



UNIVERSITY OF AMSTERDAM

MSc. Biological Sciences

Track: Ecology and Evolution

Second Research Project

**Seed dispersal connectivity among palm swamp
patches in Costa Rica and Nicaragua**

by

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August, 2017

42 ECTS Credits

January - August 2017

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An online repository with the data and results of this thesis project is hosted at:
<https://github.com/fgabriel1891/RaphiaTapirConnectivity>

Abstract:

Wetlands dominated by monospecific stands of the Yolillo palm (*Raphia taedigera*) in Costa Rica and Nicaragua are considered as one of the ecosystems with the most direct pressures over its long term conservation. This monospecific stands are distributed in patches and represent climax stages within the forest dynamics of the lowland areas in the study area. Despite the importance of this palm swamps, broad scale connectivity among palm patches have not been subject of many studies. *Raphia taedigera* fruits present megafaunal traits, making the Central American Tapir (*Tapirus bairdii*) the only effective animal seed disperser of *Raphia taedigera*. In this study, seed dispersal connectivity of *Raphia taedigera* populations is assessed structurally and functionally with information from literature, world databases and remotely sensed data. Results of the connectivity analysis can help biodiversity managers to benefit from spatially informed model outputs to prioritize conservation actions focused over the long term preservation of this palm swamp wetlands.

Keywords: *Raphia taedigera*, *Tapirus bairdii*, seed dispersal, connectivity, Costa Rica, Nicaragua.

INTRODUCTION

The consequences of biodiversity changes over the ecosystem are often expressed at broad spatio-temporal scales (Brose & Hillebrand, 2016). Ecosystems are maintained by adequate flows of individuals, species, materials, energy and (genetic) information across physical landscapes (Correa Ayram et al., 2015; Crooks & Sanjayan, 2006). Within the global biodiversity crisis (Novacek et al., 2001), ecological research faces a challenge to adequately predict the effects of biodiversity loss and to deliver products with relevance in real world ecosystems (Brose & Hillebrand, 2016).

Biological dispersal has traditionally been a difficult process to study, particularly across complex landscapes (Vasudev et al., 2015). Recently, there has been a shift in focus from dispersal studies on single populations towards integrating dispersal process with heterogeneous landscapes and the effects of humans (Worboys et al., 2010; Vasudev et al., 2015). Seed dispersal is a multiscale interaction that regulates the gene flow and spatial dynamics of plant populations (Levin et al. 2003) and is a key ecological process for the maintenance of ecosystems (Howe 1982; Wunderele 1997; Pigot 2016).

Many plants, especially in the tropics, rely on animals for the dispersion of its seeds (Howe et al. 1982; Gautier-Hion et al. 1985; Cain et al. 2000; Levey 2002). Large seeded plants (i.e. Megafaunal fruit traits) are thought to have evolved its fruit traits in response to seed dispersal pressures mediated by large animals (Barlow 2000; Guimaraes et al. 2008). However, many large animals around the globe have either faced through or are currently facing a process of rapid extinction (Dirzo and Miranda 1999; Pérez and Palacios 2007; Guimaraes et al. 2008). This creates a dispersal limitation for large seeded plant species, which makes them especially vulnerable to habitat fragmentation and defaunation (Markl et al., 2012; Galetti et al. 2006; Nuñez-Iturr et al. 2007; Corlett 2013; Vidal et al. 2013; Carvalho. et al. 2016).

The yolillo palm (*Raphia taedigera*) is one of the various species of palms (Arecaceae) with megafaunal fruit traits (Figure 1). This wetland palm species occurs in monospecific stands (Yolillales) distributed mainly in Central America (Box 1) (Serrano-Sandí et al., 2013; Yaap, et al., 2015). *Raphia taedigera* presents non-floating seeds, extended germination times and slow seedling growth (Myers, 2013b) and only the Central American Tapir (*Tapirus bairdii*) is considered to be an effective animal seed disperser of *Raphia taedigera* (Naranjo 1994,1995; (Serrano-Sandí et al., 2013; Yaap et al., 2015)) (Box 2).

Coastal wetlands, such as the *Raphia taedigera* dominated palm swamps in Central America, provide essential ecosystem services by being reservoirs of water and carbon (Hoyos-Santillan et al., 2016) or acting as endangered species refugia (Serrano-Sandí et al., 2013). Few studies have focused on understanding the ecological dynamics of these monospecific wetland ecosystems, despite of their ecological importance and representation of climax stages within the dynamics of Central American lowland ecosystems (Myers, 2013a, 2013b, 2013c).

Quantitative studies on seed dispersal are strongly tied with connectivity theory (Pascual-Hortal & Saura, 2006; Taylor et al., 1993; Saura & Rubio, 2010; Fagan et al., 2016). Connectivity is inherent to the degree of movement of individuals or ecological processes among patches in a physical landscape and is a key factor to indicate the effects of environmental change (Correa Ayram et al., 2015). Connectivity studies in Ecology can be subdivided into two main categories: **Structural connectivity** which considers only the patterns product of the spatial and topological arrangement of habitat patches in the landscape (Taylor et al., 2006) and **Functional connectivity** which incorporates the landscape effect to facilitate the movement of individuals or ecological fluxes among patches (Correa Ayram et al., 2015).

Remote sensing provides global data about the landscape at increasingly availability and higher resolutions (Persson 2016; Wang et al., 2016; Brinck et al., 2017; Gorelick et al., 2017). This remotely sensed information has already been linked with fine-scale movement data (e.g. Radio Collars) (Cagnacci et al., 2010) to develop connectivity assessments and broad scale predictive models in ecology (Clark et al., 2015; Joshi et al., 2013; Mondal et al., 2016). New advances in cloud computing (Brinck et al., 2017; Gorelick et al., 2017) in parallel with new algorithms to model animal movement (McRae et al., 2008; van Etten 2017) makes it possible to integrate high resolution remotely sensed data to represent ecological processes at landscape scales (Panzacchi et al., 2016).

Remotely sensed data can be incorporated into predictive biodiversity modelling (Kissling et al. 2017; Collins & Mitchard 2015; Davies & Asner 2014). For example, using a combination of airborne LIDAR (Light Detection and Ranging); field data and machine learning algorithms, functional canopy traits have been mapped at large scales in the peruvian Amazon (Asner 2012; Asner 2017). The results of broad scale biodiversity models can be used by conservation managers to make better-informed management decisions (Benz et al., 2016) aiming towards the preservation of landscape level processes rather than single species or populations.

For this research thesis, I aim to evaluate the seed dispersal connectivity among *Raphia taedigera* patches in Costa Rica and Nicaragua using literature derived assumptions on maximum dispersal distances, movement ecology of *Tapirus bairdii* and remotely sensed landscape data. To follow this objective, the following research questions and respective hypothesis will be addressed:

Research Question 1:

What is the variation in the seed dispersal connectivity among *Raphia taedigera* patches in function of varying *Tapirus bairdii* maximum seed dispersal distances (home range, dispersal and migration) ?

- Hypothesis 1.1 Overall connectivity increases at higher maximum dispersal distances.
- Hypothesis 1.2 Relative individual contribution of individual patches to maintain connectivity is equal for all patches

Research Question 2:

Which are the parts of the landscape that facilitates the potential seed dispersal connectivity among *Raphia taedigera* patches?

- Hypothesis 2.1: Functional corridors facilitating the movement of *Tapirus bairdii* are present among all *Raphia taedigera* patches.

Box 1: Yolillo palm (*Raphia taedigera*)

Raphia taedigera is the only representative of the genus *Raphia* for the Americas. *Raphia taedigera* is distributed mainly in Central America, along the Caribbean lowlands from Nicaragua to Panama and in the south Pacific coast of Costa Rica (Serrano-Sandi et al. 2013) where they grow forming monotypic stands called **Yolillales**. In the neotropics, The yolillo palm is also found in the coastal areas of the rivers Urabá and Atrato in Colombia (Espinol and Montenegro 1963) and in some islands in the Amazon delta in Brazil (Kanh and Moussa 1994). The origins and mode of arrival of *Raphia taedigera* to the Americas has been motive of old debates (Otedoh's 1977; Fairbanks 1989; Urquahart 1997; Carney and Hiroaka 1997). However, palynological data sets the arrival of the Yolillo palm from Africa pre-dating the arrival of first European settlers and the Atlantic slave trade (Carney and Hiroaka 1997; Wake et al. 2006).

Raphia taedigera fruits are ovoid in shape, scaly in appearance, hard and succulent in texture and measure 4.5-6.8 x 3.2-4 cm (PalmWeb 2016) Apart from the Central American Tapir, few species have been documented to consume the fruits of this palm. Monkeys (*Cebus capucinus* and *Ateles geoffroyi*) are only attracted by the immature fruits, peccaries occasionally consume the fruit (although acting as a seed predator) and an apparent small predation of fruits by rodents has been recorded (Myers 1984; Myers 2013). Tapirs are important seed dispersal agents for a variety of plant species (Farril et al. 2013). In the regions where *Raphia taedigera* occurs, tapirs have been record to use disproportionately *Raphia taedigera* stands on its time budget, showing a preference to consume its fruit (Naranjo 1995; Foerster and Vaughan 2003; Chassot et al. 2015).

Figure 1: *Raphia taedigera*.
Infructescence (a),
fruits (b,c). Source
(Palmpedia.net)



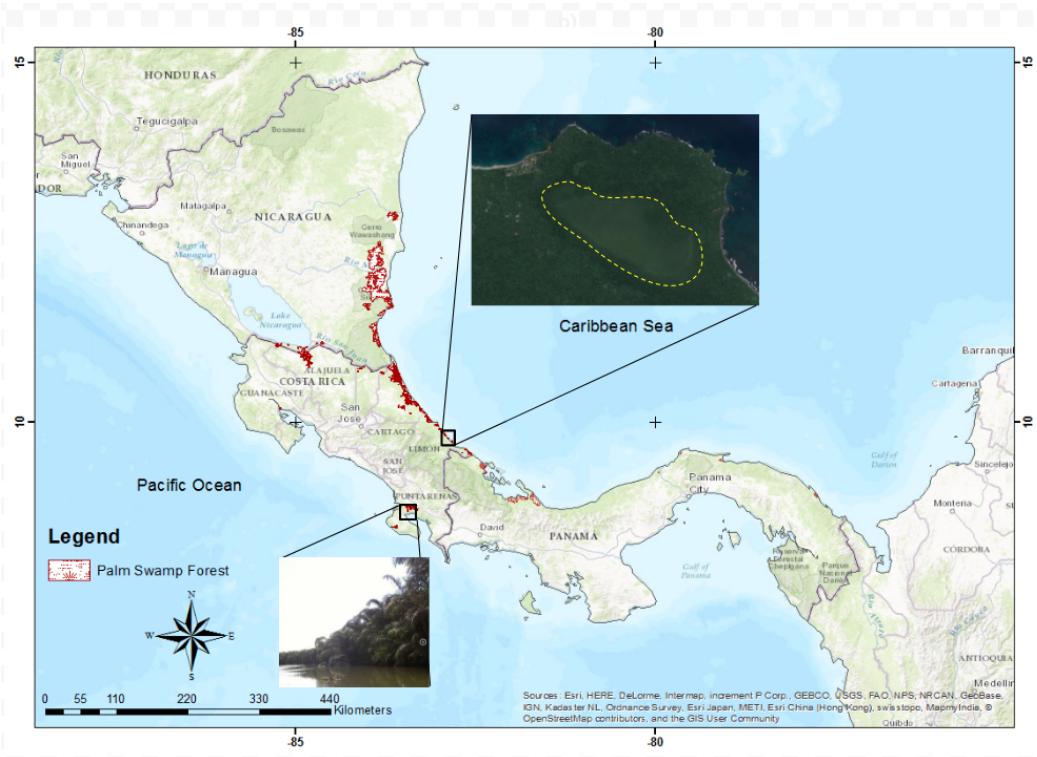


Figure 2: Distribution of palm swamps in Central America. Zoom boxes shows a *Raphia taedigera* dominated riverbank (bottomleft) and an aerial view of a *Raphia* dominated patch. *Raphia* patches are distinguishable from satellite images and aerial photographs for its relative homogeneity respect to the surrounding forest. A single patch, for which its borders have been highlighted with a yellow dashed line (Topright) is presented as example in top right zoom box. Source of pictures: Palmpedia.net and Google Earth

Box 2: Central American Tapir (*Tapirus bairdii*)

Tapirus bairdii actively forage fruits from *Raphia taedigera*, especially in the dry season. (Naranjo 1995; Foerster and Vaughan 2003; Chassot et al. 2005). In Central America, *Tapirus bairdii* is distributed from Southern Mexico to Colombia (Restrepo and Betancourt 2008). In Nicaragua, tapirs occurs in lowland tropical forest, seasonally flooded forest and swamps along the Caribbean coast, with viable populations holdings at Bosawás it the North and San Juan del Norte at the border with Costa Rica in the South (Jordan and Urquhart 2013). In Costa Rica, the tapir is present in the three mountain ranges and the lowlands along the Caribbean coast (Castellanos et al. 2008). *Tapirus bairdii* populations have undergone a steady decline with an estimated loss of more than 50% of its populations in the last 30 years (3 generations) attributed mainly to habitat loss and hunting (Garcia et al. 2016).

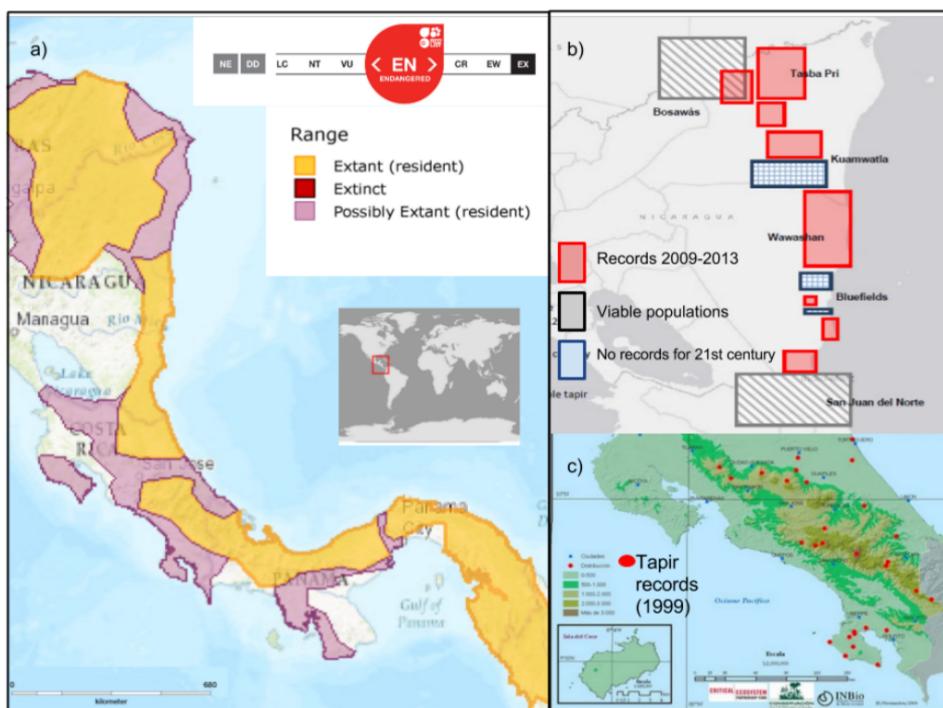


Figure 3: Distribution of *Tapirus bairdii* in Nicaragua and Costa Rica: a) Subpopulations identified by the IUCN in Nicaragua, Costa Rica and Panama. b) Tapir populations in Nicaragua according to Jordan and Urquhart 2013. c) Tapirs records in Costa Rica up to 1999 according to Elizondo (1999). Pictures modified from: a) Garcia et al. 2016; b) Jordan and Urquhart 2013; c) Elizondo 1999

Theoretical Framework

Probability of connectivity:

This graph-based metric describes a probabilistic model for the dispersal between two patches given a set of n existing links and habitat patches. PC represents the probability for two points randomly placed within the landscape fall into habitat areas that are reachable from each other (Saura and Pascual-Hortal 2007, Saura 2008, Saura and Rubio 2010) and is calculated as:

$$PC = \frac{\sum_i^n \sum_j^n a_i a_j P_{ij}^*}{A_L^2} = \frac{PCnum}{A_L^2}$$

where:

a_i and a_j are the attributes of patches i and j .

p_{ij} is the probability of direct dispersal given a distance threshold for all the links in that path.

P_{ij}^* is the maximum product probability of all possible paths between patches i and j .

$PCnum$ is a value that varies according to the topology of the network of patches i and j correspond to maximum patch attribute.

By dividing the $PCnum$ value by , PC ranges from 0 - 1 reaching higher values if there is no fragmentation or when fragmentation exists but there is a maximum interpatch connectivity, such as for each pair of patches (Saura and Rubio 2010) and it's one of the metrics that best describe the relative contributions of each node to the overall connectivity of the landscape (Pascual-Hortal and Saura 2006; Saura and Torne 2009). Absolute values of PC are dependant on the landscape area, therefore in order to prioritize and rank patches in terms on the contribution to the overall connectivity of the network the variation in PC caused by the removal of individual element from the landscape (Urban and Keitt 2001; Saura and Pascual-Hortal 2007; Saura and Rubio 2010) was calculated as:

$$dPC_k = 100 \times \frac{PC - PC_{remove,k}}{PC} = 100 \times \frac{\delta PC_k}{PC}$$

dPC_k : can be separated on its three fractions quantifying the contribution of each node to the overall connectivity (Saura and Rubio 2010). Being:

$$dPC_k = dPCI_{intra,k} + dPCF_{flux,k} + dPC_{connector,k}$$

$dPCI_{intra}$: represents the single node contribution to intrapopulation connectivity, this fraction represent an intrinsic attribute of the patch, being for this study is based on the individual patch areas.

dPCFlux: is a measure for the interpopulation connectivity of the node, this depends on the relative number of shared links from the individual patch to the other ones (i.e. How "well connected" is a patch with others).

dPCconnector: represents the "stepping stone" (Saura and Rubio 2010) contribution of a patch to the overall connectivity.

Components:

Represent sub-units | clusters | modules of highly interconnected nodes within the network of patches.

Equivalent Connectivity:

EC (Equivalent Connectivity) is equal to the square root of PCnum. Represents total habitat or area available for dispersal (nodes + links).

Google Earth Engine API:

A cloud based platform for planetary scale environmental data analysis. Acts as a data aggregator for many open source satellite imagery. Additionally the API allows to perform geospatial analysis both in Python and Javascript. <https://developers.google.com/earth-engine/>

Circuit theory:

Circuit theory in Ecology treats the landscape as a conductive surface. Circuit theory softwares model the flow of electrons among specific part of the landscape. The flow of electrons are analogous to modelling random-walks movement of animals or genes across the landscape (McRae et al. 2008)

Randomized shortest path:

Randomized shortest paths looks to minimize the cost of reaching an endpoint from a sourcepoint in a grid or network. However, at difference to standard shortests paths, a fixed level of entropy or variability is maintained (exploration). This allows to model midpoints between total random walks and shortest paths. (Saerens et al. 2009).

WORKFLOW

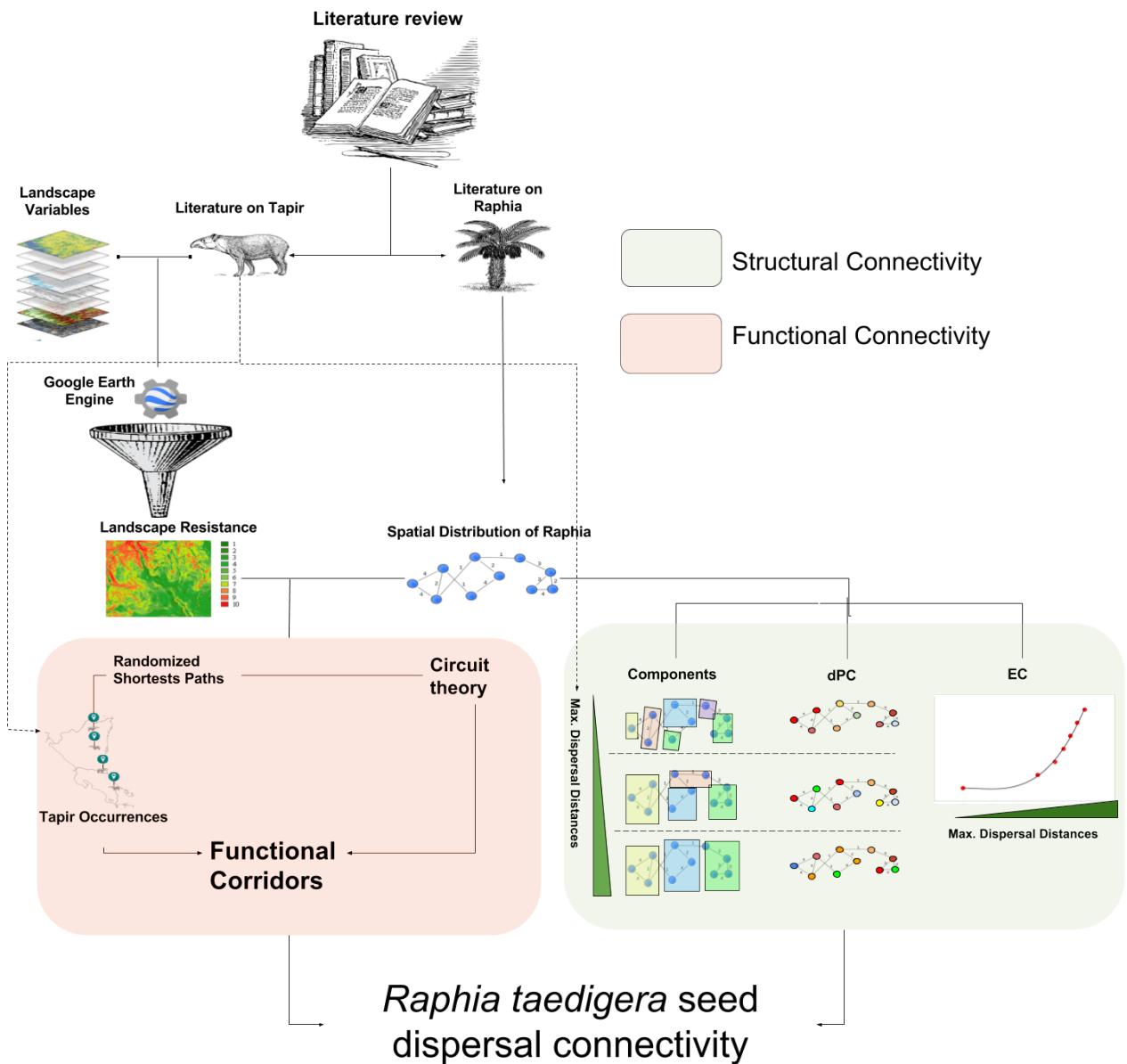


Figure 4: Workflow followed in the present study.

METHODS

Patches of Raphia taedigera

Monospecific patches of *Raphia taedigera* palm can be distinguished on aerial photographs and satellite images due its homogeneous structure relative to the nearby forest (Serrano-Sandí et al., 2013). A file with the spatial distribution of *Raphia taedigera* patches was provided by Juan Serrano-Sandi by personal communication in ArcGIS shapefile format. Polygons were converted from multipart to singlepart polygons in ArcGIS v10, exported as a KML file and uploaded to the Google Cloud as a FusionTable.

Seed Dispersal Ecology of Tapirus bairdii

Observations concerning to *Tapirus bairdii* behavior, ecology and maximum seed dispersal distances were extracted from published literature. A search for articles following (Haddaway et al., 2015) was performed in February 2017. The following keywords were limiting the search results: *Tapirus bairdii*, Costa Rica, Nicaragua, Baird's tapir, Central American, dispersal, movement, range, habitat, ecology. Several queues were performed in Google Scholar with different combinations of 2 or 3 keywords at a time conserving always either the keyword *Tapirus bairdii* or Baird's tapir. After each search step, based on titles, all new matches pointing to relevant articles were downloaded for posterior analysis.

Based on the published literature, ten maximum dispersal distances were selected ranging from 100m to 240Km (Table 1). This distance thresholds were selected to reflect the movements of *Tapirus bairdii* at home range, dispersal and migration scales. Relevant observations *Tapirus bairdii* dispersal ecology were also extracted from literature. Observations were classified into a database which included the following categories: *Habitat use, Species range, Conservation status, Natural history, Population characteristics and Species distribution*. The database was used as reference to reclassify of landscape physical variables to reflect their ability to facilitate or impede the movements of *Tapirus bairdii*.

Table 1: Maximum seed dispersal distances used as distance thresholds to calculate connectivity metrics. Increasing distances are associated with reductions on the frequency of the movement.

Dispersal distance	Source	Type of Movement	Reason
100m	NA	Home Range	Short distance seed dispersal
300m	NA	Home Range	Short distance seed dispersal
1500m	Schank et al. 2015	Home Range	Reported dispersal distance for <i>Tapirus bairdii</i>
3600m	Farril et al. 2013	Home Range	Minimum range value of the mean movement distance of <i>Tapirus terrestris</i>
5200m	Farril et al. 2013	Home Range	Mean movement distance of <i>Tapirus terrestris</i>
6700m	Farril et al. 2013	Home Range	Maximum range value of the mean movement distance of <i>Tapirus terrestris</i>
13000m	Farril et al. 2013	Home Range	Maximum movement distance within 24h of <i>Tapirus terrestris</i>
20800m	San diego Zoo	Dispersal	Mean movement distance * Minimum digestion time (4 days)
52000m	San diego Zoo	Dispersal	Mean movement distance * Mean digestion time (10 days)
240000m	San diego Zoo	Migration	Ocean to ocean length at 10° Latitude

Tapirus bairdii occurrence records

Occurrence records of *Tapirus bairdii* spanning the years 2000-2016 were downloaded from ZENODO (<https://zenodo.org/>). Records contained the detection of tapirs with camera traps in Rio Indio, Nicaragua and the known presence only locations for the distribution of *Tapirus bairdii* in Central America. Records DOI: 10.5281/zenodo.17602 and 10.5281/zenodo.18557. Records come from the last compilation of *Tapirus bairdii* presence in Central America (Schank et al., 2015) and represent camera trap observations.

Structural connectivity

Patches of *Raphia taedigera* were examined as a spatially explicit network. In this network, each patch is considered as a 'node' and its characterized by their relative area (dA). Nodes can be connected with a 'link' which represents the Euclidean distances from one patch edge to another one. Two patches are considered to be connected based on a probabilistic model in function of the Euclidean distances separating patches and a dispersal threshold. Ten scenarios were modelled with each *Tapirus bairdii* maximum dispersal distances as dispersal thresholds. A 0.05 probability of connection was fixed for distances equal to the dispersal thresholds assigned for all scenarios. Euclidean Distances between patches were calculated with the Conefor QGIS plugin v.2.9.

To estimate overall connectivity, measured as the total amount of patches and connections among them, the Equivalent Connectivity (EC) metric was calculated using CONEFOR Sensinode software v2.6 (Saura and Torne, 2012). EC corresponded to the Equivalent Connected Area (ECA) from (Saura, et al. 2011; Schank et al., 2015). Individual patch contribution to connectivity (dPC) was calculated as the variation in the Probability of Connectivity (PC) metric (Pascual-Hortal & Saura, 2006; Saura & Rubio, 2010) caused by the removal of the patch from the network (Rubio, Rodríguez-Freire, Mateo-Sánchez, Estreguil, & Saura, 2012; Saura & Rubio, 2010). Standard scores (z-scores) were calculated to compare dPC values across Maximum Dispersal Distance thresholds.

The individual patch contribution to connectivity (dPC) can be separated in its fractions PCintra, PCflux and PCconnector, describing respectively the intrapopulation, interpopulation and "stepping stone" contribution to connectivity of each patch (Rubio et al., 2012; Saura & de la Fuente, 2017; Saura & Rubio, 2010). Relative contributions from each fractions to dPC were calculated as the ratio dPCfraction (i.e. dPCintra, dPCflux, dPCconnector) /dPC .

To assess the effect of patch size (in surface area) on the overall connectivity, the association between dA and each dPCfraction values were evaluated by Pearson correlations. Latitudinal variation of dCP values and their individual fractions contributions PCintra, PCflux and PCconnector was evaluated to determine the presence of spatial patterns on the distribution of dPC values.

Number of Components

Components (or connected region) is defined by CONEFOR as a set of nodes for which a path exists between every pair of nodes (Saura & Pascual-Hortal, 2007). The number of components metric represents the number of sub-units (clusters) of patches existing in the network at each distance thresholds. Different components are not likely to share functional relationships (Pascual-Hortal & Saura, 2006). To assess the level of fragmentation of the network, the ratio between the number of components and the total number of patches was calculated for all maximum dispersal distances scenarios.

Functional connectivity

Resistance layer

To incorporate the effect of the landscape on the connectivity among patches a resistance layer was constructed to represent the overall resistance of the surrounding landscape to the movement of a *Raphia taedigera* seed from one patch to another. As the movements of *Raphia* seeds are assumed to be directly linked to those of *Tapirus bairdii* among patches of *Raphia taedigera*, the cost layer represent an aggregation of five physical variables influencing the tapir choices of movement in the study area.

Variables used to build the resistance layer were: *Population density*, *Terrain slope*, *Road network*, *Forest canopy coverage* and *Distance to water sources*. Based on the dispersal-relevant observations on *Tapirus bairdii*, each variable was reclassified into several classes and assigned a determined resistance values between 0 - 100 (Table 2). Resistance values were subjectively assigned based on information extracted from literature and intentionally skewed towards the end values of the distribution to emphasize the differences between lower and higher cost areas in the aggregated resistance layer.

Population density and road network

Tapirs prefer places where human activity is limited (Flesher and Ley 1996, Lira-Torres et al. 2014, Chassot et al. 2015). Population density was used as a proxy of the landscape resistance to tapir movement due to human presence. Population density data comes from a subset of the WorldPop Americas dataset for Costa Rica and Nicaragua. From the dataset, the 2010

estimated of people per pixel ('ppp') was used to build the cost layer. Resistance values of 3, 70, and 100 were assigned to human density ranges of 0-10, 10-50 and 50-120 respectively.

Schank et al. (2015) and Chassot et al. (2015) describe roads as effective barriers for tapir movement. To incorporate this information to the resistance layer, road network for Nicaragua and Costa Rica was obtained from the Diva-GIS free country level spatial data (<http://www.diva-gis.org/Data>). 1st and 2nd order roads were assigned resistance values of 100 whereas to 3rd and other non-paved roads a resistance of 70 was assigned.

Terrain slope

Slope was calculated with the terrain algorithm implemented in the Google Earth Engine API. The algorithm calculates the slope in degrees of a digital elevation model (DEM). Elevation data was obtained from the Shuttle Radar Topography Mission (SRTM) 1 Arc-Second (~30m) global product, clipped to the study area. Based on tapir observations, Chassot et al 2015 states the preference of smooth slopes by *Tapirus bairdii*. Therefore, slope was reclassified into three classes, 0°-15°; 15°-30° and 30°-90°, with resistance values of 0, 70 and 100 respectively.

Distance to Water

Tapirus bairdii is an animal which its movement is highly associated to water sources(Carrillo-Reyna, Reyna-Hurtado, & Schmook, 2015). Tapirs are continuously attracted to water sources (Chassot et al. 2015). Farril et al. (2013) mentions the use of *Tapirus bairdii* of waterholes and water bodies to regulate its body temperature. In addition, dung piles of *Tapirus bairdii* are found with less frequency when the waterholes are dry, suggesting that tapirs actively use water resources. Foerster and Vaughan et al. (2015) show that for nocturnal habitat selection tapirs rarely foraged or rested along creeks, but streambeds were used for easy travel between sites and for defecation. In the dry season, tapirs rest almost exclusively in wallowing holes and in the wet season tapirs rarely slept directly on water. However, they were usually less than 20m away from a waterbody. In addition, Lira-Torres et al 2014, inferring from copulatory pictures of the tapir inside water, highlights the importance of waterbodies for the reproduction of tapirs.

For the resistance layer, water presence was obtained from Sentinel-1 space-borne single aperture radar (SAR) imagery. A composite image for the study area was created with the VH band of the Sentinel 1 images corresponding to the date ranges from 2015-04-01 to 2015-08-01

which correspond mostly to the 2015 wet season. The VH band was preferred over the VV band because water is less apparent on VV than VH (MWBS 2015). A threshold method was used to delineate water bodies. A sample polygon of vertices ([-83.80,12.16], [-83.80,12.15], [-83.79,12.14], [-83.79,12.16], [-83.80,12.16], [-83.80,12.16]) was drawn over the Rio Escondido in Nicaragua to be selected as a sample region (Appendix Figure 1). The area corresponding to the sample region was selected because it offers an approximate 50/50 balance between water and non-water areas. The OTSU's method of segmentation (Carrillo-Reyna et al., 2015; Liu Jianzhuang et al. 1991) was used to calculate the threshold that will correspond to the best partition into "water" - "non-water" classes over the distribution of pixel values on the sample region. The calculated threshold value was then applied over all the study region composite to find water sources.

When globally applying the OTSU threshold to the study area, confusion appears in the mountainous regions where the scatter due of presence of water is often confused with the scatter produced by radar shadows in mountainous regions (Appendix Figure 2). Therefore, the thresholded image was masked with a 30m Height Above Nearest Drainage (HAND) model to identify "true" water areas detected with S1 radar images. The 30m HAND mask was obtained from a Global HAND mask (Donchyts et al. 2016) produced with the SRTM 30m product. The resistance layer due to water presence was calculated as a composite image with the thresholded S1 water occurrence, HAND <30m and HAND >30m. Resistance values of 0, 10 and 40 were assigned respectively.

Tree canopy cover

Forest coverage has been identified as one of the key variables driving the choice of the movements of *Tapirus bairdii* (Lira-Torres, Briones-Salas, & Sánchez-Rojas, 2014). Tree canopy cover for the year 2000 was used to estimate resistance based on canopy coverage. Data was obtained from the Global Forest Change 2000-2014 (Hansen et al., 2013) in this dataset, trees correspond to vegetation taller than 5m in height and comes from Landsat data examined at 30-meter resolution. Forest is expressed as percentage per output grid cell (Hansen et al., 2013) . According to Foerster & Vaughan (2002), secondary forest were the habitat which the tapir was using the most, followed by primary forests. Additionally, *Tapirus bairdii* seems to use habitats preferentially according depending on the season. Tapirs used secondary forests more than expected in the dry season in comparison to the wet season (Foerster & Vaughan, 2002). Naranjo (1995) in Costa Rica also shows a preference of *Tapirus bairdii* for lowland secondary

forests, avoiding primary forest. Thus, from the dataset, the 2000 tree cover layer was reclassified into five classes: 0-15%, 15-40%, 40-60%, 60-80%, >80% and 0% and assigned values of resistance values of 80, 70, 30, 10, 50 and 100 respectively. The class corresponding to 0% canopy cover was masked out with the water occurrence layer to reduce confusion between open areas with water surfaces.

Aggregated resistance layer

Each pixel of final aggregated raster resistance layer represented the cumulative sum of all individual resistance variables for that pixel.

Validation of the resistance layer

To validate if the aggregated resistance correctly represents the landscape resistance for movements of *Tapirus bairdii*, "null models" were created calculating 100 independent replicates of the means and medians of 100 random observations from a pool of pixel values. This pool was created from 10 random sampling events where each one consisted to extract 100 random pixel values from the aggregated resistance layer at 30m resolution. To validate the resistance layer output, the "null models" were compared against the mean and median of the pixel values of the resistance layer pixels matching the *Tapirus bairdii* observation points obtained from ZENODO.

Functional corridors

Circuit theory

Landscape corridors facilitating the movement of *Tapirus bairdii* among all the patches of *Raphia taedigera* were determined using circuit theory algorithms implemented in the software Circuitscape (McRae et al., 2008). Circuitscape, calculates corridors by modelling the cumulative resistance or current flow among every pair of focal nodes (patches) through a resistance layer (McRae et al. 2008). The final output consists of an aggregated raster of all node to node calculations (McRae et al., 2008; van Etten, 2017) which represents all possible paths among patches.

As calculations with Circuitscape can become computationally intensive, *Raphia taedigera* patches with areas less than 0.5Km² were excluded from the analysis. Additionally, only 10% of

all other patches were selected as focal nodes (i.e. nodes to apply current). Focal nodes were selected visually in order to reflect the topological pattern of components found at maximum dispersal distances scenarios of 1500m (Mean tapir daily movements) calculated with CONEFOR. The model output represents the cumulative resistance of the landscape calculated over 76 focal nodes. Linkage Mapper Toolkit for ArcGIS v.10 was used to call Circuitscape to perform the corridor analysis.

Randomized shortest paths

A second approach towards locating potential functional corridors in the landscape was used by calculating randomized shortest paths (RSPs) (Box 3) from each of the *Tapirus bairdii* occurrence points to a random patch of *Raphia taedigera*. In addition, the model was constrained to a middle point to reflect a tradeoff between optimization of routes (i.e. least cost paths) and free exploration of landscape (i.e. random walk) (Panzacchi et al. 2016). This was done to represent the assumptions of spatial memory of *Tapirus bairdii* (i.e. Tapirs tend to remember paths used).

The 30m x 30m resistance layer was aggregated into 90m x 90m to optimize computational time. The aggregated resistance layer was transformed into a transition matrix representing the mean cost of transitioning from one raster cell to another across its eight (8) adjacent cells. i.e. permeability (van Etten 2017). The size of this matrix is given by (Nrows x Ncols) from the resistance raster layer and is stored as a sparse matrix.

Geographical distance distortions due to latitudinal variations and diagonal vs orthogonal cell neighbors were corrected with the function `gdistance::geocorrection` (van Etten 2017) by dividing each matrix value by the distance between cell centres. The average number of passages through cells of connections between cells before arriving to a destination cell (van Etten 2017) was calculated to determine the dispersal paths.

Randomized shortest paths (RSPs) were calculated with the corrected transition matrix. The model was replicated 20 independent times, maintaining the number of tapir occurrences but randomizing the patches selected as endpoints of the RSPs. Every calculation was constrained with theta values of 1e-12. Final model output consists of the cumulative sum of each individual model replicates. All calculations were performed using the algorithms implemented in the R package **gdistance** (van Etten, 2017).

Table 2: Physical variables used to build the resistance Layer.

Variable	Class	Resistance	Resolution	Source	Year
Population Density	0-10	3	hab/100sqm	WorldPop	2010
	10-50	70	hab/100sqm	WorldPop	2010
	50-120	100	hab/100sqm	WorldPop	2010
Slope	0-15	0	30sqm	SRTM	2000
	15-30	70	30sqm	SRTM	2000
	30-90	100	30sqm	SRTM	2000
Road Network	1st & 2nd order roads	100	30sqm	OpenStreetMap	2016
	3rd order roads	70	30sqm	OpenStreetMap	2016
Distance to water	Water bodies	0	30sqm	Sentinel1	2015
	HAND ¹ (< 30m)	10	30sqm	GlobalHAND	2000
	HAND (> 30m)	40	30sqm	GlobalHAND	2000
Forest TreeCover(%)	0-15	80	30sqm	Hansen et al. 2013	2000
	15-40	70	30sqm	Hansen et al. 2013	2000
	40-60	30	30sqm	Hansen et al. 2013	2000
	60-80	10	30sqm	Hansen et al. 2013	2000
	80-100	50	30sqm	Hansen et al. 2013	2000
	0	100	30sqm	Hansen et al. 2013	2000

RESULTS

Distribution of Raphia taedigera

In Nicaragua, *Raphia taedigera* patches are only found along its Atlantic coast covering an extension of 11008,832 Km² which correspond to the 0.84% of the national territorial extent of the country. Patches in Nicaragua covers an mean area of 1.35 Km² +/-0.12 Km², with a largests patch of 60.62 Km². In Costa Rica, patches are distributed mainly along the Atlantic coast. However, *Raphia taedigera* can also be found in the Pacific coast at the south of the country and at the base of the Nicaragua lake. In Costa Rica, *Raphia* patches covers an extension of 539,313 sq Km, around 1.05% of the national territory and 16.5% of all wetlands (Muñoz, 1998; Serrano-Sandi et al. 2013).

Literature search

Tapirus bairdii Dispersal Ecology

From the literature search strategy 159 relevant seed dispersal observations for Tapirs were collected. The class "Habitat use" had the most number of observations reported. Most of the information collected comes from Chassot et al. 2005, Lira-Torres et al. 2014 and Schank et al. 2015. Observations collected were mainly focused on *Tapirus bairdii*. However, relevant observations were collected for *Tapirus terrestris* and *Tapirus indicus* species with similar habitat requirements and movements to *Tapirus bairdii* (Appendix Table S1).

Maximum Dispersal Distances

Maximum dispersal distances were selected in order to reflect the ability of *Tapirus bairdii* to move *Raphia taedigera* seeds from one patch to another. Tapirs choice of movements can be classified into three categories of movement: Home range, Dispersal and Migration. The frequency of a Tapir choosing one or another kind of movement, is inversely proportional to the total dispersal distances.

Home Range movements

Based on the literature, maximum dispersal distances ranging from 100m to 13Km can be considered as home range movements. Farril et al. (2013) describes overlapping home ranges of *Tapirus bairdi* averaging 1.3 Km² (+/- 0.73km²) with a maximum range of 2.3 Km². Reyna-Hurtado et al. 20106 In the Calkamul Biosphere Reserve over the period of 2011-2015 a home range of 2 Km² was estimated for a single individual of *Tapirus bairdii*. They also report a the occurrence trip back of 7.8Km in 2 days and a camera trap record 10km outside the main home range of the individual. According to Myers et al. (2013b) non-floating seeds of *Raphia taedigera* can be rolled away from the parent plant assisted by strong water currents that push the seed over the ground. This process may disperse the seed short distances and is likely to happen along riverine borders in the flooding season. In this study, maximum dispersal distances associated to such events (100m and 300m) were included in the category of Home Range movements

Dispersal movements

Tapirus bairdii individuals, although having overlapping home ranges (Foerster and Vaughan et al 2003), are documented that they can move big distances in search for new home ranges (Foerster 1998). Tapirs can move up to 10Km in one day, preferring to move along creeks, rivers and avoiding pronounced slopes. (Chassot et al. 2005; Farril et al. 2013). Tapir mediated dispersal events of *Raphia taedigera* will occur when a tapir that has already consumed a fruit of *Raphia taedigera* will move in search for new home ranges. Considering maximum daily movements along with the gut passage time for Tapirs in captivity (4-23 days) (*Tapirus bairdii* fact sheet: San Diego Zoo) maximum dispersal distances considered to be part of the Tapir dispersal movements are estimated as 20.8Km and 52Km.

Migration events

The present distribution of *Raphia taedigera* could suggest the presence of long distance dispersal events (+200Km). To represent long dispersal distances a maximum dispersal distance of 240Km was selected. This value represents the approximated length in Km from the Atlantic to Pacific coast. Although there is no record of a single tapir individual moving such distances. Experts suggest for *Tapirus bairdii* are capable to move such distances. Although a

highly improbable scenario, when considering the maximum reported gut passage time and the Tapir maximum daily movements, a seed inside a tapirs gut could travel more than 200Km.

Seed dispersal connectivity

Structural connectivity

Overall dispersal connectivity measured with EC (Equivalent Connectivity) shows an exponential positive relationship with Maximum Dispersal Distances associated to *Tapirus bairdii* movements (Figure 5). Maximum connectivity EC values were found at Maximum Dispersal Distances associated with migration type movements. However, the exponential nature of the relationship means that variations in *Tapirus bairdii* home range movements (0-13Km) would have a bigger impact over the overall connectivity of *Raphia taedigera* patches compared with changes in connectivity due to changes on dispersal or migration Tapir movements.

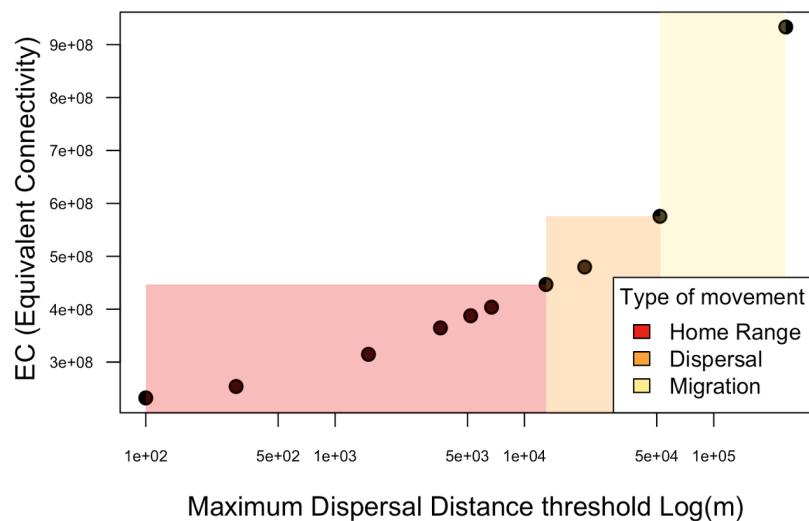


Figure 5: Changes on the Equivalent Connectivity (EC) metric with increasing *Tapirus bairdii* Maximum Dispersal Distances. EC represents the overall connectivity for dispersal among *Raphia taedigera* patches. Colored bars represents the maximum EC found for dispersal thresholds corresponding to each type of *Tapirus bairdii* movement (i.e. Home range, Dispersal and Migration). Note that the X-axis have been logarithmized.

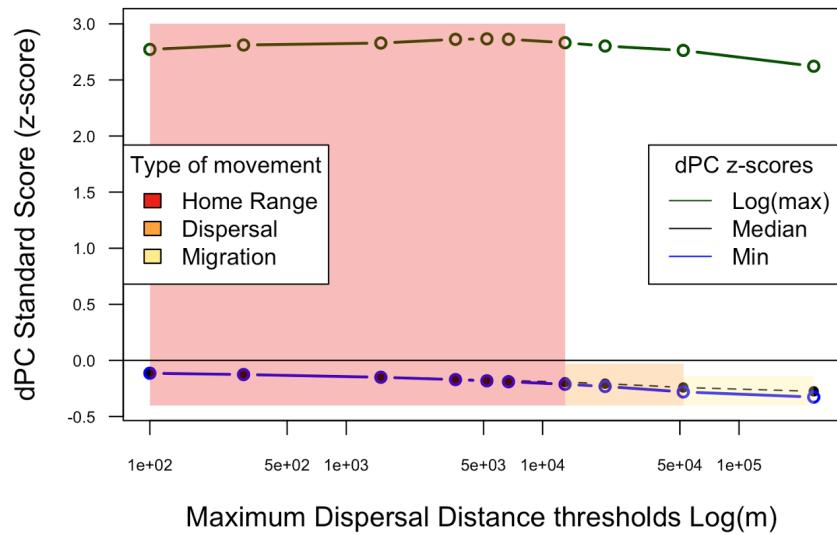


Figure 6: Changes on the dPC z-scores with increasing *Tapirus bairdii* Maximum Dispersal Distances. dPC z-scores represents the normalized contribution to connectivity of each patch. Note that the X-axis have been logarithmized.

When comparing the distribution of standardized scores (z-scores) of dPC values of patches at all *Tapirus bairdii* Maximum Dispersal Distances thresholds, there is a strong difference between median z-scores values and maximum z-scores and for all scenarios evaluated. Maximum dPC values are several folds bigger than the median values of dPC for all patches. This suggest that for all modeled scenarios connectivity is maintained only by few specific patches (Figure 6).

To identify the presence of spatial patterns on the location of patches contributing the most to maintain connectivity was observed when examining the latitudinal variation of the distribution of dPC z-scores. Patches contributing towards maintaining overall connectivity at all Maximum Dispersal Distances evaluated are highlighted by the peaks in Figure 7. Individual contribution of patches which contribute the most to maintain connectivity were higher for Maximum Dispersal Distances associated to *Tapirus bairdii* Home Range movements.

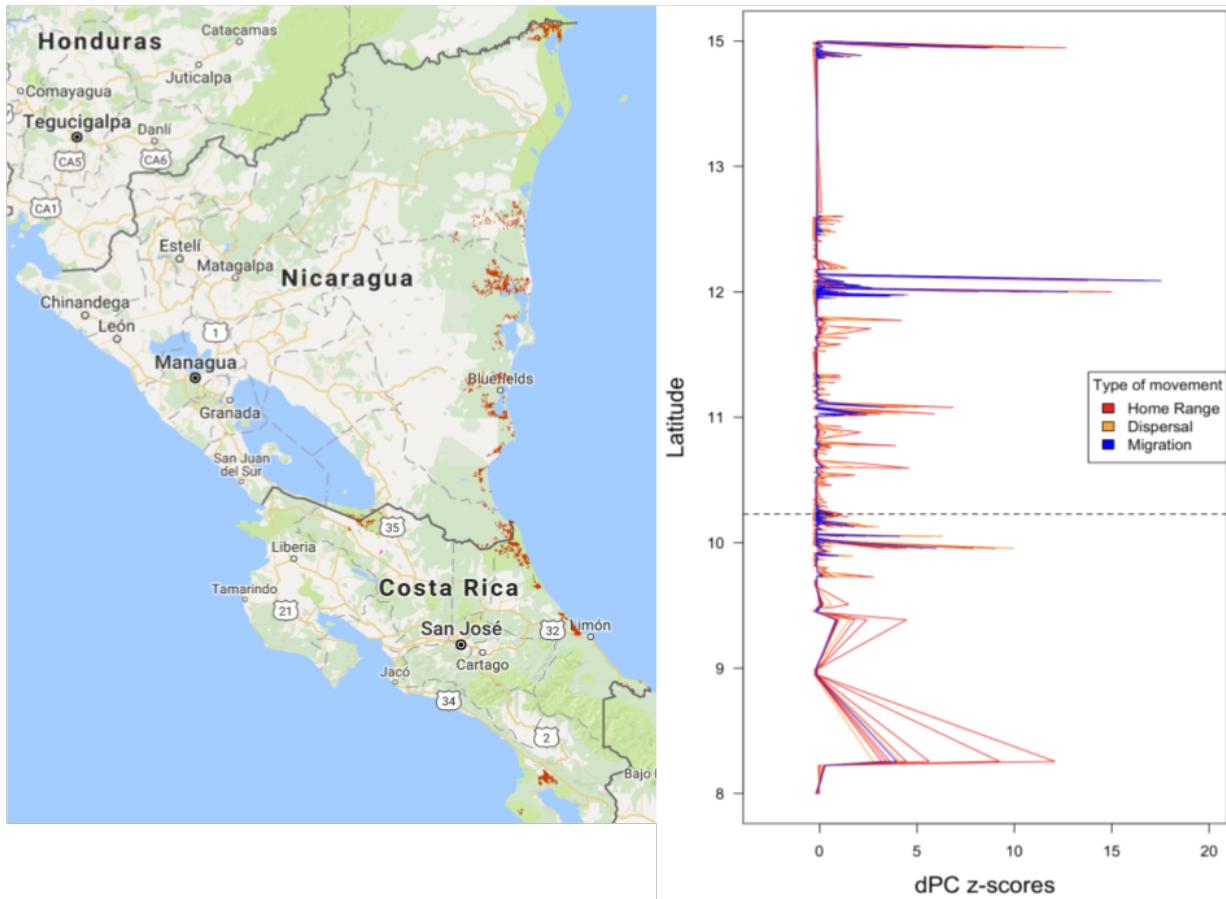
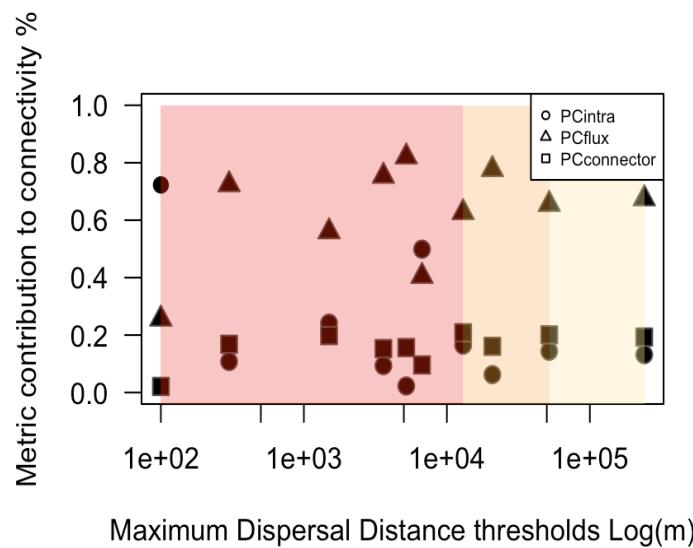


Figure 7: Latitudinal variation of the dPC z-scores. Lines represent the distribution of dPC z-scores against the latitudinal



component of the centroid of each *Raphia taedigera* patch.

Figure 8: Contribution to connectivity of each of dPC fractions.

Overall, the area weighted dispersal flux (dPCFlux) (Saura and Rubio 2010) contributed the most to habitat availability for dispersal measured by dPC, except at dispersal scenarios of 100m and 6700m, were contributed second, behind PCIntra (Figure 8). PCFlux contribution to habitat availability reaches its lowest at very short dispersal scenarios (100m). Valleys, highlighting drops in the relative contribution of PCFlux compared with the other dispersal scenarios were found at 100m, 1500m, 6700m and 52Km. Intrapatch connectivity (PCIntra) contribution to habitat availability reach its maximum at dispersal distances of 100m and 6700m with valleys at 300m, 5200m and 20.8Km. Stepping stone (PCconnect) contribution to habitat availability peaks at 1500m and 13Km and it reaches a minimum at 100m dispersal distance thresholds (Figure 8).

dPCIntra values were highly correlated with patch area for all maximum dispersal distances thresholds calculated (Figure 9). dPCFlux shows increasingly higher correlations with dA (Patch area) at increasing distance thresholds. Correlations of dPCconnector with patch area follows a similar pattern than dPCFlux but reaches a peak at maximum dispersal distances of 20.8 Km to drop at larger dispersal thresholds. Low correlation values between PCconnector and relative patch area (dPa) would imply that for scenarios at very short and very long maximum distance dispersal the patches with higher stepping stone contribution to overall landscape connectivity of are not necessarily the larger ones (measured by Patch Area). This suggests that changes in patch size could mean higher relative changes on the "stepping stone" function of the patch for such dispersal scenarios, resulting in changes up 20% in the overall seed dispersal connectivity (for tapir dispersal scenarios) of *Raphia taedigera* populations in the Costa Rica and Nicaragua.

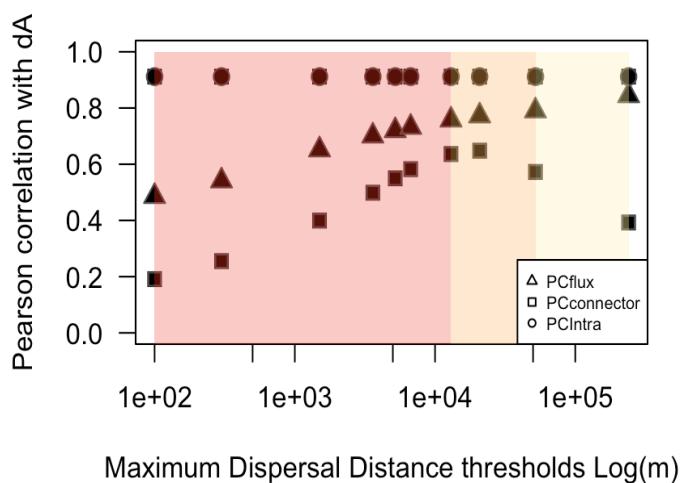


Figure 9: Pearson correlations between the dPC fractions and Patch relative area (dPa).

Number of components

An inverse relationship between the ratio values and the dispersal thresholds was found. At minimum dispersal distances (100m), the ratio No. components/ No. patches was of 0.8 meaning that 80% of patches forms clusters isolated from the overall network. Until dispersal distances of 1500m the ratio values diminishes rapidly. At 1500m, the ratio clusters/patch is lower than 0.2. Low ratio values are maintained overall the distance thresholds considered to be relevant for the tapir dispersal. At the highest dispersal threshold distances considered (240Km) this ratio equaled to 1.

Functional connectivity

Resistance layer

Final resistance layer (Figure 10) represents the aggregated resistance values for each of the spatial variables (Human population density, Distance to Water, Slope, Canopy tree cover, Road network) used to characterize the level of resistance of the landscape to the movements of *Tapirus bairdii*. Aggregated resistance values ranged from 1 to 240. Zones with low resistance values were generally found at the eastern side of the study area near to the Atlantic Coast. In Costa Rica the mountainous regions (Including the San Jose Valley at the center of the country have the highest resistance values. High resistance values correspond to areas with pronounced slopes. In Nicaragua, high resistance areas are located towards the west side of the country. In Nicaragua higher resistance values were more attributed to deforested areas. At broader scales, distance to water sources was the variable that contributed the most to the overall spatial patterns observed in the aggregated resistance layer (Figure 10).

Validation of the resistance layer shows that Tapir observations have significantly lower mean resistance values when considering the mean values of random samples to create a "null model" for comparison. However, when considering median values there is not apparent differences between the "null model" from random points and the median values of observed tapir occurrences. This could imply that in overall the aggregated resistance layer is skewed towards low resistance pixel values.

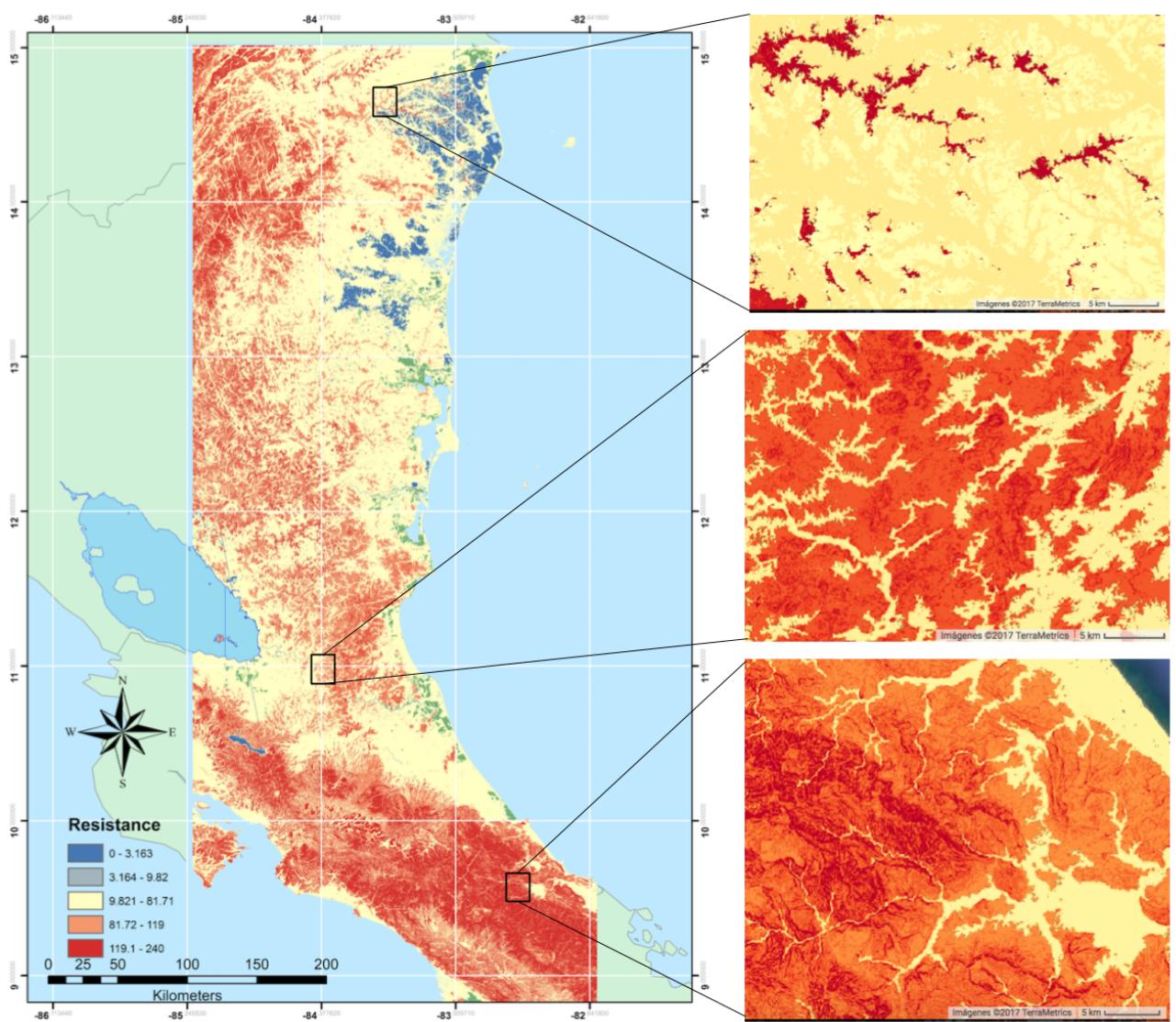


Figure 10: Final aggregated resistance layer representing the landscape resistance to *Tapirus bairdii* movements among *Raphia taedigera* patches. Higher resistance values are in red. Patches of *Raphia taedigera* are drawn in green. Pixel resolution of the Raster layer = 30mx30m.

Functional corridors

In general terms, both approaches (Circuit theory & RSPs) highlight a similar set of functional corridors linking all *Raphia taedigera* patches (Figure 11). Cumulative current map produced generated with Circuitscape shows areas with higher cumulative resistance located mainly at the central valley of Costa Rica and in the northeastern part of the Nicaraguan border. A continuous corridor is observed in the Atlantic coast connecting both countries. Corridors in Costa Rica exists connecting patches from the Pacific Coast with the ones in the Atlantic Coast. These corridors are mainly concentrated in the areas below San Jose. Main corridors connecting both coasts are found from the Talamanca Region, Cahuita and Rio Banano at the Atlantic coast., merging near Shiroles and diverging into a series of connected corridors following river basins towards the Sierpe region near the Osa Peninsula. A similar set of east-west corridors are found from the regions of Limon and the Tortuguero National Park. One of this corridors goes east from Playa Hermosa following the river basin that acts as limits for the Cartago and Limon Provinces, and another one passes towards regions near to Jabillos, Turrialba, Pejibaye and Villa Millis. This corridors merges at Rivas and follows river basins towards the Uvita region at the Pacific coast.

Patches south of the Nicaragua Lake are connected with the Atlantic coast patches by a corridor mainly found in the areas corresponding to the San Juan River at the border with Nicaragua. A corridor which links the Pacific side patches with the ones near Nicaragua lake, first follows the South Pacific coast of Costa Rica and then diverges into separate corridors near the populated center of Parrita. One along the Pacific Coast towards the regions of Puntarenas and Monteverde and the other crossing the forests near the regions, from south to north of: Santiago; Atenas; Grecia and San Ramon and Boca Arenal. Both corridors merge together near the town of San Rafael and towards the region of Caño Negro south of Nicaragua Lake.

In Nicaragua, a main corridor in the Atlantic coast flows South to North from the San Juan del Nte. region up to the patches located in the Bismuna region near the Honduras border. From Boca San Carlos, two corridors goes north and merge at the Caño Negro river to then follow the main atlantic corridor towards Bluefields. In the region of Punta Gorda, the atlantic corridor separates into three parts before merging again towards Bluefields. One follows up the Atlantic coast towards Monkey Point, the second follows the Caño Montecristo and the third one goes up following the Caño Punta Gorda. Up Bluefields, the Atlantic corridor goes almost uniformly

towards the Bismuna regions. Around seven differentiable West-East corridors are found in Nicaragua connecting the patches near the Nicaragua Lake with the ones at the Atlantic coast. From south to north this corridors start from near the Nicaragua Lake at Santa Cruz, San Carlos, San Miguelito and La Flor. This corridors also follow river basins and tributaries of the Santa Cruz, Sabalos, Palo de Arquito ,Tule, Tepenaguasapa, Oyate and Ojucuapa rivers.

There is also the presence of a "bottleneck" (i.e. narrow areas acting as corridors) are in the triangular region formed by Bluefields, Kukra Hill and El Rama between the 12 and 13 parallels. Main differences between the Circuitscape corridors and the Randomized Shortest paths is that corridors obtained with the second approach appears to be less dependant on following rivers. RSP's allows to visualize density of paths in a determined regions rather than proposed corridors. Therefore, even if the pixel size is bigger (90x90m vs 30x30m) the model is most accurate to represent local, small scale variations in the choices of movement for *Tapirus bairdii* in comparison to Circuitscape corridors.

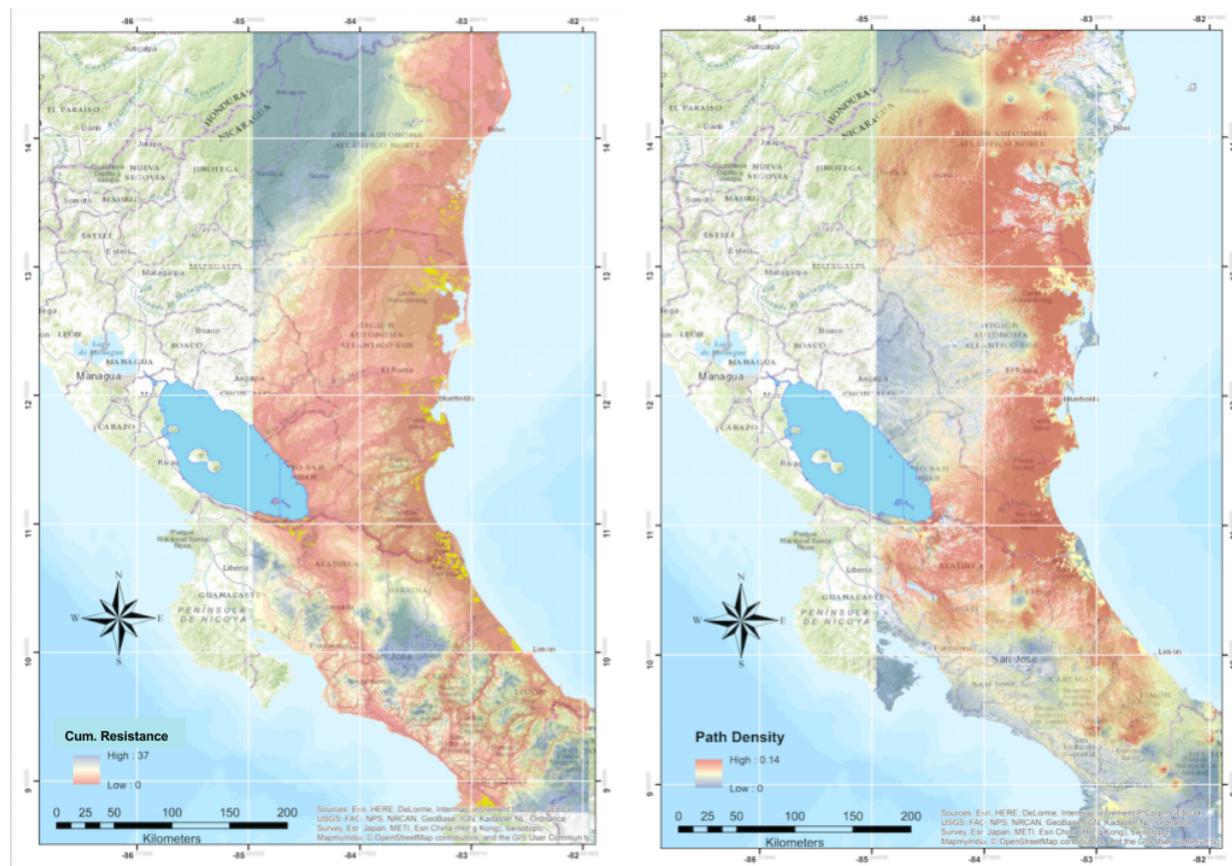


Figure 11: Seed Dispersal Functional Corridors found among *Raphia taedigera* patches in Costa Rica and Nicaragua. Left: Corridors found with Circuitscape. Right: Corridors found with the Randomized Shortest Paths approach. Main global similarities between both outputs have been highlighted with same color rectangles. Main global differences are shown with colored circles. Resolution of Circuitscape corridors layer = 30 x 30m. Resolution of RSP's corridors layer = 90mx90m.

Discussion

Preserving the spatial connectivity of populations is a key target for nature conservation. Connectivity is a complex process that is maintained by the spatial arrangement of the patch network and the adequate movement of genetic material among them. In Central America, yoliiales have been characterized as the wetlands with the biggest human-related pressures (Calvo-Gutiérrez, Bonilla-Murillo, & Sasa, 2013; Serrano-Sandí et al., 2013). During the dry season, people slash and burn the *Raphia taedigera* palms and drain the soil for agriculture or cattle ranching purposes (Calvo-Gutiérrez et al., 2013; Serrano-Sandí et al., 2013).

The importance of patches to maintain seed dispersal connectivity is not only determined by patch area but rather for the spatial location of the patch in relation to other patches. This was especially true for seed dispersal connectivity for short and long distances. This suggests that for conservation actions, directed to the long term conservation of Raphia dominated wetlands, preserving the global spatial arrangement of the patches is more important than focusing the preservation of single patches.

For all dispersal distance thresholds evaluated few patches are responsible of maintaining overall connectivity. In Costa Rica, all of this patches, with the exception of patches up the towns of Limon and Moin, fall under some degree of land protection (i.e. protected areas). In Nicaragua, important patches are located inside of protected areas, However, in the delta of the Kuringwas river, an important patch of *Raphia taedigera* to maintain seed dispersal connectivity among populations falls outside of the national network of protected areas. This patch (and surrounding satellite patches) acts as connection between the Llanos de Karawala and Wawashang National Protected Areas. Conservation efforts should prioritize the conservation of this particular patches in order to ensure the long term preservation connectivity of *Raphia taedigera* populations (Figure 12).

In addition to preserving key patches for seed dispersal to long term sustainability of *Raphia taedigera* populations requires an adequate gene flow. Gene flow among populations might be product of pollination and seed dispersal. Pollination in *Raphia taedigera* appears to be primarily wind mediated. Seed dispersal gene flow is associated to *Tapirus bairdii* movements, which are in turn limited by changes on the landscape matrix.

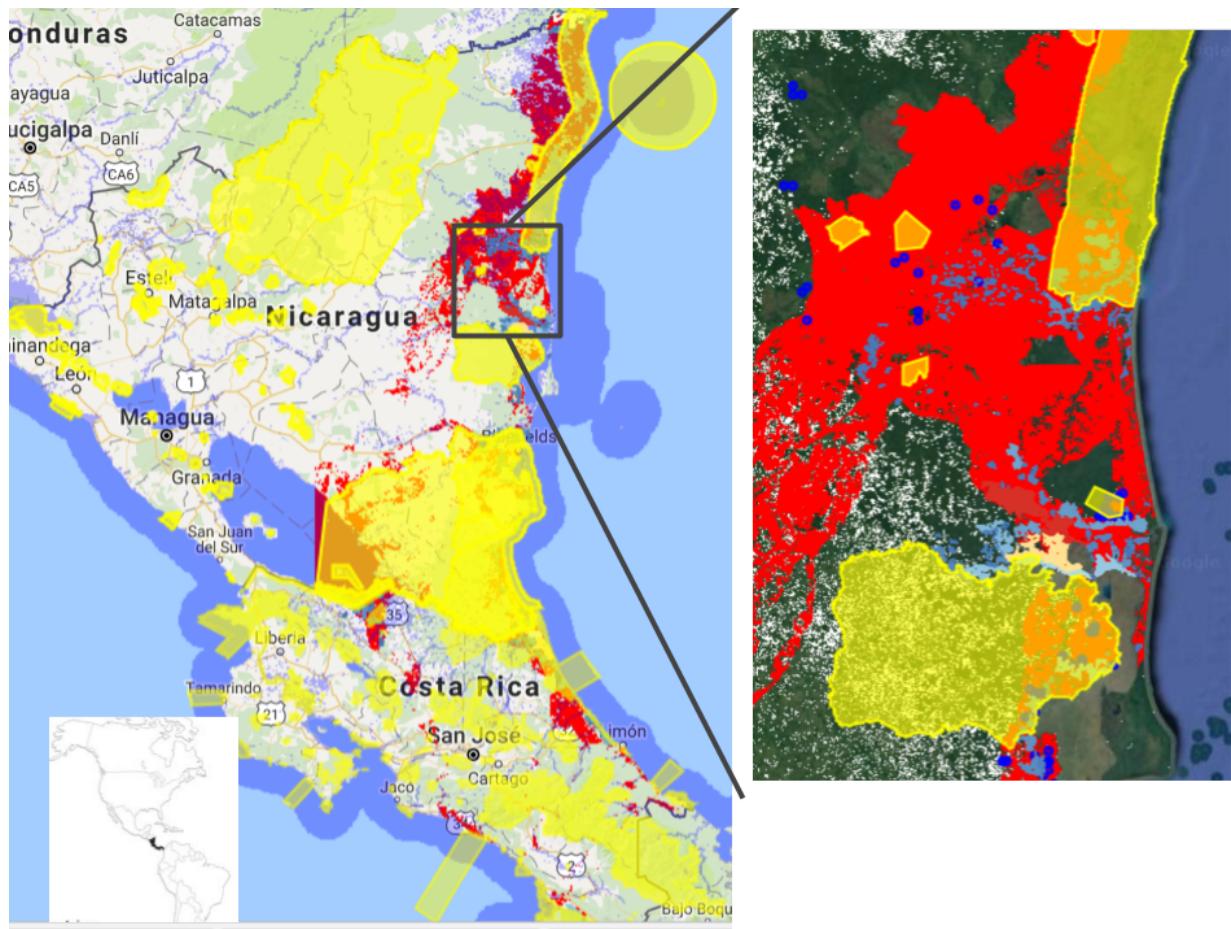


Figure 12: Important *Raphia taedigera* patches (measured by dPC) outside of protected areas in Nicaragua, important areas to prioritize conservation actions. Protected areas are shaded yellow and patches are colored based on dPC values at 5200m (Tapir mean daily movements) Blue tones represent lower dPC and reddish tones are in function to increasing dPC values.. Corridors found with Coircuitscape are in red. Deforestation losses are shown in white. Tapir occurrences (zoom box) are shown as blue points.

According to the results of the functional corridors, several portions of the landscape surrounding *Raphia taedigera* patches acts as potential corridors among all *Raphia* patches, especially on those located in the Atlantic Coast. for which seed dispersal might occur. From the landscape level variables affecting the choices of movement of *Tapirus bairdii*, forest cover and human density is the variable most associated to change due human-related pressures.

Deforestation and land transformation affects directly seed dispersal connectivity of *Raphia taedigera* populations, either by removal of patch cover or modifications on the portion of the landscape acting as corridors among *Raphia* patches. Deforestation pressures are differentially expressed between Nicaragua and Costa Rica (Sesnie et al., 2017). With forest changes being of higher proportion in Nicaragua. As forest losses is often associated with colonization and defaunation processes (Hobley, ; Kurten, 2013; Sesnie et al., 2017) . This is expected to have

an impact over *Tapirus bairdii* populations which in turn will be expressed over the long term persistence of *Raphia taedigera*.

The forest cover layer used in this study represents the forest coverage estimated for the year 2000. Since then deforestation in Nicaragua have incremented despite the national network of protected areas. In the zone of Bluefields, functional corridors have undergone a sustancia deforestation that threaten to severe the Atlantic corridor linking population patches of *Raphia taedigera* (Figure 13).

An additional threat towards severing the connectivity of *Raphia taedigera* populations in the near future is the project of the Chinese government to the creation of a cross-oceanic canal (Figure 14). This would imply a direct modification of the landscape at different levels.

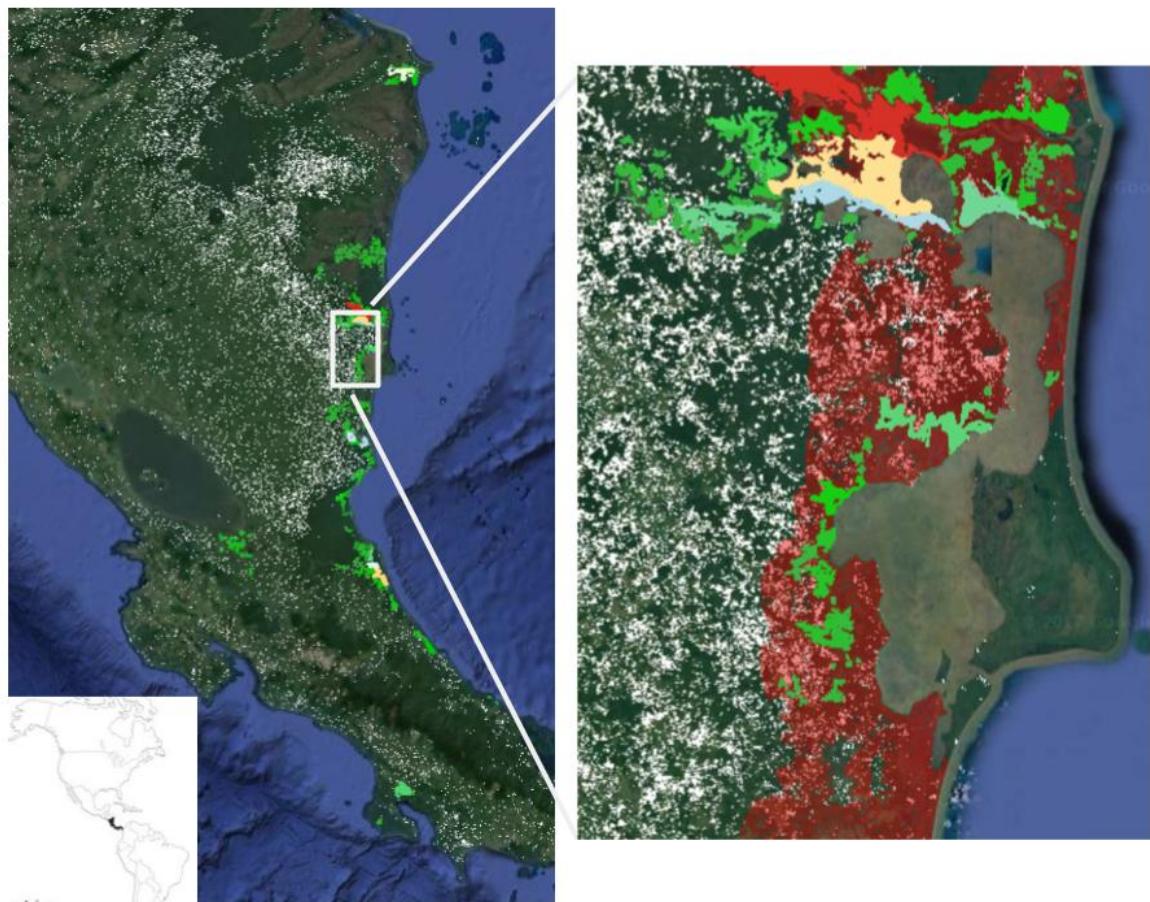


Figure 13: Example of the deforestation effect on the corridors near Bluefields, Nicaragua. Corridor found with Circuitscape is colored in red. Forest loss changes from 2000-2013 (Hansen et al. 2013) are shown in white.

Although increasing of flooded areas in some parts of the landscape may result beneficial to the local expansion of nearby *Raphia taedigera* patches, the overall effect of the canal would imply a physical barrier for home range, dispersal and migration movements of tapir individuals north and south the canal (Meyer & Huete-Pérez, 2014), becoming an important barrier also for the gene flow among *Raphia taedigera* populations. This modification in the connectivity of populations could have cascading implications over the long term persistence of *Raphia taedigera* in the study area.

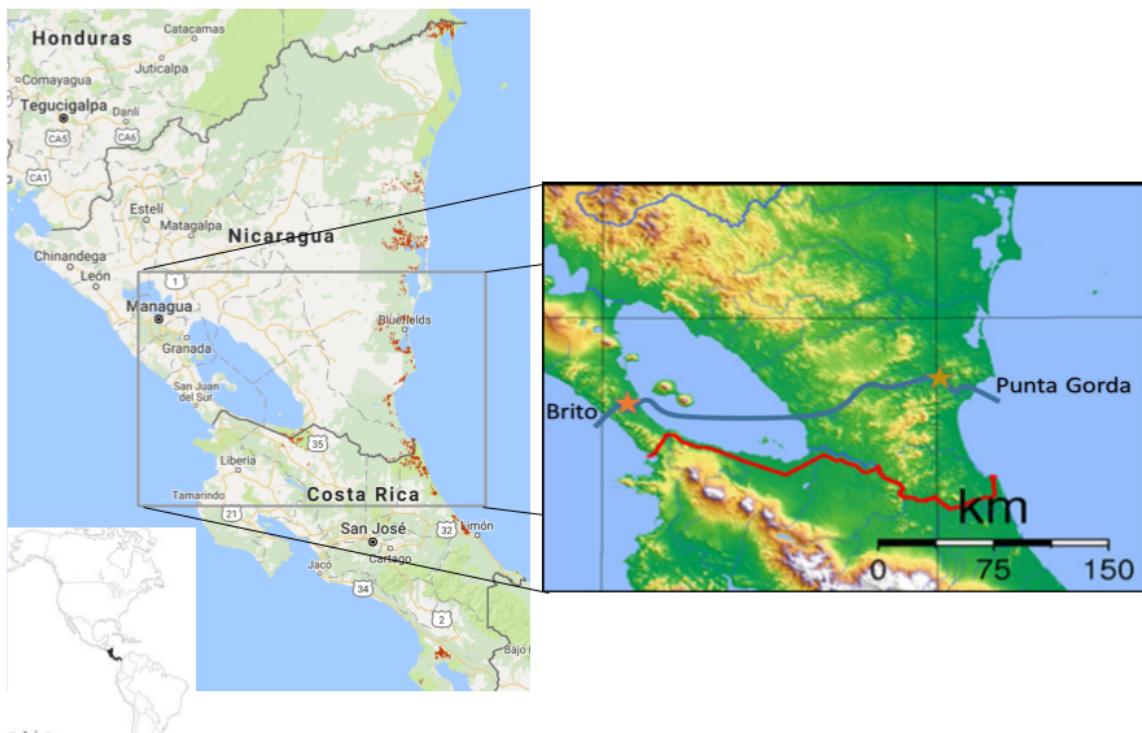


Figure 13. Route of the proposed Nicaraguan Canal (Blue). The canal begins in Punta Gorda at 11.5° Latitude.

Assumptions of the study

The study of seed dispersal connectivity, a multiscale interaction, is particularly complex and results have to be always interpreted according to the assumptions realized in the models. For this study assumptions made in this study deserve some discussion. For the structural connectivity analyses, distances among patches were calculated as euclidean distances (i.e. straight lines). Although structural connectivity metrics have positively associated to reflect gene flow patterns among populations (Aavik et al., 2014), euclidean distances could not necessarily reflect real travel distances at large scales. A second assumption is the assignment of resistance values to particular landscape variable category. Despite the resistance values were

selected based on literature observation on the Tapir movement ecology, local processes which might influence the resistance of the landscape to tapir movements have not been addressed. Nevertheless, the validation of the resistance layer show a level of agreement between the tapir occurrence records and a lower resistance values (Figure 14).

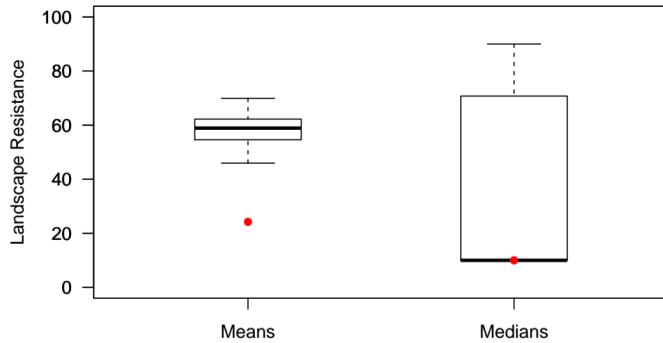


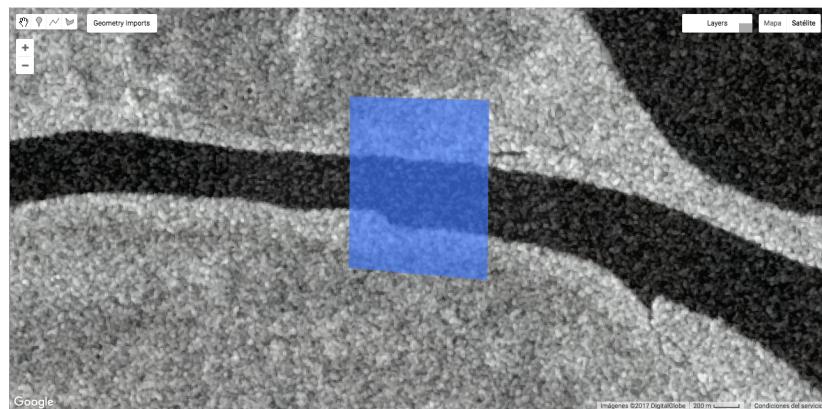
Figure 14: Validation of the resistance layer. Boxplots represents the Null model (see methods). Mean and median observed resistance values for the occurrence of Tapirs are shown with the red dot.

Impact and Future Perspectives

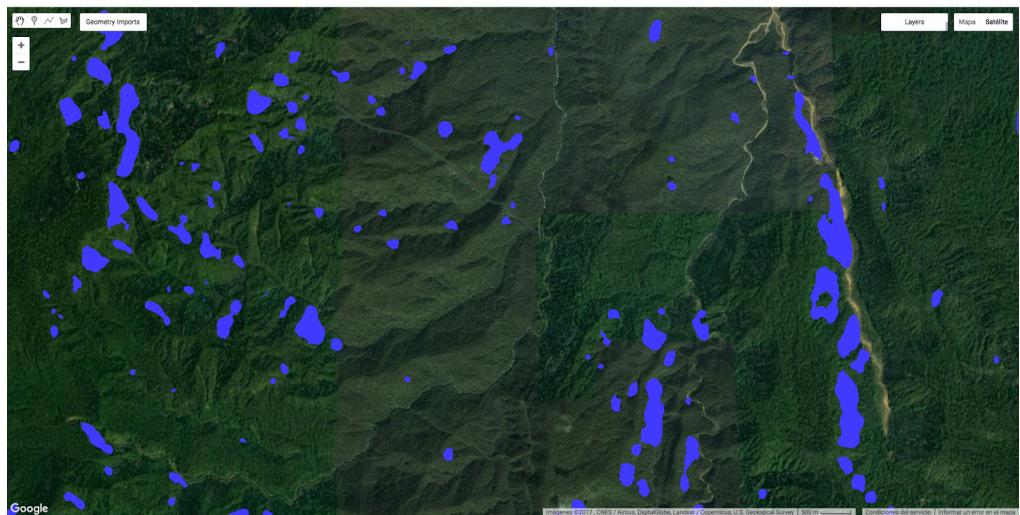
New advances on computational ecology and cloud computing made possible to scale up to macroecological patterns from focalized observations to enhance the understanding of complex ecological systems such as the spatial patterns of the seed dispersal interaction between *Raphia taedigera* and *Tapirus bairdii*.

Frameworks such as the ones presented in this study could be applied, independently of taxa or study area, to leverage from localized research to scale up predictions and create baselines for monitoring. The increasing availability of remotely sensed data at higher resolutions appears as an opportunity for ecologists, conservationists and developers to create replicable and re-scalable products (e.g. https://earthengine.google.com/case_studies/). Such products, aside of providing insights on the functioning of ecological macrosystems (Aavik et al., 2014; Heffernan et al., 2014) are of increasing importance to provide decision and policy makers spatially explicit conclusions to prioritize conservation efforts.

APPENDIX



Appendix Figure 1: Area selected as sample for the global separation between water-non-water for S1 imagery. Bounding box = $([-83.80, 12.16], [-83.80, 12.15], [-83.79, 12.14], [-83.79, 12.16], [-83.80, 12.16], [-83.80, 12.16])$.



Appendix Figure S2: Example of the confusion on the OTSU separation of S1 radar images in mountainous regions in the Talamanca Cordillera in Costa Rica. Center point of image (9.51N -83.29W)

Acknowledgements:

To my supervisors: Renske Onstein, A.C. Harry Seijmonsbergen for their time and invaluable comments and discussion that help the development of this research project.

To Daniel Kissling for helpful discussions and the use of his server for the calculations of the randomized shortest paths.

To Suzette Flantua for her key help and knowledge on connectivity and corridor concepts.

To the UvA GIS Studio to let me use the computers to run Circuitscape.

To Jose Serrano-Sandi, Mahmood Sasa and Ronald Myers for providing me literature and spatial information about *Raphia taedigera* in Costa Rica and Nicaragua.

To Charlotte Laurin for patience and help with the final presentation pitch.

To all my friends and family whom are my base support.

Finally, to SENESCYT (Secretaría Nacional de Educación Superior, Ciencia y Tecnología) [Ecuador] for financing my MSc studies with the Scholarship “Convocatoria Abierta 1 Fase, 2014”.

Appendix Table S1. Relevant observations on the Ecology of the Tapir extracted from literature

Species	Observation	Source	VariableClass	Location
<i>Tapirus bairdii</i>	Habitat in North of Wawashang Nature Reserve	Jordan et al. 2016	Habitat use	Nicaragua
<i>Tapirus bairdii</i>	Habitat in wetlands in the southeastern corner of of Wawashang Nature Reserve	Jordan et al. 2016	Habitat use	Nicaragua
<i>Tapirus bairdii</i>	Habitat in mangrove swamps in the east of of Wawashang Reserve	Jordan et al. 2016	Habitat use	Nicaragua
<i>Tapirus bairdii</i>	Habitat of importance in the wetlands behind Bluefields Severe nature degradation in Cerro Silva and Punta Gorda Nature Reserve, low probability of harboring tapirs	Jordan et al. 2016	Habitat use	Nicaragua
<i>Tapirus bairdii</i>	None of the areas classified as agriculture before 2000 retain habitat occupancy of Tapirs	Jordan et al. 2016	Habitat use	Nicaragua & Costa Rica
<i>Tayasuu pecari</i>	None of the areas classified as agriculture before 2000 retain habitat occupancy of White lipped peccaries	Jordan et al. 2016	Habitat use	Nicaragua & Costa Rica
<i>Tapirus bairdii</i>	Distance to agriculture frontier has a much larger impact for terrestrial mammal occupancy	Jordan et al. 2016	Habitat use	Nicaragua & Costa Rica
<i>Panthera onca</i>	None of the areas classified as agriculture before 2000 retain habitat occupancy of Jaguars	Jordan et al. 2016	Habitat use	Nicaragua & Costa Rica
<i>Tapirus bairdii</i>	Home range of ** <i>Tapirus bairdii</i> **: 2.32sqKm	Schank et al. 2015	Natural history	Central America
<i>Tapirus terrestris</i>	For ** <i>Tapirus terrestris</i> ** dispersal distances up to 1.5Km	Schank et al. 2015	Natural history	Brazil
<i>Tapirus bairdii</i>	Temperature seasonality explains 33.9% of predicted habitat	Schank et al. 2015	Habitat use	Central America
<i>Tapirus bairdii</i>	Precipitation seasonality explains 31.5% of predicted habitat	Schank et al. 2015	Habitat use	Central America
<i>Tapirus bairdii</i>	Precipitation of dryest quarter explains 9.7% of predicted habitat	Schank et al. 2015	Habitat use	Central America
<i>Tapirus bairdii</i>	Maximum temperature of warmest month explains 9.1% of predicted habitat	Schank et al. 2015	Habitat use	Central America
<i>Tapirus bairdii</i>	Tapirs are found in Tropical Rainforest, Semievergreen tropical rainforest, Montane fores, Pine and oak forest	Schank et al. 2015	Habitat use	Mexico
<i>Tapirus bairdii</i>	Tapirs are present in Dry forest	Schank et al. 2015	Habitat use	Costa Rica
<i>Tapirus bairdii</i>	Bosawas Biosphere a stronghold for Tapir populations	Schank et al. 2016	Population distributi	Nicaragua
<i>Tapirus bairdii</i>	Indio Ma'z Biosphere reserve a stronghold for Tapir populations	Schank et al. 2017	Population distributi	Nicaragua
<i>Tapirus bairdii</i>	Forest remnants of the Caribbean Coast may function as important corridor of suitable habitat between ** <i>Tapirus bairdii</i> ** populations Poaching, deforestation more probably eliminated connectivity	Schank et al. 2015	Population character	Nicaragua
<i>Tapirus bairdii</i>	between tapir populations in the far north and in the far south West part, far from the Caribbean Coast populations were hunted and is unsustainable for tapir populations	Schank et al. 2015	Population character	Nicaragua
<i>Tapirus bairdii</i>	Apparent Corridor in the Caribbean coast from Honduras to Costa Rica	Schank et al. 2015	Population distributi	Nicaragua
<i>Tapirus bairdii</i>	Tapirs were observed using forest and exotic tree plantations in northern Costa Rica	Schank et al. 2015	Population character	Nicaragua
<i>Tapirus bairdii</i>		Schank et al. 2015	Population character	Costa Rica

	Tapirs may be resilient to colonize new forest patches if there is not enough forage and cover available in the biological corridors between them	Schank et al. 2015	Population character Costa Rica
Tapirus bairdii	Tapirs are found in Santa Rosa National Park	Schank et al. 2015	Population distributi Costa Rica
Tapirus bairdii	Tapirs are found in Guanacaste National Park	Schank et al. 2015	Population distributi Costa Rica
Tapirus bairdii	Tapirs are found in Palo Verde National Park	Schank et al. 2015	Population distributi Costa Rica
Tapirus bairdii	Tapirs presence in dry forest may be undersampled	Schank et al. 2015	Population distributi Costa Rica
Tapirus bairdii	No Tapirs are present in the Nicoya Peninsula	Schank et al. 2015	Population distributi Costa Rica
	Areas along caribbean coast between Limon and Cahuita National park likely represent areas where <i>Tapirus bairdii</i> is no longer present	Schank et al. 2015	Population distributi Costa Rica
Tapirus bairdii	The increase in pineapple production limits tapirs movements	Schank et al. 2015	Population character Costa Rica
Tapirus bairdii	Paved roads and multilane highways are barrier to tapirs	Schank et al. 2015	Population character Costa Rica
Tapirus bairdii	Tapirs are found in Santa Rosa National PArk	Schank et al. 2015	Population distributi Costa Rica
	Most of tapir suitable habitat is along the atlantic coast, protected areas connected by primary forests in indigenous territories such as Embara and Guna	Schank et al. 2015	Population distributi Panama
Tapirus bairdii	Darien National Park could harbor tapirs, but no evidence is reported	Schank et al. 2015	Population distributi Panama
Tapirus bairdii	<i>Tapirus bairdii</i> in the IUCN red list (Castellanos 2008). In Mexico is considered an endangered species	Lira-Torres et al. 201	Conservation status Mexico
Tapirus bairdii	<i>Tapirus bairdii</i> listed in the Appendix 1 of CITES%	Lira-Torres et al. 201	Conservation status Mexico
Tapirus bairdii	Population of <i>Tapirus bairdii</i> have decreased more than 50% in the last 30 years	Lira-Torres et al. 201	Conservation status Mexico
Tapirus bairdii	Globally, population is estimated to be of 5500 adult individuals	Lira-Torres et al. 201	Population character Central America
Tapirus bairdii	Mexico has a population of less than 1500 individuals (Castellanos 2008)	Lira-Torres et al. 201	Population character Mexico
Tapirus bairdii	Fortaleza (Study area) has a population of 120 people grouped in 30 families, they hunt in the sourrounding tropical forest, including species like the tapir	Lira-Torres et al. 201	Conservation status Mexico
Tapirus bairdii	Preys of the Jaguar includes the central american Tapir (Chavez et al. 2007)	Lira-Torres et al. 201	Natural history Central America
Tapirus bairdii	The relative abundance index for the four year sampling study was of 6.77/1000 camera-night (n=61)	Lira-Torres et al. 201	Population character Mexico
Tapirus bairdii	16 (26.22%) males, 3 (4.91%) females and unidentified (67.21%)	Lira-Torres et al. 201	Population character Mexico
Tapirus bairdii	95.08% adults, 3.27% juveniles, and 1.63% with a cub	Lira-Torres et al. 201	Population character Mexico
Tapirus bairdii	<i>Tapirus bairdii</i> is a nocturnal species	Lira-Torres et al. 201	Habitat use Mexico
Tapirus bairdii	In dry season Bosque Tropical Perennifolio without hunting was the habitat more used by the tapir	Lira-Torres et al. 201	Habitat use Mexico
Tapirus bairdii	In dry season Secondary vegetation with hunting was used according to availability	Lira-Torres et al. 201	Habitat use Mexico

<i>Tapirus bairdii</i>	In dry season Bosque Tropical Perennifolio with hunting was the habitat less used by the tapir In wet season secondary with hunting habitat was used more than expected	Lira-Torres et al. 201 Habitat use	Mexico
<i>Tapirus bairdii</i>	In wet season Bosque Tropical Perennifolio without hunting was the habitat less used by the tapir	Lira-Torres et al. 201 Habitat use	Mexico
<i>Tapirus bairdii</i>	In dry season Bosque Tropical Perennifolio with hunting was used more than expected	Lira-Torres et al. 201 Habitat use	Mexico
<i>Tapirus terrestris</i>	Tapirus terrestris in Bolivian Chaco 11-60 records per 1000 night camera nights	Lira-Torres et al. 201 Population character Bolivia	
<i>Tapirus terrestris</i>	Tapirus terrestris in Bolivian humid forests 7 records pero 1000 night camera nights	Lira-Torres et al. 201 Population character Bolivia	
<i>Tapirus terrestris</i>	Tapirus terrestris in Brazil humid forests 2.71 records pero 1000 night camera nights	Lira-Torres et al. 201 Population character Brazil	
<i>Tapirus terrestris</i>	Tapirus indicus 4-19 records per 1000 night camera nights	Lira-Torres et al. 201 Population character Sumatra	
<i>Tapirus bairdii</i>	Tapirus bairdii 12 records per 1000 night camera traps in Chiquibul Tapirus bairdii 37.57 record per 1000 night camera traps in Calakmul Biosphere reserve (Data probably is biased because sampling restricted to only aguadas lagoons which heavily influences the presence and recurrence in that particular biosphere reserve, due to scarcity of water bodies)	Lira-Torres et al. 201 Population character Belice	
<i>Tapirus bairdii</i>	Sex estructure slightly favor females than males. But not significantly different from 1:1 (Naranjo 2009)	Lira-Torres et al. 201 Population character Mexico	
<i>Tapirus bairdii</i>	Tapirus bairdii can live up to 30 years	Lira-Torres et al. 201 Natural history	Central America
<i>Tapirus bairdii</i>	Tapirus bairdii is a solitary species	Lira-Torres et al. 201 Habitat use	Central America
<i>Tapirus bairdii</i>	Water bodies are important for the reproduction of the species (Inferred after observation of photographies of tapirs copulating inside water bodies)	Lira-Torres et al. 201 Habitat use	Mexico
<i>Tapirus bairdii</i>	Water availability, forest coverage and food are indispensable factors for the habitat selection of <i>Tapirus bairdii</i>	Lira-Torres et al. 201 Natural history	Central America
<i>Tapirus bairdii</i>	In dry seasons, forest patches in between agricultural zones are important as food source of native trees and water	Lira-Torres et al. 201 Habitat use	Mexico
<i>Tapirus bairdii</i>	In flooded areas favor a succession state that provides plenty of tree and shrub sprouts wch the tapir activily looks for in the wet seasons because of the high nutrient concentration of such sprouts Grassland or secondary vegetation can be used by the tapir as long as human activity is limited and hunting pressure is small	Lira-Torres et al. 201 Habitat use	Mexico
<i>Tapirus bairdii</i>	Protected areas are not more important for tapir populations In San Juan - La Selca Corridor <i>Tapirus bairdii</i> is frequent where there is forest coverage, wetlands and a combination of yolliales and hebaeuous wetlands	Lira-Torres et al. 201 Habitat use	Mexico
<i>Tapirus bairdii</i>	Population density 0.22 ind/sqKm in Lacandon Chiapas	Chassot et al. 2005 Habitat use	Costa Rica
<i>Tapirus bairdii</i>		Chassot et al. 2005 Population character	Mexico

Tapirus bairdii	Population density of 0.53 ind/sqKm in Barro Colorado 1.23 ind/sqKm in Corcovado National Park	Chassot et al. 2005 Population character Panama Chassot et al. 2005 Population character Costa Rica
	Preference of habitat use in landscapes with important fragments of intervened lowland forest and secondary forest. With natural or human-made gaps, wetland combinations, water bodies, quebradas, ca-os, yolliales riparian forests and herbaceous swamps	Chassot et al. 2005 Habitat use
Tapirus bairdii	Preference of habitat with smooth slopes	Chassot et al. 2005 Habitat use
Tapirus bairdii	An exclusion zone of at least 290 mts round population centers (Flesher and Ley, 1996)	Chassot et al. 2005 Habitat use
Tapirus bairdii	Home range of Tapirus bairdii 125ha (Forester and Vaughan 2002)	Chassot et al. 2005 Natural history
Tapirus bairdii	Home range of Tapirus bairdii 135ha Corcovado National Park (Forester 2002)	Chassot et al. 2005 Natural history
Tapirus bairdii	Tapirus bairdii can move big distances in search for new home ranges in Corcovado National Park (Foerster 1998)	Chassot et al. 2005 Natural history
Tapirus bairdii	Forest fragments <125ha = deficient	Chassot et al. 2005 Habitat use
Tapirus bairdii	Forest fragments >125 ha <136ha = adequate	Chassot et al. 2005 Habitat use
Tapirus bairdii	Forest fragments >136ha = excellent	Chassot et al. 2005 Habitat use
Tapirus bairdii	Tapirus bairdii is attracted to water sources	Chassot et al. 2005 Habitat use
Tapirus bairdii	Lagoons = excellent	Chassot et al. 2005 Habitat use
Tapirus bairdii	Lagoon buffer 1-100m = Excellent	Chassot et al. 2005 Habitat use
Tapirus bairdii	Lagoon buffer 101-200m = Adequate	Chassot et al. 2005 Habitat use
Tapirus bairdii	Lagoon buffer 201-300m = Adequate	Chassot et al. 2005 Habitat use
Tapirus bairdii	Tapirus bairdii is attracted to highly flooded areas	Chassot et al. 2005 Habitat use
Tapirus bairdii	Wetlands = Excellent	Chassot et al. 2005 Habitat use
Tapirus bairdii	Wetland buffer 1-100m = Excellent	Chassot et al. 2005 Habitat use
Tapirus bairdii	Wetland buffer 101 - 200m = Adequate	Chassot et al. 2005 Habitat use
Tapirus bairdii	Wetland buffer 201 - 300m = Adequate	Chassot et al. 2005 Habitat use
Tapirus bairdii	Rivers, quebradas and ca-os = Excellent	Chassot et al. 2005 Habitat use
Tapirus bairdii	Rivers, quebradas and ca-os buffer 1-40m = Excellent	Chassot et al. 2005 Habitat use
Tapirus bairdii	Rivers, quebradas and ca-os buffer 41-80m = Excellent	Chassot et al. 2005 Habitat use
Tapirus bairdii	Rivers, quebradas and ca-os buffer 41-80m = Adequate	Chassot et al. 2005 Habitat use
Tapirus bairdii	Rivers, quebradas and ca-os buffer 81-120m = Adequate	Chassot et al. 2005 Habitat use
Tapirus bairdii	10m both side of roads low probability of finding tapirs	Chassot et al. 2005 Habitat use
Tapirus bairdii	Slope of terrain flat to 15% = Excellent	Chassot et al. 2005 Habitat use
Tapirus bairdii	Slope of terrain 16% to 30% = Adequate	Chassot et al. 2005 Habitat use
Tapirus bairdii	Slope of terrain> 31% = Deficient	Chassot et al. 2005 Habitat use
Tapirus bairdii	Biological Corridor La Selva-San Juan is estimated to have a population density of 0.53ind/sqKm to 1.60 ind/sqKm	Chassot et al. 2005 Population character Costa Rica
Tapirus bairdii	Tapirus bairdii is considered locally extirpated from most of its historic range in Costa Rica	Cove et al. 2013 Natural history

	Although <i>Tapirus bairdii</i> is considered as rare. Their findings suggest that it is more resilient and better able to use available habitat in the fragmented corridor than previously thought In Costa Rica <i>Tapirus bairdii</i> is protected and there is little economic gain on killing this species Best predictor of lowland tapir (<i>Tapirus terrestris</i>) occurrence was travel time from the nearest city, serving as an index of a site innacesibility to people (Licona et al. 2011) Tobler 2002 found that <i>Tapirus bairdii</i> occurred in areas of dense vegetation and rarely used open habitats in the Cordillera de Talamanca, southern Costa Rica	Cove et al. 2013	Habitat use	Costa Rica
	Fruit constitutes 1.4-18.6% of <i>Tapirus bairdii</i> diet camera sites were selected at least 2Km apart to ensure independece among forest sites 500m is an insignificant travel distance for <i>Tapirus bairdii</i> Sites within and adjacent to the Maquenque National Wildlife Refuge and Braulio Carrillo National Park had a stron postivi relationship with tapir occurrence Habitat suitability of Maquenque NWR because of forest cover and limit human density	Cove et al. 2013	Natural history	Costa Rica
	Tapirs are usually left alone in hunting and poaching activities <i>Tapirus bairdii</i> uses waterholes and waterbodies to regulate temperature Reported home range of <i>Tapirus bairdii</i> 1.3sqKm (+/- 0.73km ²) with a maximun range of 2.3sqKm during the wet season tapirs share 26% of their annual home range, whereas overlap in the dry season is usually null	Cove et al. 2013	Habitat use	Costa Rica
	Jaguars mean daily travelled distance was 2.24km with a maximal daily distance travelled of 10km based on radio collar data Tobler reported lowland tapir (<i>Tapirus terrestris</i>) individuals moving up to 13Km overa 24 hr period (GPS Radio collared data), with a mean movement distance in a 24hr period of 5.2Km (range 3.6 - 6.7kmm)	Farril et al. 2013	Natural history	Mexico
	Hurtado et al found that white lipped peccaries require visits to water bodies on an almost daily basis in our study region, performing search patterns at two spatial scales: they search one area intensively by moving no more tha 3km every day and occasionally perform long displacements (9 to >16KM) Animals dung near samll and large waterholes and are found at lower densitiens when waterholes are dry, suggesting that animals use waterholes mainly for water	Farril et al. 2013	Habitat use	Peru
				Mexico
				Mexico

<i>Odocoileus virginianus</i>	Animals dung near small and large waterholes and are found at lower densities when waterholes are dry, suggesting that animals use waterholes mainly for water	Farril et al. 2013	Habitat use	Mexico
<i>Tayasuu pecari</i>	Animals dung near small and large waterholes and are found at lower densities when waterholes are dry, suggesting that animals use waterholes mainly for water	Farril et al. 2013	Habitat use	Mexico
<i>Tayasuu pecari</i>	Species are in general unwilling to travel long distances in search for resources on a daily basis, thus their movement patterns will likely occur mostly within a small area surrounding a waterhole as has been observed for the white lipped peccary	Farril et al. 2013	Natural history	Mexico
<i>Tapirus bairdii</i>	Secondary forests most common used habitat type (61.3%)	Foerster and Vaughn	Habitat use	Costa Rica
<i>Tapirus bairdii</i>	Primary forests was used (0.25%)	Foerster and Vaughn	Habitat use	Costa Rica
<i>Tapirus bairdii</i>	Tapirus bairdii was classified as the tenth Neotropical forest mammal by Dobson and Jinping (1993) based on population density and distribution	Foerster and Vaughn	Population character	Central America
<i>Tapirus bairdii</i>	Ripe bananas were found to be the most effective bait for attracting tapirs to capture sites	Foerster and Vaughn	Natural history	Central America
<i>Tapirus bairdii</i>	Tapirs used the primary forest and airstrip/compound habitats more during the wet season compared to the dry season while secondary forest, beach, water, and coastal grassland habitat had higher usage ratios in the dry season.	Foerster and Vaughn	Habitat use	Costa Rica
<i>Tapirus bairdii</i>	Large animals such as tapirs (150-300 kg) have a difficult time dissipating excess body heat due to their low surface to volume ratio (Schmidt-Nielson 1990)	Foerster and Vaughn	Natural history	Costa Rica
<i>Tapirus bairdii</i>	Study-long 95 percent MHR ranges averaged 125.0 ha (SD 57.7) for all tapirs combined in la sirena	Foerster and Vaughn	Natural history	Costa Rica
<i>Tapirus bairdii</i>	All tapirs shared a 32.5 ha area of overlap between study-long home ranges representing 19-37% of home ranges in dry season	Foerster and Vaughn	Natural history	Costa Rica
<i>Tapirus bairdii</i>	All tapirs shared a 25.9 ha area of overlap between study-long home ranges representing 21-36.9% of home ranges in wet season	Foerster and Vaughn	Natural history	Costa Rica
<i>Tapirus bairdii</i>	Four of the five tapirs utilized the secondary forest habitat more during the dry season than the wet. All tapirs used the secondary forest habitat in proportion to its availability during the wet season, the Sirena area appear to provide an excellent balance of diversity to the resident tapir population, resulting in smaller home ranges	Foerster and Vaughn	Habitat use	Costa Rica
<i>Tapirus bairdii</i>		Foerster and Vaughn	Habitat use	Costa Rica

Tapirus bairdii	Naranjo (1995a) determined that <i>T. bairdii</i> in CNP preferred lowland secondary forests and avoided primary forests. Baird's tapirs in Belize prefer secondary forests and floodplains (Fragoso 1990)	Foerster and Vaugh Habitat use	Costa Rica
Tapirus bairdii	Williams (1984) found most nocturnal activity of two Baird's tapirs in Santa Rosa National Park, Costa Rica, centered in lowland riparian forest and regenerating riparian forest.	Foerster and Vaugh Habitat use	Costa Rica
Tapirus bairdii	<i>Tapirus terrestris</i> in Venezuela was found to forage preferentially in lower elevation gaps, keying in on higher biomass of palatable plant species and abundance of certain plants (Salas & Fuller 1996). In this study, secondary forest was the most utilized habitat during both seasons. We concur with other researchers in that tapirs forage more in secondary forests because it contains high densities of understory plants.	Foerster and Vaugh Habitat use	Costa Rica
Tapirus terrestris		Foerster and Vaugh Habitat use	Venezuela
Tapirus bairdii	Tapirs are strict herbivores (browser/frugivore) and must obtain their forage between the forest floor and ca 1.5 m height.	Foerster and Vaugh Habitat use	Costa Rica
Tapirus bairdii	We believe the high percentage of secondary forest habitat in the area was a major factor in allowing the study animals to maintain such small home ranges. Based on this assumption, we would expect home range sizes for tapirs in the Sirena area to increase as the regeneration process modifies available habitat.	Foerster and Vaugh Habitat use	Costa Rica
Tapirus bairdii	water plays only a minor role in nocturnal habitat selection. The study animals rarely foraged or rested along creek sides, although streambeds were often utilized for easy travel between feeding sites and for defecation.	Foerster and Vaugh Habitat use	Costa Rica
Tapirus bairdii	In the wet season, however, tapirs seldom slept in water, although they were usually less than 20 m from a creek or river.	Foerster and Vaugh Habitat use	Costa Rica
Tapirus bairdii	Dry season diurnal resting sites were almost exclusively in wallowing holes associated with freshwater sources.	Foerster and Vaugh Habitat use	Costa Rica

	<p>Tapirs were seen eating fallen fruits during the majority of our direct observations in primary forest, particularly <i>Licania platypus</i> (Chrysobalanaceae). In following radio-tagged tapirs in these forest patches, they appeared to travel directly from one <i>L. platypus</i> to another, circling the bases of the trees in search of fruit while essentially ignoring the remaining vegetation. In a similar manner, Bodmer (1990) reported that <i>T. terrestris</i> encountered fruits more frequently when ranging in <i>Mauritia flexuosa</i> palm forests than in non-palm forests because they changed their searching behavior.</p>	Foerster and Vaugh Natural history	Costa Rica
Tapirus bairdii	<p>Naranjo (1995b) also found a disproportionately heavy use of monotypic stands of <i>Raphia taedigera</i> (Palmae) by <i>T. bairdii</i> in CNP, Costa Rica. A mixture of primary and secondary forest appears to suit tapirs very well</p>	Foerster and Vaugh Natural history	South America
Tapirus bairdii	<p>All animals had several hundred ticks on and around the aural, inguinal, axillary and perineal regions year round, being highest during December - May, the dryest season in La Sirena. Ticks were either <i>Amblyomma oblongoguttatum</i> or <i>Amblyomma coelebs</i>. <i>Amblyomma coelebs</i> is most frequently found on lowland tapirs (<i>Tapirus terrestris</i>)</p>	Foerster and Vaugh Habitat use	Costa Rica
Tapirus bairdii	<p><i>Amblyomma coelebs</i> This tick has also been described on Baird's tapirs and horses in Panama. 7,28 <i>Amblyomma oblongoguttatum</i> has been reported on birds and at least 21 species of mammals, including Baird's tapirs, and a variety of rainforest mammals in Venezuela</p>	Hernandes-divers et Natural history	Costa Rica
Tapirus bairdii	<p>In Costa Rica, the largest remaining populations of tapirs are in Corcovado/Osa, Guanacaste/Santa Rosa, Arenal, the Cordillera Volcanica Central, the Llanuras de Tortuguero, and in the Cordillera de Talamanca/La Amistad (Matola et al. 1997).</p>	Hernandes-divers et Natural history	Venezuela
Tapirus bairdii		Tobler et al 2002	Population distribution Costa Rica

	The forests of the Talamanca mountain range are not only the largest continuous forested area in Costa Rica but also play an important role as biological corridors for tapirs and other large mammals. This is because they connect tropical rain forests of the lowlands with montane forests, as well as connecting the Atlantic and Pacific sides of the country. . The height and cover of the herb layer did not seem to influence the choice	Tobler et al 2002	Population distribution	Costa Rica
Tapirus bairdii	of a browsing site. Although tapirs have been reported to preferentially defecate in water (Terwilliger 1978, Naranjo 1995b; cf. Acosta et al. 1996), four of the five defecation sites discovered in this study were located on land (two of them less than 50 m from a small river	Tobler et al 2002	Natural history	Costa Rica
Tapirus bairdii	in this study, trails were found almost exclusively in places with dense vegetation and were scarce in more open areas. Foraging and sleeping places were only used a few times. Tracks were rarely found twice at the same place. Areas with gentle slope were preferred for browsing but virtually all available slopes were used to some degree	Tobler et al 2002	Natural history	Costa Rica
Tapirus bairdii	Although fruits were found to be an important part of the tapir diet in the lowlands (Terwilliger 1978, Williams 1984, Bodmer 1991, Naranjo 1995b, Foerster 1998), they seem to be of little importance in this study area. This can be explained by the low availability and small size of the fruits in montane cloud forests at this elevation. Therefore, tapirs in this study area do not seem to have an important role	Tobler et al 2002	Population characteristics	Costa Rica
Tapirus bairdii	as seed dispersers as suggested by Olmos (1997) for the lowlands. La danta es aficionada de las semillas de Óyolillo, las cuales se traga entera. Sus heces, parecidas a las del caballo, permiten identificar sus sitios de alimentación con facilidad	Tobler et al 2002 Chassot et al. 2005	Natural history	Costa Rica

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