter, La Amistad) in the Cordillera de Talamanca (Fig. 1A). The Osa Peninsula alone houses approximately 2.5 % of global biodiversity despite its small size (~1100 km^2), including the largest primary lowland rainforest remaining in Pacific Mesoamerica (Gutierrez et al., 2019; Friedlander et al., 2022). We considered the Zona Protectora Las Tablas and Reserva Biológica del Bicentenario Pájaro Campana, which form a continuous forest block adjacent to La Amistad as part of La Amistad for our analyses. Elevation generally increases from the Pacific coast toward La Amistad, reaching a maximum of 3240 m (Fig. 1B). A small, mid-elevation mountain range (Fila Cruces) lies between lowland protected areas and La Amistad and reaches a maximum elevation of approximately 1700 m. There are several large, lowland protected areas, including Corcovado and Piedras Blancas National Parks, Golfo Dulce Forest Reserve, Terraba-Sierpe National Wetland and Golfito, Osa, and Pejeperro National Wildlife Refuges (Fig. 1A, Table A.1). Including all lowland protected areas and La Amistad, 30.5 % of the study landscape is currently protected (UNEP-WCMC and IUCN, 2023). Additionally, 31.4 % of the landscape is covered by Biological Corridors. The Costa Rican government established the Biological Corridor program in 2006 to provide connections among protected areas (SINAC, 2022). However, Biological Corridors are not officially protected, often consist of private land, and vary widely in terms of size, habitat characteristics, and restoration or conservation effort (Beita et al., 2021). Whilst the landscape is primarily forested (63.1 %) and Biological Corridors fall between lowland protected areas and La Amistad, forest cover is highly fragmented by agriculture and roads (Nikolova and Soto-Navarro, 2024) (Fig. A.1). Agriculture cover is approximately 24.5 % and is particularly concentrated within the central portions of the landscape (Fig. A.1). Please see Appendix for details on land cover in the study area.

2.2. Conductance surface

We created a conductance surface (inverse of resistance) based on the land cover classification (Fig. A.2., Table 1). Conductance refers to habitat permeability or the likelihood of a random walker choosing to move through a given cell in the landscape (McRae et al., 2008). Land cover-specific conductance values were based on the general assumption that intact forests increase conductance for medium-large terrestrial mammals present in the landscape (Baird's tapir [*Tapirus bairdii*], white-lipped peccary [*Tayassu pecari*], and jaguar [*Panthera onca*]; de la Torre et al., 2017, Meyer et al., 2020, Rabinowitz and Zeller, 2010). We opted to combine forest and riparian classes because both facilitate connectivity, but riparian areas constituted <0.1 % of the landscape, so we referred to these collectively as "forest". We treated the combination of low vegetation (cropland+pasture), pineapple, and oil palm as "agriculture", but low vegetation within protected areas remained as "low vegetation". We modified forested areas based on canopy height, so that mature forested locations had greater conductance. This was primarily based on a 10 m resolution global forest canopy dataset from 2020 imagery (Lang et al., 2023). Due to gaps (approximately 5 % of the landscape, presumably from clouds), we substituted 10 m resampled canopy height values from Potapov et al. (2020) (30 m resolution; 2019 imagery). Because canopy >30 m high was not accurately represented in Potapov et al. (2020), we set all values >30 m to 30 m (as well as from Lang et al. (2023) for consistency). We calculated the conductance modifier by dividing canopy height by 30 and then multiplied conductance values by this modifier. Finally, we incorporated roads using a layer from the Atlas of Costa Rica (Ortíz-Malavasi, 2014). Primary, secondary, and all other roads were buffered by 250 m, 125 m, and 50 m, respectively, to account for the broader spatial footprint of roads beyond roads themselves (Liu et al., 2014).

2.3. Objective 1: potential climate-resilient corridors

We used the centerpoint of lowland protected areas <500 m elevation as origins (n = 8) and points every 10 km along the border of La Amistad (within our landscape) as end points (n = 14) for least cost paths. Terraba-Sierpe National Wetland was treated as two separate origins because it consists of two large, non-contiguous blocks. We converted the conductance surface to a conductance matrix using the "create_cs" function and 8-directional connectivity in the "leastcostpath" R package (Lewis, 2023). We calculated least cost paths between each origin and end point using the "create_lcp" function in the "leastcostpath" package (112 total paths). We then identified the five least cost paths with the lowest accumulated cost (i.e., most permeability) from each origin, resulting in 40 total potential corridors for further analysis.

We used Circuitscape v5.0.0 in Julia v1.9.3 to model connectivity (Anantharaman et al., 2020) using the same conductance surface as for least cost paths. Starting locations were gridded points every 1 km within lowland protected areas. This is in contrast to least cost paths (for which we used centerpoints) given that Circuitscape more efficiently models connectivity throughout the entire landscape. Destinations were the same end points used for least cost paths. We also designated parts of La Amistad that overlapped with our study area as "short-circuit regions", which Circuitscape treats as uniformly without movement costs. We used the conjugate gradient algebraic multigrid solver and 8-directional connectivity and performed all analyses at 10 m resolution. This method produces a landscape-wide surface of current flow values, with higher values representing greater connectivity potential (Anantharaman et al., 2020). Current refers to expected movement probabilities for a random walker through a given cell en route from start to end points (in contrast to conductance, which is unaffected by spatial position) (McRae et al., 2008). Finally, we identified high-

Table 1
Conductance values by land cover type.

Type	Conductance	Area (km^2)	Percentage
Agriculture	30	1545	24.5
Developed	NA	8	0.1
Forest	1000[a]	3990	63.1
Low vegetation	30	75	1.2
Road	50	502	7.9
Water	20	103	1.5
Wetland/mangrove	20	86	1.6

[a] Multiplied by forest canopy height modifier (see Section 2.2 in main text). See section Appendix for land cover type descriptions and classification details.

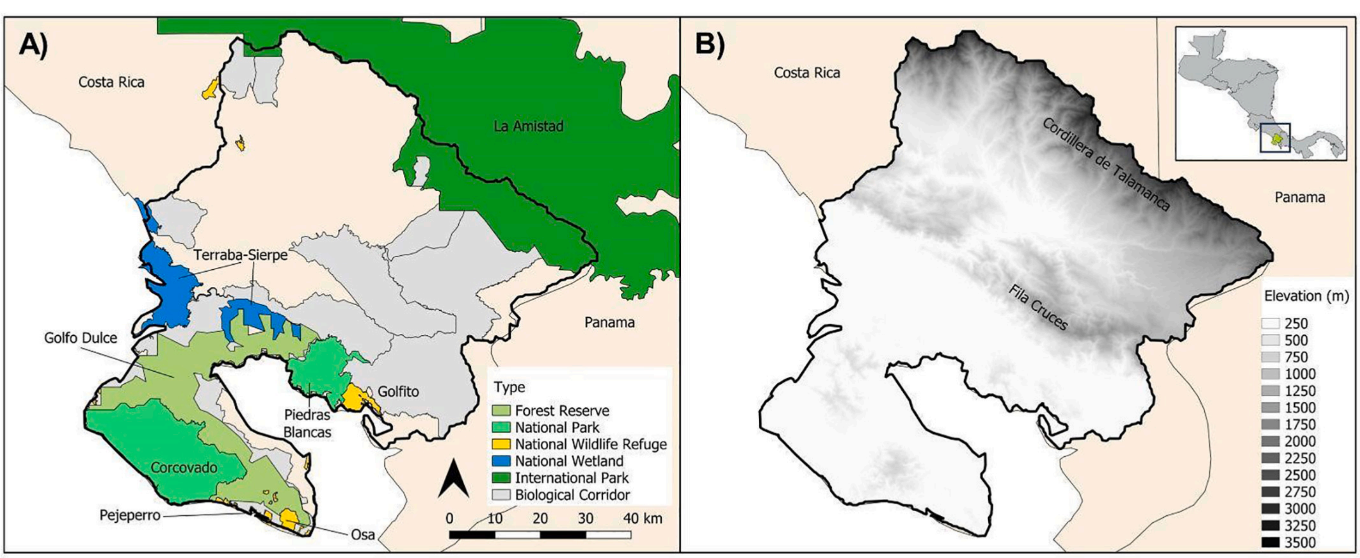

Fig. 1. A) Lowland protected areas (origins) and La Amistad International Park (destination) for mapping potential climate-resilient corridors. For this analysis, we considered the western and eastern portions of Terraba-Sierpe as two separate origins. Designated Costa Rican Biological Corridors are shown for context. B) Elevation based on 30 m resolution Shuttle Radar Topography Mission data (Jarvis et al., 2008).

connectivity forest and agriculture patches by quantifying mean current flow (cumulative) within each existing patch. We focused this analysis on unprotected areas because current within origin protected areas is skewed by the directionality of current flow and because our focus is on identifying corridors between lowland and highland protected areas.

2.4. *Objective 2: ecological characteristics and conservation status of potential climate-resilient corridors*

A corridor width of at least 2 km is considered a “rule-of-thumb” for facilitating long-term gene flow and habitat recolonization for terrestrial mammals (Beier, 2019). Therefore, we applied 1 km buffers on each side of least cost paths to assess their ecological characteristics and conservation status. We quantified number and percentage overlap of protected areas and Biological Corridors in each buffer using the World Database of Protected Areas, downloaded in October 2023 (UNEP-WCMC and IUCN, 2023), and a shapefile of current Biological Corridors, respectively (SINAC, 2022). We then assessed distance and elevational gradients, percentage forest and agriculture cover, number of forest patches and agriculture patches, total road crossings, and number of forest patches, agriculture patches, and road crossings per kilometer within each buffer using land cover data described in the Appendix and 30 m elevation data from the Shuttle Radar Topography Mission (Jarvis et al., 2008). Road crossings and forest and agriculture patches function as metrics of habitat fragmentation within potential corridors and are important because overall forest cover alone does not ensure connectivity (Brumberg et al., 2024). Forest and agriculture patches were identified using the “patches” function and 8-directional contiguity in the R “terra” package (Hijmans, 2023). We also quantified mean forest canopy height within buffers using canopy data described in Section 2.2. We used Spearman’s rank correlation coefficients (rho) and a *p*-value of 0.05 to analyze relationships among least cost path characteristics while accommodating non-normal distributions.

2.5. *Objective 3: validation of potential climate-resilient corridors using camera trap data*

We synthesized data from 330 camera trap stations from 4 separate studies conducted between 2018 and 2023 to examine recent landscape use by local wildlife and evaluate corridor functionality (Vargas Soto et al., 2022; Whitworth et al., 2022) (Fig. A.3). Overall, cameras were deployed for 23–334 days (median = 127 days) and were located a median of 913 m apart (cameras active <21 days were excluded). Cameras were located along an elevational gradient of 0–2,551 m (median = 165 m) and were primarily located in forested areas (median 85 % forest cover within 500 m buffers around cameras). Totals of 171 (52 %), 62 (19 %), and 101 (31 %) cameras were located in protected areas, national parks, and least cost paths (2 km buffers), respectively.

Analyses of capture rates help account for uneven sampling effort, particularly when considering both rare and common species (Carbone et al., 2001). We calculated capture rate as the number of independent detections for a given species (using a 30-minute threshold) at a given camera location divided by the number of active days for that camera (expressed as capture rate per 100 days). If deployment start or end dates were unknown, we used dates of first and last images recorded by a given camera, respectively. We then analyzed effects of conductance and current on capture rates for 7 focal species using negative binomial generalized linear models (“glm.nb” function in the R “MASS” package; Venables and Ripley, 2002). Focal species were medium-large vertebrates (primarily mammals) with variable sensitivity to human disturbance (Vargas Soto et al., 2022). These included disturbance-sensitive species: Baird’s tapir (*T. bairdii*), jaguar (*P. onca*), and white-lipped peccary (*T. pecari*); generalist species: puma (*Puma concolor*) and collared peccary (*Pecari tajacu*), and generalist, commonly hunted species: spotted paca (*Cuniculus paca*) and great curassow (*Crax rubra*), a large bird. We expected our focal species to have higher capture rates in areas with greater conductance (high permeability) or current (high probability of supporting corridors). We used mean conductance and mean cumulative current within 500 m buffers of camera trap locations as predictors of capture rates and compared performance to null models (i.e., no predictors) based on second-order Akaike Information Criterion using the “model.sel” function in the R “MuMIn” package (Bartoń, 2023). We only used cameras in unprotected locations for models assessing current because current was skewed by flow directionality within protected areas. All models included log-transformed active camera days as an offset term to control for variable survey effort.

Data and R scripts are available on Zenodo (https://doi.org/10.5281/zenodo.11122373). We used R v4.3.1 for analyses (R Core Team, 2023).

3. Results

3.1. *Potential climate-resilient corridors*

Least cost path analysis identified a few key pathways connecting multiple lowland protected areas to La Amistad (Fig. 2A). Of 40 least cost paths analyzed, the greatest concentrations occurred in the neck of the Osa Peninsula through the eastern portion of the landscape. An exception was routes leading from the western portion of Terraba-Sierpe National Wetland, which were most spatially distinct from other least cost paths. Generally in alignment with least cost paths, circuit theory analysis demonstrated high potential current flow through the neck of the Osa Peninsula and the eastern portion of the landscape (Fig. 2B). However, there were some notable differences between least cost path and circuit theory results. There were many potential pathways connecting lowland and upland protected areas identified using circuit theory that were not identified in the least cost paths analysis, particularly through central portions of the landscape (Fig. 2B). These results indicated that least cost paths existed within a broader mosaic of many potential routes.

3.2. *Ecological characteristics and conservation status of potential climate-resilient corridors*

Least cost paths were predominantly forested (median = 76 %, range = 57–82 %) with relatively tall mean canopy heights (median = 26 m, range = 22–27 m), limited coverage within protected areas (median = 31 %, range = 3–55 % overlap) and often located within Biological Corridors outside protected areas (median = 87 %, range = 3–100 % overlap) (Fig. A.4, Table A.2). Least cost paths ranged between 64 and 166 km in length (median = 104 km) and 1,415–2,932 m in elevation (median = 1,700 m) from lowest to highest point. Despite relatively high forest cover, least cost paths were significantly fragmented, traversing ranges of 162–328 (median = 252) forest patches, 812–1237 (median = 1,063) agriculture patches, and 50–252 (median = 117) roads. These translated to 1–4 (median = 2) forest patches, 9–17 (median = 11) agriculture patches, and 0–3 (median = 1) roads crossed per kilometer. Differences among least cost paths and relationships among their ecological characteristics are addressed in the Appendix and Fig. A.4).

Current analysis in existing forest and agriculture patches showed that a small number of patches held relatively high connectivity value (≥ 80th percentile mean current). We identified 11,600 unprotected forest patches (median area = 0.07 ha, range = 0.01–42,475 ha) whose mean current followed a right-skewed distribution (Fig. 3a, c). Of the high-connectivity forest patches (n = 2,315; median area = 0.18 ha, range = 0.01–42,475 ha), just 12 patches were >1,000 ha (Fig. 3e). We also identified 26,414 agriculture patches (median area = 0.12 ha, range = 0.01–2,361 ha) whose mean current also followed a right-skewed distribution (Fig. 3b, d). However, only four of the high-connectivity agriculture patches (n = 5,281, median area = 0.02 ha, range = 0.01–568 ha) were >100 ha (Fig. 3f).

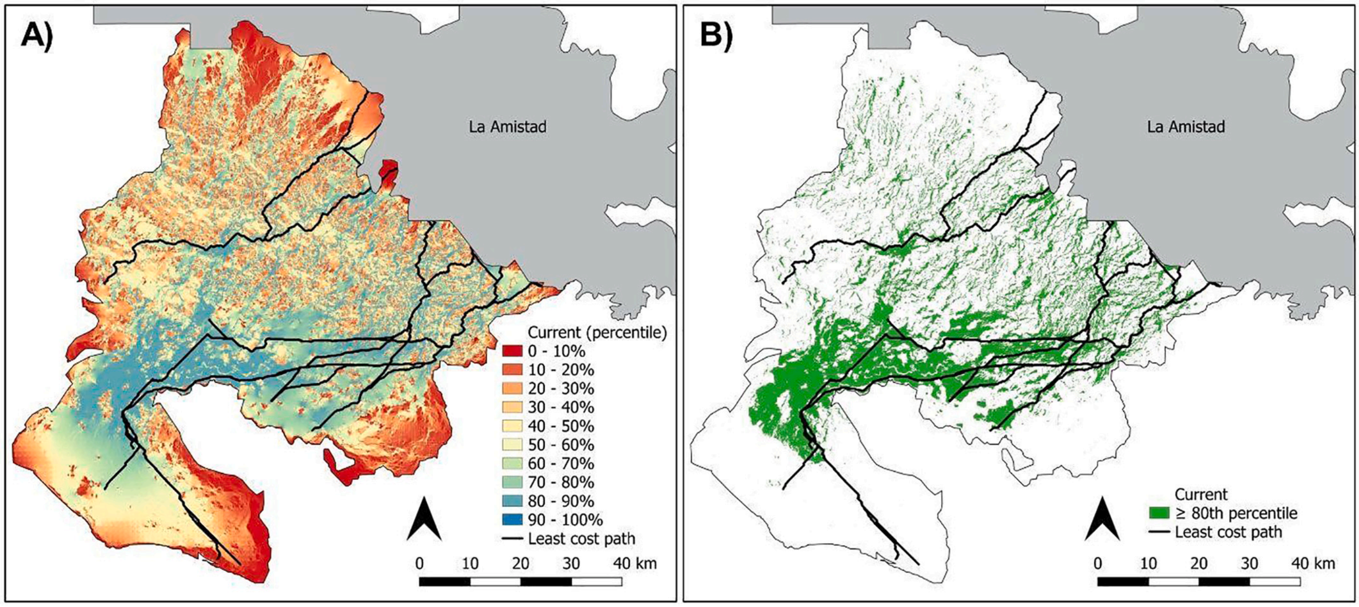

Fig. 2. Least cost paths overlaid on A) current (modeled movement probability) B) and 80th percentile of current and greater.

3.3. Influence of conductance and current on camera trap capture rates

Across 330 camera traps, there were 7,411 independent detections of our 7 focal species. Capture rates were generally greater for more common, generalist species and lower for rarer, more disturbance-sensitive species. Collared peccary (61 % of cameras), curassow (54 %), and paca (45 %) were most frequently detected, whereas puma, tapir, white-lipped peccary, and jaguar were detected at 31 %, 22 %, 9 %, and 8 % of cameras, respectively. Detections for all species were more common in protected areas (especially within the Osa Peninsula) (Fig. A.5). Conversely, detections within central portions of the landscape, including Biological Corridors, least cost paths, and high-connectivity (high-current) areas, were relatively uncommon, especially for tapir, jaguar, and white-lipped peccary.

Capture rates were positively and significantly associated with conductance, indicating that all focal species use parts of the landscape presumed to favor movement, such as forests (Fig. 4, Table A.3). However, models without predictors outperformed models using current to predict capture rates for 6 of 7 focal species, indicating that these 6 species are not using unprotected parts of the landscape presumed to represent potential corridors. The exception was Baird's tapir, but this species still had lower expected capture rates with higher current ($\beta = -6.64$, 95%CI: -12.56, -1.74; $p = 0.0372$). This suggests that tapirs are not often using potential corridors. Although focal species appeared to use portions of the landscape thought to facilitate movement (i.e., high conductance), focal species were not detected frequently in unprotected, fragmented areas between lowland protected areas and La Amistad.

4. Discussion

Our study combined least cost paths and circuit theory at high spatial resolution to identify numerous potential climate-resilient corridors between lowland protected areas on the Osa Peninsula and La Amistad, a potential highland climate change refugium. Our fine-scale analyses demonstrated that all potential corridors identified using structural connectivity in this region are highly fragmented and only partially protected (least cost paths: median 31 % area protected). Specifically, least cost paths traverse an average of 249 forest patches, 1,062 agriculture patches, and 117 roads, suggesting that even the "best" available routes contain numerous obstacles. Finally, our extensive camera trap dataset provided limited evidence of functional connectivity (short-term) between lowland protected areas and La Amistad, suggesting that improving connectivity should be a conservation priority. Whereas there was some evidence of connectivity for a portion of the generalist community, there was little evidence for relatively rare, sensitive species (i.e., tapir, jaguar, and white-lipped peccary). Without additional investment in conservation and restoration, it will be challenging to form functional corridors due to thousands of mostly small forest and agriculture patches outside protected areas. Nevertheless, our fine-scale approach offers numerous candidate locations to guide conservation actions to enhance landscape connectivity.

4.1. Designated corridors are insufficient for climate resilience in southwestern Costa Rica

The lack of relationship between capture rates and current suggests that the various possible routes between lowland protected areas and La Amistad are likely still too fragmented, degraded, or inaccessible to constitute functional corridors, particularly for disturbance-sensitive species. These findings are especially discouraging considering that designated Biological Corridors not only overlap considerably with many least cost paths and high connectivity (high-current) areas, but also constitute much of the land between lowland protected areas and La Amistad. Therefore, corridors we identified are still only potential corridors, highlighting the urgency for on-the-ground conservation interventions such as habitat restoration and road crossing structures to improve regional connectivity.

Increasing connectivity among protected areas has long been recognized as a major global conservation priority for climate resilience. Target 3 of the Kunming-Montreal Global Biodiversity Framework aims to protect and connect 30 % of global land area by 2030. By 2020, Costa Rica already had over 27 % of its land protected, but only 40 % of protected lands were interconnected (Álvarez Malvido et al., 2021). This suggests that the current portfolio of Biological Corridors in Costa Rica provides insufficient connectivity for climate resilience. Although Biological Corridors cover 38 % of the country, previous research has also shown that Biological Corridors are insufficient for connecting protected areas under climate change (Beita et al., 2021). Therefore, our study exemplifies the pressing need for a locally actionable Costa Rican corridor network explicitly designed to support ecological connectivity under climate change.

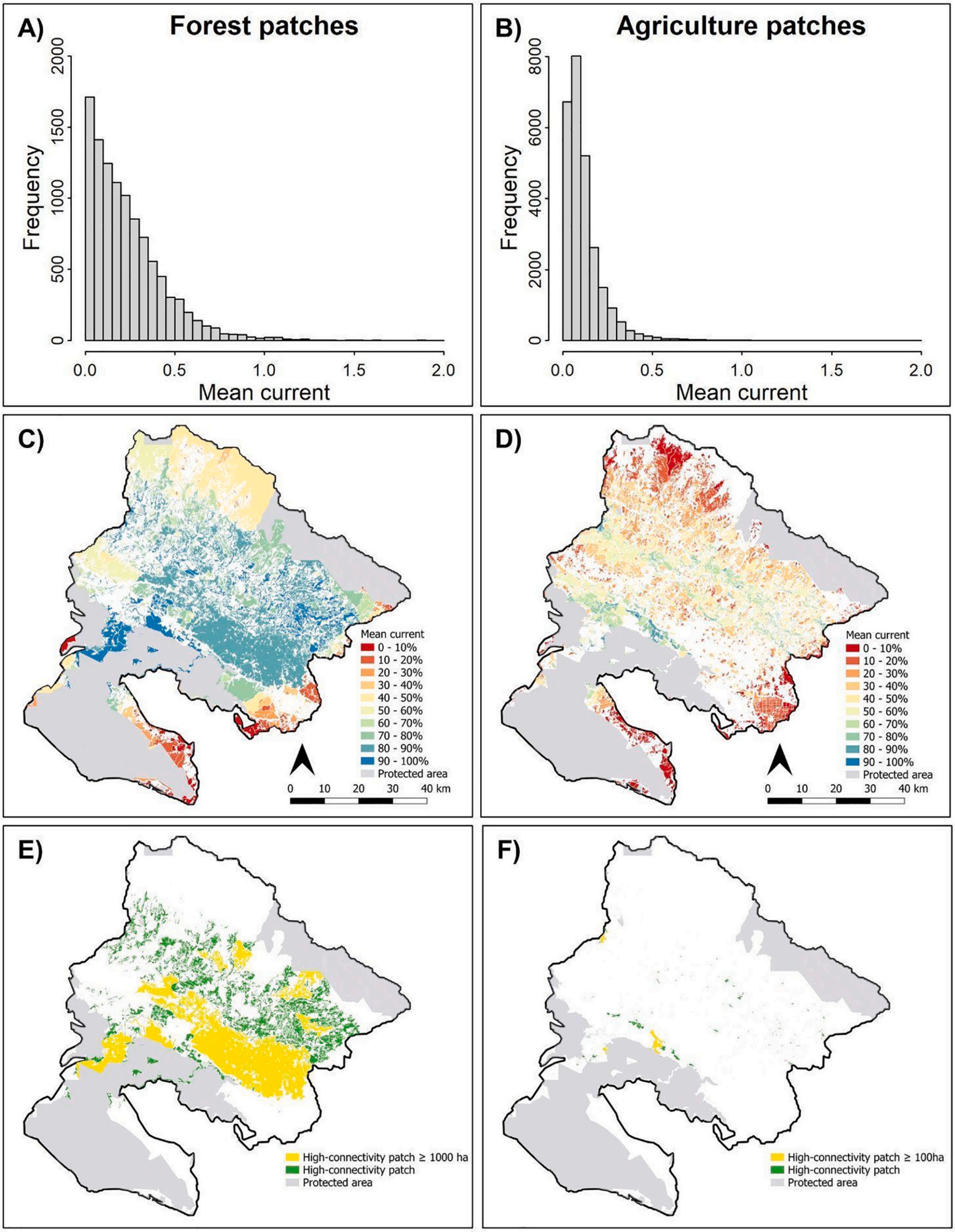

Fig. 3. A) mean current (modeled movement probability) in unprotected forest patches ($n = 11{,}600$), B) mean current in agriculture patches ($n = 26{,}414$), C) mean current in forest patches in percentile bins, D) mean current in agriculture patches in percentile bins, E) high-connectivity forest patches (mean current $\geq$80th percentile) ($n = 2315$) and high-connectivity forest patches $\geq$1,000 ha (10 km^2) ($n = 12$) (maximum = 425 km^2), and F) high-connectivity agriculture patches (mean current $\geq$80th percentile) ($n = 5{,}281$) and high-connectivity agriculture patches $\geq$100 ha (1 km^2) ($n = 4$) (maximum = 6 km^2).

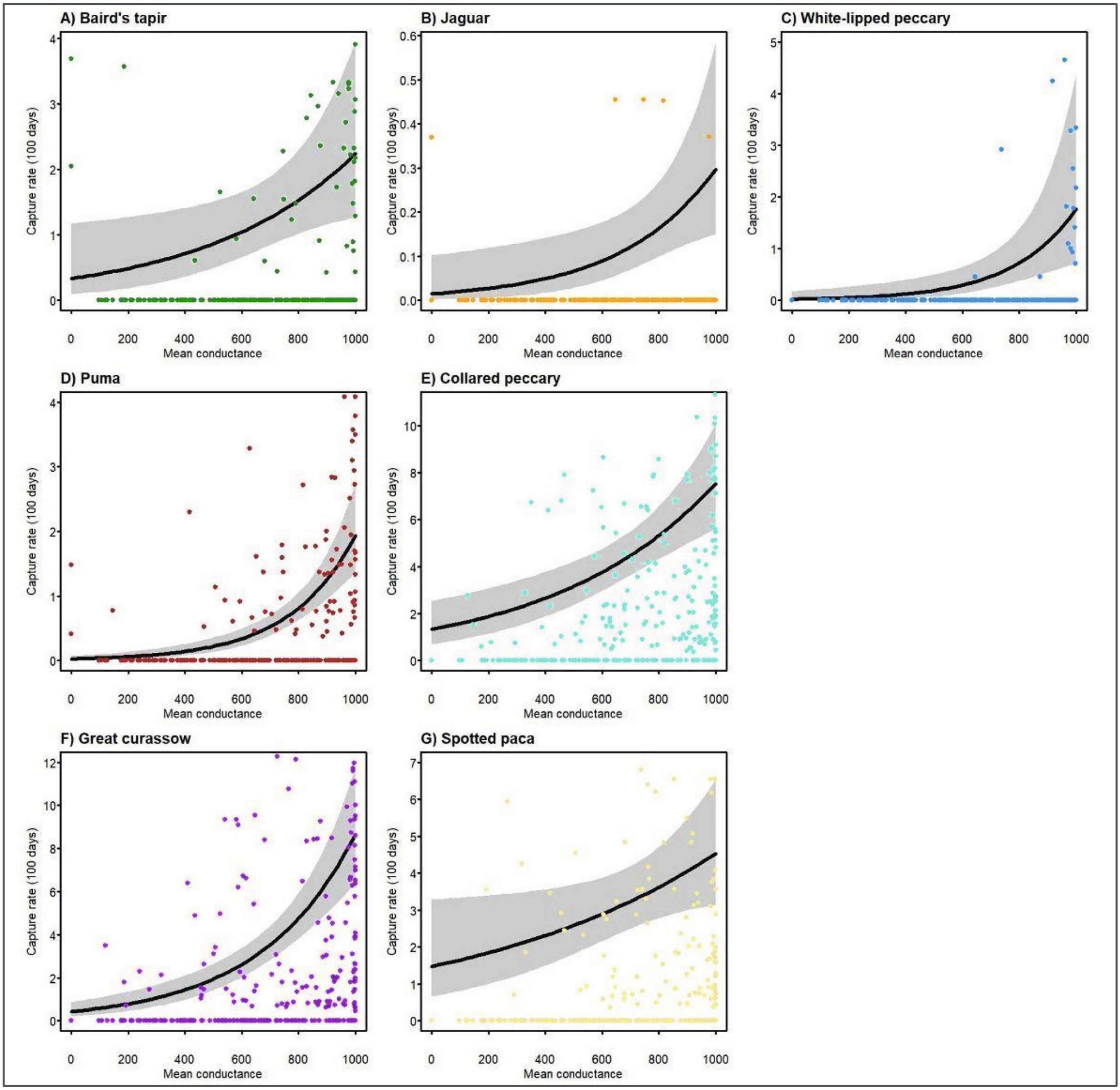

Fig. 4. Relationships between capture rate and conductance (habitat permeability; mean within 500 m buffers around camera traps) for A) Baird's tapir (*Tapirus bairdii*), B) jaguar (*Panthera onca*), C) white-lipped peccary (*Tayassu pecari*), D) puma (*Puma concolor*), E) collared peccary (*Pecari tajacu*), F) great curassow (*Crax rubra*) and G) spotted paca (*Cuniculus paca*). Lines represent predictions from negative binomial generalized linear regression and gray areas represent associated 95 % confidence intervals. Points represent actual data. Note different y-axes among plots.

4.2. Working toward multi-species corridors for facilitating range shifts

One of the ultimate goals of connectivity research is establishing functional, multi-species corridors (Wang et al., 2018). Whereas many studies rely on umbrella species (often large, charismatic mammals), such an approach often does not meet the connectivity requirements of co-occurring species or is not thoroughly tested (Brennan et al., 2020). Similar to our study, previous studies of large tropical mammals have suggested designing corridors based on the connectivity needs of sensitive species (Brodie et al., 2015; Meyer et al., 2020). This approach resembles using functional traits to design multi-species corridors (Salgueiro et al., 2021). Another approach is to apply species distribution modeling to identify habitat for a suite of species, which may be useful in the tropics where there are many specialist species potentially sensitive to climate change (Linero-Triana et al., 2023). Nonetheless, achieving multi-species connectivity in a climate change context likely requires addressing taxonomic bias in previous research toward large mammals as well as spatial biases in model calibration and validation data (often also biased toward large mammals; Delisle et al., 2021). Although our study was one of few to assess multi-species functional connectivity using local observational data, our validation was made possible by synthesizing several separate camera trap studies, none of which was designed to assess regional connectivity. Ideally, multi-species connectivity validation would be designed to sample multiple taxa across local, ecologically relevant gradients (e.g., forest cover, elevation) or stratified across available habitat types, but this is often difficult due to resource or accessibility constraints (Lalechère and Bergès, 2021). Taken together, multiple approaches may need to be combined both to design and validate multi-species corridor functionality, particularly in highly biodiverse, multi-use tropical landscapes.

A key assumption of our analyses is that connectivity across elevational gradients can promote climate resilience for biodiversity. Although we investigated the extent to which focal species use potential corridors across elevational gradients and our data can serve as a reference point for future work in southwestern Costa Rica, we did not explicitly examine range shifts. The ecological complexities of elevational range shifts would require additional years of observations and are beyond the scope of our study, but should be prioritized in future research. Documented range shifts in the tropics are relatively rare, but have been mostly elevational with no clear evidence of latitudinal range shifts (Colwell and Feeley, 2024). This underscores the importance of connectivity across elevational gradients in the tropics, particularly for lowland species threatened by climate change. Our focal species already inhabit lowland and highland protected areas within our landscape, but the lack of connectivity in intermediate portions of the landscape could preclude upward shifts in abundances or seasonal movements. Nonetheless, our focus is on landscape capacity to support biodiversity resilience under climate change and our findings suggest that such capacity is currently limited (at least for the suite of species assessed), possibly due to habitat fragmentation and degradation separating lowland and highland protected areas.

4.3. Facilitating implementation of climate-resilient corridors in southwestern Costa Rica and beyond

Our study shows that strategically protecting, restoring, and linking forest fragments important for connectivity may represent the best path to creating functional climate-resilient corridors in tropical multi-use landscapes such as ours. While providing a detailed, stakeholder-driven corridor implementation plan is beyond the scope of this paper, we show how this approach is beneficial for locally actionable conservation by identifying forest and agriculture patches with high connectivity value (high current) that could be targeted for on-the-ground efforts (Fig. 4). For example, the small number of relatively large unprotected forest and agriculture patches with high connectivity value could be priority candidates for conservation. Although other prioritization factors could be considered, including property values, biodiversity indices, or agriculture aptitude, patches with high connectivity value represent a starting point for engaging with landowners and other stakeholders.

4.4. Conclusion

Climate-resilient corridors represent a key nature-based solution for promoting biodiversity resilience under climate change by encouraging gene flow, providing buffers from extreme temperatures, and enabling access to potential highland climate change refugia. Our findings underscore the urgent need for more conservation and restoration in fragmented, multi-use tropical landscapes to support connectivity. Furthermore, possible mismatches between structural and functional connectivity demonstrate the importance of validating potential corridors using biological data, particularly considering the potentially widespread negative effects of habitat fragmentation or degradation on landscape connectivity. Our study emphasizes that simply designating corridors does not necessarily create functional corridors for all taxa. Finally, integrating coarse- and fine-scale research can help provide local conservation practitioners with the information necessary to overcome common corridor implementation gaps.

CRediT authorship contribution statement

Ian M. McCullough: Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Christopher Beirne:** Writing – review & editing, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Formal analysis, Data curation. **Carolina Soto-Navarro:** Writing – review & editing, Supervision, Conceptualization. **Amy Eppert:** Data curation, Writing – review & editing. **Eleanor Flatt:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation. **Yvonne J.M. Kemp:** Writing – review & editing, Resources, Investigation. **Péter K. Molnár:** Writing – review & editing, Supervision, Resources, Methodology, Funding acquisition. **Michael S. Mooring:** Writing – review & editing, Investigation, Data curation. **Yana Nikolova:** Software, Data curation. **Erik R. Olson:** Writing – review & editing, Resources, Investigation, Data curation, Conceptualization. **Carolina Pinto:** Writing – review & editing, Resources, Investigation. **Junior Porras:** Writing – review & editing, Resources, Investigation, Data curation. **María José Mata Quirós:** Writing – review & editing, Resources. **Guido Saborío Rodriguez:** Writing – review & editing, Resources. **Jan Schipper:** Writing – review & editing, Resources, Investigation, Conceptualization. **Chelsey R. Tellez:** Writing – review & editing, Investigation. **Juan S. Vargas Soto:** Writing – review & editing, Methodology, Investigation. **Andrew Whitworth:** Writing – review & editing, Supervision, Resources, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Analysis data and R scripts are available on Zenodo (https://doi.org/10.5281/zenodo.11122373).

Acknowledgements

We are thankful for the support of the Osa Camera Trap Network members and the communities of Dos Brazos de Rio Tigre, Los Planes, Rancho Quemado, and Indigenous Reserve Alto Laguna. Finally, we thank the volunteers of Osa Conservation and Universidad National de Costa Rica who assisted in fieldwork and data sorting.

Funding

This research was supported by the International Conservation Fund of Canada, the Bobolink Foundation, the BAND Foundation, the Gordon and Betty Moore Foundation, the Krystyna and Dan Houser Foundation, the SENSE Foundation Brussels, the Mazar Family Charitable Foundation Trust, Fundación ProCAT, Las Alturas del Bosque Verde, the Phoenix Zoo, Sabrina Karklins, Michael Simons, NSERC (Natural Sciences and Engineering Research, Council of Canada) Discovery Grant, CFI (Canada Foundation for Innovation) John R. Evans Leader Funds, MRIS Ontario Research Funds, University of Toronto Scarborough Research Competitiveness Funds, Northland College, JaguarOsa, and the Costa Rican National System of Conservation Areas (SINAC).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110763.

References

Almasieh, K., et al., 2023. Identifying core habitats and connectivity paths for the conservation of mouflon (*Ovis gmelini*) in Western Iran. Global Ecol. Conserv. 41, e02377 https://doi.org/10.1016/j.gecco.2023.e02377.

Álvarez Malvido, M., et al. (Editores). (2021). Latin America and the Caribbean Protected Planet Report 2021. Mexico City, Mexico; Cambridge UK; Gland, Switzerland; Bogota, Colombia: Red-Parques, UNEP-WCMC, WCPA-IUCN, WWF, CONANP and IAPA Project.

Anantharaman, R., et al., 2020. Circuitscape in Julia: high performance connectivity modelling to support conservation decisions. JuliaCon Proceedings 1(1), 58. https://doi.org/10.21105/jcon.00058.

Bartoń K (2023). _MuMIn: multi-model Inference_. R package version 1.47.5, <https://CRAN.R-project.org/package=MuMIn>.

Beier, P., 2012. Conceptualizing and designing corridors for climate change. Ecol. Restor. 30 (4), 312–319. https://doi.org/10.3368/er.30.4.312.

Beier, P., 2019. A rule of thumb for widths of conservation corridors. Conserv. Biol. 33 (4), 976–978. https://doi.org/10.1111/cobi.13256.

Beita, C.M., et al., 2021. Ecological corridors in Costa Rica: an evaluation applying landscape structure, fragmentation-connectivity process, and climate adaptation. Conserv. Sci. Pract. 3 (8), e475 https://doi.org/10.1111/csp2.475.

Brennan, A., et al., 2020. Characterizing multispecies connectivity across a transfrontier conservation landscape. J. Appl. Ecol. 57 (9), 1700–1710.

Brodie, J.F., et al., 2015. Evaluating multispecies landscape connectivity in a threatened tropical mammal community. Conserv. Biol. 29 (1), 122–132.

Brumberg, H., et al., 2024. Increasing Forest cover and connectivity both inside and outside of protected areas in southwestern Costa Rica. Remote Sens. 16 (6), 1088. https://doi.org/10.3390/rs16061088.

Carbone, C., et al. (2001). The use of photographic rates to estimate densities of tigers and other cryptic mammals. In Animal Conservation Forum (Vol. 4, No. 1, pp. 75–79). Cambridge University Press.

Colwell, R.K., Feeley, K.J., 2024. Still little evidence of poleward range shifts in the tropics, but lowland biotic attrition may be underway. Biotropica e13358.

Correa Ayram, C.A., et al., 2016. Habitat connectivity in biodiversity conservation: a review of recent studies and applications. Prog. Phys. Geogr. 40 (1), 7–37. https://doi.org/10.1177/0309133315598713.

de la Torre, J.A., et al., 2017. Habitat availability and connectivity for jaguars (*Panthera onca*) in the southern Mayan Forest: conservation priorities for a fragmented landscape. Biol. Conserv. 206, 270–282.

Delisle, Z.J., et al., 2021. Next-generation camera trapping: systematic review of historic trends suggests keys to expanded research applications in ecology and conservation. Front. Ecol. Evol. 9, 617996.

Dobrowski, S.Z., 2011. A climatic basis for microrefugia: the influence of terrain on climate. Glob. Chang. Biol. 17 (2), 1022–1035. https://doi.org/10.1111/j.1365-2486.2010.02263.x.

Friedlander, A.M., et al., 2022. Nearshore marine biodiversity of Osa peninsula, Costa Rica: where the ocean meets the rainforest. PLoS One 17 (7), e0271731. https://doi.org/10.1371/journal.pone.0271731.

Fung, E., et al., 2017. Mapping conservation priorities and connectivity pathways under climate change for tropical ecosystems. Clim. Chang. 141, 77–92. https://doi.org/10.1007/s10584-016-1789-8.

Gutierrez, B.L., et al., 2019. An island of wildlife in a human-dominated landscape: the last fragment of primary forest on the Osa Peninsula's Golfo Dulce coastline. Costa Rica. PLOS One 14 (3), e0214390. https://doi.org/10.1371/journal.pone.0214390.

Heller, N.E., Zavaleta, E.S., 2009. Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biol. Conserv. 142 (1), 14–32. https://doi.org/10.1016/j.biocon.2008.10.006.

Hijmans, R., 2023. terra: Spatial Data Analysis. R package version 1, 7–29. https://CRAN.R-project.org/package=terra.

Hilty, J., et al., 2020. Guidelines for conserving connectivity through ecological networks and corridors. Best Practice Protected Area Guidelines Series No. 30. IUCN, Gland, Switzerland.

Iannella, M., et al., 2024. Functional connectivity and the current arrangement of protected areas show multiple, poorly protected dispersal corridors for the Eurasian lynx. Biol. Conserv. 291, 110498 https://doi.org/10.1016/j.biocon.2024.110498.

Jantz, P., et al., 2014. Carbon stock corridors to mitigate climate change and promote biodiversity in the tropics. Nat. Clim. Chang. 4 (2), 138–142. https://doi.org/10.1038/nclimate2105.

Jarvis, A., et al. (2008). Hole-filled SRTM for the globe Version 4, available from the CGIAR-CSI SRTM Database: https://srtm.csi.cgiar.org.

Jucker, T., et al., 2018. Canopy structure and topography jointly constrain the microclimate of human-modified tropical landscapes. Glob. Chang. Biol. 24 (11), 5243–5258. https://doi.org/10.1111/gcb.14415.

Keeley, A.T., et al., 2018. Making habitat connectivity a reality. Conserv. Biol. 32 (6), 1221–1232. https://doi.org/10.1111/cobi.13158.

Kindlmann, P., Burel, F., 2008. Connectivity measures: a review. Landsc. Ecol. 23, 879–890. https://doi.org/10.1007/s10980-008-9245-4.

Krosby, M., et al., 2018. Identifying riparian climate corridors to inform climate adaptation planning. PLoS One 13 (11), e0205156. https://doi.org/10.1371/journal.pone.0205156.

Lalechère, E., Bergès, L., 2021. A validation procedure for ecological corridor locations. Land 10 (12), 1320. https://doi.org/10.3390/land10121320.

Lang, N., et al., 2023. A high-resolution canopy height model of the earth. Nat. Ecol. Evol. 1-12 https://doi.org/10.1038/s41559-023-02206-6.

LaPoint, S., et al., 2013. Animal behavior, cost-based corridor models, and real corridors. Landsc. Ecol. 28, 1615–1630. https://doi.org/10.1007/s10980-013-9910-0.

Lewis J (2023). leastcostpath: Modelling Pathways and Movement Potential Within a Landscape_. Available at: https://CRAN.R-project.org/package=leastcostpath.

Lewis, S.L., et al., 2015. Increasing human dominance of tropical forests. Science 349 (6250), 827–832. https://doi.org/10.1126/science.aaa9932.

Linero-Triana, D., et al., 2023. Prioritizing ecological connectivity among protected areas in Colombia using a functional approach for birds. Global Ecol. Conserv. 48, e02713.

Liu, S., et al., 2014. Forest fragmentation and landscape connectivity change associated with road network extension and city expansion: a case study in the Lancang River valley. Ecol. Indic. 36, 160–168. https://doi.org/10.1016/j.ecolind.2013.07.018.

McCullough, I.M., et al., 2024. Mapping climate adaptation corridors for biodiversity - a regional-scale case study in Central America. PLoS One 19 (5), e0304756. https://doi.org/10.1371/journal.pone.0304756.

McRae, B.H., et al., 2008. Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89 (10), 2712–2724. https://doi.org/10.1890/07-1861.1.

Meyer, N.F., et al., 2020. Towards the restoration of the Mesoamerican biological corridor for large mammals in Panama: comparing multi-species occupancy to movement models. Mov. Ecol. 8 (1), 1–14.

Mohammadi, A., Almasieh, K., Vaissi, S., 2024. Ungulates conservation in the face of human development: Mining and roads' influences on habitat and connectivity in Iran's central plateau. Ecol. Inform., 102656 https://doi.org/10.1016/j.ecoinf.2024.102656.

Nikolova, Y.S., Soto-Navarro, C., 2024. Land-Cover Classification of Mesoamerica's Climate Hubs (1.0.0) [Data set]. Zenodo. https://doi.org/10.5281/zenodo.13329296.

Ortíz-Malavasi, E., 2014. Atlas Digital de Costa Rica 2014. Instituto Tecnológico de Costa Rica, Costa Rica.https://repositoriotec.tec.ac.cr/handle/2238/6749?show=full.

Pineda-Zapata, S., et al., 2024. Mapping the way: identifying priority potential corridors for protected areas connectivity in Colombia. Perspect. Ecol. Conserv. 22 (2), 156–166. https://doi.org/10.1016/j.pecon.2024.02.003.

Pinto, C.M., et al., 2024. Identifying wildlife road crossing mitigation sites using a multi-data approach-a case study from southwestern Costa Rica. J. Environ. Manag. 361, 121263 https://doi.org/10.1016/j.jenvman.2024.121263.

Potapov, P., et al., 2020. Mapping and monitoring global forest canopy height through integration of GEDI and Landsat data. Remote Sens. Environ. 112165 https://doi.org/10.1016/j.rse.2020.112165.

R Core Team, 2023. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/>.

Rabinowitz, A., Zeller, K.A., 2010. A range-wide model of landscape connectivity and conservation for the jaguar. Panthera onca. Biol. Conserv. 143 (4), 939–945.

Sales, L.P., Pires, M.M., 2023. Identifying climate change refugia for South American biodiversity. Conserv. Biol. 37 (4), e14087 https://doi.org/10.1111/cobi.14087.

Salgueiro, P.A., et al., 2021. Multispecies landscape functional connectivity enhances local bird species' diversity in a highly fragmented landscape. J. Environ. Manag. 284, 112066.

Scheffers, B.R., et al., 2017. Extreme thermal heterogeneity in structurally complex tropical rain forests. Biotropica 49 (1), 35–44. https://doi.org/10.1111/btp.12355.

Senior, R.A., et al., 2019. Global loss of climate connectivity in tropical forests. Nat. Clim. Chang. 9 (8), 623–626. https://doi.org/10.1038/s41558-019-0529-2.

Sistema Nacional de Áreas de Conservación [SINAC]. 2022. Mapas de corredores biológicos de Costa Rica. https://www.sinac.go.cr/ES/correbiolo/Paginas/default.aspx.

Stralberg, D., et al., 2020. Toward a climate-informed north American protected areas network: incorporating climate-change refugia and corridors in conservation planning. Conserv. Lett. 13 (4), e12712 https://doi.org/10.1111/conl.12712.

Trew, B.T., Maclean, I.M., 2021. Vulnerability of global biodiversity hotspots to climate change. Glob. Ecol. Biogeogr. 30 (4), 768–783. https://doi.org/10.1111/geb.13272.

UNEP-WCMC and IUCN (2023) Protected Planet: The World Database on Protected Areas (WDPA), October 2023, Cambridge, UK: UNEP-WCMC and IUCN. Available at: www.protectedplanet.net.

Vargas Soto, J.S., et al., 2022. Human disturbance and shifts in vertebrate community composition in a biodiversity hotspot. Conserv. Biol. 36 (2), e13813 https://doi.org/10.1111/cobi.13813.

Venables, W. N. & Ripley, B. D. (2002) Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0–387–95457-0.

Wang, F., et al., 2018. Does one size fit all? A multispecies approach to regional landscape corridor planning. Divers. Distrib. 24 (3), 415–425.

Whitworth, A. et al. (2022). Last updated January 2024. Osa Peninsula . http://n2t.net/ark:/63614/w12003884. Accessed via wildlifeinsights.org on 2024-01-26.

Zeller, K.A., et al., 2012. Estimating landscape resistance to movement: a review. Landsc. Ecol. 27, 777–797. https://doi.org/10.1007/s10980-012-9737-0.