Habitat connectivity of three threatened ungulate species in the high plains native savanna of northern South America

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Abstract

The high plains native savanna landscape (HPNSL) northeast of the Orinoco River is the habitat of 50% of the wild ungulate species (WUS) reported for Colombia. Over the last 20 years, this high species diversity has been strongly threatened by the accelerated human transformation of the natural land cover causing connectivity loss of the habitats. Despite this situation, the region lacks a biological connectivity analysis with a multi-species approach involving species groups that are representative of the savanna ecosystem such as the WUS. Understanding the spatial distributions of suitable habitats and the main habitats that act as primary habitats for ungulate focal species (UFS) in these landscapes is fundamental for the design of effective conservation strategies. Here, we use an occurrence dataset for *Tapirus terrestris*, *Odocoileus virginianus*, and *Tayassu pecari* in the development of species’ potential distribution models, the binarization process, and morphological spatial pattern analysis. This information was used for the modelling of dispersal corridors connecting the core habitats of the UFS using the randomized shortest path algorithm and quantifying the weighted global connectivity metrics. Our results suggest an integral corridor with potential least-cost dispersal routes between the HPNSL on the middle and lower-middle basins of the savanna rivers and, to a lesser extent, the lower basin of the Meta River. These areas associated with the fluvial dendritic systems are connected, while the core habitats in the eastern part of the savanna landscape are largely disconnected. We discuss how the application of such knowledge on the spatial ecology of ungulate species might improve management of the metapopulations in the Colombian HPNSL.

Introduction

Human activities have drastically shaped the earth's surface, causing fluctuations in the connectivity of the landscape that lower species diversity (Palmara et al. 2023), besides negatively impacting the ecological, genotypes, species, and functional characteristics of landscape units (de Chazal and Rounsevell 2009; Haddad et al. 2015; IPBES 2019). On a global scale, loss of landscape connectivity generates an increase in the costs of dispersal of mammals, limiting, in turn, the large movements by increasing the distances between habitat patches (Bolger et al. 2008; Bonte et al. 2012; Seidler et al. 2015). Dispersing individuals in unconnected landscapes must travel longer distances through unsuitable parts of the landscape (the matrix), requiring time and energy with the additional risk of an unsuccessful dispersal (Baguette et al. 2013; Bonte et al. 2012). The risk is greater for species from biomes with low levels of connectivity, like savanna landscapes. Savanna is the biome with the lowest connectivity of the 14 world's biomes assessed (Saura et al. 2017; Herrera et al. 2017). In this context, connectivity of wildlife populations that inhabit the Neotropical savannas is a critical factor in their long-term survival, particularly for large mammals facing multiple threats such as habitat loss and hunting pressure (Bogoni et al. 2020; 2022). At present, wildlife is increasingly confined in ever more smaller and sparse habitat patches (Fahrig 2003; Boitani et al. 2007); and low habitat connectivity impedes ecological processes like daily foraging, seasonal migration, successful reproduction, and juvenile dispersal (Rayfield et al. 2011; Braaker et al. 2014). In the long term, poor connectivity increases extinction risk and
decreases genetic diversity because of population isolation, inbreeding depression, demography stochasticity, and limitation of their evolutionary potential and response to fluctuations in landscape connectivity (Hayward and Kerley 2009; Dirzo et al. 2014; Koen et al. 2014; Correa Ayram et al. 2016). These effects are mainly seen in the large mammal species with broad-scale spatial requirements (Bogoni et al. 2023). These are the WUS that require large areas (Crooks et al. 2017). It should be noted some ungulates are reported as species threatened because of habitat loss and degradation of their habitats (Lino et al. 2019).

The Perissodactyla represent three families and a total of 16 species, and the Artiodactyla is represented by 10 families and 380 species (Fennessy et al. 2016; Wilson and Mittermeier 2011). These WUS are distributed mainly in savannas, grasslands, and forests of Africa, America, Asia, and Europe; and they also appear in Australia as introduced species (Wilson and Mittermeier 2011). The Neotropics contain about 30% of the total world mammalian diversity (Carrillo et al. 2015). In the northern South American savannas, ungulates are particularly vulnerable to different anthropogenic threats (Gallina-Tessaro et al. 2019). In Colombia, twelve species of WUS are known, represented by three species of tapir, two peccary species, and seven species of deer. Of this diversity 50% of the species are reported in the HPNSL of the Orinoco basin, containing one tapir species, two peccary species, and three deer species (Montenegro et al. 2019). The WUS are typically herbivorous and inhabit a wide range of diverse habitats (Wilson and Mittermeier 2011), and generally show high dispersal capacity, allowing individuals to find suitable habitat. Ecological conditions indicate some degree of connectivity of these terrestrial landscapes, converting these WUS to “focal species” allowing the creation of connectivity networks, habitat modelling, selection of conservation areas, and the assessment of functional connectivity across large landscapes such as the savanna ecosystems (Riggio et al. 2017, 2022). In this context, it is crucial to assess connectivity patterns and identify key areas for implementation of conservation actions for the metapopulations of these mammals (Saranholi et al. 2022). Such patterns must satisfy the ecological requirements of a wide range of organisms in biodiverse countries like Colombia where human transformation has affected nearly 50% of the ecosystems and more than 1500 species of fauna and flora are classified in some category of threat (Andrade-Correa 2011; Etter et al. 2017).

At present, landscape connectivity assessments and corridor designs are being conducted in savanna ecosystems on a global scale. These assessments are being carried out to maintain a suite of ecological processes for this landscape that can only be sustained if multiple species can move across it. These assessments have been explored in a multi-species context (e.g. Brodie et al. 2016; Riggio et al. 2017, Niyogi et al. 2021; Crego et al. 2021; Riggio et al. 2022). Evaluating landscape connectivity and identifying corridors could be done by using different approaches (Littefield et al. 2019). One of the most used is least-cost modelling or circuit theory (McClure et al. 2016, Jackson et al. 2016). This involves (i) the collection of focal species occurrences or movement data, (ii) assembling spatial variables that are hypothesized to be associated with species occurrence or movement, (iii) fitting appropriate habitat models that allow the prediction of how spatially variables promote or impede species movement or presence in the landscape, and (iv) estimating corridors based on the spatial arrangement of the resistance surface (Bond et al. 2017). Landscape metric indices have been used to estimate and quantify
the connectivity of patches (Saura and Pascual-Hortal 2007; Saura and Tomé 2009; Niyogi et al. 2021). These indices are based on estimation of the distances between habitats that allow the calculation of the Euclidean distance as the shortest straight line between habitats (Jordan et al. 2007; Andersson & Bodin 2009; Norman and Boesch 2009).

This paper presents a comprehensive assessment of connectivity and corridor designs for three WUS in the HPNSL located in Vichada department, Colombia. Our approach involved four key steps: (i) modeling suitable areas of occurrence for UFS, (ii) classifying these areas into either suitable or unsuitable habitats, as well as identifying core patches within those that were deemed viable, (iii) designing dispersal corridors to connect these essential habitat cores, and finally (iv) quantifying weighted global connectivity metrics to measure the overall connectedness across this expansive region. Our research aims to provide valuable scientific information useful for prioritizing conservation management efforts within eastern Colombia's native savanna ecosystems. Given the increasing vulnerability of the region to climate change and other global factors affecting wildlife populations, our findings can support decision-making processes concerning effective measures toward ensuring the long-term sustainability of both HPNSL and associated wild ungulate metapopulations.

Methods

Study area

The Colombian Orinoquia represents 33% of the Orinoco River basin and 34% of the national territory (Romero et al. 2011). In this region, there are three main types of native savannas: (i) floodplain savanna, (ii) piedmont savanna, and (iii) high plains savanna; and each contains different landforms, soil, savanna formations, and vegetation patterns that belong to a macrosystem of global importance (the tropical savannas; Rippstein et al. 2001). The HPNSL are represented by the flat and dissected highlands and rocky outcrops associated with the Guiana Shield made up of Tertiary sedimentary rocks, overlying crystalline Precambrian rocks and sediments of the Paleozoic Era and Cretaceous Period of the Mesozoic Era that stand out from the savanna landscape matrix (Huber 2006, SGC 2020). We conducted the study, encompassing 36.841,4 km² of the HPNSL associated with the Meta, Bita, Tomo, Tuparro, and Tuparro rivers in the Vichada department (4°38’N, 69°14’W; 65 m altitude), in the Orinoco River basin, within and in the area of influence of the El Tuparro Biosphere Reserve, east of the Colombian Andes (Rippstein et al. 2001, Fig. 1). The Orinoquian region is biogeographically located east of the Andes with Amazonia to the south, the Caribbean to the northwest, and the Guiana Shield to the east. The region has a tropical climate with an average annual temperature and precipitation of 30ºC and 1115 mm yr⁻¹ with a unimodal pattern in the temporal distribution of precipitation during the annual rainy season cycle from April to October and with a dry season from November to March and is largely associated with activity generated by the southern migration of the Intertropical Convergence Zone (Pimentel et al. 2021). The Vichada department’s landscapes are made up of a mosaic of extensive HPNSL with riparian forests associated with the dendritic pattern of the complex hydric network (Veneklaas et al. 2005; Romero et al. 2011;
This landcover functions as a biological corridor connecting fauna from the west to the east and south to north (Mosquera-Guerra et al. 2018).

**Focal species**

We focus on three of the six species of WUS reported for the Orinoquian ecoregion: (i) lowland tapir (*Tapirus terrestris*) categorized as Vulnerable (VU) by the International Union for Conservation of Nature - IUCN, (ii) white-tailed deer (*Odocoileus virginianus*) Least Concern (LC), and (iii) white-lipped peccary (*Tayassu pecari*) Vulnerable (VU–Montenegro et al. 2019). The three other species of WUS, the collared peccary (*Diclotyles tajacu*), red brocket deer (*Mazama americana*), and the Amazonian brown brocket deer (*Mazama nemorivaga*), have a limited number of records of occurrence for the native savanna ecosystems of Vichada. The UFS are morphologically and behaviorally heterogeneous and have different habitat and foraging preferences in the HPNSL. Lowland tapir (LT) is forest dependent species where are the prime seed dispersers for the palm (*Mauritia flexuosa*), indicating the close evolutionary relationship between both species (Varela et al. 2019; González et al. 2021; Álviz et al. 2023), white-lipped peccary (WLP) is primarily frugivorous, but will eat other plant resources, invertebrates, fungi and even occasional fish, and prefer natural forests (Keuroghlian et al. 2008, 2012, 2013), and white-tailed deer (WTD) consume leaves, shoots, fruits, seeds and grasses, a generalist condition that explains their wide distribution in savanna ecosystems (Gallina and López-Arévalo 2016; Roden-Reynolds et al. 2022). WLP has an average weight of less than 40 kg (Dubost et al. 2003), while the WTD is over 80 kg (Weber and Hidalgo 1999) while the LT average weight is 200 kg (Medici 2010).

**Wild ungulate species occurrence data**

Our analyses used a set of occurrence data of the UFS distributed in the HPNSL associated with five of the main rivers in Vichada. The data corresponded to the following: results of photo-trap campaigns carried out by the Fundación Omacha, Wildlife Conservation Society - WCS Colombia, Parque Nacional Natural El Tuparro, and the Instituto de Investigaciones de Recursos Biológicos Alexander von Humboldt – IAvH; direct observations reported in the social media iNaturalist; and specimens deposited in the mammals’ reference collection of the IAvH-M. This information is reported in the Global Biodiversity Information Facility (GBIF [www.gbif.org](http://www.gbif.org)). Subsequently, we created a presence-absence matrix by removing duplicate records and taking the coordinates of each record, and establishing a value of 1 for each place when present and 0 otherwise, obtained a matrix where the occurrences of the UFS were 985 registers LT, n = 338 (34%); WTD, n = 205 (21%), and WLP, n = 442 (45%). This dataset was used in the construction of UFS distribution models. Geographic coordinates of occurrence records were reported in decimal degrees based on WGS 84 data.

**Species distribution model suitable habitats**

We modeled the UFS using the MaxEnt algorithm version 3.4.3. Habitat suitability was then used to derive the resistance surface and the core habitat patches (Niyogi et al. 2021). We evaluated the performance of the MaxEnt models by calculating commission and omission errors (Anderson et al. 2003), the area under
the curve (AUC) of the receiver operating characteristic (ROC) curve (Elith et al. 2006, 2011), as well as by testing partial ROC curves (Lobo et al. 2008). The construction of the suitability models for the UFS considered 12 predictors: Climatic predictors were temperature seasonality (BIO 04), temperature annual range (BIO 07), precipitation of driest month (BIO 14), precipitation of coldest quarter (BIO 19), and isothermality (BIO 03). Habitat quality predictors were a normalized difference vegetation index - NDVI of the dry season (October to March) for the last 10 years, distance to rivers and forests, elevation, distance to roads and urban centers, and human modification. Collinearity between variables was evaluated using the variance inflation factor (VIF, Babak et al. 2014; Akinwande et al. 2015) analysis in the open-source software R 4.0.3 (R Core Team 2023). The spatial resolution of the bioclimatic predictors was 500 m; and they were obtained from the WorldClim dataset (Hijmans et al. 2005), habitat quality predictors (Farr et al. 2007; Didan 2015; IDEAM 2021; IGAC 2021), and human footprint (Kennedy et al. 2019).

**Binarization process and morphological spatial pattern analysis (MSPA)**

We applied the specificity-sensitivity threshold using the R package presence-absence test (Freeman 2012), and binarization converted the continuous gradient maps into binary distributions of suitable and unsuitable classes (Niyogi et al. 2021). Subsequently, we performed the Morphological Spatial Pattern Analysis (MSPA) on the suitable areas using the Guidos Toolbox (Soille and Vogt 2009; Vogt and Ritters 2017) to identify core habitat patches (Niyogi et al. 2021). Additionally, the MSPA classifies the image into seven categories: (i) core, (ii) islet, (iii) loop, (iv) bridge, (v) perforation, (vi) edge, and (vii) branch (Soille and Vogt 2009), based on the shape and physical appearance of its features. MSPAs are useful for mapping core habitats, however their use for mapping corridors is not recommended due to the non-inclusion of spatial metrics such as dispersal capabilities (maximum dispersal distance) of species (Niyogi et al. 2021). In this context, our approach to corridor modelling considered the dispersal capabilities of UFS reported in the scientific literature.

**Modelling dispersal corridors**

We modeled dispersal corridors connecting core habitats of UFS using the randomized shortest path algorithm (RSPA) from the R package "gdistance" (Van Etten et al. 2017). The conceptual approach considered was that of circuit theory (setting \( \theta \) equal to 0 in RSPA). This method is reported by Zeller et al. (2018) as the most appropriate for modelling dispersal corridors when the starting data are locations of species presence (\( \theta \) equal to 1 would simulate the least-cost path) (Niyogi et al. 2021). RSPA estimates density values for each grid cell in the landscape, where higher values represent a higher probability of a random walker passing through the cell (McRae et al. 2007). The data used for this analysis were (i) core habitat patches, (ii) resistance surface, and (iii) maximum dispersal distances of UFS (Niyogi et al. 2021). The resistance surface was generated using a negative exponential transformation of the habitat suitability gradient maps following Trainor et al. (2013). For dispersal ability, we used the maximum dispersal distances reported for LT (Medici 2010), WTD (Roden-Reynolds et al. 2022), and WLP (Hofman et al. 2016) were used.
The resistance values of each grid cell in the HPNSL connecting the core habitats and the maximum dispersal capacity of the species were used to derive the probabilistic dispersal area, where each cell was assigned a corridor value (range 0 to 100). The corridor values, together with core habitats, were used to create an integrated conservation area for the four UFS that highlighted regions with high probability corridors and core habitats (Niyogi et al. 2021).

Quantifying Functional Connectivity in the Savanna Landscapes

The weighted global connectivity metrics used in the process of quantifying the connectivity of HPNSL for UFS were as follow: (i) flux (F), (ii) equivalent probability (EC), (iii) probability of connectivity (PC), and (iv) integral index of connectivity (IIC), calculated using Graphab version 2.4 software (Clauzel et al. 2019 – Supplementary Information). Input data were (i) core habitats, (ii) resistance surfaces, and (iii) maximum dispersal costs (threshold) for each species (Niyogi et al. 2021).

Statistical analysis

Sample size was limited and influenced the type of statistical analysis of the results carried out. A Kruskal–Wallis test was performed to determine whether or not there was a statistically significant difference between the areas suitable and core habitats for the UFS. The tests reported in this paper were calculated using the open-source software R.4.0.3 (R Core Team 2023) for the graphical representation using the R software package ggplot2.

Results

Modelling suitable habitats, binarization process, and morphological spatial pattern analysis (MSPA)

The VIF analysis made it possible to exclude four highly correlated climatic variables with the variables initially considered: mean annual temperature (BIO 01), mean diurnal range (BIO 02), annual precipitation (BIO 12), and precipitation of the driest quarter (BIO 17). The models obtained using the Maxent’s algorithm gave AUC values > 0.9 (LT = 0.94, WTD = 0.95, WLP = 0.96 and integrated = 0.94). Habitat suitability ensemble output maps, binarized suitability maps, and MSPA output maps of UFS and integrated across species showed the spatial distribution of suitable and core habitats (Fig. 2).

The areas values of suitable and core habitats reported for the UFS analyzed vary between land-use categories (i) unprotected areas, (ii) protected areas (PAs), (iii) forests, and (iv) savanna (suitable habitats $p = 0.002$, and core habitats $p = 0.004$ values; Figs. 3 and 4). The integrated cross species areas reported for suitable habitats were 4694 km$^2$ and core habitats 1905 km$^2$, respectively.

Modelling dispersal corridors
The dispersal corridor maps for UFS and the integrated cross species show patches of riparian forest associated with the fluvial dendritic network that offers low resistance for dispersal in the HPNSL (Fig. 5). The patterns are relatively similar across the species and the integrated area considers the minimal requirement for allowing dispersal across all the WUS in the savanna ecosystem of Vichada.

**Quantifying potential functional connectivity**

The reported values of global connectivity metrics show that there will be much lower global connectivity in the HPNSL if habitats outside the protected areas are not conserved (see Supplementary Information). The mapping of the nodes and their linkages clearly demonstrate that the connections between most patches will be destroyed if the riparian forests associated with the dendritic pattern of the hydric network cease to exist (Figs. 6 and 7). The riparian forests play a central role in the connectivity network of the savanna landscape in the Orinoco River basin. The habitat networks of the UFS have a low degree of cohesion if some nodes are removed, and removal will disconnect the entire graph, making each node very important for guaranteeing the functional connectivity of the savanna landscape.

**Discussion**

Multispecies connectivity analyses that include WUS have been used successfully in savanna landscapes of Asia (e.g. Liang et al. 2021; Niyogi et al. 2021; Malakoutikhah et al. 2020), Africa (e.g. Riggio et al. 2017, 2022), and South America (e.g. Herrera et al. 2017; Sancha et al. 2021; Saranholi et al. 2022). Our study is the first to use a multi-species approach to evaluate biological connectivity in the HPNSL in eastern Colombia, besides presenting detailed analyses that identify suitable habitats and potential corridors for three vulnerable ungulate species. The information here generated is of utility for the conservation interventions focused on WUS based on their dispersal and geographical distributions for the Orinoquia region.

The distribution of the suitable habitats and the core habitats suggests that large areas are outside the PAs and act as primary habitats for the UFS. The maps show that most of the core habitats are located in the middle and lower-middle basins of the Bita, Tomo, Tuparrito, and Tuparro savanna rivers and, to a lesser extent, the lower basin of the Meta River. These areas are located in the riparian forests of the connected dendritic systems, while the core habitats in the eastern part of the savanna rivers are largely disconnected. Our results agree with that reported by Ang’ila et al. (2023) on the influences of (i) plant communities, (ii) topography and (iii) soil for the distributional patterns of large mammals in the savanna landscapes. In recent decades the increases in the HPNSL areas transformed by livestock and agro-industrial models and the increases in the frequency and extent of forest fires are considered degradation factors for riparian forests in Vichada department, due to recurrent burnings of the surrounding savanna landscapes. These conditions could affect the connectivity on the regional scale (Armenteras et al. 2005; Huidobro et al. 2021; Jiménez et al. 2022; Ramírez-Restrepo et al. 2023). In this context, maintaining or improving the quality of the larger patches associated with the fluvial dendritic network will contribute to more successful use of these patches that can function as “stepping stones” by focal species (Saura and
Rubio 2010; Herrera et al. 2017). Fundamental areas that facilitate the movement across savanna matrix for these species can traverse relatively long distances, e.g., tapirs greater than 5000 meters (Medici 2010) or intermediate distances \(>4000\) for peccary and deer (Hofman et al. 2016; Roden-Reynolds et al. 2022). For example, during the rainy season, the riparian forests of the savanna rivers are flooded, causing wildlife to move to higher elevations where the \(M.\ flexuosa\) formations are located (Mosquera-Guerra et al. 2018). Throughout this climatic season, the “savanna” matrix plays a fundamental role in connecting the riparian forest and the palm formations where wildlife can feed the fruit of this palm, the main resource for some large mammal species including the UFS (González et al. 2021; Álviz et al. 2023). Thus, within the HPNSL and for the UFS different elements of landscape structure may play different roles depending on their topological position and intrinsic habitat characteristics. One of these is passage patches used as intermediate points to subsequently reach other habitat patches in a dispersal process that encompasses multiple movements as steps through the dendritic network of the savanna landscape (Herrera et al. 2017; Riggio et al. 2017).

The intra- and inter-specific variations in the dispersal of UFS demonstrate the difficulty of implementing suitable corridors and stepping stones to provide functional ecological networks (Baguette et al. 2013). Connectivity models have proven useful for designing biological corridors (Beier et al. 2008; Freeman et al. 2019). There is a growing recognition that wild mammal corridors should be planned, designed, and implemented for multiple species so that, ideally, the full range of crucial ecosystem processes can be maintained across large spatial scales (Brodie et al. 2015; Lawer et al. 2020; Crego et al. 2021; Riggio et al. 2022). The circuit theory is a useful tool for modeling species dispersal patterns (McRae et al. 2008; Liang et al. 2021). When interpreting the maps resulting from circuit models, the individual connectivity analyses for the three UFS yielded “traffic hubs” similar to connecting paths through the middle and lower basins of the Meta and savanna rivers. Thus, the integral corridor largely confirmed potential least-cost dispersal routes within and between the HPNSL. This outcome was not unexpected since these WUS share habitat affinities. The three species positively select riparian forests associated with rivers and streams of the savanna landscape in search of shelter (predators and high temperatures), water, and food in addition to avoiding human proximity and the open conditions of savannas (Mosquera-Guerra et al. 2018).

The three UFS are considered landscape species because they have extensive area requirements, low population densities, and importance for local human communities. As such, their conservation contributes to maintaining ecological integrity and ecosystem services provided by savanna landscapes (Alviz and Pérez 2015; Mosquera-Guerra et al. 2018; Montenegro et al. 2019; Khosravi and Mahmoud-Reza 2019). Consequently, it is not surprising that the main corridors identified in the present study overlapped with important areas for biodiversity conservation with different approaches as follow: “\textit{Bita Corredor para la Vida}” (Bita Life Corredor) in the framework of designation of wetlands of international importance, Ramsar site (Mosquera-Guerra et al. 2018), “\textit{Proyecto Vida Silvestre}” (Wildlife Project) (Alviz and Pérez 2015), Natural National Park El Tuparro, and the El Tuparro Biosphere Reserve designated recently as other effective area-based conservation measures - OECMs (Protected Planet 2022). Our results suggest that optimizing UFS corridors by using either a multi-species or a focal species approach
can be a cost-effective method for securing savanna landscape permeability for a large mammal assemblage associated with these ecosystems (e.g., predators of UFS such as *Panthera onca*, *Puma concolor*, and *Speothos venaticus*). Therefore, the riparian forests that give rise to the dendritic network of the middle and lower river basins of the savanna rivers and Meta River are crucial for maintaining connectivity for all three UFS and deserve to be granted conservation priority, because once that is denied, the dispersal and gene flow of all three species will be inhibited with serious consequences for the biodiversity of the HPNSL (Mosquera-Guerra et al. 2018).

Functional connectivity estimates are mainly used to design viable metapopulations of UFS (Saranholi et al. 2022). The spatial dynamics of these metapopulations are often described as continuous source-sink dynamics, whereby upstream populations serve as sources and downstream populations serve as sinks (Baguette et al. 2013). Global connectivity metrics and corridor structure for the three UFS reported for the HPNSL of the Colombian Orinoquia support the view that some species are better connected in these landscapes, for example the LT. This may be a function of their home range size and dispersal ability, so while LT is widely distributed with largely contiguous habitats, WTD, and WLP remain limited to certain patches, and their core habitats are connected only when they are in proximity. Therefore, some species are more prone to geographic isolation and population decline compared to others within the same landscape (Poethke et al. 2003; Reinhardt et al. 2005; Niyogui et al. 2021). Connectivity per se also affects the dispersal of organisms in dendritic networks (Carrara et al. 2012). Headwaters are often distinct evolutionary populations, whereas confluence patches are a genetic mix of several headwater patches and hence reservoirs for genetic diversity (Baguette et al. 2013). Confluence patches are thought to be more stable; however, headwater patches are the sources of diversity in a basin and therefore very important from a conservation viewpoint (Campbell Grant et al. 2007; Baguette et al. 2013). Our results show high disconnection of the patches of riparian forest that forms the dendritic network associated with sectors of the upper basin of the rivers evaluated. Similar results are reported in the Serra do Mar Biodiversity Corridor designed in the Brazilian largest Atlantic forest to promote the conservation of LT and WLP where anthropogenic barriers can influence the corridor effectiveness for promoting gene flow at some scales (e.g., within 30 km). This corridor may not be fully effective over its entire extension (Saranholi et al. 2022). The situation is possibly similar to what is happening with the populations of UFS in our study area.

Consequently, the HPNSL are underrepresented within the national system of PAs. However, the region has a network of private nature reserves that contribute to the conservation of the biodiversity associated with those ecosystems located in the area of influence and inside the Tuparro Biosphere Reserve (López-Arévalo et al. 2021). These private nature reserves are generally small and isolated from each other (RUNAP 2023). This condition translates into different levels of connectivity for UFS ranging from networks with few large areas and distant from each other, to networks consisting of many small areas where connectivity depends mainly on the dispersal capacity of mammal species (Santini et al. 2016). Limitations in the dispersal capacity of individuals between patches of the APs reduce the opportunities for adaptation in response to global changes in subpopulations (Riggio et al. 2017). In this context, it is a priority to plan the conservation and restoration actions of the riparian forest in the savanna ecosystems.
at a landscape scale focused on facilitating dispersal between subpopulations to ensure long-term survival as a metapopulation (Hanski and Ovaskainen 2000; Blazquez-Cabrera et al. 2014). It is also necessary to integrate connectivity analyses with management plans for vulnerable ungulate species (e.g. Álviz and Pérez 2015). Additionally, HPNSL are listed among the ecosystems most vulnerable to degradation processes driven by climate change in Colombia, a situation that could increase the levels of land cover transformation in the region (Etter et al. 2017). This condition makes necessary the construction and integration of adaptation strategies against climate change in the planning of conservation actions and the design of new PAs (Heller and Zavaleta 2009; Hannah 2011; Magris et al. 2014). It is also necessary to consider factors such as variation in habitat connectivity levels of vulnerable ungulate species as individuals move within their areas of occurrence, as well as the uncertainties of connectivity changes driven by current and future climate variability (Albert et al. 2017).

We suggest that our results should be considered in the national programme for the conservation of *Tapirus* in Colombia (Montenegro 2005) and other strategic planners engaged in the conservation of UFS and large mammals in the Colombian savanna ecosystem. These actions will be in line with a recent claim to conserve biodiversity conservation under the Convention on Biological Diversity, CDB and the Aichi Target 11 (Hoban et al. 2020; Saranholi et al. 2022). We also suggest that in the El Tuparro Biosphere Reserve and the Bita River Ramsar site, considered the conservation figures with the greatest extension of savanna landscape in Colombia, that policies for the conservation of the WUS should include reinforcement (or perhaps restoration) of population connectivity and reduction of illegal hunting pressures (Saranholi et al. 2022), including subsequent protection or restoration of wildlife corridors—i.e., patches of land that connect two or more protected areas or seasonal ranges of focal species (Jones et al. 2012; Beale et al. 2013; Bond et al. 2017) because of the contribution that ungulates make in carbon exchange and accumulation in the Orinoco HPNSL (Morales-Rincon et al. 2021). This is essential in the current global climate crisis. Finally, we recommend (i) exploring the combined effects of climate, land cover, and anthropogenic influences such as wildfire on UFS in the climate change scenarios, (ii) incorporating more detailed species information such as dispersal limitation, biotic interactions, and population density into the connectivity analysis, and (iii) conducting fine-scale monitoring with camera traps and GPS collars to verify the proposed connectivity priority.

**Declarations**

**Supplementary Information** The online version contains supplementary material available at https://doi.org/

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**Availability of data and material** The data sets generated and analysed during the current study are available from the corresponding author on reasonable request.

**Code availability** The code supporting the current study is available from the corresponding author on request.

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethics approval** Ethical approval was granted by Universidad Nacional de Colombia and Natural National Park El Tuparro.

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**References**


**Figures**
Figure 1

Study area in the HPNSL in Vichada department, main rivers, highways, protected areas (PAs), forest and non-forest land (savanna), and occurrence registers of the UFS.
Figure 2

(a), (d), (g), (l) Habitat suitability maps, (b), (e), (h), (k) binarized suitability maps, and (c), (f), (i), (l) MSPA output maps of three UFS and integrated in the HPNSL of Vichada department.
Figure 3

Suitable habitats for the UFS and integrated and the allocation of these areas among the three land-use categories in the HPNSL.
Figure 4

Core habitats for the UFS and integrated across species, and the allocation of these areas among the three land-use categories in the HPNSL.
Figure 5

Dispersal corridors for the UFS and integrated cross species in the HPNSL.
Figure 6

Mapping of UFS and integrated core habitats and links. Core habitat patches are shown as nodes, while the connections between the nodes are shown as edges. The size of the nodes is proportional to the area of the different habitat patches in the high plain native savanna landscape.
Figure 7

Comparison of number of nodes by dispersal distance for UFS and integrated across species.

Supplementary Files

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