UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN GEOGRAFÍA

CENTRO DE INVESTIGACIONES EN GEOGRAFÍA AMBIENTAL

INTEGRACIÓN DE MODELOS DE CONECTIVIDAD DEL PAISAJE PARA LA CONSERVACIÓN DE LA BIODIVERSIDAD EN EL SISTEMA VOLCÁNICO TRANSVERSAL DE MICHOACÁN, MÉXICO

TESIS
QUE PARA OPTAR POR EL GRADO DE:
DOCTOR EN GEOGRAFÍA

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PONTIFICIA UNIVERSIDAD JAVERIANA DE BOGOTÁ

MÉXICO, D. F. AGOSTO 2016

Cami, mi adorada esposa, mi mejor amiga, mi compañera de vida, te dedico con todo mi amor este logro. Han sido muchos etapas que hemos pasado juntos, ésta ya se está terminando para darle paso a muchas más; recuerdo que hace cuatro años te escribía en la dedicatoria de la tesis de maestría "espero que toda la vida cosechemos juntos muchos más logros y podamos seguir cumpliendo nuestros sueños, para mí no hay alegría más grande que estar siempre a tu lado". Ahora me llena de felicidad y de orgullo saber que todo eso se ha cumplido, hemos cosechado más logros, seguimos cumpliendo nuestros sueños y nos hemos mantenido juntos con el apoyo mutuo y la alegría que nos caracteriza. No dudo que esto permanecerá a lo largo de nuestra vida. TE AMO

AGRADECIMIENTOS

Esta tesis hace parte del proyecto titulado “Evaluación de la importancia relativa del bosque húmedo de niebla bajo un enfoque de paisaje (clave 179386). Agradezco la beca otorgada por la Comisión Nacional de Ciencia y Tecnología- CONACYT (beca 256412) para realizar los estudios de posgrado. En general agradezco a la Universidad Nacional Autónoma de México y en especial al Centro de Investigaciones en Geografía Ambiental (CIGA) por permitirme hacer parte del programa de Doctorado en Geografía.

Un agradecimiento especial al tutor de este trabajo Dr. Manuel E. Mendoza Cantú, por su constante apoyo en el desarrollo de la investigación y al Dr. Diego Pérez Salicrup del IIES-UNAM por los enriquecedores comentarios e interés a lo largo del doctorado. Quiero dar un profundo agradecimiento al Dr. Andrés Etter Rothlisberger de la Facultad de Estudios Ambientales y Rurales de la Pontificia Universidad Javeriana de Bogotá porque de nuevo hizo parte de mi crecimiento académico y profesional y sobre todo por los acertados comentarios al trabajo, en especial sus aportes en la preparación de los artículos derivados de la tesis.

Al Dr. Víctor Sánchez Cordero del Instituto de Biología de la UNAM por brindarme su tiempo para conocer mi investigación y por aceptar ser parte del sínodo de este trabajo. Al Dr. Eduardo Mendoza del INIRENA-UMSNH por invitarme a compartir los conocimientos adquiridos en esta tesis con sus estudiantes y también por ser parte del sínodo.

Al cuerpo docente del CIGA en especial al Dr Jean Francois Mas por su amistad, por asesorarme en el modelamiento espacial y por darme la oportunidad para compartir en su clase el tema de conectividad y fragmentación del paisaje. A la Dra. Isabel Ramírez

porque siempre estuvo pendiente de mis avances y por valorar el esfuerzo de mi trabajo desde mi tesis de maestría. Al Dr. Adrian Ghilardi porque siempre quiso estar al tanto del desarrollo de la tesis y por su buena disposición para apoyarme. Por supuesto al Dr. Pedro Urquijo por brindarme su amistad desde que entré a ser estudiante del CIGA y por encontrar años después mi premio refundido.

A todos mis amigos del CIGA por los momentos inolvidables en mis visitas relámpago a Morelia, en especial a Yuri, Brian e Iván por los buenos mezcales. Al grupo GEOS por todo tipo de mensajes. Agradezco a Abe por su amistad y porque siempre me brindó su casa. Un agradecimiento especial a mi colega Nico Vargas por su amistad, apoyo y generosidad. Siempre me abrió las puertas de su casa y me tendió la mano con trámites y estadía en Morelia. Igualmente a Gemma por brindarme su amistad y las charlas sobre nuestros gatos.

A mis amigos en Colombia y en el DF por todos los buenos momentos que hemos compartido. A Vane y Dago por ser excelentes amigos desde que llegamos a México, Sebastián por apoyarnos tanto en los momentos difíciles, Nata y Alex por estar siempre pendientes de nosotros. Un agradecimiento especial a nuestra querida amiga Cami Quintero que nos abrió las puertas de su casa e hizo parte de un viaje inolvidable y certero para finalizar este proceso. A Beth por la amistad incondicional y por siempre estar dispuesta a ayudarnos.

Finalmente quiero dar un profundo agradecimiento a mi familia en Colombia la cual extraño inmensamente. A Elizabeth mi madre, a mi padre Hernando y a mis cinco hermanos (Chabi, Maito, Kiss, Soni y Rocy) y a todos mis adorados sobrinos. Un especial agradecimiento a mis suegros Ruth y Fernando por toda la ayuda y amor que nos han brindado, gracias por hacerme sentir como otro hijo más y por quererme tanto.

A mi esposa Camila con la que he compartido trece años de mi vida, termino esta tesis gracias a ti, te adoro con todo mi corazón, eres como ya te había escrito la chispa de mi vida, gracias por llenarme de ilusiones y por tus enseñanzas, definitivamente mantienes mi corazón en forma. A nuestra hija Tita por su compañía y ternura, y a nuestro hijo Balam por llegar a nuestro hogar y aumentar su felicidad. Los dos son un ejemplo de amor incondicional y fidelidad.

TABLA DE CONTENIDO

RESUMEN

El estudio de la conectividad del paisaje es importante en la identificación de prioridades para la conservación de la biodiversidad y para la correcta toma de decisiones en cuanto al manejo del paisaje. En esta tesis se presenta la aplicación de un conjunto de modelos de conectividad para identificar áreas importantes para conservar la movilidad de los organismos a través del paisaje. Primero se lleva a cabo una revisión de los estudios recientes de conectividad en la conservación de la biodiversidad, se discuten los principales avances en el conocimiento y se presenta un marco teórico-conceptual para la posterior aplicación de los modelos. Luego se utiliza un modelo de conectividad basado en grafos y se aplica a un tipo de vegetación (bosque de niebla) en particular apoyado en su distribución potencial, para analizar las diferentes formas en que dichos bosques aportan a la conectividad del paisaje. A continuación se propone un índice de huella espacial humana ajustado para evaluar el impacto humano sobre la conectividad en el nivel de especies individuales y de múltiples especies, se presentan las diferencias espaciales del impacto antrópico sobre la conectividad del hábitat de tres grupos de especies de mamíferos terrestres con distribuciones y requerimientos ecológicos diferentes. Por último, se aplica un modelo híbrido en el cual se combina la teoría de circuitos con el enfoque de priorización espacial de la conservación para identificar las mejores áreas para la conservación de la conectividad multi-especie. Los resultados obtenidos en este trabajo son útiles para orientar las discusiones e implementación de iniciativas de conservación de la biodiversidad y el enfoque es aplicable en diferentes escalas y paisajes. Así mismo, la priorización de áreas para la conservación que tienen en cuenta los elementos del paisaje externos a los parches de hábitat es útil en la planificación del uso del suelo y puede ser clave como estrategia de adaptación al cambio climático.

Palabras clave: Planificación de la conservación, conectividad del hábitat, teoría de circuitos, teoría de grafos, priorización espacial de la conservación, corredores, México.

ABSTRACT

The study of landscape connectivity is important in identifying priorities for biodiversity conservation and for proper decision-making about landscape management. In this thesis, I presented the application of a set of connectivity models to identify important areas to maintain mobility of organisms through the landscape. First, I presented a review of recent studies of connectivity in biodiversity conservation. Major advances in understanding of connectivity was discussed. I discussed a theoretical-conceptual framework for subsequent application of the connectivity models. Then, I used a graph-based connectivity model applied to a particular type of vegetation (mountain cloud forest), supported by its potential distribution to analyze the different ways in which it forests can provide landscape connectivity. Subsequently I proposed a spatial human footprint index adjusted to assess the human impact on single species and multi-species connectivity. I presented spatial differences of anthropogenic impacts on habitat connectivity of three groups of terrestrial mammal with different distributions and ecological requirements. Finally, I applied a hybrid model in which circuit theory approach with spatial prioritization of conservation was combined to identify best areas for conservation of multi-species connectivity. The results obtained in this study are useful to guide discussions and implementation of initiatives for biodiversity conservation and the approach is applicable on different scales and landscapes. Likewise, prioritization of conservation areas that take into account the landscape elements external to habitat patches is useful in land use planning and can be essential as an adaptation strategy to climate change.

Key words: conservation planning, habitat connectivity, circuit theory, graph theory, Spatial conservation prioritization, wildlife corridors, Mexico

INTRODUCCIÓN

La definición más habitual de conectividad del paisaje es: "el grado en el cual el paisaje facilita o impide el movimiento a través de los parches de recursos " (Taylor et al., 1993). En este sentido, son los elementos del paisaje y su configuración los que determinen la capacidad de los organismos para acceder a los parches que ofrecen cierta aptitud de hábitat. De ello se deriva la importancia de crear modelos que identifiquen los aportes de dichos elementos para proveer conectividad y de esta forma priorizarlos para su conservación.

La conservación de la conectividad del paisaje es indispensable para asegurar la permanencia de la biodiversidad debido a que facilita la dispersión de los organismos a través del paisaje, el flujo genético y la recolonización de hábitats marginales, entre otros procesos ecológicos (Kool et al., 2013). Así mismo, la capacidad de los ecosistemas para proveer los servicios ambientales depende de la disponibilidad y la calidad del hábitat que aportan los fragmentos remanentes, su grado de conectividad, y la forma en que los afectan otras perturbaciones causadas por el hombre, como el cambio climático y las especies invasoras (Haddad et al. 2015).

Por lo tanto la conectividad es un requisito ecológico necesario en la planificación de la conservación (Moilanen et al., 2005; Early, 2007) y en las prácticas adecuadas de conservación y manejo del paisaje (Laita et al., 2011; Rayfield et al. 2015). Sin embargo, es imprescindible saber cómo medirla antes de integrarla en los protocolos de conservación (Saura et al., 2011). Así mismo, las actividades humanas en el paisaje han influido sobre la conectividad del hábitat de las especies individuales en diferente grado (Baldwin et al., 2010; Alagador et al., 2012; Theobald et al., 2012). Es necesario medir dicho efecto incorporando variables de fragmentación y pérdida de hábitat para derivar estrategias que ayuden a mantener poblaciones viables de múltiples especies, extendiendo su análisis no solo a los parches de hábitat sino a través de la matriz del paisaje (Rayfield et al. 2015). En este sentido, la presente tesis analiza como los modelos de conectividad del paisaje y otros modelos espacialmente explícitos pueden ser integrados para identificar los elementos del paisaje que compensen las necesidades de conservación de la conectividad y así mismo buscar alternativas que fomenten o mantengan la movilidad de los organismos.

El Sistema Volcánico Transversal de Michoacán (SVT_{Mich}) es idónea como área de estudio porque es un paisaje altamente biodiverso con una riqueza promedio de 105 especies de mamíferos terrestres (Escalante et al., 2007) y contiene importantes áreas protegidas que necesitan tener continuidad (Fuller et al., 2006). Así mismo las actividades humanas han configurado un paisaje en su mayoría dominado por coberturas antrópicas pero con parches de hábitat remanente con alta aptitud de hábitat y una densa red de carreteras que ha limitado potencialmente la movilidad de las especies (Correa et al. 2014).

Objetivo general:

Evaluar la conectividad del paisaje integrando para la priorización de áreas para la conservación de la biodiversidad en el Sistema volcánico Transversal de Michoacán, México

Objetivos específicos:

- Aplicar modelos de conectividad del paisaje integrados con otros enfoques espacialmente explicitos para priorizar áreas para la conservación de la conectividad.

- Analizar la conectividad de los bosques húmedos de montaña en el área de estudio para identificar áreas prioritarias de conservación, tomando como referente su distribución potencial y su relación con otros ecosistemas montanos.

- Evaluar el efecto de la huella humana sobre la conectividad del hábitat en el $\mathrm{SVT}_{\mathrm{Mich}}$ en escenarios multi-especie con diferentes distribuciones y requerimientos espaciales.

- Identificar los sectores de la matriz del paisaje que son más importantes para permitir la movilidad de múltiples especies a través de los parches de hábitat

- Identificar otras alternativas de conectividad por medio de corredores potenciales y priorizarlos con base en su capacidad para facilitar flujos de dispersión y el aporte de los parches que conectan a la conectividad general en el área de estudio

Estructura de la tesis:

La presente tesis está estructurada en 4 capítulos (Figura 1). Cada capítulo corresponde a un artículo científico publicado o en revisión. El diseño, el análisis y la escritura de los manuscritos fue parte de mi labor como estudiante de doctorado. El tutor y los miembros del comité tutorial asesoraron todo el proceso de investigación y son coautores de los artículos.

En el **capítulo 1** se hace una revisión detallada de la literatura reciente sobre el estudio de la conectividad en la conservación de la biodiversidad y se presenta una aproximación teórica y conceptual sobre los objetivos, tendencias y futuros desafíos de investigación en términos de conservación y conectividad. Este capítulo es una introducción para los siguientes porque describe y contextualiza los métodos actuales más utilizados en el análisis de la conectividad haciendo énfasis en la priorización de áreas para la conservación. En el **capítulo 2** se presenta una aplicación mixta que integra modelos de distribución potencial basados en nicho ecológico y modelos de conectividad basados en grafos. Se modelaron las áreas de hábitat óptimo para el desarrollo del Bosque Húmedo de Montaña (BHM) en el Sistema Volcánico Transversal de Michoacán (SVT_{Mich}), y se analizó el rol de las superficies identificadas de este tipo de vegetación para la conectividad del paisaje. Se muestra la importancia potencial del BHM para proveer conectividad estructural y funcional del paisaje y su articulación en la priorización de áreas para la conservación. En el **capítulo 3** se reporta una nueva forma de evaluar el impacto humano sobre la conectividad del paisaje. En el documento se explica cómo la huella espacial humana acumulada afecta la conectividad del hábitat de múltiples especies. Se presenta también la utilidad de la aplicación en la identificación de subrogados para los protocolos de conservación. Como anexo de este capítulo se presenta un artículo donde se describe la construcción de un modelo espacial del tiempo de intervención humana sobre el paisaje, el cual es un componente integral del índice de huella espacial humana aplicado en esta investigación. En el **capítulo 4** se utiliza gran parte de los datos de conectividad obtenidos en el capítulo 3 para identificar sitios prioritarios para la conservación de la conectividad. Se aplicó un modelo híbrido entre modelos de flujos de dispersión basados en teoría de circuitos y un enfoque de priorización espacial de la conservación. Los resultados obtenidos en este capítulo son un insumo útil que puede orientar futuras acciones de conservación en el SVT_{Mich}.

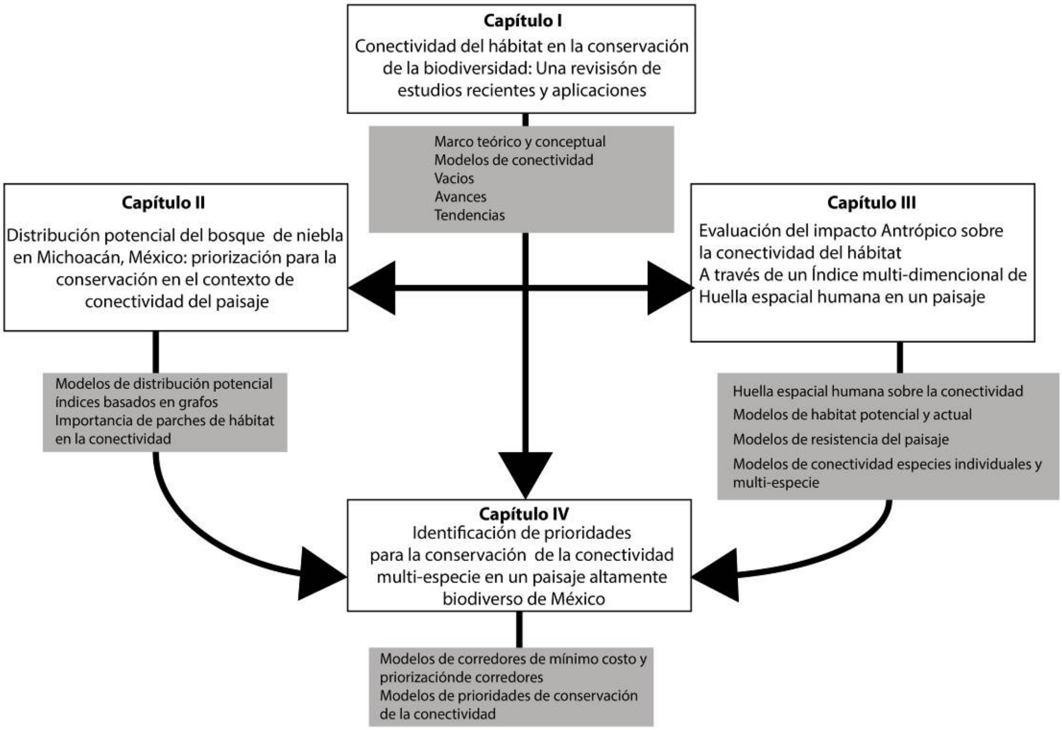

Figura 1. Diagrama de Interacción entre los capítulos de la tesis. Recuadros en gris corresponden a los principales productos obtenidos en cada capítulo.

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CAPITULO I

LA CONECTIVIDAD DEL HÁBITAT EN LA CONSERVACIÓN DE LA BIODIVERSIDAD: UNA REVISIÓN DE ESTUDIOS RECIENTES Y APLICACIONES

HABITAT CONNECTIVITY IN BIODIVERSITY CONSERVATION: A REVIEW OF RECENT STUDIES AND APPLICATIONS

Artículo publicado en *Progress in Physical Geography*
Correa Ayram CA, Mendoza ME, Etter A, Salicrup DRP (2016) Habitat connectivity in biodiversity conservation: A review of recent studies and applications. Progress in Physical Geography 40(1):7-37. doi: 10.1177/0309133315598713
Reseña del artículo en: http://conservationcorridor.org/2016/03/review-a-decade-of-research-on-connectivity-for-biodiversity-conservation/

Article

Progress in Physical Geography
2016, Vol. 40(1) 7–37
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DOI: 10.1177/0309133315598713
ppg.sagepub.com
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Habitat connectivity in biodiversity conservation: A review of recent studies and applications

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Abstract

The study of landscape connectivity in conservation has increased considerably since the early part of the 21st century. While the implications of landscape connectivity are self-evident for conservation, they are also important for physical geography since a proper understanding of landscape patterns and processes allows for better landscape management practices, which are at the core of geography. This paper presents a review of the literature based on 162 publications from 2000 to 2013, in which we evaluated the current state and recent advances in the integration of landscape connectivity in the identification and planning of conservation areas. The literature review and data analysis were based on a database organized into five categories: General information, study areas, research objectives, research methods in connectivity studies, and integration of connectivity with conservation. We found a substantial increase in the number of publications relating to connectivity and conservation from 2008 to 2013. Least cost analysis was the method most commonly applied. We found no implementation of landscape connectivity proposals generated by the studies (e.g. potential corridors) into real landscape elements to ensure the permanence and functionality of ecosystems. We identified four important niches for potential future research projects: a) connectivity and climate change, b) contribution of connectivity studies to restoration planning, c) connectivity and land cover/land use change modeling and planning, d) contribution of connectivity analysis in the provision of ecosystem services across landscapes.

Keywords
connectivity, biodiversity, conservation planning, corridors, prioritization

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I Introduction

The integrity and functionality of ecosystems and the maintenance of biodiversity and ecosystem services are made possible by the flow of organisms, materials, energy, and information across landscapes (Crooks and Sanjayan, 2006). Because of the importance of these flows in the maintenance of landscapes and biodiversity conservation, the concept and study of landscape connectivity has emerged and steadily grown.

The physical landscape is a key factor determining the spatial structure and arrangement of landscape elements, and on how humans use the land and change the way those elements relate to one another (Forman, 1995; Zonneveld 1995). The physical geography of a landscape is a fundamental input to address and understand how connectivity links the spatial and functional structure of a geographical area, shaping ecological processes and their connectivity, and therefore for the planning of appropriate spatial structures to ensure continuity. Connectivity is a key factor in indicating the ecological effects of environmental change. For example, protected areas cannot meet their conservation goals if they do not have functional linkages between them that allow ecological processes like gene flow, migration, re-colonization of areas with threatened populations, and, most importantly, the possibility by individuals and populations to adapt to climate change (Rudnick et al., 2012). Structural and functional isolation of areas with high conservation value severely limits the capacity of the system to maintain ecological processes (Rudnick et al., 2012). Improving functionality of at-risk conservation areas (or any conservation area for that matter) will depend a great deal on its connectivity to other areas. Because of this, connectivity studies focus on landscape elements and probable dispersal routes, which are intrinsic in prioritizing conservation areas (key terms used throughout this review are defined in Table 1).

The definition of landscape connectivity includes two fundamental concepts: a) structural connectivity, corresponding to spatial relationships (continuity and adjacency) between the structural elements of the landscape (e.g. Forest patches), which is independent on the ecological characteristics of the species (Taylor et al., 2006; Tischendorf and Fahrig, 2000), and b) functional connectivity, which refers to landscape features that facilitate or impede the movement of species between habitat patches (Taylor, 1993; Taylor et al., 2006). Consequently, the ability of species to move or disperse through the landscape is integrated with structural features of the landscape (Adriaensen et al., 2003). Connectivity is mainly applied in the context of terrestrial landscapes (Landscape connectivity) to "the extent to which landscape facilitates or impedes movement among resource patches" (Taylor et al., 1993). However, based on the same premise it can also be applied to other environments such as seascapes (Seascape connectivity) (Caldwell and Gergel, 2013; Grober-Dunsmore et al., 2009; Mumby, 2006), fluvial landscapes (Riverscape connectivity) (Fausch et al., 2002;Wiens, 2002), as well as in different processes like gene flow (Genetic connectivity) (Clinton et al., 2007; Cushman et al., 2006; McRae and Beier, 2007) or dispersal across discreet populations (Population connectivity) (Crooks and Sanjayan, 2006; Lowe and Allendorf, 2010).

A related term is Habitat connectivity, which refers to the degree of functional connectivity (Taylor et al., 2006) between patches of optimal habitat for individual species (Lindenmayer and Fischer, 2006). It is assumed that landscape elements (terrestrial as well as marine or others) present different levels of habitat suitability, so that areas of high suitability comprise more optimal habitat patches. At the same time, however, they are also immersed in matrices of growing human influence that facilitate or impede mobility of species, depending on their characteristics. In order to refer consistently to

Table 1. Definition of key terms used throughout this review.

Terms	Definitions	Key references
Graph theory	Is a mathematical approach in which problems are solved using graphs. A graph is defined as a collection of points (nodes) connected by lines (edges). This theory has been applied in landscape ecology to analyze the connectivity through graphs. A graph representing a landscape composed of nodes (patches) connected by a line that can be expressed as the adjacency or linkages between patches (corridors).	Bunn et al. (2000); Urban and Keitt (2001); Minor and Urban (2008)
Circuit theory	The circuit theory is applied to generate measures of connectivity or isolation of habitat patches, and connecting elements to identify wildlife corridors and conservation planning. In circuit theory, a model graph is an electrical circuit to predict the movement and dispersal patterns across the landscape. Circuits are networks of nodes connected by electrical components that conduct current flows and are used for analyzing graphs. A basic measure of connectivity from circuit theory is the "resistance distance" defined as the effective resistance between a pair of nodes, similar to the concept of ecological effective distance but incorporating multiple pathways.	McRae (2006); McRae and Beier (2007); McRae et al. (2008)
Current flow	In circuit theory. The current flow is represented on a map as the spatial distribution of dispersal probability of a random walker (per cell) through all habitat patches.	McRae and Beier (2007); McRae et al. (2008)
Resistance surface	It describes the degree of difficulty (cost) of an organism to move through the landscape. High resistance values are assigned to elements that facilitate the movement of the target species, in contrast, high strength values for difficulties or barriers to the movement.	Singleton et al. (2002); Spear et al. (2010); Zeller et al. (2012)
Corridors	Landscape elements that provide physical links between habitat patches and facilitate the movement of organisms and process through an inhospitable matrix.	Forman (1995); Bennet (1998)
Least cost analysis	Approach used to identify the least cost path between a pair of habitat patches. Least cost analysis determines the path that follows the shorter and less costly distance between two points through a resistance surface.	Adriaensen et al. (2003)
Least cost path (LCP)	In a GIS context, the least-cost path (LCP) represents the "individual" path of least resistance between two points habitat patches.	Adriaensen et al. (2003); Pinto and Keitt (2009); Rayfield et al. (2010)
Least cost corridor (LCC)	Least cost corridors (LCC) are similar to LCP but identified the "accumulated" cost between two points and are normalized in a layer that combines the least cost values. LCC is expressed in a corridor that represents a gradient or threshold of the least "accumulated" cost paths.	Pinto and Keitt (2009); McRae and Kavanagh (2011);

(continued)

Table 1. (continued)

Terms	Definitions	Key references
Habitat suitability	Habitat suitability is defined as the probability that a species uses a particular habitat based on ideal conditions that the habitat provides. An area with high habitat suitability value provides a high probability that the species will survive.	Wang et al. (2008)
Habitat patches	Habitat patches are relatively homogeneous areas that differ from their surroundings and provide high habitat suitability for a particular species.	Forman (1995); Girvetz and Greco (2007)
Focal especies	In landscape ecological context, species that are used to define different spatial and compositional attributes that must be present in a landscape and their appropriate management requirements.	Lambeck (1997)

the particular connectivity without limiting it to terrestrial environments, we use the term Habitat connectivity.

The interaction and the parallel evolution of landscape ecology with physical geography allow the integration of topics that are related to the landscape's patterns and process (e.g. landscape structure and connectivity). Because of the increasing inclusion and application of habitat connectivity in landscape ecology and conservation planning during the last decade, a variety of connectivity study cases are now available. For example, in forest landscapes, Saura and Pascual-Hortal (2007) demonstrated the importance of habitat patches in maintaining the general connectivity of *Accipiter gentilis* in Cataluña. In seascapes, Anadon et al. (2011) evaluated the connectivity potential of a network of marine reserves. Hermoso et al. (2012a) applied a connectivity analysis in the identification of priority conservation areas in a riverscape using a longitudinal connectivity analysis with the intention of mitigating the impacts of the reserve design. Other cases have focused on identifying potential corridors between habitat patches for focal species (Beier et al., 2009; Cushman et al., 2009; Roever et al., 2013) or in cases of explicit action in systematic conservation planning (Gordon et al., 2009; Lehtomäki et al., 2009; Linke et al., 2012). Although those concepts, methods, and applications related to habitat connectivity are variable, there is no synthesis available to elucidate progress and advances in the field. Thus, it is useful to review the methods and research objectives in the literature to evaluate the current state of scientific production in habitat connectivity studies – particularly in the identification, prioritization and conservation planning to signal gaps and offer practical suggestions for future studies in this area.

In this article, we review current analytical approaches and the applications of the study of connectivity in biodiversity conservation. In particular, we identify and describe the methods that currently incorporate connectivity in habitat conservation planning. We identify the countries, regions, and institutions where connectivity associated research is being conducted. Additionally, we identify research tools, techniques, and emphases that are integrated into conservation planning.

II Methodology

The review was based on scientific literature using the following databases: ISI Web of Knowledge, Springer, ScienceDirect, EBSCO, and WILEY. The key words were selected so that the search would integrate connectivity studies with the prioritization and planning of conservation areas. The literature selected was limited to studies that suggest or propose explicit action in conservation by applying landscape connectivity as a tool to: a) identify priority conservation areas, b) select protected areas, c) identify potential corridors or corridor design, d) define networks of habitat patches, and e) select restoration or reforestation areas. These included not only terrestrial landscapes, but also seascapes (Pittman et al., 2011) and riverscapes (Fausch et al., 2002).

Only articles written between 2000 and 2013 were chosen with the intention of highlighting recent research trends from this time period as the baseline. The boolean search criteria included the following key words: (“landscape connectivity” OR “habitat connectivity “OR “functional connectivity” OR “wildlife corridors” OR “potential corridors” OR “graph theory “OR” circuit theory” OR “patch network” OR “matrix resistance “OR “landscape resistance” OR “modeling connectivity” OR “landscape permeability” OR “resistance distances “OR “least cost distances “OR” least cost path”) AND (“conservation planning” OR “protected areas” OR “landscape conservation” OR “conservation areas” OR “landscape-scale conservation planning” OR “prioritization of conservation areas “OR” protected area networks” OR “conservation networks”). The first list resulted in 2,092 articles. We limited the results obtained from ISI Web of Knowledge based on the following research areas: Environmental Sciences Ecology, Science Technology Other Topics, Agriculture, Biodiversity Conservation, Evolutionary Biology, Remote Sensing, Zoology, Geography, Entomology, Freshwater Marine Biology, Oceanography, Fisheries, Forestry, Biochemistry Molecular Biology, Reproductive Biology, Mathematical Computational Biology, Plant Sciences, Water Resources, and Genetics Heredity. In Springer we limited the results to: Life Sciences, Environmental Sciences, Earth Sciences and Geography, Genetics and Molecular Biology. Finally, in ScienceDirect we limited the results to: Agricultural and Biological Sciences, EBSCO, and WILEY as the original search. This reduced the results to 882 articles.

The resultant list was purged of studies that referred to computer programs, reviews, theoretical articles, description of landscape metrics, and duplicate studies. This filter was applied to obtain a manageable sample that included only practical studies, explicit methods, and direct applications of connectivity in biodiversity conservation. Therefore, the exclusion of papers about computer programs allowed us to filter out a large number of contributions that referred to specialized descriptions of tools to measure and model connectivity, but which did not include case studies (e.g. Landguth et al., 2012; Ray, 2005; Saura and Torné, 2009). However, recent trends in software use were evaluated in each of the papers selected for further evaluation. Theoretical articles and critical reviews were discarded in the analysis because we did not intend to discuss theoretical developments of the discipline, since these have been widely documented in other recently published reviews (e.g. Baguette et al., 2013; Kool et al., 2013; McRae et al., 2008; Minor and Urban, 2008; Mitchell et al., 2013; Rudnick et al., 2012). Nevertheless, the trends in the use of theoretical approaches that served as background in the selected manuscripts were analyzed. Articles about indices to measure connectivity were excluded (e.g. Kindlmann and Burel, 2008; Laita et al., 2011; Moilanen and Nieminen, 2002; Pascual-Hortal and Saura, 2006), because we only tried to study their application for each selected case and not in their descriptions per se. In total, 162 articles were selected for the analysis.

We completed the systematization and the analysis of the reviewed manuscripts by standardizing a database with information from each article divided into five categories: general information, study area, research objectives, connectivity methods, and connectivity in conservation planning. Each category was further divided (Table 2) into sections that answered the proposed research questions.

We are aware that our criteria of selection may have discarded articles that are generally related to connectivity conservation. However, search keywords and specification of applied case studies resulted in an evaluation of articles that have an explicit link between the approaches of connectivity and direct conservation actions. We did not expect to make a complete inventory of the articles on connectivity and conservation. Therefore, we carefully identified current analytical approaches, the methods used to analyze connectivity and its application into conservation planning in the set of articles we selected. Finally, as a result of our selection process, we obtained a relative proportion of papers whose contents were disaggregated into categories that we consider appropriate to answer our research questions (see Table 2). Hence, the results of our review may be affected by this set of articles and the categorization for evaluation. Thus, because the results are based on a set of articles, the review may provide a partial view of the field of study.

III Results

1 When and where is habitat connectivity pursued and applied to conservation?

Of the 162 papers analyzed, half were carried out in the last three years indicating an increase in application of connectivity analyses during this time. The number of case studies incremented yearly, particularly since 2008 (Figure 1). The reviewed articles were published in 45 scientific journals, 28% of which were published in *Biological Conservation* and 14% in *Landscape and Urban Planning*; other journals, such as *Landscape Ecology* (10%) and *Conservation Biology* (9%), also presented a relatively high number of publications. The large majority were conducted in Europe (68) and North America (60) – particularly in the US (55) and Spain (16) (Figure 2).

The scale most commonly used was regional (133 articles), which covers more than a municipality and can be as large as several States, followed by local (a city and/or municipality) with 14 studies, and then six transnational studies (more than one country but less than a continent). Only one study was conducted at the global level. No information was presented with regard to the extent of study area in 30% of the articles. The limits of the study areas were mostly defined by political boundaries (59%) and to a lesser extent by natural boundaries (41%). Geographic boundaries defined by mountain chains were the most common (19% of articles). The most representative political boundaries were the municipal and State boundaries (14% and 12%, respectively). Study areas were defined by limits of protected areas in 9% of the studies. Natural boundaries were also represented by watersheds (9% of articles) and valleys (6%). The extent of study areas was from 20,000 to 50,000 km^2 in 12% of studies, for areas of 1000 to 5000 km^2 in 10%, while very large areas of 100,000 to 500,000 km^2 were represented in 9% of the studies. The most frequent spatial resolution varied between 10 m and 50 m pixel value.

2 Study emphases

Terrestrial landscapes represented 88% of studies, fluvial 9%, marine 7%, and 2% in mixed environments (fluvial-terrestrial). According to the classification of terrestrial eco-regions (Olson et al., 2001), 13 biomes were represented in the sample (Figure 3). The most frequent were the temperate broadleaf and mixed forests (35%), temperate conifer forest (19%), and Mediterranean forests, woodlands and scrublands (17%).

With regard to family, genus, and species content, 83% of studies used focal species

Table 2. General description of the variables used in the individual evaluation of the article contents.* We used the classification and mapping of the biomes and eco-regions of the world la (Olson et al. 2001) based originally on 14 terrestrial biomes.

	Variable	Description
General information	When, Who	
	Author	Who wrote it?
	Year	When was it published?
	Title	What is the title?
	Journal	In what journal was it published?
	Volume	In what volume was it published?
	Number	In what issue was it published?
	Institution	What institution was responsible (First author)?
	Country	In what country was it done (First author)?
Study area	Where	
	Study scale	At what level was the study conducted (continental, transnational, national, regional, local)?
	Continent	On what continent was it conducted?
	Country	In what country was it done?
	Location	In what location was it done?
	LA	Was it done in Latin America?
	Area (Km^2)	How large was the area in Km^2?
	Pixel	What was the resolution used (m)?
Research objectives	What, Why	
	Environment	What was the type of environment where it was conducted (terrestrial, marine, fluvial)?
	Biome*	In what biome was it conducted (Olson et al. 2001)?
	EF?	Were focal species used?
	Tax group/CLASS	If focal species were utilized, what class?
	Tax group/ORDER	If focal species were utilized, what order?
	Tax group/FAMILY	If focal species were utilized, what family?
	Focal species	Which focal species were used?
	Type of information presented per spp	What type of information about the focal species was used?
	Conservation action/ proposal	What conservation objective was proposed?
Connectivity study methods	How	
	Analytic approaches	What foci in connectivity studies were used?
	Type of connectivity measure	How was connectivity measured?
	Expert opinion	Was expert opinion used?
	Use of OE	For what was expert opinion used?
	MAH/MCH	Presence of habitat suitability models Habitat or habitat quality
	Tools	What specific programs were used for connectivity studies?
	LCP/LCC/CF	Were least cost paths/corridors or current flows used?
	Description	Brief description of how connectivity was analyzed

(continued)

Table 2. (continued)

	Variable	Description
Connectivity/ conservation integrity	How	
	Specific threats	What type of threat to conservation was the study addressing?
	Management/ Mitigation/ Strategy	What strategy was used to mitigate or manage the threat?
	SAP/IAPC?	Was there explicit selection or identification of conservation areas? (yes, no)
	Criteria	What criteria were used in the selection or identification?
	What do they link?	Was there identification of potential corridors, what do they link?
	Role of pot. links	What was the proposed role of the corridors?
	AMC?	Was a multi-criteria analysis used for some aspect of conservation?
	Legal Asp.	Were legal aspects of the study taken into account?
	CP Tools	What specific conservation planning tools were used?
	Observations	General review of the tools used in planning/identification/ prioritizing

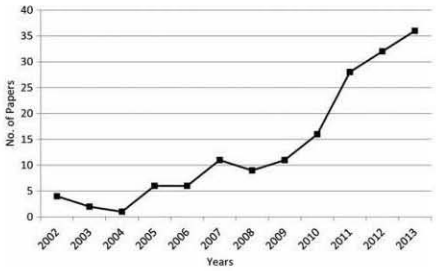

Figure 1. Number of articles published by year.

corresponding to 9 classes, 40 orders, 59 families and 131 species. The three most frequent classes were all vertebrates: Mammals (68 articles), Birds (37 articles), and Reptiles (13 articles). The most studied order was the Carnivores (45 articles). The most frequent family was the Felidae (23 articles), while the most studied species was the *Puma concolor* (seven articles) (Figure 4). Eight studies focused on hypothetical species, while 18 did not use focal species at all.

Biological data (occurrence, dispersal distances, current distribution, population size, and habitat preferences and requirements) for the focal species were obtained through the bibliography and secondary information in 32% of studies, 30% through field data collection, 8% were unspecified, and 30% did not use this kind of data. Sixty-seven articles reported the use of field methods to collect data of occurrence and movement of focal species. We identified 14 field methods to collect data on occurrence and movement of focal species, of which tracking telemetry was the most frequent (24%), followed by genetic data (DNA samples from feathers, manure, pellet, and blood) (15%), direct sightings (13%), and camera traps (3%) (Figure 5).

We identified 16 different conservation objectives, actions, or proposals (Figure 6). The most frequent included the identification and selection of important conservation areas (54 articles), followed by connectivity in corridor identification (44 articles), and finally the integration of connectivity within conservation planning (18 articles).

3 Connectivity study methods

The predominant analytic approach was functional connectivity (78%), followed by structural

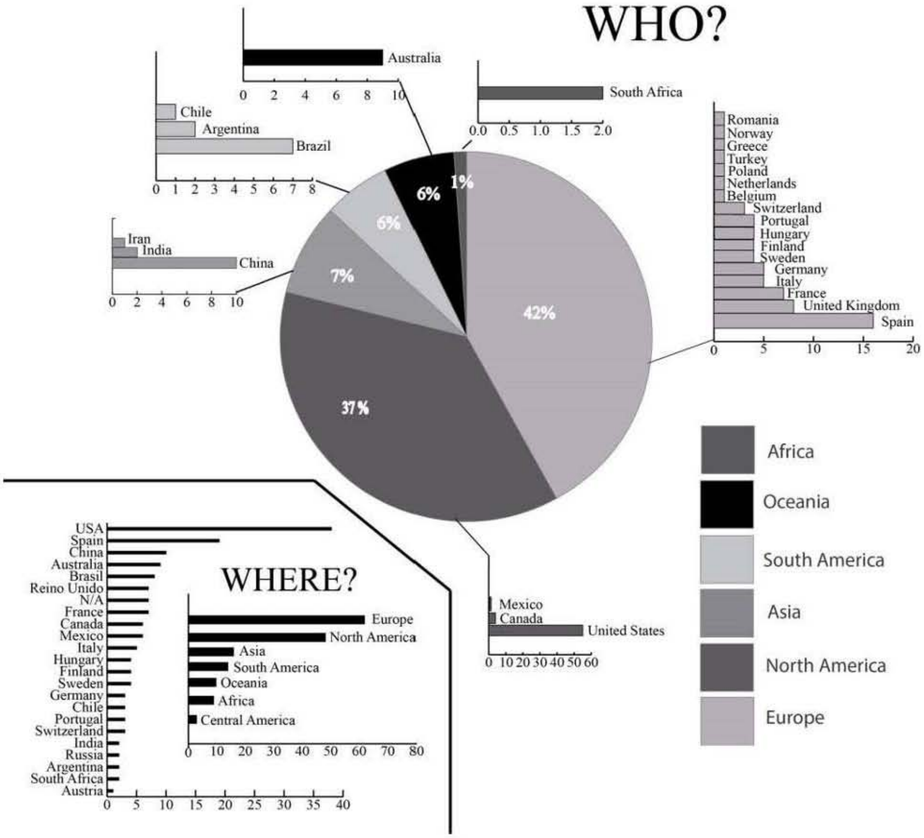

Figure 2. Where case studies were performed and by whom.

connectivity (9%), genetic connectivity (4%), riverscape connectivity (3%), and finally seascape connectivity (2%). We identified 23 methods to measure connectivity (Figure 7). The three most utilized were the least cost analysis (67 articles), graph theory (54 articles), and functional connectivity indexes (30 articles). In 34% of the studies (56 articles) expert opinion was used as input largely to evaluate the resistance of the matrix (23 of 56 articles) and to evaluate habitat suitability (12 of 56 articles) (see Figure 7).

Habitat suitability models were used in 44% of the articles we reviewed to estimate accumulated resistance to movement. Of the 162 analyzed studies, 130 utilized software tools to analyze connectivity and conservation priorities. Within this sample (n = 130), we found 44 different software tools. The majority (21%) used CONEFOR to calculate functional connectivity indexes based in graph theory (Saura and Torné, 2009). The "cost distance" tool in ArcGis (ESRI, California) was used in 15% of the articles to calculate least cost paths

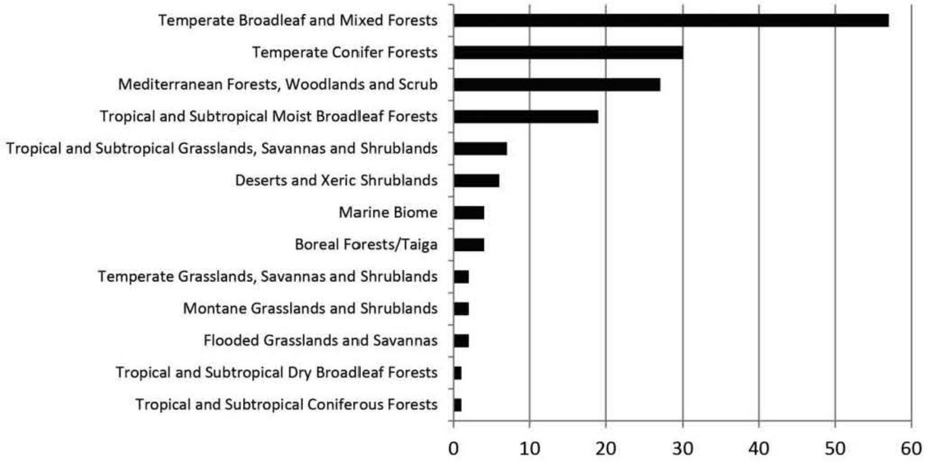

Figure 3. Number of articles and the biomes that were studied in them. Classification and mapping of the biomes and eco-regions of the world (Olson et al. 2001).

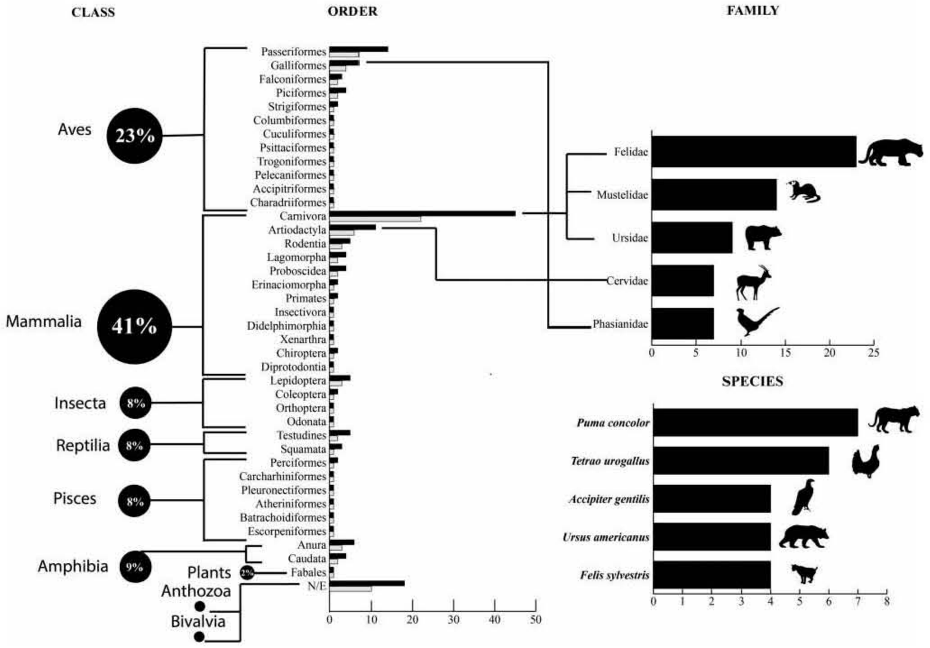

Figure 4. Taxonomic groups represented in the studies included in the review. N/E: No Order specified. “Order” in grey represents the percentage represented and in black the number of articles.

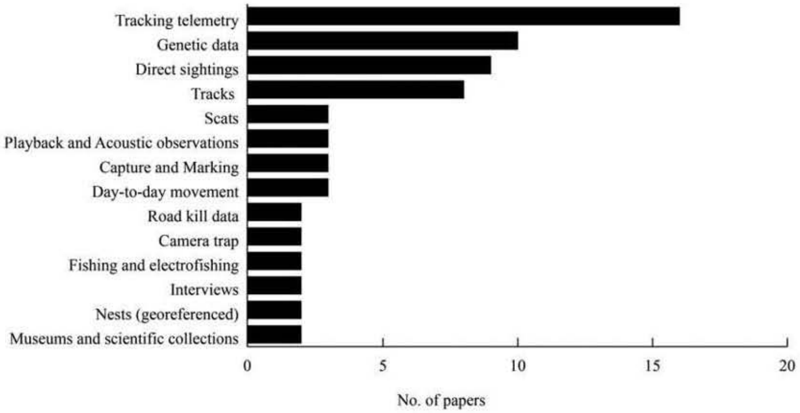

Figure 5. Field techniques used to collect data of occurrence and movement of focal species.

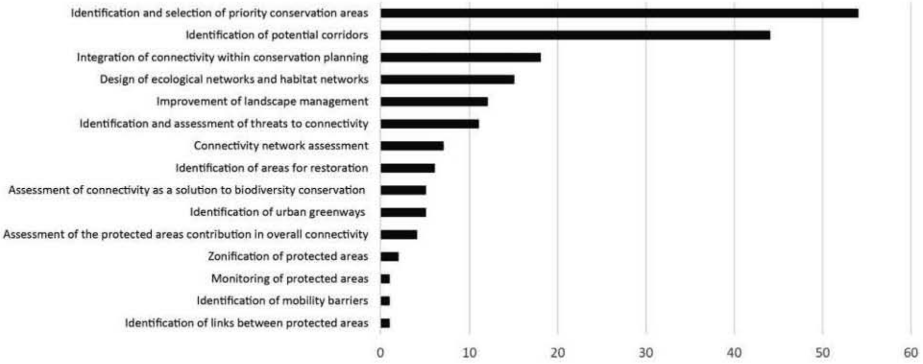

Figure 6. Objectives, actions, or proposals for conservation.

through habitat patches and 8% used FRAGSTATS (McGarigal et al., 2002) to calculate structural landscape indexes. Specialized conservation planning programs like MARXAN (Ball et al., 2009), ZONATION (Moilanen, 2007), and ConsNet (Ciarleglio et al., 2009) were present in lower percentages (see Figure 7, with an asterisk). We found four types of connectors in these programs: a) least cost paths (45), b) least cost corridors (19), c) current flows (9), and d) least cost maximum flow (1).

4 How to integrate connectivity studies with conservation goals?

The most common application in integrative, conservation goal-oriented connectivity studies was to devise strategies to manage or buffer specific threats to biodiversity, such as fragmentation (43% of the total articles), habitat loss (26%), and urban expansion (9%). Others discussed specific threats to focal species populations, such as poaching (4%) and deaths as a

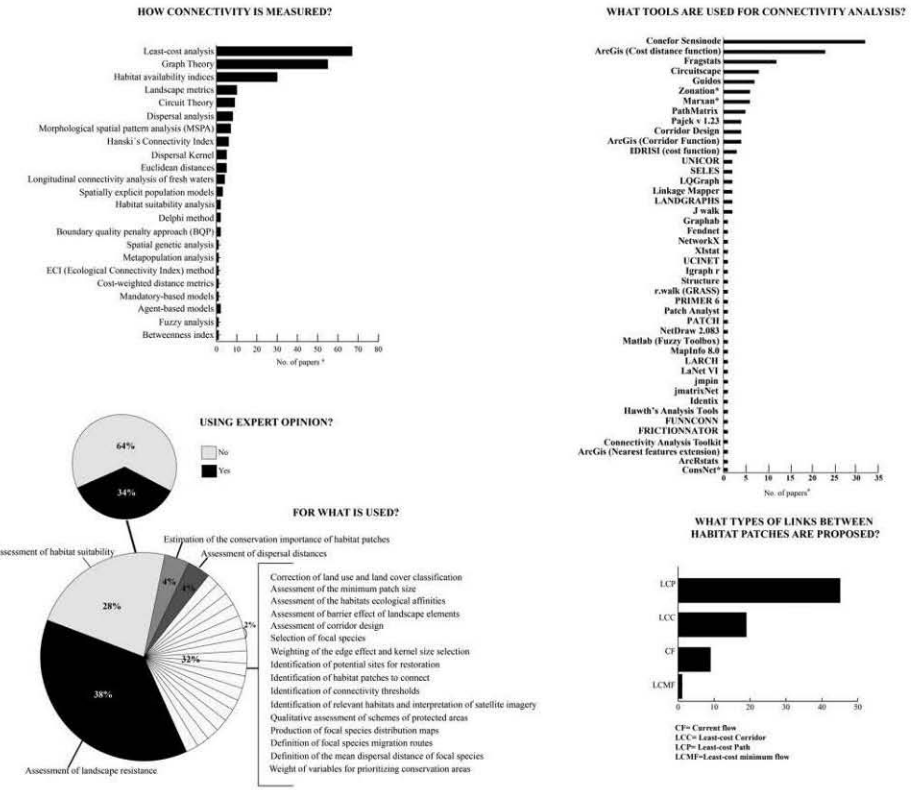

Figure 7. How connectivity was analyzed.

result of crossing highways (1.5%). The general strategies developed in these studies were principally based in the selection of networks that incorporate functional connectivity between priority sites with a high degree of irreplaceability. This highlights the importance given to identifying connection corridors between areas of high habitat suitability, identification of significant patches in the general maintenance of connective corridors, and the restoration of habitat networks that allow for the re-colonization and dispersal of focal species.

The majority of the articles (62%) addressed the selection or identification of protected areas integrating connectivity with conservation planning by using 60 selection criteria, of which dispersal distances for focal species (30 articles) and habitat availability (30 articles) were the most common. The third most represented criterion was connectivity (26 articles). The other notable criteria used in systematic conservation planning (Figure 8) were irreplaceability (9 articles) and representation (6 articles).

Nearly half of the articles (78 articles) explicitly raised the issue of identifying or proposing potential corridors. The most important role of potential corridors corresponded to connecting habitat patches to facilitate movement of focal species (45 articles). The proposed potential corridors looked to link habitat patches to facilitate re-colonization, increase migration, and genetic dispersal as well as promote the persistence of ecological processes at the landscape level.

IV Discussion

1 General trend in number of publications

The last decade showed a notable increase in the number of publications that incorporate habitat connectivity in conservation analyses, indicating that there is an expanding research interest in this topic. This increase is most apparent since 2008 (see Figure 1) and is largely related to the boom in new methodologies based on the application of indexes related to habitat availability that integrate conservation planning at a landscape scale (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007; Saura and Rubio, 2010); for example, the application of circuit theory in connectivity studies (McRae and Beier, 2007) and graph theory in the evaluation of connectivity and conservation planning (Minor and Urban, 2008). The application of methods focused on systematic and spatial planning in conservation have also contributed to the increase in publications of this research topic by the integrating habitat connectivity in reserve selection strategies (Early and Thomas, 2007; Lehtomäki et al., 2009; Moilanen, 2007). The increase in connectivity studies we observed, may also be related to concerns about habitat fragmentation and its impact on biodiversity (Leidner and Haddad, 2011; Parks et al, 2013; Severns et al, 2013; Vergara et al, 2010; Watts et al., 2010). There was also a significant increase in publications in 2013 related to climate change adaptation, indicating a growing interest in the different ways connectivity can support biodiversity resilience studies. Examples of this latter topic include studies identifying the suitability of functional linkages to address effects of climate change on habitat (Wasserman et al., 2013) and the evaluation of the effectiveness of protected areas to conserve biodiversity under different climate change scenarios (Mazaris et al., 2013).

We observed a marked preference for publishing in scientific journals specializing in ecology and urban planning (*Landscape Ecology*, *Landscape*, and *Urban Planning*) as well as in conservation sciences (*Biological Conservation* and *Conservation Biology*). These journals coincide with common objectives of publishing on advances in conservation and management at different scales.

2 Principal countries in scientific production and recent research trends

Connectivity and landscape fragmentation studies are currently considered within the top 10 key research topics in landscape ecology (Wu, 2013). In this sense connectivity as a tool is being studied thoroughly, mainly by North American and European scientists. The US is the country with the highest number of articles on the subject (45/162 sample articles) showing a greater dissemination capacity compared with other countries. This tendency is associated with the number of research contributions made by government organizations in the field of forest habitat conservation such as the USDA Forest Service Rocky Mountain Research Station with four contributions in this review. The research conducted by this organization focuses on the identification of potential corridors between habitat patches for umbrella species in the Rocky Mountains (Cushman et al., 2009; Cushman and Landguth, 2012; Parks et al., 2013; Squires et al., 2013). Although the literature included in this review only corresponds to articles published in peer reviewed journals (see methods), we believe that it is important to highlight the governmental contributions of the California Essential Habitat Connectivity Project: A Strategy for Conserving a Connected California and the Washington

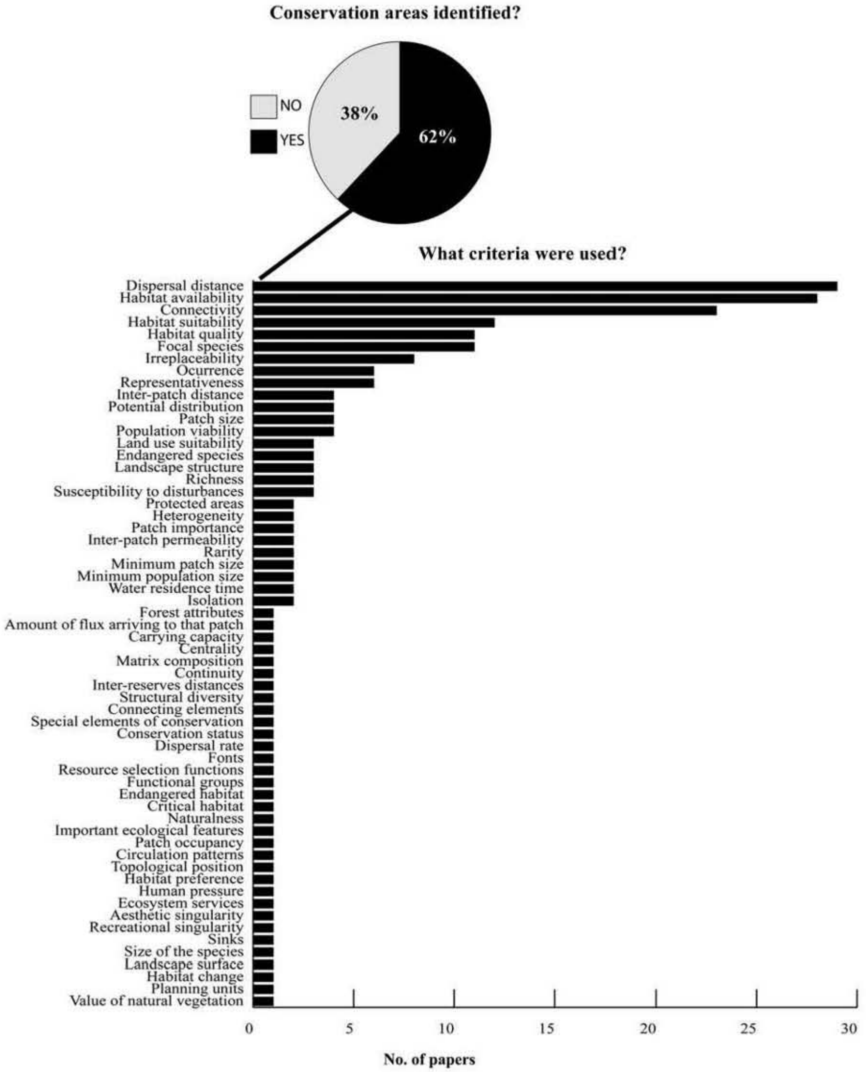

Figure 8. Criteria for the identification of conservation priority areas.

Connected Landscapes Project, which share the principal objectives of identifying natural remnant of habitat patches and modeling the connectivity between them (see Spencer et al., 2010 peer reviewed technical report), and to help prioritize areas in need of habitat connectivity for biodiversity conservation in the western US (see WHCWG, 2010 peer reviewed technical report). Some research centers (e.g. Klamath Center for Conservation Research) have contributed with recent research on the re-colonization of critical habitats through connectivity (Carroll et al., 2012). Along the same lines, seven US universities report more than one contribution in this review in different related topics; for example, in connectivity analysis between protected areas (Minor and Lookingbill, 2010), dispersal models to evaluate habitat connectivity (Lookingbill et al., 2010), conservation strategies for umbrella species (Thorne et al., 2006), proposed corridors and connectivity conservation strategy comparison (Beier al., 2009; Brost and Beier, 2012), among others.

In Europe, Spain and the UK are the leaders in connectivity studies (15 and 8 articles, respectively; see Figure 1). However, according to the data, compared with the US these countries published three to five times fewer articles. In Spain, habitat connectivity and conservation publications correspond to 25% of European and 11% of the total published globally. This could be a result of the large quantity of works contributed by the following organizations: Departamento de Economía y Gestión Forestal, ETSI Montes from the Universidad Politécnica de Madrid, and by authors at other European institutions. Approximately 50 articles on connectivity have been published since 2000, of which 15 were included in our analysis. The studies focused primarily on prioritizing areas that maintain habitat connectivity (Bodin and Saura, 2010; García-Feced et al., 2011; Gurrutxaga et al., 2011; Rubio and Saura, 2012; Saura and Rubio, 2010), and index formulation and tools to analyze them (Pascual-Hortal and Saura, 2006; Pascual-Hortal and Saura, 2008; Saura, 2010; Saura and Pascual-Hortal, 2007; Saura and Torné, 2009), among others. The publications from the UK represented 13% for Europe and 6% globally. Half of the studies were done by government institutions dedicated to forest studies (four of eight articles) and the focus on least cost models to evaluate biodiversity and in designing habitat networks (Nikolakaki and Dunnett, 2005).

The continents with the lowest number of contributions were Asia (9%), South America (6%), Oceania (5%), and Africa (1%). In Asia, China – with 10 articles (7%) – dominates 77% of Asia's publications. This tendency may well be related to a number of studies that aim at prioritizing conservation areas of the Giant Panda, *Ailuropoda melanoleuca* (Li et al., 2010; Qi et al., 2012; Shen et al., 2008; Xu et al., 2006) and an interest in studying connectivity of green spaces in urban areas (Chang et al., 2011; Chang et al., 2012; Kong et al., 2010).

In South America, the country with the best information dissemination with respect to connectivity and conservation is Brazil, with 4.3% of the total number of articles and 67% of the total publications from South America. This result is likely on account of the early increase in lines of research in landscape ecology from 1995 and the growing interest in spatial pattern studies between the years 2000 to 2005 (Pivello and Metzger, 2007). According to our results, Brazilian universities that study landscape ecology (e.g. Universidade de São Paulo and Universidade Federal do Rio de Janeiro), favor functional connectivity in fragmented landscapes – principally in "Mata Atlántica" (Awade and Metzger, 2008; Uezu et al., 2005) – and in the identification and design of protected area networks (Crouzeilles et al., 2011; Crouzeilles et al., 2013).

In Oceania, Australia contributes 5% globally within the reviewed articles. In spite of the fact that their contribution in this analysis is limited compared with Spain or the US, Australian contributions provide practical information on habitat connectivity and the creation of biodiversity network promoted by government institutions, NGOs, and private organizations (Fitzsimons and Wescott, 2008). At the same time, they have developed studies in the use of connectivity in riverscapes for use as criteria for prioritizing conservation areas (Hermoso et al., 2012a; Hermoso et al., 2012b; Linke et al., 2012).

3 Objects of study

We identified a prevalence of studies in terrestrial environments, largely represented by forest biomes, and mostly of temperate broad leaf and mixed forests types. This result may be because of the predominance of this biome in Europe and North America where the majority of the study areas are carried out (see Figure 1). This bias, however, shows that only a small fraction of global eco-regions have been studied in terms of connectivity, and have low species richness and structural complexity (Olson and Dinerstein, 2002). There was a small number in more complex forest biomes in terms of biological richness and diversity, including tropical and subtropical moist forests, which contain a high percentage (75%) of cataloged eco-regions that are critical or endangered (Olson and Dinerstein, 2002). These more complex biomes are distributed in countries with limited information dissemination, predominantly in Africa and Latin American (63%). There is a similar trend in the tropical and subtropical grasslands, savannas, and scrublands, which have a high level of endemism, habitat complexity (e.g. the variation between eco-regions of "los Llanos" and "el Cerrado" in Latin America), and large mammal richness (e.g. East African savannas) in spite of the strong anthropic pressure as a result of agricultural expansion (Klink and Machado, 2005). We found a small number of publications related to the conservation through connectivity of these habitats (e.g. Epps et al., 2011; Roever et al., 2013); and this is without taking into account the biome least protected at the global level, the temperate savannas (Hoekstra et al., 2005).

The preference for the study of connectivity in terrestrial systems may be a consequence of humans being a terrestrial species, but also because the approaches are relatively less complex (e.g. least cost analysis or landscape metrics) than connectivity studies in aquatic systems. Their implementation requires less information for modeling connectivity (usually two types: habitat patches and resistance surface), and additional information on the dispersal of species is relatively easy to obtain either with fieldwork or in literature (Ormerod et al., 2011). In contrast, studies of aquatic systems are more difficult because they have complex mechanisms for dispersal of organisms (e.g. seascapes larvae) influenced by other factors such as depth and ocean currents that limit measurability of mobility patterns with currently available tools (Anadon et al., 2013; Cowen and Sponaugle, 2009; Treml and Halpin, 2012).

Most of the studies in this review analyzed focal carnivorous species, similar to Zeller et al. (2012), such as Puma (*Puma concolor*) and other large mammals including the black bear (*Ursus americanus*) (see Figure 4). Usually, carnivorous focal species are selected because they require large areas of habitat, have relatively low densities and large dispersal distances, as well as being "charismatic" and of concern for conservation (Beier et al., 2008; Carroll, 2006). These characteristics have been proposed as beneficial for conservation of other species with shorter dispersal ranges and serve to implement wildlife corridors (Rabinowitz and Zeller, 2010). However, Beier et al. (2008) suggest that the selection of focal species should be approached not only by the individual carnivores but also by a wider variety of native species since the majority are generalist species and the corridors designed for the others will not be appropriate for specialist species with more reduced ranges. In this analysis, 83% of the studies concentrated on focal species and of these only 29% used more than one species in the connectivity analysis.

Recent articles treat connectivity as a major criterion to address the identification and maintenance of ecological integrity of the landscape, above all as a strategy to mitigate the negative effects of fragmentation (Rudnick et al., 2012) and other anthropic threats such as those related to global climate change (Kool et al., 2013). To this end, the identification and proposal of corridors, ecological networks, and habitat networks derived from habitat connectivity analysis are used as tools to design conservation strategies. Such frameworks, have benefited from the development of new tools associated with geographic information systems (GIS), allowing observers to integrate structural landscape characteristics with functional connectivity to support the design and implementation of corridors in management plans (Chetkiewicz et al., 2006).

We believe that the identification of landscape elements for the design of ecological network's could be helpful the integration of "homogeneous land units" approaches, which have been less frequently applied in this field (Blasi et al., 2008; Brost and Beier, 2012). These units provide a geographic framework that composes the basic physical characteristics of the landscape (Zonneveld, 1995). Thus, the role of physical geography is key to enhance comprehensive approaches to biodiversity conservation.

4 Methods in connectivity studies and integration with conservation objectives

Least cost analysis was the most utilized method in connectivity analyses (see Figure 7). This approach assumes that the ability of focal species to disperse results from the characteristics of the landscape matrix facilitating or impeding their mobility between patches (Adriaensen et al., 2003). Least cost paths (LCP) are used to determine the closest route with the fewest impediments between habitat patches. Nevertheless, the results are of limited use to conservation efforts as they only represent a line between two points, which is not a realistic corridor (Rudnick et al., 2012). Since 2009, researchers have been increasingly focused on least cost corridors (LCC), although the LCC have been used since 1997 (Walker and Craighead, 1997) as well as during the early 2000s (e.g. Singleton and Lehmkuhl, 2001; Singleton et al., 2002). LCC represents the accumulated cost gradient, which makes them closer to being functional areas to link habitats and therefore more realistic representations from a conservation objective standpoint (Beier et al., 2009). In the review by Zeller et al. (2012) only one study reported the use of LCC. In contrast, our review identified 19 studies implementing LCC, mostly between 2012 and 2013 (12 of 19 articles). This was probably because of the availability of new and better tools to calculate LCC (Beier et al., 2011; McRae and Kavanagh, 2011).

The second method most used in connectivity analysis is based on graph theory, where the landscape is translated into a graph composed of habitat patches (nodes) more or less interconnected by a network where the links represent the dispersal of individuals or flows through the landscape (Bunn et al., 2000; Minor and Urban, 2008; Urban and Keitt, 2001). Graph theory is useful as it facilitates the evaluation of the landscape connectivity (Laita et al., 2011) and identifies the contribution of each individual patch (Rubio and Saura, 2012). A direct relationship exists between graph theory and habitat availability indexes (Integral Index of Connectivity (IIC) and Probability of Connectivity (PC), which, according to our review, correspond to the third most utilized method. Graph theory-based indexes elucidate the optimal habitat area for focal species and the relative connectivity between all the patches that make up the whole habitat area. The application of these indexes in prioritizing conservation areas is useful as it allows for the identification of the important patch networks for general landscape connectivity, the analysis of the effect of the disappearance/removal of individual patches, and/or the selection of individual patches that could be linked to corridors along with the evaluation of emerging landscape structure. These indexes have been applied in identifying the effect on the dispersal of focal species and other ecological flows (Decout et al., 2012; Rubio and Saura, 2012; Ziolkowska et al., 2012).

The description of habitat availability indexes and their applicability is detailed in Pascual-Hortal and Saura (2006), Saura and Pascual-Hortal (2007) and Pascual-Hortal and Saura (2008). According to this assessment, the use of index derivations is significant. According to Saura and Rubio (2010) they can be partitioned in three groups (intra, flux, and connector) that measure the contribution of patches in connectivity among other elements, such as "stepping stone" habitat. As they allow for the identification and incorporation of patches in conservation planning, this can be useful in conservation. The determination of which patches contain suboptimal habitat (like stepping stones) that favor general connectivity among others that comply with the habitat requirements for each species is quite essential (Rubio and Saura, 2012).

Mixed methods were reported in five of the reviewed papers; for example, complementing morphological spatial pattern analysis (MSPA) with habitat availability indexes (Vogt et al., 2007a). MSPA uses image-based morphological classification (geometry and elemental forms), which has been applied in landscape ecology to identify and map structural landscape patterns, to identify internal and external fragmentation (Vogt et al., 2007a) as well as the connective elements like corridors (Vogt et al., 2007b). This method is relevant for biodiversity conservation and management purposes as it elucidates key structural elements that comply with the connective function of integrating classification results with habitat availability indexes (Saura et al., 2011b), which can help to establish valuation criteria for conservation plans (Clerici and Vogt, 2013).

Another modeling tool present in the reviewed papers was circuit theory (six articles). It has been applied in connectivity analysis as a complementary method to graph theory because of its ability to integrate all possible routes between habitat patches while calculating the LCP specifically through the designated optimal path (McRae and Beier, 2007). This approach presents some advantages, compared with least cost analysis and graph theory alone, as it permits the identification of alternative routes between all patches (not simply a pair of patches) and detects points where the loss of some habitat area may mean increased loss of connectivity (Cushman et al., 2013; McRae et al., 2008). It also measures isolation, supposing the focal species moves randomly along LCP. The assumption in least cost analysis is that the individuals choose to move or disperse between two specific patches, something unusual in focal species (McRae et al., 2008). In predicting possible movements through the established nodes, the current flow densities are used to identify corridors or pinch-points. In other words, this estimates the corridors where there is a higher likelihood of use by focal individuals when moving between habitat patches (McRae et al., 2008). Castilho et al. (2011) applied circuit theory to study gene flow between habitat patches of *Puma concolor* with the goal of connecting protected areas to enhance population recovery by reducing the likelihood that the pumas would return to insecure areas. Poor et al. (2012) applied an integrative method using the least cost analysis and circuit theory to identify priority conservation areas for *Antilocapra americana* and proposing connections between them. Other studies, such as Zeigler et al. (2011), integrate circuit theory, functional connectivity indexes, and least cost analysis to compare areas with high dispersal likelihood for animals with different behavior types and their influence in habitat connectivity.

Connectivity analysis in riverscapes and seascapes was represented by a variety of methods that differ from those utilized in terrestrial environments. In the case of marine environments, functional connectivity was analyzed based on three dimensions. To prioritize networks of marine areas in places where there is a high level of connectivity, Berglund et al. (2012) analyzed the horizontal, vertical, and temporal dispersal of mollusk larvae in the ocean. In the case of river environments, the majority of the methods apply longitudinal connectivity indexes to establish the degree of continuity of rivers that allows the movement of ecological flows upriver and downriver (Branco et al., 2012), suggesting that success of conservation efforts comes down to maintaining the integrity of planning units (subsystems) across the entire fluvial system (Hermoso et al., 2011).

Expert opinion was often used to evaluate the resistance of the landscape matrix and to qualify habitat suitability for focal species, a trend also reported by Zeller et al. (2012). Expert opinion was used to a lesser degree to evaluate the importance of habitat fragment conservation and to estimate approximate dispersal distances. Most studies included expert opinion because of the lack of current information and the difficulty in obtaining empirical resistance data. However, this procedure has been criticized on account of the subjectivity inherent in assigning “correct” values in models as a result of the differences in perception of landscape between humans and other species in terms of mobility and habitat suitability (Cushman et al., 2013).

Empirical methods in estimating resistance have been used as an alternative to expert opinion. Richard and Armstrong (2010) completed a connectivity analysis based on the combination of a cost–distance model with step selection functions and in qualifying resistance to movement by replacing the assigned values to specific land cover in function of proximity to the habitat patches. Baldwin et al. (2010) and Alagador et al. (2012) used values of the human footprint index (Sanderson et al., 2002) as a substitute for resistance, assuming a negative relationship between the footprint and the permeability of the landscape. Poor et al. (2012) applied a method based on two models of habitat suitability –one calculated using MaxEnt (Phillips et al., 2006) and the other through a multi-criteria analysis assuming that the high habitat suitability values correspond with low resistance values.

Several studies employed field methods using telemetry that allow for the modeling of the influence of barriers and other landscape characteristics in focal species mobility (Cushman et al., 2010; Roever et al., 2013), or those based on captures and DNA collection in the analysis of gene flow (Atwood et al., 2011). We thought that the resistance evaluation methods, based on empirical data, would be more robust than those based on expert opinion, in the sense that they are more objective and realistic in measuring resistance. However, this requires a large quantity of information that is more difficult to obtain and demands more time in the parameterization of models (e.g. telemetry). Expert opinion will likely continue to be a widely utilized method and has advantages in comparison with others forms of empirical data extrapolation because, in many cases, little field data information is available with regard to species mobility and the practical short term conservation efforts required to increase them (Zeller et al., 2012)

5 Trends in the use of software tools

CONEFOR (Saura and Torné, 2009) was the preferred tool in connectivity analysis. This software is based on graph theory and is easily integrated into conservation efforts because of its ability to calculate habitat availability indexes (Pascual-Hortal and Saura, 2006; Saura and Pascual-Hortal, 2007) quantifying the importance of habitat patches in general landscape connectivity. This tool provides a more objective means for selecting priority conservation areas and landscape management (Saura and Torné, 2009). For this reason, and the ease of integrating GIS data, CONEFOR has been applied to biodiversity and conservation planning. For example, it has been used in the selection of agricultural areas for reforesting efforts (García-Feced et al., 2011), identification of ecological networks in riparian habitats (Looy et al., 2013), identification of priority habitat patches for conservation (Bodin and Saura, 2010; Crouzeilles et al., 2013; Rubio and Saura, 2012; Shanthala Devi et al., 2013), characterizing the effects of highways in landscape connectivity Fu et al., 2010; (Gurrutxaga et al., 2011), evaluating past and future effects of connectivity in protected area networks and in forests (Rubio et al., 2012; Saura et al., 2011a), prioritizing restoration areas for fluvial systems (Segurado et al., 2013), identification of green urban areas for connectivity conservation (Tannier et al., 2012), and identification of future reintroduction areas and maintenance of faunal populations (Ziolkowska et al., 2012), among others.

Structural connectivity is mainly analyzed with the FRAGSTATS software (McGarigal et al., 2002). However, its usefulness in conservation has been questioned because of the limited relationship between landscape indexes and the functional characteristics of landscape (Li and Wu, 2004). Nevertheless, this review showed that the incorporation of this program with other software can be useful to integrate structural analysis with the functional analysis of connectivity (e.g. Freeman and Bell, 2011; Goetz et al., 2009). GUIDOS (Vogt et al., 2007a), was useful as it gives a spatial patterns analysis (fragmentation and structural connectivity) and easily integrates the results from other tools for a variety of conservation actions. Saura et al. (2011b), selected habitat patches with CONEFOR (network connectivity analysis) and integrated the morphological spatial pattern analysis using GUIDOS (MSPA), identifying important elements in habitat connectivity such as core area and bridges.

The calculations of LCP were conducted largely with the distance–cost function in ArcGIS and PATHMATRIX (Ray, 2005). However, the calculation of LCC (its advantages as compared with a LCP are discussed in section IV) was predominantly through the corridor function in ArcGIS. The use of LINKAGE MAPPER was emphasized (McRae and Kavanagh, 2011), but in our review it was only observed in two studies (McRae et al., 2012; Nuñez et al., 2013). We believe that its use will increase on account of its application in conservation planning. Not only does it identify LCC, but also delineates them through temperature gradients modeling movements in response to climate change (Nuñez et al., 2013) and additionally detects barriers that could impede movement across landscapes, making it useful in identifying optimal restoration sites (Shah and McRae, 2008) by identifying corridors and areas of high likelihood of focal species movement (McRae, 2012).

CIRCUITSCAPE is a free tool based in circuit theory that models patterns of mobility and gene flow across landscapes (Sha and McRae, 2008). In this review it was represented in five articles (e.g. Poor et al., 2012). We supposed that the preference would be to use LINKAGE MAPPER as it is being used more and more as a complementary method to the least cost models (McRae et al., 2008; see section IV), and for designing conservation networks in the context of gene flow and dispersal probabilities (Castilho et al., 2011; Zeigler et al., 2011).

The use of specific software for conservation, such as MARXAN (Ball et al., 2009), CONSNET (Ciarleglio et al., 2009), and ZONATION (Moilanen, 2007), is notable in spatial planning. All three of them incorporate habitat connectivity for multiple species as a criteria for prioritizing conservation areas and, in general, to resolve spatial issues in conservation (Early and Thomas, 2007). These tools represent robust methodologies to identify important maintenance areas for habitat quality and connectivity (Moilanen, 2005, 2007) and could be appropriate as complements to other corridor identification approaches that are commonly used (e.g. Least cost analysis and circuit theory) and corresponding tools (e.g. Linkage Mapper and Circuitscape). However, in our review we found no case studies that would exemplify this.

6 Scope and future research challenges

a Limitations in validating connectivity models. Potential corridors resulting from habitat connectivity modeling have, in their majority, not been validated (Cushman et al., 2013). No study reported an explicit evaluation of the corridors that were obtained through such analyses. However, their validation is necessary to corroborate the contribution of LCC to mobility and, in general, in the provision of ecosystem services. Validation is an essential step in the design and implementation of corridors so that they can be implemented once their efficiency is verified (Cushman et al., 2013). However, the empirical validation of corridors is scarce because of the difficulty in obtaining field data with regard to dispersal, the number of individual species with particular behaviors, and the existence of matrices with low resistance.

Some empirical validation methods have been utilized recently that are principally based on telemetric GPS data, un-invasive methods like camera traps, application of genetically derived landscape analyses, mark and recapture, and field interviews. One way to validate models partially is by verifying whether focal species use proposed LCC to move between habitat patches. For example, Stevenson et al. (2013) used telemetric GPS data to register grey squirrel (*Sciurus carolinensis*) movements and provide information about their use of proposed corridors and the probability of movement through them. This validation aided in demonstrating that the LCC were in fact able to predict the squirrels' movements. Another example of the utility of potential corridor validation is that of Li et al. (2013), who employed genetic differentiation data of the Przewalski gazelle (*Procapra przewalskii*), obtained in a previous study, to look for genetic similarity between populations connected by potential corridors. They used interviews with herders in the area to identify migrations between the habitat patches. The results showed connectivity patterns before actually establishing the current corridors. Bergerot et al. (2013) used a combination of dispersal models between patches and graph theory to analyze the functional connectivity with a species of butterfly (*Pieris brassicae*). To validate the models, they used field observation after massive release of marked butterflies to corroborate whether the dispersal patterns used for the butterflies were valid.

b Scaling issues in the study of habitat connectivity. Haines-Young and Chopping (1996) mention that there are numerous studies addressing scale considerations; they point out the essential role it plays in geography and landscape ecology. Turner (1990) showed that information is often lost as spatial data are converted to coarser resolutions. It is recognized that the nature of the pattern detected in the landscape depends on the scale of the spatial data used for interpretation; also, Turner (1990) cautions that the parameters and processes that are relevant at one scale are frequently not important or predictive at another scale. This also applies to the issue of connectivity, which depends on the scale at which the landscape is analyzed. In consequence, the spatial scale plays an essential role in the determination of conservation priorities that should be based on connectivity. Haines-Young and Chopping (1996) strongly suggest interpreting the spatial document with the highest resolution possible, although this depends on the objectives of the study.

Objectives in conservation planning depend on the geographical scale. Although many of the articles focused on the regional level (see results section), some addressed coarser scales, such as transnational or global (Alagador et al., 2012; Crooks et al., 2011; Saura et al., 2011b). Their analyses were based on focal species requirements with wide dispersal and large home ranges, such as those of big terrestrial mammals (Bruinderink et al., 2003; Rabinowitz and Zeller, 2010). Such studies give support to the design of a wide protected area network (interregional or transnational), suitable for maintaining viable populations and favoring sound environmental public policies. However, because these models are based on coarse scale data (> 1 km^2), they cannot recognize key elements for landscape connectivity, such as stepping stones.

In this review we observed that although there is progress in the knowledge of impact of spatial scale in the provision of connectivity, it is necessary for the viability of conservation actions to take into account carefully the spatial scale both at the stage of research (e.g. evaluation of habitat connectivity) and of implementation (e.g. restoration actions). Physical geography, biogeography, and landscape ecology could guide connectivity conservation studies on the basis of the following considerations: a) Determine the appropriate spatial scale based on the ecological requirements of the focal species, since species are affected by ecological phenomena including biogeophysical processes that occur at multiple spatial scales (e.g. Dispersal distance, landscape perception) (Baguette and Van Dyck, 2007); b) Collect data from the landscape at based on the spatial extent and grain size (Gustafson, 1998); c) Identify the spatial scale at which the landscape barriers could be an obstacle to species' dispersal (McRae et al., 2012); and d) When possible, apply a multi-scale approach to assess the overall habitat connectivity, or conservation actions such as ecological restoration (D'Eon, et al., 2002; Lindenmayer and Franklin, 2002). The challenge of spatial scale and habitat connectivity becomes a bigger issue in seascapes and riverscapes, in which the scale issue is still poorly developed or even not reported (Boström et al., 2011). Physical geography also has a great deal to contribute in the understanding of the biogeophysical processes involved; for example, the extension of graph-based approaches, which have been adapted successfully across a hierarchy of spatial scales to model connectivity in freshwater environments (Erős et al., 2011).

c Promising topics in habitat connectivity. We determined four important topics of further development in the study of habitat connectivity and biodiversity conservation.

Connectivity and climate change. Although landscape ecology in general and connectivity approach in particular are almost completely absent in the concept of global climate change (Li and Mander, 2009), they would be greatly improved if physical geographers to get more involved. One of the main adaptive climate change strategies for biodiversity conservation is the maintenance of protected area networks that include corridors, stepping stones, and refuges where the impact of climate change is lower (Mawdsley et al., 2009), which depends on the development of connectivity models that take into account physical geographical inputs such as climate change projections and how landscapes change over time that impact the design of corridors at different scales. Some advances include the McIntyre et al. (2014) use of graph theory, to establish the impact of climate change on projected habitat connectivity between wetlands that allowed them to determine how dispersal of focal species was affected by rapid variations in climate at regional and continental scales. Also, Nuñez et al. (2013) used a cost–distance analysis to delineate mobility corridors between areas of low human influence along temperature gradients, to determine how organisms' movement is affected by changes in climate.

Connectivity and its potential in restoration planning. The study of habitat connectivity is useful in restoration actions because it identifies areas where the implementation of new connector elements would help to optimize connectivity in fragmented landscapes. For example, studies based on graph theory assess the impact on connectivity as a result of removal or eventual restoration of habitat patches (Tambosi and Metzger, 2013; Tambosi et al., 2014). In addition, the least cost distance-based approach and circuit theory enable the identification of areas with high (or low) probability of connectivity and landscape elements that are barriers to dispersal of focal species. These sites could be prioritized for restoration or conservation efforts (McRae et al., 2012). However, the need to incorporate new variables to spatial modeling (such as the cost of restoration) to bridge the gap between connectivity models (e.g. potential corridors) and actual restoration actions (McRae et al., 2012, Torrubia et al., 2014) has been recently discussed. Nevertheless, this requires a higher level of information and an interdisciplinary approach. In this sense, for example, a clearer comprehension of how soils and landform limit or enhance the possibility of ecosystem recovery or restoration could benefit from closer work with physical geographers.

Connectivity and land cover/land use change modeling and planning. One of the principle variables used in connectivity modeling is land cover and land use change (LCLUC), which can affect to greater or lesser degrees landscape resistance, and thus the capacity of the organisms to move within its matrix. Identifying trends in connectivity change is important as it is directly related to conservation efforts in a timely and more efficient manner, especially in cases of accelerated changes. Modeling of changes in LCLU into the future, to project changes in the landscape, is an obvious area where physical geographers need to be included because of their expertise. Piquer-Rodríguez et al. (2012) used projections to analyze the relationship between LCLUC and structural connectivity and were able to define the dynamics of the connecting elements in the landscape. Rubio et al. (2012) used various scenarios of changes in LCLU, which showed different levels of resistance to species movements. To analyze the variation in time of the connectivity of landscape elements, a probability of connectivity index (PC) was assigned to various temporal scenarios (Saura and Pascual-Hortal, 2007). Other recent studies analyzed multi-temporal changes in structural connectivity (Khalyani and Mayer, 2013; Pătru-Stupariu et al., 2013) and functional connectivity (Vergara et al., 2013) based on LCLUC resulting from deforestation and urban growth.

Connectivity and ecosystem services across the landscape. Connectivity is a key factor in the provision of ecosystem services because their maintenance depends on the mobility of the organisms and, in general, of the ecological flows in the landscape (Mitchell et al., 2013). Few studies provide methods to evaluate ecosystem services using landscape attributes like connectivity (Mitchell et al., 2013). Ng et al. (2013) assumed that if a habitat patch has an important role in general habitat connectivity it would also have a high ecosystem service value. Applying the PC index (Saura and Pascual-Hortal, 2007), the change in values for ecosystem services were analyzed to identify habitat patches that would be of high priority in restoring ecosystem services. According to Mitchell et al. (2013), there is a need for more research in this area as the majority of studies focus on the regulation of ecosystem services, and in the specific ways that connectivity can influence the provision of services in terms of the mechanisms and scale in which connectivity affects them. Reduction in connectivity may affect the flows (exchange, compensation, recovering, etc.) of ecosystem services, especially for regulation; for instance, pollination process change, if there is a breakdown of flows given by connectivity, because the ability of organisms to pollinate is affected.

Connectivity analyses are fundamental to the design of ecological networks and the assessment of the effectiveness of protected areas. However, for this to happen it is necessary to work on the limitations that hinder the inclusion of connectivity in conservation planning, such as validation of the connectivity models, improving in field data collection and sharing between researchers, studying the particular behavior of focal species, habitat preferences, and not relying solely on species occurrence data. Although the outlook from this review suggests that these needs are being resolved rapidly, the biggest challenge is making progress in the transition between the academic views to public policy, ensuring that plans incorporate conservation connectivity with the real elements that would promote conservation.

V Conclusions

Our review reaffirms the importance of integrating habitat connectivity studies with explicit biodiversity conservation efforts. Connectivity, as for much of landscape ecology studies, still tends to be overwhelmingly focused on terrestrial environments. There is a strong need to increase the research on ecological networks in seascapes and riverscapes. Furthermore, studies are also mostly focused in temperate broad leaf and mixed forests, with fewer studies in tropical landscapes, which often are more complex and support higher diversity levels. Also, connectivity studies are dominated by focal species that are carnivorous, "charismatic," and with wide ranges of dispersal, leaving out less visible, but often more important, species and features.

The amount of literature found was so large and diverse that it was necessary to apply a rigorous selection method, which allowed only a subset of papers related to the study of habitat connectivity in biodiversity conservation to be chosen. The filter may have biased the results (e.g. identifying conservation goals) and limited their subsequent interpretation. However, our review is a rigorous survey of practical applications, current approaches, and research tools that can be applied in explicit conservation actions. In addition, if needed, the review methods can be replicated at a later time to track progress in this field.

There is a general lack of validation of proposed corridors and networks resulting from the connectivity models. The predominant analytical approach is that of functional connectivity, arising from the integration of spatial relationships between landscape elements (e.g. habitat patches) and functionality of ecological processes (e.g. species dispersal). Therefore, the practical application of the results of connectivity studies in actual conservation programs is still weak and needs to be resolved if the functionality and permanence of ecosystems in protected area networks and elsewhere is a priority (e.g. potential corridors vs. real corridors). Our findings may help to strengthen such links between research and execution of conservation plans. This should, however, also be backed by increased efforts to obtain occurrence data, genetic data, tracking telemetry, and exchange of this information between researchers and conservation institutions to improve the implementation of conservation actions to assure concrete results.

To exploit fully the potential for connectivity studies to contribute to sustainable management, model validation needs to be applied. It is also imperative to include more diverse environments and a more complete account of species and ecosystem services. We make a call for physical geography and wider applications of landscape ecology to play a more prominent role in the analysis of ecological processes and their connectivity, as well as the planning of appropriate spatial structures to that end. Habitat connectivity is a key issue in landscape ecology and is increasingly important in physical geography (e.g. integrating graph theoretical approaches, Kent, 2009) to take advantage of their comprehensive view in understanding the different landscape processes.

Acknowledgements

The authors would like to thank the project 179386 financed by CONACYT. We would also like to thank the researchers who so kindly collaborated with their commentaries on previous versions of this article. We would like to thank M. Mishkin (a colleague and native English speaker) for reviewing the manuscript. Finally, we would like to thank three anonymous referees and the editor for their valuable comments and suggestions that have significantly improved this manuscript.

Funding

The author(s) disclosed receipt of the following financial support for the research, authorship, and/or publication of this article: CCA received a grant from CONACYT to complete a PhD in Geography at UNAM, of which this study is a part. The remaining authors received no financial support for the research, authorship, and/or publication of this article.

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CAPITULO II

DISTRIBUCIÓN POTENCIAL DEL BOSQUE DE NIEBLA EN MICHOACÁN, MÉXICO: PRIORIZACIÓN PARA LA CONSERVACIÓN EN EL CONTEXTO DE CONECTIVIDAD DEL PAISAJE

POTENTIAL DISTRIBUTION OF MOUNTAIN CLOUD FOREST IN MICHOACAN, MEXICO: PRIORITIZATION FOR CONSERVATION IN THE CONTEXT OF LANDSCAPE CONNECTIVITY

Artículo en revisión en Applied Geography

POTENTIAL DISTRIBUTION OF MOUNTAIN CLOUD FOREST IN MICHOACAN, MEXICO: PRIORITIZATION FOR CONSERVATION IN THE CONTEXT OF LANDSCAPE CONNECTIVITY

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ABSTRACT

Potential distribution models and landscape connectivity studies have increased with regard to their utility in identifying priority areas for conservation in recent years. The principal objective of this study was to model the potential distribution of Mountain Cloud Forests (MCF) in the Transversal Volcanic System, Michoacán (TVS_{Mich}), and to analyze the role of these areas in landscape connectivity. Potential distribution was modeled for the MCF based on maximum entropy using 95 occurrence points and 26 ecological variables at 30 m spatial resolution. Potential connectivity was then evaluated using a probability of connectivity (PC) index based on graph theory. The percentage of variation (dPC_k) was used to identify the individual contribution of each potential area of MCF in overall connectivity. The different ways in which the potential areas of MCF can contribute to connectivity were evaluated using the three fractions derived from dPC_k ($dPCintra_k$, $dPCflux_k$ and $dPCconnector_k$). We determined that 1.3% of the TVS_{Mich} is optimal for the presence of MCF. The contribution of said area in maintenance of connectivity was low. However, the conservation of MCF is indispensable to provide or receive dispersion flows through TVS_{Mich} and another forest type (ex. Coniferous forest) as well as its role as a connector element between habitat types. The knowledge of potential capacity of the MCF to promote structural and functional landscape connectivity is key in the prioritization of conservation areas and is useful for future analyses complimented with the current distribution data.

Key words: Potential distribution modeling, potential connectivity, graph theory, conservation planning, Mexico.

INTRODUCTION

Mountain ecosystems occupy 24 % of the earth’s surface, of which 40% correspond to forest ecosystems (Kapos et al., 2000). In the interior and areas surrounding mountain ecosystems resides 26% of the world’s population and depends on the ecosystem services that these systems provide, particularly hydric resources (Körner & Ohsawa, 2005). At the same time, mountain ecosystems are considered among the most vulnerable to climate change (IPCC, 2007), and at a global level only 17% of its surface (5.6 millions of km^2) are within protected areas (Rodríguez-Rodríguez et al., 2011).

At a global level, mountain forests play a fundamental role in biodiversity conservation, hydric regulation of large watersheds and carbon storage. For this reason there is a greater need to conserve these remnant areas as an adaptive strategy to mitigate climate change (Spracklen & Righelato, 2014). These areas also provide cultural value in terms of aesthetic, spiritual and recreation value of great importance in a world increasingly transformed by human activities (Price et al., 2011).

In Mexico, the MCF are known as “mesophylous mountain forests” and at a global level they are known as “mountain cloud forests” (Villaseñor, 2010). These ecosystems are important for their wealth of endemic flora and fauna and for their role in providing environmental goods and services; Above all, for hydric regulation and maintenance of the loading capacity of aquifer mantles (Hamilton et al., 1995; Challenger, 1998). As with the majority of forest ecosystems, the MCF are threatened by anthropogenic pressures including deforestation, illegal logging, mining activities, construction of roads and clear-cutting for grazing and agriculture. These forests are especially vulnerable to climate change, particularly taking into account the low cloud cover that has diminished drastically as a result of global climate change (Bazzaz, 1998; Foster, 2001). It is estimated that 50% of the MCF in Mexico have been transformed into pastures and agricultural plots and close to 71% of the tree species that make them up fall under varying categories of ecological threat (CONABIO, 2010; González-Espinosa et al., 2011).

In the State of Michoacán, the MCF are generally dispersed between pine forests and mixed pine-oak forests that are currently fragmented principally due to avocado orchards, illegal logging and firewood extraction (CONABIO, 2010; Barsimantov & Antezana, 2012). Likewise, under natural conditions, the MCF is distributed in a discontinuous spatial patterns along the TVS$_{\text{Mich}}$ (Vázquez-García, 1995; CONABIO, 2010). Studies have been conducted on the occurrence potential of the MCF at national level (Rzedowsky, 1978; Rzedowsky, 1990; Cruz-Cárdenas et al., 2012) offering relevant information about their distribution and spatial configuration (CONABIO, 2010). However, spatial resolution used for this data ($\geq$ 1 km^2) does not permit detailed understanding of how its distribution impacts landscape connectivity.

Recently, Cuervo-Robayo et al. (2014) updated bioclimatic data available for Mexico (Hijmans et al., 2005; Saenz-Romero et al., 2010; Téllez-Valdés, 2011) with the idea of strengthening previous models and improving their quality. This allows for better spatial resolution of the distribution potential models and eventually the ability to evaluate changes in connectivity.

Connectivity is an indicator for the degree that habitat patches permit the movement of organisms and their genes across the landscape (Taylor et al., 1993; Taylor et al., 2006). The degree of connectivity is a result of the interaction of spatial factors (structural configuration) and functions of the landscape (e.g. species dispersal), and plays a crucial role in maintaining the exchange of organisms and gene flows between isolated populations, particularly in the context of biodiversity conservation (Bennet, 1999). It is an important variable in adapting to climate change, showing the possibilities for dispersal of organisms between optimal habitats improving resilience (Heller y Zavaleta, 2009; Brost y Beier, 2011; Schloss et al., 2011).

Landscape connectivity allows for the identification of the ecologically interconnected network of landscape elements. The use of graph theory has been widely used in landscape ecology to identify and analyze ecological networks for conservation purposes with the goal to increase connectivity or to evaluate the impacts of anthropogenic infrastructural modification (Urban y Keitt, 2001, Zettterberg et al., 2010; Foltête et al., 2014). These studies use several indices based on graph theory, for example the Integrate Connectivity Index (*IIC*) and the Probability of Connectivity Index (*PC*) (Pascual-Hortal & Saura, 2006; Pascual-Hortal & Saura, 2008) used as practical tools to identify networks in interconnected landscapes. In this way, more recent studies have applied the percentage of variation of the IIC (*dIIC)* and PC (*dPC*) to prioritize habitat patches (García-Feced et al., 2011; Shanthala et al., 2014; Correa et al., 2014) and the three fractions that make them up (*intra, flux, connector*) (Bodin y Saura, 2010; Baranyi et al., 2011) to improve the connectivity and mobility of species (Saura & Rubio, 2010). In Mexico, graph theory has been applied to conservation. For example, Villavicencio et al. (2009) determined the state of connectivity in four protected areas in the State of Jalisco, while López (2010) analyzed the differences between structural and functional connectivity in protected areas in the State of Veracruz. Correa et al. (2014) identified potential conservation areas using a multitemporal landscape connectivity analysis in the State of Michoacán. However, in particular in the MCF of the Transversal Volcanic System, there are gaps in information about the spatial and functional relationship between connectivity and habitat availability.

The purpose of this study was to analyze the connectivity of the MCF for the identification of priority conservation areas, based on their potential distribution and their relationship with other mountain ecosystems. We developed a spatial predictive distribution model of MCF and analyzed their contribution in landscape connectivity. We identified priority areas for the maintenance and improvement of connectivity in the framework of conservation management of the MCF.

METHODS

Study area

The Transversal Volcanic System (TVS) is a volcanic chain that crosses Mexico from the Pacific Ocean to the el Gulf of Mexico, that extends approximately 160,000 km^2 (Ferrari et al., 2012). It is not only known for its complex geology but also for its richness in biodiversity and endemism, apart from acting as a transitional zone between nearctic and neotropical biogeographical regions (Gámez et al., 2012). The study area corresponds to the central portion of the TVS in the northern of the State of Michoacán (TVS$_{Mich}$; Fig 1).

The central TVS$_{Mich}$ occupies an area of 28,100 km^2 and its altitude range varies from 1,000 to 3,800 m above sea level. The annual average precipitation goes from 600 to 2000 mm (Vidal-Zepeda, 1990). The most humid sector (1000-2000 mm) is concentrated in the southern slopes of the TVS$_{Mich}$ (García, 1990), principally represented by a subhumid, temperate climate (Cw$_2$), with an annual average temperature between 12°C a 18°C (García, 2004). This sector is characterized by the bioclimatic factors ideal for the distribution of coniferous forests (CF) and in a lower proportion ideal for the MCF. The occurrence of MCF requires a temperate climate with a high relative humidity, hilly terrain and soils with a deep humus layer (Velázquez et al., 2000; López-Mata et al., 2012). In the State of Michoacán 410 vegetative species found solely in the MCF and 19 in the CF (Cué Bär et al., 2006; Villaseñor, 2010). Species richness of the MCF has a significant relationship with precipitation in the wet months and annual evapotranspiration rates (López-Mata et al., 2012). There are eight natural protected areas in the TVS$_{Mich}$. The majority are distributed in the mountainous sector (Figure 1) that covers 2.4% of the study area (Bezaury-Creel et al., 2009), but does not include relicts of the MCF y and only includes 0.5% of the area of the CF.

The MCF in the TVS$_{Mich}$ is currently in a relict state and a now corresponds to a highly reduced area of 79 Km^2 (0.28% of the TVS$_{Mich}$) (INEGI, 2005). The relict areas are located in zones with a very steep topography, which limited its accessiblity—Nevertheless, its has not been an obstacle for land cover change (CONABIO, 2010).

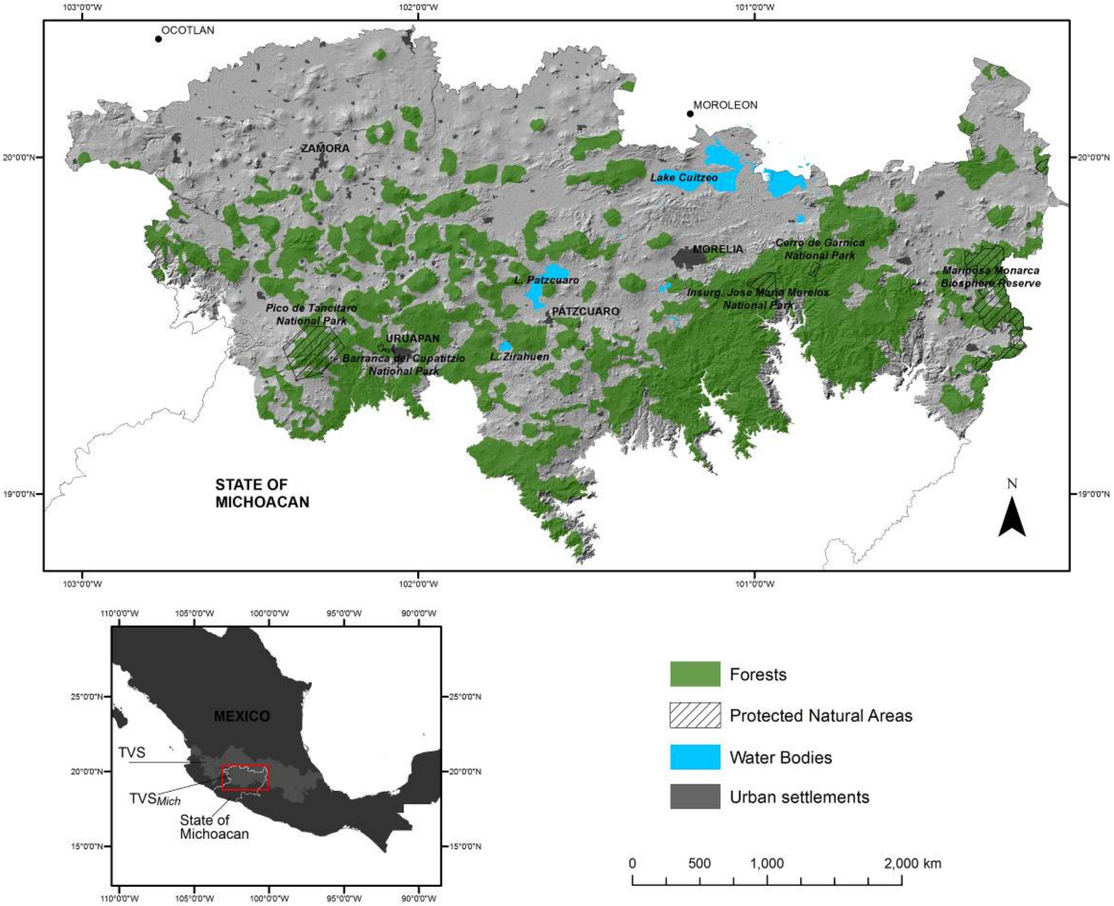


Figure 1 Area of study, showing forest cover in the Transversal Volcanic System of Michoacan-TVSMich (INEGI, 2005).

Spatial modeling of the potential distribution of Mountain Cloud Forests (PDM MCF) and of Coniferous Forests (CF)

Currently, the best conserved relicts of MCF in theTVS_{Mich} are inside the CF matrix of and mixed oak-pine forests (CONABIO, 2010). Considering the characteristics of the landscape (e.g. patch size, habitat suitability, position, aspect, etc.), MCF have a fundamental role in the functional and structural connectivity of all areas of secondary vegetation and even primary vegetation in some portions of the TVS_{Mich}. To identify the origin of the MCF and analyze its role in landscape connectivity we carried out a potential distribution model (PDM) for MCF and other for CF. With the goal of contextualizing the connectivity analysis of the current remnants of the MCF, we developed a protocol for modeling the potential distribution of both types of forest that are strongly interrelated. The modeling was carried out using the software MaxEnt 3.3.3 (Philips et al. 2006).

-*Occurrence data and predictive variables*

We used occurrence data of the types of forests to create the potential distribution models in the following way:

> Mountain Cloud Forest: (a) we used a species diagnostic consisting of 72 presence reports based on vegetative samples to ensure the presence of characteristic vegetation of the MCF (see Santana et al, 2014); and (b) we used 23 occurrence data points obtained from the INEGI (2005) database for Michoacán and presence data for the MCF based on previous vegetative studies in the study area (Medina et al., 2000; García et al., 2002).
>
> Coniferous Forest: We used 167 occurrence points of 7 representative species of the CF in Michoacán (Villaseñor, 2005; Rzedowski, 2006; Cué-Bar, 2006): *Pinus leiophylla* (58 points), *Pinus pseudostrobus* (31 points), *Abies religiosa* (29 points), *Pinus montezumae* (18 points), *Pinus michoacana* (14 points), *Cupressus lusitanica* (11 points), *Pinus hartwegii* (5 points).

A total of 27 predictive variables were divided in 2 groups:

a) Bioclimatic variables: We selected 20 variables, 19 at high resolution (30m) taken from the variables from WorldClim (Hijmans et al., 2005) developed by Cuervo-Robayo et al., (2014) based on the multiplication of climatic coefficients interpolated for the whole country with a basis in a digital high resolution elevation model (ASTER GDEM) focusing in the study area. We included an additional bioclimatic variable, evapotranspiration, based on the Turc (1954) model (Cruz-Cárdenas et al., 2012) (Table1).

b) Topographical variables: Starting with six-scenes of ASTER GDEM at 30m resolution that covers the State of Michoacán downloaded from the NASA database (http://reverb.echo.nasa.gov) and a unified mosaic that was created from the final DEM. Based on this process we extracted 7 variables: aspect, curvature, elevation, topographic humidity index, rugosity, slope and topographical position index.

Table 1. Predictive variables employed in the study to model potential occurrence of MCF

Class	Code	Variable

Bioclimatic	bio1	Annual Mean Temperature
	bio2	Mean Diurnal Range (Mean of monthly (max temp - min temp))
	bio3	**Isothermality (BIO2/BIO7) (* 100)**
	bio4	**Temperature Seasonality (standard deviation *100)**
	bio5	Max Temperature of Warmest Month
	bio6	Min Temperature of Coldest Month
	bio7	Temperature Annual Range (BIO5-BIO6)
	bio8	Mean Temperature of Wettest Quarter
	bio9	Mean Temperature of Driest Quarter
	bio10	Mean Temperature of Warmest Quarter
	bio11	Mean Temperature of Coldest Quarter
	bio12	**Annual Precipitation**
	bio13	**Precipitation of Wettest Month**
	bio14	**Precipitation of Driest Month**
	bio15	**Precipitation Seasonality (Coefficient of Variation)**
	bio16	Precipitation of Wettest Quarter
	bio17	**Precipitation of Driest Quarter**
	bio18	**Precipitation of Warmest Quarter**
	bio19	**Precipitation of Coldest Quarter**
	EvTR	**Evapotranspiration**
Topographic	**asp_class**	**Orientation**
	curv	**Curvature**
	dem30m	**Elevation**
	rect_twi	**Topographic wetness index**
	rugg	**Rugosity**
	slope	**Slope**
	TPI	**Topographic position index**

Note: The variables in bold correspond to the variables used in the final MCF and CF models, chosen based on a correlation test. T= Temperature, P=Precipitation.

To reduce redundancy between predictive variables we used a cross correlation analysis (correlation coefficient from Pearson *(r)*) for each of the 27 initial variables, using *Band Collection Statistics (Spatial Analyst)* in ArcGis 10.x. (ESRI, 2012). When a pair of variables presented a correlation > 0.80, one was excluded from the spatial model, which leads to the exclusion of 10 variables leaving 17 variables in the final model (Table1).

The selected variables were integrated into the software MaxEnt (Philips et al. 2006), which models distribution of species using the maximum entropy principle, which estimates the probability of distribution based on presence data and the environmental conditions where the species have been observed (Philips et al. 2006). The potential distribution is subject to the limitations imposed by the availability of information with respect to occurrence points and environmental conditions in the study area (Peterson et al. 2011). The evaluation of the predictive quality of the models used the Area Under the Curve test (AUC), and was classified according the ranges proposed by Thuiller et al. (2005): poor AUC (AUC < 0.8), moderate (0.8 < AUC < 0.9), good (0.9 < AUC < 0.95) and very good (0.95 < AUC < 1.0). The models with values >0.75 were considered potentially useful (Phillips et al., 2008). The *Jacknife* test was used to establish the importance of the variables in the potential distribution model and to select those variables that could be excluded apart from the correlation test.

The spatial projection of the model was restricted to the limits of the TVS_{Mich} study area using the following parameters for modeling: 75% of occurrence points for training and 25% for validation. We used 1000 iterations and eliminated any occurrence points that were found inside the same pixel (30m). Due to potential overestimation in the results, we excluded the data for diagnostic species in the final model using only the presence data of the MCF and CF.

To identify the optimal presence areas of the MCF and CF we applied the acceptance range used by (2007) and Stiels et al. (2011) of the *10 percentile training presence logistic threshold*—determining which pixel is apt if its value is higher than the tenth percentile of probability of presence. All pixels above that threshold were preliminarily reclassified as potential MCF or CF.

To establish the degree of superposition of the two models (*niche overlap*) and attain a distribution adjustment of MCF (taking into account their spatial relationship with CF), we applied the relative range test (Warren y Seifert, 2010). The relative range values are values from 0 to 1. The values closest to 1 represent a higher probability that two habitat patches are the same for both models (Warren y Seifert, 2010). The calculation of niche overlap was completed using ENM tools 1.3 (Warren et al., 2008; Warren, Glor, y Turelli, 2010).

Based on the niche overlap test, we assumed that the low probability occurrence values of MCF in some sectors of TVS_{Mich} could correspond to the CF potential. So, to avoid overestimating the final PDM/MCF, we constructed an adjustment criteria of the occurrence values in which the values of the differences between the preliminary models of PDM MCF and PDM CF greater than 0 were assigned to MCF, while the values that resulted in 0 or lower were assigned to CF.

Landscape Connectivity Analysis and priority areas

-*Graph -based connectivity modeling*

The first step in constructing the connectivity model is based on the definition of patches (*nodes*), and connections (links) that make up the landscape (*graph*), and the patch parameters like patch area and habitat quality (Galpern, Manseau & Fall, 2011; Foltête et al., 2014), using a binary map of potential distribution of the MCF. Two graphs were constructed with different spatial extent: 1) A overall graph using the TVS_{Mich} as the basis of the landscape to analyze the role of the potential MCF areas in connectivity along the TVS_{Mich}., 2) a graph that takes into account the potential distribution of CF as the basis of the landscape to analyze the importance of potential MCF areas as connector elements and/or dispersal elements within other types of habitat.

We used a general median dispersal distance of 10,000 m (*d=10,000;* Fig 2) as a threshold for connectivity based on the habitat requirements of the Mexican bobcat (*Linx rufus escuinapae*) that inhabit the TVS_{Mich}, (Nuñez, 2002 & 2005) that has previously been used as a focal species to identify potential conservation areas (Correa et al., 2014). Species with intermediate dispersion ranges can better explain the state of connectivity than those with more limited ranges, showing more sensitivity to loss of habitat patches (Saura & Rubio, 2010). However, to analyze the change in the degree of overall connectivity (*PC_overall*) various dispersal ranges were used to represent small to large mammals: d=50m, d=100m, d=500m, d=1,000m, d=5,000m, d=10,000m, d=20,000m.

A total of 9,829 potential MCF polygons made up the graph-based models. The connections between nodes (*link geometry*) were based on Euclidian distances (Pascual-Hortal & Saura, 2008; Andersson & Bodin, 2009) because in order to model connectivity under an approximate connectivity potential it is assumed that the natural state offers no resistance to mobility of the focal species. If the objective were to analyze the impact of anthropic activities on connectivity, the anthropic modifications offer different levels of difficulty for mobility and in this case it was relevant to use a cost distance analysis (Gurrutxaga et al., 2011; Correa et al., 2014).

-*Evaluating the importance of patches in landscape connectivity*

Connectivity was evaluated for each graph model through the PC index proposed by Saura y Pascual-Hortal (2007) and the three components (*dPCintra*, *dPCflux* and *dPCconnecto*r) described in Saura y Rubio (2010). According to Saura (2013), *PC* index is considered a landscape index because it takes into account the intrinsic attributes of each unit (e.g. patch area, habitat quality, probability of occurrence of focal species, etc.) and the topological relationships among the other elements of the connectivity network (e.g. position, aspect, location, etc.). The *PC* index (Ec. (1)) is defined as "the probability that two animals randomly placed within the landscape fall into habitat areas that are reachable from each other (interconnected) given a set of n habitat patches and the connections (pij) among them" (Saura & Pascual-Hortal, 2007).

$$PC = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n} a_i \times a_j \times p_{ij}^{*}}{A_L^2}$$

(1)

In this equation a_{i} and a_{j} are attributes of the nodes i and j. In this case, the attribute of the node corresponds to the patch area i weighted by the average of the probability of occurrence inside the patch i. Here, p^{*}_{ij} is the maximum probability all possible routes between patches *i, j* and A_{L} represents the total landscape area. The PC index is calculated in a range from 0 to 1 and increases as general connectivity increases (Saura & Pascual-Hortal, 2007; Saura & Rubio, 2010). This weighting approach is appropriate to this study as it is likely that there are small patches that do not add to general connectivity, but have a high probability of occurrence or conversely add to general connectivity, but do not have a high probability of occurrence, with varying ranges of habitat quality.

To analyze the individual importance of potential patches of MCF in overall connectivity of CF and of the $\mathrm{TVS}_{\mathrm{Mich,}}$ we applied the dPC_k from the *PC* index (Ec. (2)) (Pascual-Hortal & Saura; Saura & Pascual-Hortal, 2007; Saura & Rubio, 2010). The dPC_k quantifies the loss of connectivity when potential MCF patches are systematically removed (Saura & Pascual-Hortal, 2007). This individual calculation helped to calculate the percentage associated with the importance of each patch and allows for the prioritization of patches in the context of connectivity conservation.

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

(2)

Here, PC is the index value when the landscape is intact (with no patch loss) and $PC_{\mathrm{remove,k}}$ is the PC value when there is the loss of patch *k* (Saura & Pascual-Hortal, 2007). To analyze the distinct ways that the potential MCF patches can contribute to connectivity in the study area and inside the CF, we analyzed the three fractions that integrate the PC index (Ec. (3)) (Bodin y Saura, 2010):

$$dPC_k = dPC\,\mathrm{intra}_k + dPCflux_k + dPCconnect_k$$

(3)

The three fractions of dPC_K takes into account the different ways that a patch *k* can contribute to connectivity and habitat availability. The $dPCintra_k$ (*intra patch connectivity*) value corresponds to the area of habitat consistent with the patch *k*. In other words, it corresponds to the connected area between the habitat patches and is completely independent of dispersal distances and dependent of the patch area. Here, $dPCflux_k$ corresponds to the dispersal flux weighted by the patch attribute (in this case, area of the patch *k* weighted by the probability of occurrence of the same patch value, *k*) received or originated from the patch *k* links with the rest of the patches that integrate the landscape; $dPCflux_k$ is dependent of the attribute of the patch *k* and the topological position of *k* with respect to the other patches *(interpatch connectivity*). $dPCconnector_k$ evaluates the role that *k* as a connector element has between the other habitat areas (*stepping stones*), measures the importance of the patch *k* as an enhancer element of connectivity, is independent of the area of patch *k*, but dependent on its topological positioning with respect to the other patches (Bodin & Saura, 2010; Saura, 2013).

We used Pearson’s coefficient correlation (Wessa, 2012) to evaluate the differences and measure the relationship between the value of the three dPC_k components, the *k* attribute and the patch (*k*) area. To evaluate the relative contribution of each dPC_k fraction in overall connectivity (*ϴPCintra*, *ϴPCflux*, *ϴPCconnect*), the total *dPC* were added and divided by the sum of the values of each element and the result multiplied by 100 to interpret it as a percentage (Saura & Rubio, 2010). The same method was applied to each of the sectors that were divided the PDM MCF to facilitate analysis of the results (Fig 3). The construction of the graph-based models and the calculation of connectivity metrics (Saura & Pascual-Hortal, 2007; Saura & Rubio, 2010) were completed using GRAPHAB 1.2.1 software (Foltête, Clauzel & Vuidel, 2012).

RESULTS

Potential distribution of Forests in the $\mathbf{TVS}_{\mathbf{Mich}}$

The results of the relative range test (0.79) indicate that the values of habitat suitability defined for PDM MCF and PDM CF are ecologically similar. In this case, we assume that there is a high relative similarity between the potential MCF areas and those of the CF, independent of the quantitative difference between the suitability values.

- *Mountain Cloud Forest (MCF)*

The optimum area for the presence of MCF was approximately 37,567 ha, which represents 1.3 % of the $\mathrm{TVS}_{\mathrm{Mich}}$ and is composed of 9,829 potential patches. Approximately 97 % of the estimated potential MCF area was distributed between 2000 and 3000 m (75% between 2000 and 2500 m while 22% was between 2500 and 3000 m). Only 7% was inside protected areas present in the zone (2,625 ha). In general, we identified three sectors where the main MFC areas were located (Figure 2): The first sector (west) was in the mountain Tancítaro, Sector 2 (center) corresponds to the area near lake Zirahuén, and is where we found the highest probability of occurrence values, but in the absence of protected areas, and sector 3 (east) is the area that partially covers the municipalities of Zitácuaro and Hidalgo.

The PDM MCF showed a median AUC value of 0.98 based on training data and 0.97 on verification data set, reaching the “very good” category (Thuiller et al., 2005), which indicates that the model differentiated the distribution potential of the MCF properly. The logistic presence threshold (*10th percentile training presence logistic threshold*) was 0.163; all the pixels greater than this value were considered as potential MCF. The predictor variables with the highest contribution in the model were the precipitation of coldest quarter (bio19), elevation (dem_30m) and aspect (asp_class) (Table2).

Table2. Percentage of contribution (>5%) of the environmental and topographical variables for the PDM MCF and PDM CF.

Mountain Cloud Forest (MCF)		Coniferous Forest (CF)	
Variable	Percent Contribution (%)	Variable	Percent Contribution (%)
Precipitation of Coldest Quarter	48.1	Precipitation of Coldest Quarter	29.2
Elevation	13	Precipitation of Driest Quarter	17.1
Aspect	10.8	Annual Precipitation	14.7
Annual Precipitation	6.3	Isothermality	8.6
Precipitation of Warmest Quarter	6.3	Annual Precipitation	7.4
		Elevation	6.3

-
- *Coniferous Forest (CF)*

The optimal CF area in the TVS_{Mich} was 691,068 ha, which would occupy 24 % of the total $TVS_{Mich.}$ (Fig 2). The majority of the potential CF area was concentrated in the mountain chain located in the southern portion of the TVS_{Mich}, forming a corridor that links the study area to the central part of the Mexican TVS.

The PDM CF used for this analysis showed a median AUC value of 0.91 for the training data and 0.82 for the verification data, falling into the “moderate” category (Thuiller et al., 2005). The logistic presence threshold (*10th percentile training presence logistic threshold*) was 0.26; all of the pixels greater than this value were accepted as potential CF. The precipitation of coldest quarter(bio19), precipitation of driest quarter (bio17) and annual precipitation (bio12) were, respectively, the environmental variables that contributed most to the -model (Table 2).

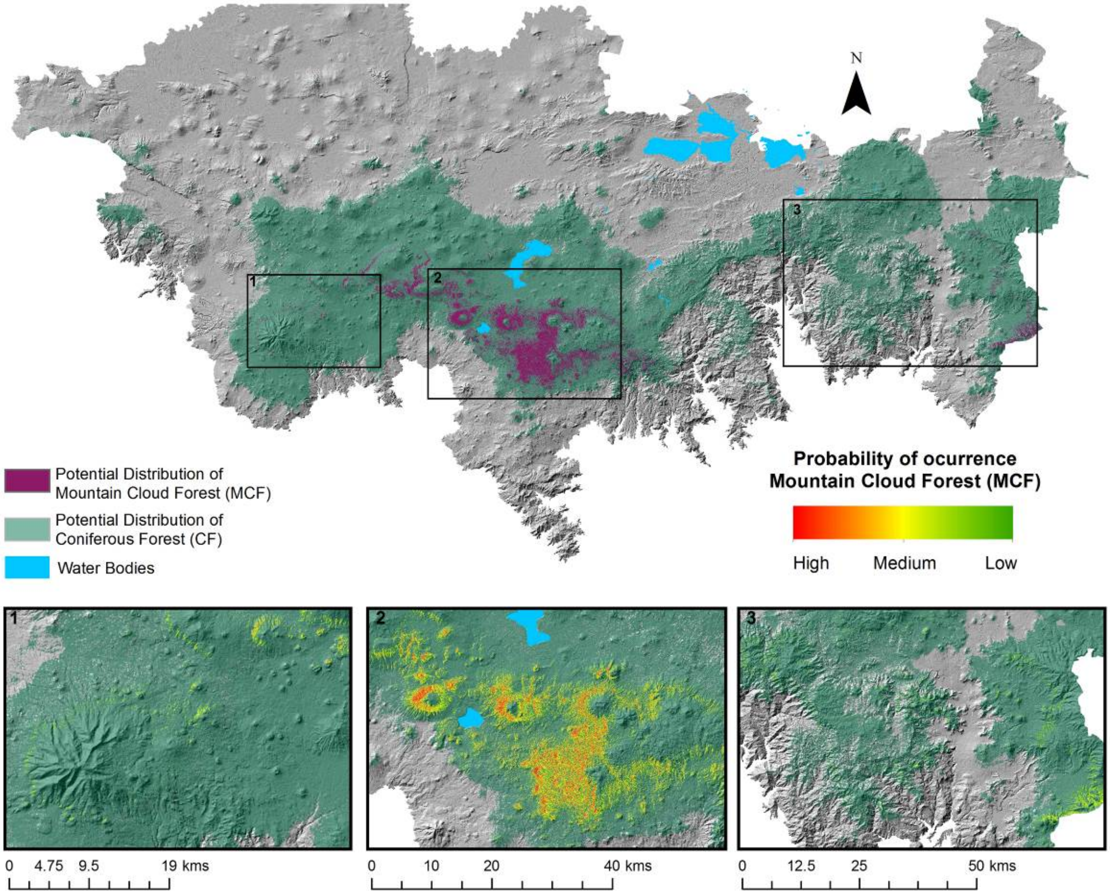


Figure 2. Map of the potential distribution of the MCF and the CF in the TVS$_{\text{Mich}}$ and the 3 principle sectors in connectivity evaluation. Sector 1 (west) corresponds to the mountain Tancítaro and part of the municipalities of Uruapan and San Juan Parangaricutiro. Sector 2 (center) is located in the area near lake Zirahuén and south of lake Pátzcuaro. Sector 3 (east) in the rural areas in the municipalities of Zitácuaro and Hidalgo.

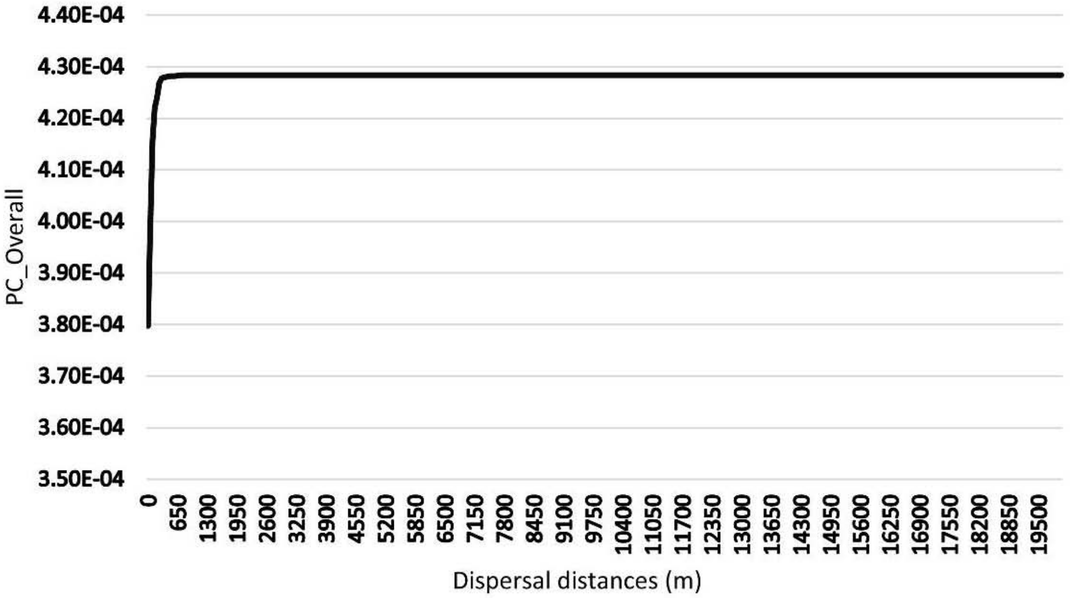
Analysis of connectivity and prioritization of conservation areas

-*Contribution of the PDM MCF to general connectivity in the TVSM$_{ich}$ and the PDM CF*

The general PC index values were very low for the two areas. The PC average between the different dispersal distances analyzed in the TVS$_{\text{Mich}}$ was 8.6 x 10^{-6} and 1.8 x 10^{-5} for the potential CF (MDP CF). The low PC index values show that the potential contribution of the

MCF to overall connectivity and habitat availability in the two areas is limited. A slight increase in connectivity was identified between the short and intermediate dispersal distances (0 m – 3,700 m for CF and 0 m- 3,800 m for the TVS_{Mich}), which was stabilized as the distances increase (Fig 3).

1


PC_Overall
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4.30E-04
4.20E-04
4.10E-04
4.00E-04
3.90E-04
3.80E-04
3.70E-04
3.60E-04
3.50E-04
0
650
1300
1950
2600
3250
3900
4550
5200
5850
6500
7150
7800
8450
9100
9750
10400
11050
11700
12350
13000
13650
14300
14950
15600
16250
16900
17550
18200
18850
19500
Dispersal distances (m)

2

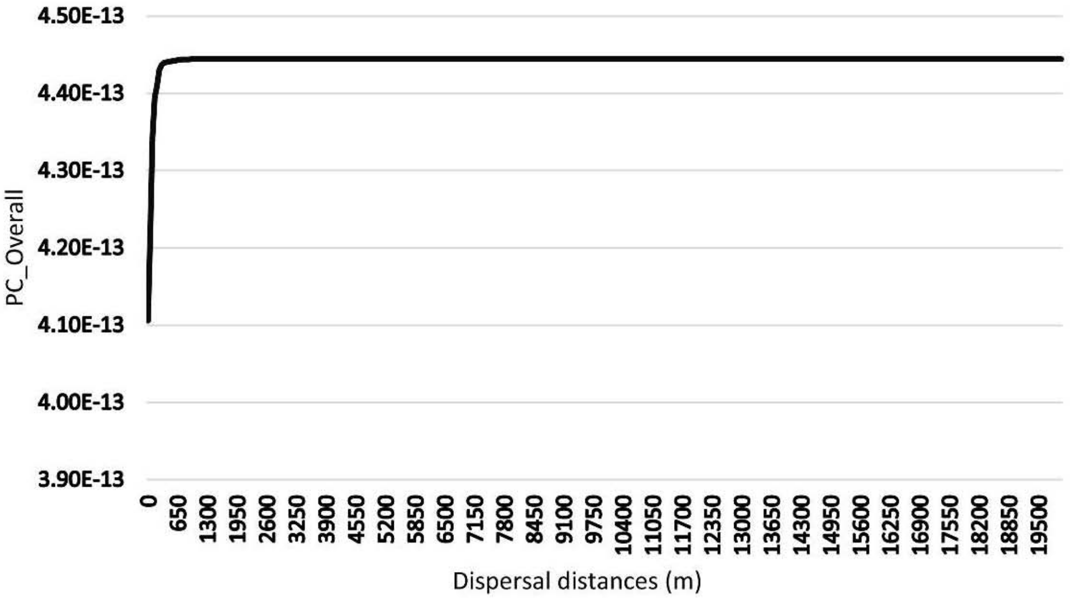

PC_Overall
4.50E-13
4.40E-13
4.30E-13
4.20E-13
4.10E-13
4.00E-13
3.90E-13
0
650
1300
1950
2600
3250
3900
4550
5200
5850
6500
7150
7800
8450
9100
9750
10400
11050
11700
12350
13000
13650
14300
14950
15600
16250
16900
17550
18200
18850
19500
Dispersal distances (m)

Figure 3. PC index (PC). 1) PC index values based on the potential CF area and 2) PC index values based on the TVS_{Mich}

-*Prioritizing potential MCF areas for maintenance of landscape connectivity*

Figure 4 shows the distribution of the importance of the dPC_k for each potential patch of MCF inside the PDM CF, and was calculated for all 9,829 potential patches of MCF. Different levels of importance were identified for the patches in each sector, which depended on the intrinsic characteristics of each (area (ha) × habitat suitability) and the topological characteristics of each patch. For example, in sector 2 the connectivity conservation priority area showed a value of 77.5% importance based on an average dispersion distance of 10,000 m ($d=10,000$). The sum of the *dPC* values was 238%. The remaining percentages were distributed among the other patches and none of them showed values above 20 % importance. Sector 1 showed predominantly low *d*PC index values and in sector 3 the values varied from very low to high importance. Conversely, the patches of “very high” importance were predominant in sector 2 but are not present in sectors 1 and 3 (Fig 3).

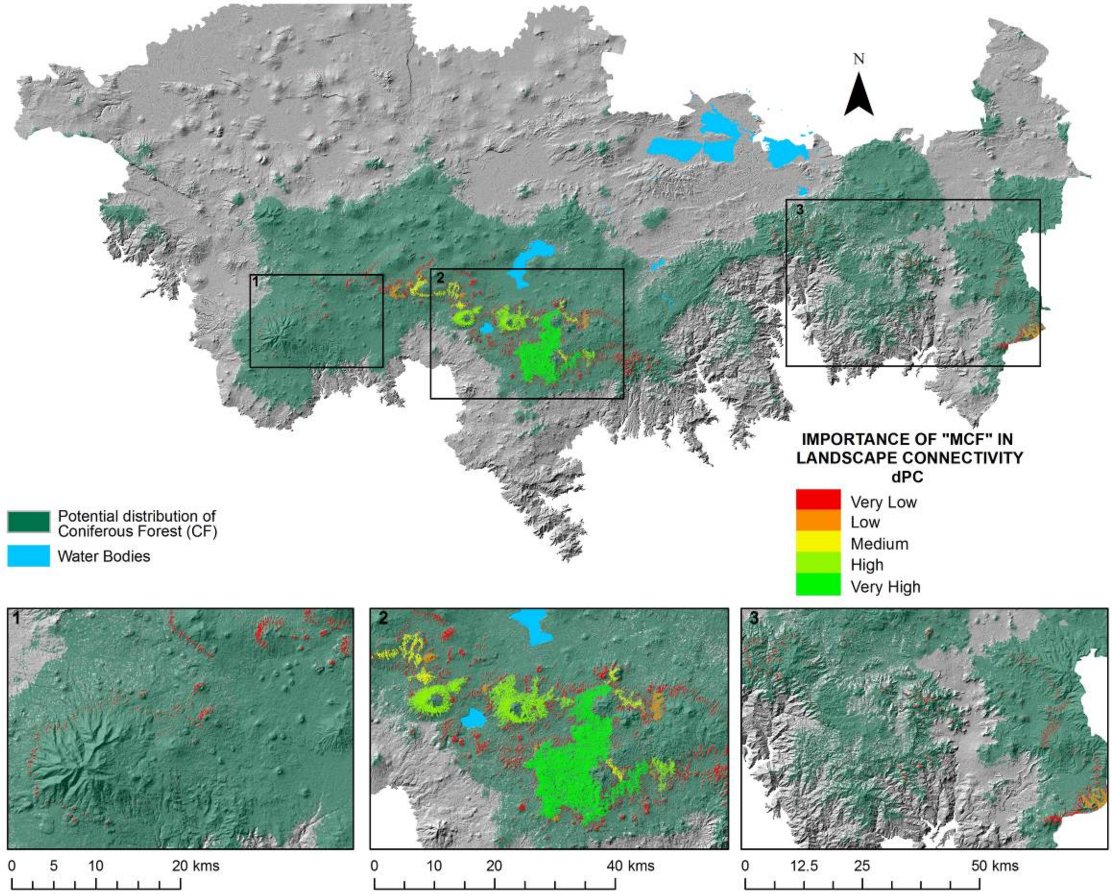


Figure 4. Distribution of the importance of potential MCF areas in general landscape connectivity based on *dPC*.

The potential patch most important in connectivity (sector 2) showed a significant difference between its attribute (area (ha) × habitat suitability; 11,249 for the largest and 2,751 for the one that followed) and those of the other patches and we found a relatively high relationship between the attribute of the potential MCF areas and the *dPC* index (Coef. Pearson= 0.70, excluding the largest patch and that with the highest attribute value).

-*Evaluation the different ways in which the potential MCF areas contribute to connectivity conservation*

The potential areas of MCF in their majority were found in the CF (Fig 2) and apparently comply with the following functions in landscape connectivity maintenance: 1) providers of connected areas inside the CF that, at the same time, provide connectivity in the TVS_{Mich} (*dPCintra*), 2) as elements that receive and disperse fluxes for the other habitat patches (*dPCflux*) and 3) as connector elements or *stepping stones* between other patches whether they be from MCF or other habitat areas like those of the CF (*dPCconnect*). *dPCflux* is the component that contributed most to general connectivity and habitat availability (*ϴPCflux*= 46.7 %), followed by *dPCconnect* (*ϴPCconnect*= 34.7 %) and finally by *dPCintra* with a value of *ϴPCintra*= 18.6%.

Importance of the potential MCF as an intra-patch provider of connectivity

The potential MCF area that contributes most to intra-patch connectivity (34.8%), was the largest (11,250 ha) and had the highest attribute value (3,036). There was a strong relationship between the attribute of each potential MCF area and the *dPCintra* (Coef. Pearson= 0.94). When the largest area was excluded the correlation slightly decreased (Coef. Pearson= 0.92). So we can infer that the potential MCF areas with higher attribute values (ha × habitat suitability) was the most important for intra-patch connectivity. Specifically, the contribution of the largest patch located in sector 2 (Id 5038) was concentrated inside the potential CF. However, the contribution of the other areas was low if we take into account that Id 5038 is four times larger than the second largest patch located in sector 3 (Id 4505) (Table 3). The results based on *dPCintra* show a high correlation with dPC_k (Coef. Pearson= 0.95).

Table3. The 10 potential MCF areas with the highest patch attribute values and the contribution (%) in each *dPC* component *(d=10,000m)*. Note that the only component that shows a decrease in *dPCIntra*. **Attribute*** corresponds to the area of patch *k* weighted by the median probability of occurrence inside the patch $_{k.}$ **Id** is the identifier number of each patch MCF in the potential distribution map.

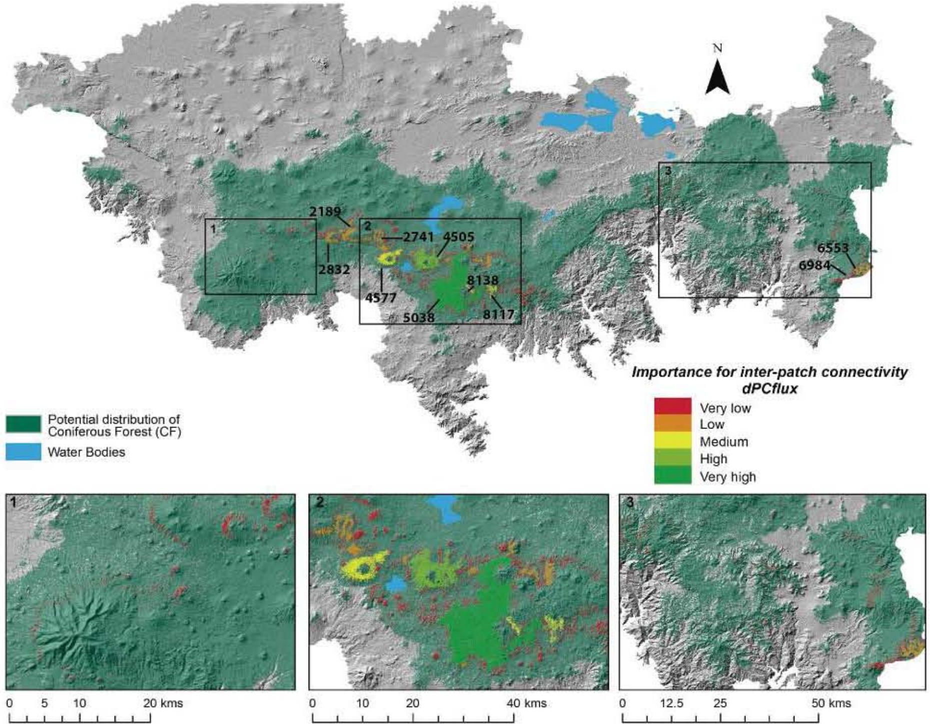
No	Id	Area (ha)	Attribute*	dPC_k	$dPCIntra_k$	$dPCFlux_k$	$dPCConnect_k$
1	5038	11,249	3,035.96	77.53	34.82	35.39	7.32
2	4577	1,834	1,117.38	8.91	4.72	3.94	0.26
3	4505	2,751	823.71	18.16	2.56	12.73	2.87
4	6553	565	438.85	1.66	0.73	0.89	0.05
5	2189	579	326.36	3.96	0.40	2.10	1.46
6	2741	406	247.60	4.26	0.23	1.95	2.08
7	2832	520	226.07	1.29	0.19	0.84	0.26
8	8117	448	215.35	7.03	0.18	5.54	1.32
9	8138	177	133.99	4.48	0.07	4.13	0.28
10	6984	162	128.89	0.85	0.06	0.54	0.25

Importance of potential MCF as providing or receiving dispersial fluxes.

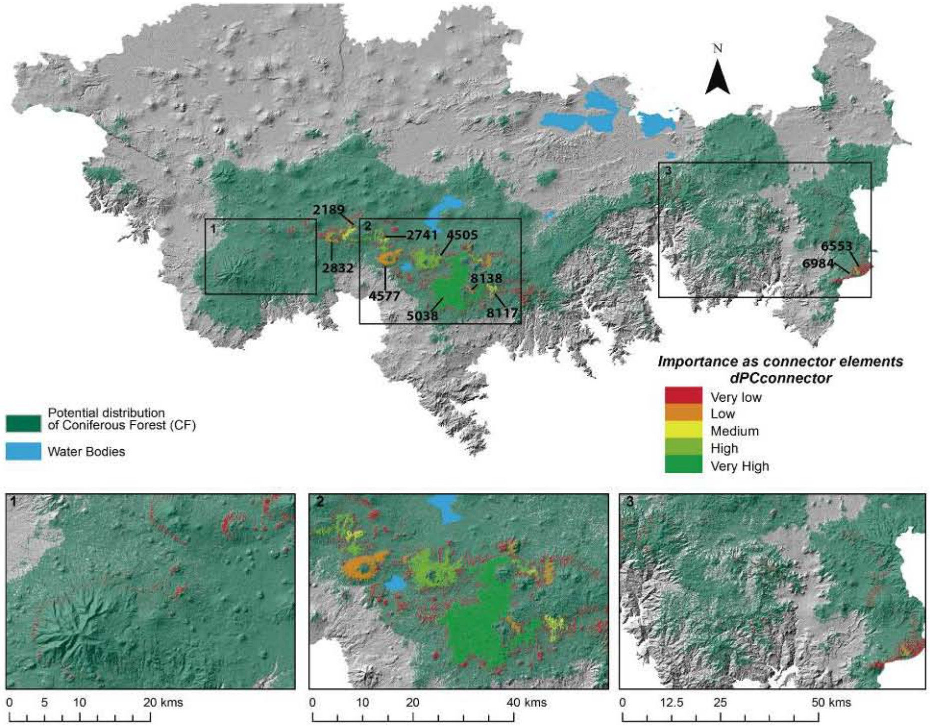
The potential MCF area with the greatest importance in *dPCflux* (35.4%) corresponds to Id 5038, which also shows the highest k attribute value. However, the *dPCflux* values are higher with comparison to *dPCintra* (i.e. areas with Id 4505, Id 8117 and Id 8138, see Table 3), which indicates that there is a higher contribution of potential MCF as an inter-patch connectivity provider. The rest of the *dPCflux* values did not rise above 13% importance. The correlation between *dPCflux* and attribute *k* is considerably high (0.95) determined largely by the attribute value corresponding to Id 5038, which is much greater than the other optimal patches (Table3). However, excluding the maximum *k* value the correlation decreases to 0.76. We infer then that the *dPCflux* value does not depend strictly on the patch area. For example the area Id 8117 (No 8) shows a *dPCflux* value greater than that of Id 2189 (No 5), which has a higher relative k attribute value. The correlation between dPC_k and *dPCflux* was close to 1 and decreased to 0.82 when the patch with the highest attribute *k* value was excluded (Id 5038).

The individual importance of the potential MCF areas continued showing low values in sector 1 (Figure 4) with respect to the dPC_k index (Fig 3) where low values associates with smaller potential areas were predominate ($dPC_{ksector1}$= 0.1%). The general contribution of $dPCflux_k$ in sector 1 was the highest (74%) in comparison to the others ($\Theta PCintra_{sector1}=8.4\%$; $\Theta PCconnector_{sector1}$=17%). In sector 2 there were no significant differences in the distribution of values of *dPCflux* in comparison with dPC_k. Conversely, in sector 3 the contribution of *dPCflux* is considerable (54%) taking into account that the general contribution value for the total dPC_k was the highest (46.68%).

a)


N
1
2
3
2189
2832
2741
4505
4577
8138
5038
8117
6553
6984
Importance for inter-patch connectivity
dPCflux
Very low
Low
Medium
High
Very high
Potential distribution of Coniferous Forest (CF)
Water Bodies
0 5 10 20 kms
0 10 20 40 kms
0 12.5 25 50 kms

b)


N
1
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2189
2832
2741
4505
4577
8138
5038
8117
6553
6984
Importance as connector elements
dPCconnector
Very low
Low
Medium
High
Very High
Potential distribution of Coniferous Forest (CF)
Water Bodies
0 5 10 20 kms
0 10 20 40 kms
0 12.5 25 50 kms

Figure 5. Importance of the potential MCF areas as providers of connectivity based on *dPCflux* (a) and *dPCconnector (b)*. Note: The numbers in the figure correspond to the coding (column Id in Table3) utilized to identify the 10 potential MCF patches with the highest *k* attribute values.

Importance of the potential MCF areas as landscape connector elements

In general, the $dPCconnector_k$ values were low in comparison to the other components and the *dPCk* index. The correlations between $dPCconnector_k$ and the other components were low (close to 0). However, the correlation between *dPCk* and $dPCconnector_k$ increased considerably from 0.61 to 0.77 when the habitat area with the highest attribute value was excluded (Id 5038).

In some sectors of potential CF and in general for the $\mathrm{TVS}_{\mathrm{Mich}}$ the importance of $dPCconnector_k$ differed in comparison with that of dPC_K (Fig 5). For example, in sector 1 where small areas of MCF predominated the dPC_K index was considerably low (Figure 4). However, the contribution of $dPCconnector_{\mathrm{sector1}}$ (41%) was greater than that of $dPCintra_{sector1}$(8 %), showing a significant role as connector elements and to a lesser degree as providers of proximity. The potential MCF areas of sector 2 contributed significantly as connector elements ($\Theta PCconnector_{sector2}$= 34%) but very little in terms of proximity ($\Theta PCintra_{sector2}$= 19.5%), where $dPCflux_k$ showed the highest contribution ($\Theta PCflux_{sector2}$= 46%). Similarly, the contribution of $dPCconnector_k$ in sector 3 was relatively high (26%) and greater than $\Theta PCintra_{sector3}$ (18%).

DISCUSSION

Modeling the potential distribution of the MCF

In spite of the fact that maximum entropy models have been more commonly used to model the distribution of species, they have also been used to model forest ecosystems (Weber, 2011; Culmsee et al., 2013) as well as other ecosystems like scrublands and wetlands (Riordan & Runden, 2009; Benito et al., 2014). Here we show a detailed model (30 m resolution) based on maximum entropy (MaxEnt) that represents the optimal zones where MCF could be potentially distributed under natural conditions along the $\mathrm{TVS}_{\mathrm{Mich}}$ (Fig. 1). It was important to complete the study with detailed spatial resolution because under natural conditions the MCF is distributed in relatively small and discontinuous areas along the $\mathrm{TVS}_{\mathrm{Mich}}$ (Vázquez-García, 1995; CONABIO, 2010). Nevertheless, for previous studies the variables of lower resolution (~1km) were useful to model the potential occurrence of the MCF in places where the MCF areas were larger or where the scale needed to be more general (Cruz-Cárdenas et al., 2012; Ponce-Reyes et al., 2012; Monterroso-Rivas et al., 2013).

The distribution model allowed us to differentiate the MCF of potential CF zones, the two types of vegetation could be confused because they occur in ecologically similar areas inside the study area (CONABIO, 2010). This could be due to the high predictive capacity obtained with the use of environmental variables used, like precipitation of coldest quarter (*bio19*), topographic variables like elevation (*dem30m*) and aspect (*asp_class*), and moreover by the adjustment of the final model by comparing and subtracting occurrence probabilities in the two models.

When comparing our MCF distribution map with others modeled in Mexico (Rzedowisky, 1990; Cruz-Cárdenas et al., 2012; Ponce-Reyes et al., 2012; Monterroso-Rivas et al., 2013), we found that the optimal distribution area for MCF in the TVS_{Mich} is much lower than those previously reported. For example, Cruz Cárdenas et al. (2012) reported approximately 850,000 ha of potential MCF in the TVS_{Mich} while our model showed only 37,567 ha. This could indicate that the models based on low resolution data overestimate the MCF area or include other vegetative types like CF that do not correspond to MCF, as in our case study. In making the final adjustments to the model, the potential ocurrence of MDF was underestimated in a few small isolated areas in sector 1 and sector 3 (Fig. 2) because, when subtracting the two models, the resulting probability values were lower than the acceptance threshold (≤ 0 = CF), being classified as BC. On the other hand, in sector 2 there was a minor adjustment after the subtraction method was applied-- in this case the original model showed a high quantity of pixels with probability values close to the lower limit of the acceptance threshold, resulting in an overestimation of the prediction of occurrence of MCF. However, based on the adjustment criteria the pixels with the highest probability values were selected (high suitability values) which allowed us to discard the pixels lower than the final acceptance threshold (≤ 0 =CF), and thus reducing the area that could have been over estimated.

Landscape connectivity analysis and prioritization of potential MCF patches

- *Original contribution of the MCF to overall landscape connectivity*

The optimal distribution areas of the MCF do not show a continuous spatial pattern, as noted by Vázquez (1995) and CONABIO (2010). This reinforces that under natural conditions the MCF shows a low structural connectivity. Moreover, the PC index values in the TVS_{Mich} and the potential CF area were very low (Fig 4.) indicating that the contribution potential of general connectivity the MCF is very limited. If the connectivity of the MCF is already low under natural conditions, it would now be even lower taking into account that the current area has been seriously reduced to approximately 60% (INEGI, 2005). However, these data would be more precise if the spatial resolution used were more compatible with those of this study or a multitemporal database (Mendoza et al., 2011), which would permit the analysis of changes in landscape connectivity similar to a study done by Correa et al. (2014) in the TVS_{Mich}.

The areas for potential MCF located in the central portion of the TVS_{Mich} (sector 2) would be the most important to increase general connectivity in the study area (Fig 4.). These areas have been deforested for the purposes of agriculture, primarily for avocado cultivation (Barsimantov & Antezana, 2012; Chavez- León et al., 2012; Bravo-Espinosa et al., 2014), which has seriously reduced habitat availability and habitat quality. This negatively impacts biodiversity, likely to a more serious degree than fragmentation (Fahrig, 1997) due to the fact that MCF was originally part of the understory of other forest structures (eg. Coniferous forest). Its disappearance creates gaps that diminish intra-patch connectivity of the original matrix, eliminating stepping stones that facilitate inter-patch connectivity (Rubio &Saura, 2012; Gil-Tena et al., 2013).

We found that the larger areas and those with greater likelihood for MCF occurrence (> attribute k value) tend to be more important for general connectivity maintenance than the smaller areas with lower suitability. This indicates a considerable contribution to intra-patch connectivity that is related to the intrinsic characteristics of each area in this case represented by weighting the area size and habitat suitability. The contribution of aspects related to topographic characteristics (e.g. position and location) is relevant in the TVS_{Mich}, and in the natural matrix of the CF. To better understand connectivity we analyzed the *dPC* components separately (Saura & Rubio, 2010) and evaluated the specific role that optimal MCF areas play in landscape connectivity (see following section).

-Different ways in which potential MCF areas contribute to landscape connectivity

In spite of a low general connectivity for potential MCF, its importance in biodiversity maintenance may be significant in the TVS_{Mich} due to the fact that the potential MCF areas show a high influence on dispersal and ecological fluxes between a particular modeled areas (which could serve as the origin or destination of fluxes) and the others (*ϴPCflux* domain). This is demonstrated in the high importance values obtained under the *dPCflux* component of the area with the highest attribute *k* value located in sector 2 (Id 5038, Fig. 5). At this time, taking into account that said area is in a relict state, its effectiveness has been diminished. However, the MCF areas that showed considerable potential dispersal flux to or from other habitat areas could be considered of high conservation priority to promote gene flow thinking about a eventual reintroduction of species (Saura & Rubio, 2010; Araiza et al., 2012; Saura, 2013).

We observed that under natural conditions the MCF has an important role in inter-patch connectivity due to the high contribution in the *connector* (d*PCconnector*) fraction. The results suggest that the discontinuous pattern of distribution is adequate in contributing to connectivity as bridges or stepping-stones between other areas of high habitat suitability; For example, to promote movement between breeding areas and other habitat areas separated by natural barriers or to aid in colonizing new habitat areas by alternate routes (Saura et al., 2014).

We differentiated the contribution of the *connector* component in different sectors of the study area (Fig. 5). We found that sector 2 is the most important, which could be explained by its topological position with respect to the other sectors. Transformation of the landscape diminishes general connectivity considerably. For this reason, we recommend that conservation actions in the TVS_{Mich} take into account the MCF relicts that are clearly of great importance as connector elements and increase the resilience of the landscape matrix. For example, in one sector of the TVS_{Mich}, Correa et al. (2014) highlighted the importance of stepping stone habitats in connectivity conservation since they increase the probability of dispersal between optimal habitat patches (though sub-optimal habitat are included as key elements, as well) and the identification of potential corridors that act as bridges between areas of high habitat suitability.

The component *dPCintra* showed a strong correlation with the patch areas, which indicates that for this component the larger patches are the areas that provide greater habitat availability (Bodin & Saura, 2010; Saura & Rubio, 2010). In this case, *dPCintra* was the fraction that showed the lowest contribution to general connectivity (*ƟPCintra)* in contrast with *ƟPCflux,* which showed the highest contribution of the three fractions. The dispersal distance that we used as the basis for connectivity evaluation (d=10,000; Correa et al., 2014) corresponds with the results of *ƟPCintra.* This has little relevance for an organism that has large to intermediate dispersal distances as they have a greater capacity to move between patches and would not find a large patch with internal connectivity as necessary. To the contrary, *dPCintra* would have greater impact for an organism with a lower dispersal capacity or short dispersal distance as it could move more easily inside the available area inside a larger patch but would be limited in moving between more isolated patches if there was need (Saura & Rubio, 2010). The largest potential area (and higher attribute *k* value, Id 5038) showed the highest importance value in comparison with the others, which were notably smaller (Table 3). This indicates that the loss of these larger areas would have a large impact on the populations of organisms with a more limited dispersal capacity. In spite of the gap in actual relative loss figures for the MCF with respect to the total area of the TVS_{Mich}, some studies have shown that the current distribution (INEGI, 2005; Dobler, 2013; Alvarez, 2013) is concentrated mainly in sector 2, which largely corresponds to the expansion zone of the avocado orchards indicating that the MCF areas that previously existed have been reduced to approximately 60 %, greatly compromising the intra-patch connectivity in this sector.

A limitation of this study is the scarce information regarding the current distribution of the MCF, which impedes a precise comparative analysis with regard to the change in connectivity with the potential MCF areas. However, if we consider this study as an important contribution to the distribution potential of the MCF in Mexico, particularly with regard to the TVS_{Mich} with a spatial resolution previously unreported, it acts as a baseline for more profound analysis in a later study. Moreover, it is a key contribution in mountain-ecosystem conservation in Mexico as it allows for the recognition of the contribution of landscape connectivity under natural conditions, which is generally reported for human-dominated landscapes (García-Feced et al., 2011; Rubio et al., 2012; Liu et al., 2014). It also allows for a detailed evaluation of the different ways that habitat loss can impact landscape connectivity (Bodin & Saura, 2010; Rubio & Saura, 2012).

CONCLUSIONS

This study shows that the potential MCF area and its spatial distribution currently have a diminished contribution to overall connectivity in the TVS_{Mich} as compared to its original distribution. However, based on the values of the three fractions of *PC*, the conservation of the MCF in Michoacan is key for the maintenance of dispersal and ecological fluxes (i.e. MCF insector 2) to and from the other potential areas as well as the contribution of the MCF as a connector element between other habitat units. The importance of said areas in conservation should not only be considered with the intrinsic ecological characteristics of each area (i.e. habitat suitability and size), but also their location or position in the landscape. This work allowed for the evaluation of the impact of connectivity loss in those areas that, in their majority, have been subject to anthropic transformation. The results of this study can aid in the identification of optimal areas where MCF should be distributed and conserved to establish restoration activities, as their inclusion would reestablish necessary connectivity. Thus, this study is the first stage of research in prioritizing MCF conservation areas and contributes to the future evaluation of landscape connectivity change to concentrate conservation efforts on current patches most influential in connectivity.

ACKNOWLEDGEMENTS

The authors would like to thank the project “Evaluación de la importancia relativa de bosque húmedo de niebla bajo un enfoque de paisaje" (clave 179386)”, funded by CONACYT. The first author would like to personally thank CONACYT for the grant awarded to complete his doctoral studies in Geography at UNAM. We would also like to thank Dra. Ángela Cuervo for her valuable feedback on earlier versions of this article and Dr. Oswaldo Téllez for his support in the creation of the bioclimatic layers used in the modeling process. We also thank the two anonymous reviewers for their suggestions and constructive commentary, which aided greatly in improving the manuscript. Finally, we would also like to thank Miramanni Mishkin, Ph.D. ABD for a previous review of this article.

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CAPITULO III

EVALUACIÓN DEL IMPACTO ANTRÓPICO SOBRE LA CONECTIVIDAD DEL PAISAJE A TRAVÉS DE UN ÍNDICE MULTI-DIMENSIONAL DE HUELLA ESPACIAL HUMANA EN UN PAISAJE ALTAMENTE BIODIVERSO DEL CENTRO DE MEXICO

EVALUATION OF ANTHROPOGENIC IMPACT ON HABITAT CONNECTIVITY THROUGH A MULTIDIMENSIONAL SPATIAL HUMAN FOOTPRINT INDEX IN A HIGHLY BIODIVERSE LANDSCAPE OF CENTRAL MEXICO

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ABSTRACT

Evaluating the cumulative effects of the human footprint on landscape connectivity is crucial for implementing policies for the appropriate management and conservation of landscapes. We present an adjusted multidimensional spatial human footprint index (SHFI) to analyze the effects of landscape transformation on the remnant habitat connectivity for 40 terrestrial mammal species representative of the Trans-Mexican Volcanic System in Michoacán ($\text{TMVS}_{\text{Mich}}$), in western central Mexico. We adjusted the SHFI by adding fragmentation and habitat loss to its original three components: land use intensity, time of human landscape intervention, and biophysical vulnerability. The adjusted SHFI was applied to four scenarios: one grouping all species and three grouping several species by habitat spatial requirements. Using the SHFI as a dispersal resistance surface and applying a circuit theory based approach, we analyzed the effects of cumulative human impact on the probability of connectivity in the different scenarios. For evaluating the relationship between habitat loss and connectivity, we applied graph theory-based equivalent connected area (*ECA*) index. Results show over 60% of the $\text{TMVS}_{\text{Mich}}$ has high SHFI values, considerably lowering the probability of connectivity for all species. Nevertheless, the effect on connectivity of human impact is higher for species with limited dispersal capacity (100-500 m). Our approach provides a new form of evaluating human impact on habitat connectivity that can be applied to different scales and landscapes. Furthermore, the approach is useful for guiding discussions and implementing future biodiversity conservation initiatives that promote landscape connectivity as an adaptive strategy for climate change.

Key words: Cumulative human impact, habitat connectivity, multi-species, Mexico.

1. INTRODUCTION

The cumulative human footprint on the landscape has reduced the resilience capacity of ecosystems and their provision of goods and environmental services, generating irreversible effects on biodiversity, such as local species´ extinction (Bennet, 1990; Saunders et al., 1991; Laurance et al., 2008; Pavlacky et al., 2012). The spatial impacts of this process on the landscape have been quantified either by means of the human footprint indexes (HFI) (Sanderson, 2013) or through indexes of naturalness (Theobald, 2010), both providing opposite readings. These methods to measure the influence of human activities on the landscapes have been applied at different levels: at the global level to understand human impact on biomes (Sanderson et al., 2002), at the national level for the spatial evaluation of human influence on ecosystems and natural regions (Etter et al., 2011; Gonzalez-Abraham et al., 2015), and at the regional level to evaluate the human impact on terrestrial ecoregions (Woolmer et al., 2008; Trombulack et al., 2010).

In studies on biodiversity conservation, HFIs have been used to evaluate landscape connectivity, based on the assumption that the intensity of the human footprint is positively correlated with the landscapes' resistance to dispersal (Baldwin et al., 2010; Alagador et al., 2012; Hand et al., 2014). The disadvantage of parameterizing HFIs as a surface of resistance is that, in general, it assumes that the effect of the human footprint is the same for all focal species, which can result in an overgeneralized representation of human effect on organisms' dispersal. To correct these biases, several approaches have been proposed (Krosby et al., 2015; Alagador et al., 2012), such as considering multiple species and integrating their response to human footprints, while differentiating the spatial distributions of organisms to identify optimal habitat areas that harbor groups of species with similar environmental requirements (i.e., environmentally similar habitats; Alagador et al., 2012). Additionally, the construction of HFIs with finer spatial resolutions (Leu et al., 2008; Woolmer et al., 2008; Theobald, 2010) or an incorporation of additional variables describing human effects over ecological processes (Leu et al., 2008; Etter et al., 2011) also constitute better inputs for connectivity models.

Following the methodology of Sanderson et al. (2002), González-Abraham et al. (2015) developed a human footprint map for Mexico and identified ecological regions having a higher degree of transformation from human activities. They found that areas with high ecological importance and biodiversity, such as the Trans-Mexican Volcanic System (TMVS), presented a high degree of human disturbance. To date, however, few studies in Mexico have evaluated the effect of the human footprint on landscape connectivity (Fuller et al., 2006; Correa et al., 2014). By integrating the three spatial footprint dimensions: intensity of land use (F_{int}), the time of intervention on the landscape (F_{time}), and biophysical vulnerability (F_{vul}), the model proposed by Etter et al. (2011) provides a more comprehensive approach for addressing the spatial human footprint for applications in conservation planning (Ocampo-Peñuela and Pimm, 2014; Qiu et al., 2015). Etter et al. (2011) defined F_{int} as the degree of modification of habitat determined by resource extraction and predominant land use, including management forms, F_{time} as the time passed since the landscape has been subject to current human activity, and F_{vul} as the degree to which a system suffers damages caused by land use. However, in the context of connectivity, this methodology could be supplemented by enhancing the incorporation variables of fragmentation and habitat loss and making them explicit both for individual species or from a multi-species approach (Brodie et al., 2015; Rayfield et al., 2015).

Our paper evaluates the effect of using human footprint measures on the assessment of habitat connectivity in the Trans-Mexican Volcanic System in Michoacán ($TMVS_{Mich}$) in western central Mexico. We apply the multidimensional HFI (Etter et al. 2011) modified by the addition of data about habitat loss and fragmentation. We integrated the information on human effects on individual species (single-species approach) and on multi-species scenarios in order to analyze anthropic impacts on groups of species with different spatial requirements.

2. METHODOLOGY

2.1 Study area

The TMVS is a volcanic chain extending across central Mexico from the Pacific Ocean to the Gulf of Mexico (Ferrari et al., 2012). The TMVS covers an area of 160,000 km^2 and is recognized as the most heterogeneous biogeographic province of Mexico in terms of its geological and biotic history, reflected by its richness in biodiversity and endemisms, by being a speciation center (Fa and Morales, 1991; Ramamoorthy et al., 1998) and by being a transitional area between the Nearctic and the Neotropical biogeographical regions (Gámez et al., 2012). Sánchez Cordero et al. (2005) estimated that 70% of the original habitat in the TMVS has been transformed and presents a high risk of extinction of endemic mammals because of the threats represented by land use and land cover changes, in particular from forest ecosystems to agriculture and urban areas.

Our study encompasses the central portion of the TMVS including the northern part of the state of Michoacán with an approximate area of 28,100 km^2 ($TMVS_{Mich}$; Figure 1). It covers an altitudinal range from 1,000 to 3,800 m and includes the following physiographic sub-provinces: Chapala, bajío Guanajuatense, bajío Michoacano, llanuras y sierras de Querétaro e Hidalgo, cordillera Costera del sur, Neovolcánica Tarasca, depresión del Balsas, Mil Cumbres, and depresión del -Tepalcatepec. Anthropic land use and land cover occupy 70% of the $TMVS_{Mich}$, suggesting a strong influence of human footprint on connectivity. Natural land covers are mostly of temperate forests (conifer, mixed conifer and oak forests, and localized mountain cloud forests) and, to a lesser extent, of low deciduous tropical forest and aquatic vegetation (INEGI, 2013). Gámez et al. (2012) and Escalante et al. (2007) consider the central TMVS as a highly biodiverse landscape with an average richness of 105 species of terrestrial mammals. Eight natural protected areas are included within the $TMVS_{Mich}$ (Figure 1), mostly distributed in the mountainous portions, but covering a meager 2.4% of the study area (Bezaury-Creel et al., 2009).

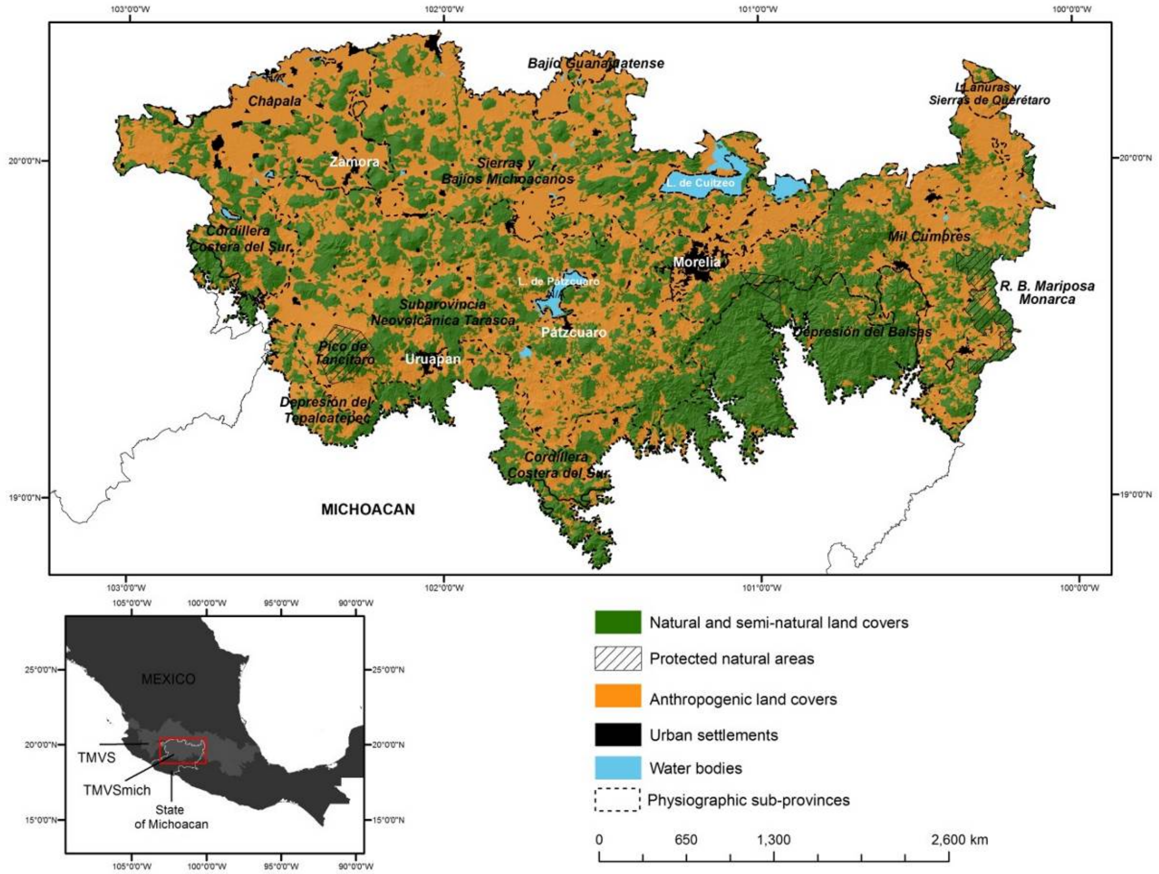

Figure 1. Localization of study area showing the spatial distribution of natural and semi natural land cover (including secondary vegetation), as well as anthropic land covers. Source: Land cover and land use map, series V (INEGI, 2013).

2.2 Selection of focal species and habitat modeling

Based on a previous study of connectivity in the TMVS (Fuller et al., 2006), we initially selected 99 species of terrestrial mammals. We then compiled occurrence data for each species from the databases of the *Global Biodiversity Information Facility* (http://www.gbif.org/), CONABIO (http://www.conabio.gob.mx/) and from the literature (e.g., Orduña, 2008; Chávez-León and Zaragoza, 2009; Charre-Medellín et al., 2015), choosing only the points within the $\mathrm{TMVS}_{\mathrm{Mich}}$. We applied a second filter to eliminate duplicate and overlapping points and selected those species that had at least 10 occurrence points (Pearson et al., 2007). The depurated list resulting from this process included 40 species of terrestrial mammals within the $\mathrm{TMVS}_{\mathrm{Mich}}$ (Table S1). For each chosen species, we modeled its potential habitat with a 30 m spatial resolution using the software MaxEnt 3.3.3 (Philips et al., 2006) and updated climatic layers for Mexico as independent variables (Cuervo-Robayo et al., 2014). Subsequently, following the methodology of Fuller et al. (2006), we generated actual or remnant habitat by overlapping the natural land covers (Figure 1) with the models of potential habitat, excluding transformed areas. These actual remnant habitat patches of each species were used for the analysis of connectivity (see Section 2.4).

2.3 Adaptation of SHFI and description of data sources

2.3.1 Description of the selected SHFI and adjustment in the context of connectivity

We used the spatial human footprint index (SHFI) proposed by Etter et al. (2011) as a spatial proxy for evaluating the human impact on connectivity. In order to better take into account the effects of the human footprint for the connectivity analysis, we added a new component expressing habitat loss and fragmentation (F_{frag}), to the original index. The incorporation of F_{frag} to the SHFI requires species specific values, given they depend on the species' spatial distribution and actual and potential habitat.

$$SHFI = \frac{\left(F_{\mathrm{int}} + F_{time} + F_{vul} + \boldsymbol{F}_{\boldsymbol{frag}}\right)\times 100}{\sum(F_{\mathrm{int}}\max + F_{time}\max + F_{vul}\max + \boldsymbol{F}_{\boldsymbol{frag}}\mathbf{max})} \qquad \text{(Eq.1)}$$

$$F_{\mathrm{int}} = LU + PD + DR + DS + FI + BI$$
$$F_{time} = TI$$
$$F_{vul} = SF + SL + MI + ED$$
$$\boldsymbol{F_{frag} = IRH + PTH + IET}$$

Where LU is the type of land use, PD is the rural population density, DR is the distance to roads, DS is the distance to settlements, FI is the fragmentation index of natural vegetation, BI is the biomass index relative to natural potential, TI is the time of intervention on ecosystems in years, SF is the soil fertility index, SL is the slope, MI is the available moisture index, and ED is the number of endemic species. For a conceptual framework with the details of each subindex and its application in the original case study (see Etter et al., 2011.

The new F_{frag} component integrates three variables:

1) *Isolation of remnant habitat (IRH)*: Distance of transformed areas to remnant patches.
2) *Percentage of transformed habitat (PTH)*: Percentage of habitat transformed by human activities in 1 km^2.
3) *Index of "extensiveness" of transformation (IET)*: Mean distance between each pixel and the centroid of each patch of transformed habitat. Known as the "Gyrate" or "Radius of Gyration" index (McGarigal et al., 2002). Establishes a value to the mean distance an organism should travel from a random point inside a patch before encountering its limit (Botequilha Leitão et al., 2006).

2.3.3 Data sources and calculation of the SHFI adjusted to the case study

Data for calculation of the human footprint in the TMVS$_{\mathrm{Mich}}$ were grouped according to the methodology of Etter et al. (2011). Six variables were used to inform land use intensity, one for time of intervention, four for biophysical vulnerability, and three related to habitat fragmentation for each species. Some databases were elaborated for the present study (e.g., map of potential ecosystems for the component F_{time}, map of endemic species richness for variable F_{int} (Table 1), which also aided us in obtaining a SHFI map with a more detailed resolution than the original (1 km). The input databases and models for the connectivity analysis were standardized to a 100 m resolution using Albers equal-area conic projection. Following Etter et al. (2011), all variables in the SHFI were rescaled between 0 and 5, indicating in ascending order a null to very high contribution to the human footprint (Table 2).

As in the original method (Etter et al., 2011), values for each subindex were added to produce partial footprint maps. Finally, the four maps were added and normalized to a scale between 0-100, to produce a general cumulative human footprint map (omitting component F_{frag}), and 40 maps of human footprint were produced for the habitat of each focal species (including component F_{frag}).

2.4 Construction of multi-species scenarios and evaluation of human footprint on habitat connectivity

To assess the differences in human footprint among groups of species with contrasting spatial requirements, we constructed three multi-species scenarios and another one grouping all the species. Because the degree of connectivity largely depends on the capability of species to move between patches of suitable habitat (Cushman and Landguth, 2012), we grouped terrestrial mammal species according to their requirements of dispersal distance and minimum habitat area (Appendix 1); variables that are well documented (e.g., Jones et al., 2009; Pe'er et al., 2014) and are easily incorporated into spatial models. Group 1, which includes species with large dispersal ranges (>3000 m) and large minimum habitat areas (>350 ha), is composed of seven species in the order Carnivora, one in the order Didelphimorphia, and one in the order Artyodactila; the species are listed in Appendix 1. Group 2 includes 21 species with medium dispersal ranges (250-1500 m) and minimum habitat areas (3-350 ha), three in the order Lagomorpha, two in the order Insectivora, 17 in the order Rodentia. Group 3 includes 10 species of Rodentia with small dispersal ranges (<250 m) and small minimum habitat areas (3 ha). Group 4 includes all of the species (McShea and Madison, 1992; Bowman et al., 2002; Saura et al., 2011; Santini et al., 2013; Saura et al., 2014).

The mobility of species was characterized by means of a resistance/friction surface calculated with the SHFI map by assuming that high human footprint areas are less permeable to species displacement (see ranges in Figure 2; Baldwin et al., 2010; Alagador et al., 2012).

Areas within the limits of the $TMVS_{Mich}$, but beyond the suitable habitat of individual species, were considered as restricted mobility areas (Resistance=100), although not being strict barriers common to all species or to multi-species groups. For obtaining maps for groups of species, the cumulative resistance calculated by adding the resistance surfaces of each species of each of the multi-species group (sum of the human footprint of species in groups 1, 2, and 3, and of all species). The four resulting maps were rescaled in an interval going from 0 to 100 (Cushman and Languth, 2012; Brodie et al., 2015). We also unified the habitat patches of individual species in order to obtain common high habitat suitability areas for each multi-species group.

The evaluation of the effect of the human footprint on connectivity was based on circuit theory (McRae, 2006; McRae et al., 2008), using the cumulative resistance maps and the common habitat patches for all species and for each multi-species group for analyzing how human impact affects the probability of connectivity of species with different dispersal capabilities and spatial requirements. Although we analyzed the impact on the habitat of each individual species, we only present the results for multi-species groups. The spatial distribution of current flows (probability of connectivity) in each scenario was assessed by using Circuitscape 4.0 (McRae et al., 2013), assuming that groups of low current density pixels show a stronger effect of human footprint and vice versa. The resulting maps were reclassified regarding impact levels (ranges shown in Figure 5). To evaluate the spatial differences between all pairs of human footprints maps and all pairs of probability of connectivity maps, we applied the relative rank test of Warren et al. (2011). The test was applied using the ENM software tools 1.4 (Warren et al., 2010). Results from the test range from 0 to 1, with values closer to 1 indicating more spatial similarity and 0 indicating that the inferred model shows no similarity to the observed model (Warren et al., 2011). Additionally, we applied the Pearson correlation to evaluate the differences between pairs of maps and to measure the relationship between the SHFI and current flow categories.

To complement the analysis based on circuit theory for assessing the relation between the SHFI and the inter-patch connectivity, we applied the equivalent connected area (*ECA*) index. The index measures the size of continuous habitat patch needed to produce the same probability of connectivity, than the one produced by all the habitat patches of the landscape being evaluated (for details on *ECA* see Saura et al., 2011). To incorporate the effects that the landscape matrix has on connectivity, we used the cost distances between habitat patches based on the calculated resistance surfaces of the multi-species scenarios and the cumulative resistance for all the species. Finally, we compared the relative variation in the *ECA* index (*dECA*) caused by the effect on the distribution of habitat patches of the human footprint with the relative variation in the surface area of remnant habitat patches (*dA*). *ECA* calculations were made using the software Conefor 2.6 (Saura and Torné, 2009).

3. RESULTS

3.1 The cumulative human footprint on habitat scenarios

The highest values of human footprint were coincident in all scenarios and for all the species, concentrated in the northern part of the $\text{TMVS}_{\text{Mich}}$ (Figure 2a), the Bajío Michoacano, and mainly in the lowlands of the Lake Cuitzeo and Lake Chapala sub-provinces, where agro-industrial land use is predominant. Inversely, the lowest values of human footprint were localized in the southern part of the $\text{TMVS}_{\text{Mich}}$, concentrated in the Neovolcánica Tarasca sub-province, mainly in mountain landscapes of the Lake Pátzcuaro basin and the Pico de Tancítaro. The low values are also distributed to the east of the $\text{TMVS}_{\text{Mich}}$ in the Mil Cumbres sub-province (characterized by the presence of large patches of temperate forests and stands of mountain forest) and in the natural protected area of the Monarch Butterfly Biosphere Reserve (Figure 2a).

Over 62% of the area of all habitat scenarios were dominated by high values of human footprint (SHFI >60), indicating a high degree of transformation and resistance to species mobility (Figure 3). Nevertheless, the maps of the spatial human footprint show particular patterns for each scenario, which result in various spatial patterns levels of landscape resistance to connectivity. For the scenario by grouping all species we found that 58% of the surface has a high cumulative impact on species' habitat (SHFI >60), and only 27% was dominated by low to very low values of human footprint (SHFI <50). Scenario 3 (order Rodentia) and 1 (mostly Carnivora) showed that over 65% of its surface area was dominated by high values of human footprint (Figure 3). Scenarios 4 (all species) and 1 showed lower human footprint values (27% and 24%, respectively), indicating that relative to scenarios 2 and 3 they concentrate more sectors with low resistance and high probability of connectivity (e.g., Lake Pátzcuaro basin and Mil Cumbres sub-provinces; Figures 2b and 2d). Scenario 2 had a limited distribution of high values of human footprint values (62%) in relation to the remaining scenarios, and 22% corresponded to low human footprint values. Similarly, the distribution pattern of high human footprint values for scenario 2 differs from the others in not being concentrated in the Bajío Michoacano sub-province (Figure 2c).

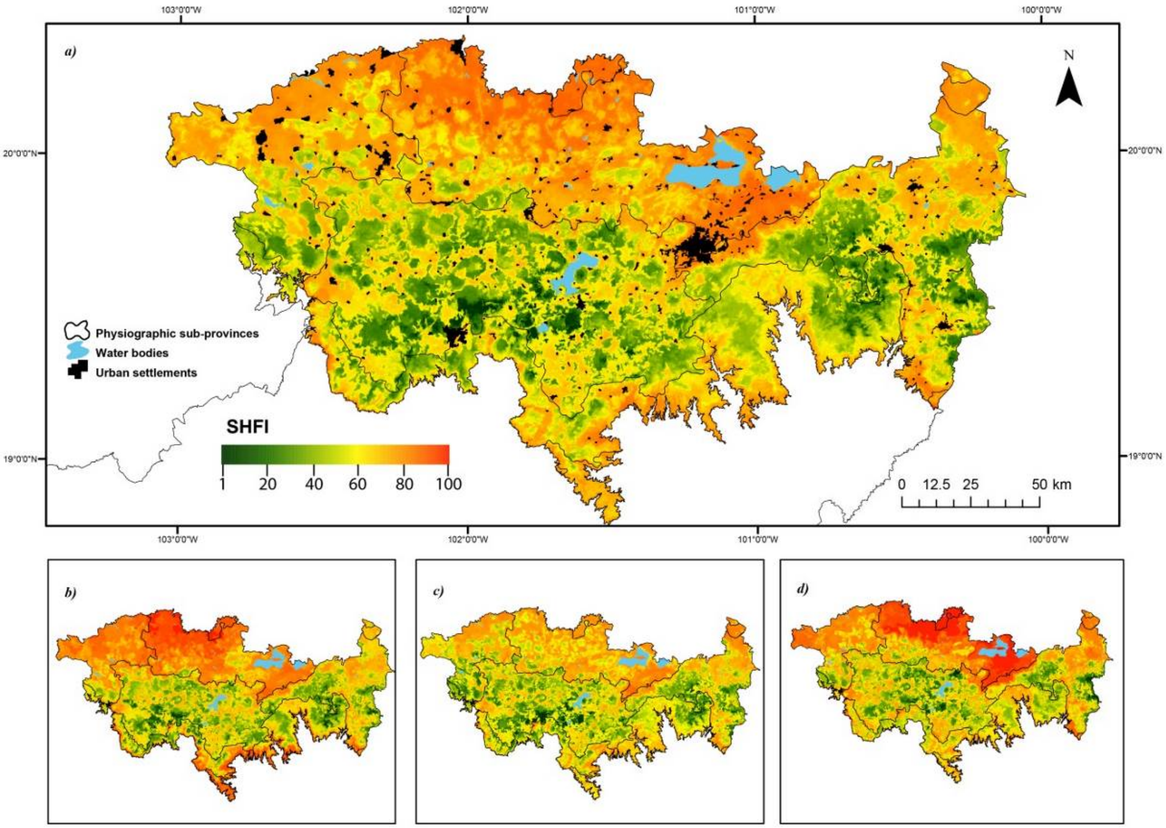

Figure 2. Distribution of the spatial human footprint index (SHFI) in the four studied scenarios. a) Scenario 4 (all species). b) Multi-species scenario 1. c) Multi-species scenario 2. d) Multi-species scenario 3.

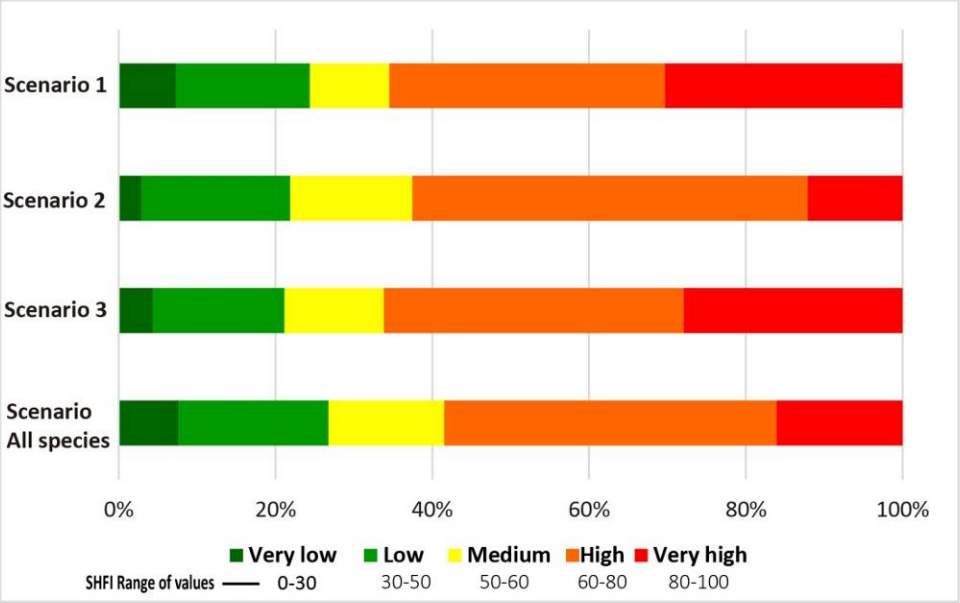

Figure 3. Distribution of the spatial human footprint index (SHFI) in the studied area. Note: Colors correspond to the ranges of SHFI spatially represented in Figure 2.

The relative rank test depicted that all scenarios have a similar distribution, but they do not have the same spatial distribution (0.65 to 0.78). The correlation between the SHFI maps depicted a general relationship between their distributions (>0.79). The comparison between scenario 2 and all-species scenario depicted the highest value (>0.78), indicating that the spatial distribution of the ranges of SHFI are the most congruent in comparison with the other scenarios. In contrast, the comparison between scenario 1 and 2 showed the lowest value (0.65).

The relative rank test applied by categories of SHFI (Table 4), shows that the scenarios of multi-species groups (1, 2 and 3), in comparison with the all-species scenario, generally, have higher values of spatial overlap that when compared among themselves (e.g. scenario 1 compared to scenario 2). The categories “very high” and “high” have the highest spatial correlation, mainly between multi-species groups (1 and 2) with the all-species scenario. The "low" category of the SHFI has the highest spatial differences when it is compared between models.

In general, the relative rank test showed that the spatial distribution of scenarios largely overlap, but in no case are they spatially identical (Warren’s relative rank value between 0.65 and 0.78). Similarly, the correlations between SHFI maps in general show a direct relation with their distributions (>0.79). The highest value for the test that we observed was for the comparison between scenario 2 and the all-species scenario (>0.78), indicating that the spatial distribution of levels of human footprint is the most congruent of all combinations. Contrastingly, the comparison between scenarios 1 and 2 showed the lowest relative rank value (0.65).

The results from the relative rank test by categories of SHFI (Table 4) reveal that all

multi-species scenarios (1,2, and 3) show higher values when compared with the all-species scenario (e.g., scenario 2 compared with the all-species scenario) than when compared between them (e.g., scenario 1 compared with scenario 2).

3.2 Effect on habitat connectivity of the cumulative human footprint for different groups of species

The result of the circuit model showed the level of human impact on the probability of mobility of organisms and other ecological flows (e.g., dispersal and gene flow), which is determined by the interaction with the landscape of the intensity of human activities, the temporal span of such activities, the biophysical vulnerability, and particularly, the loss of habitat availability and habitat fragmentation. We found a predominance of a high degree of impact on connectivity in the $\mathrm{TMVS_{Mich}}$ (Figure 4a), with over 65% of the study area being dominated by low to very low values of connectivity, which considerably compromise the mobility of terrestrial mammals in the landscape (Figure 5). According to the current flow maps, the spatial patterns of impact are coincident for all four scenarios. Low values of connectivity concentrate mostly in the sub-provinces of Chapala and Bajío Michoacano (Figure 4), areas that are related to a high human footprint (Figure 2). However, the current flow maps corresponding to scenario 4 (all species; Figure 4a) and the multi-species scenarios 1 and 2 (Figures 4b and 4c) show a predominance of a high degree of connectivity for the habitat patches in the lowlands of the lake Cuitzeo basin (Figure 1), despite the very high human footprint there. On the contrary, the multi-species scenario for group 3–containing species with short dispersal ranges and requiring less extensive habitats (Figure 4d)–showed in the same area a low degree of connectivity and a considerable effect of the human footprint (Figure 2d).

The spatial distribution of high values of current flow was also very similar in the four scenarios (yellow color in Figure 4). Areas with a high probability of connectivity and relatively low anthropic impact were mostly concentrated in the highlands of the lake Pátzcuaro and lake Cuitzeo basins, in the Mil Cumbres sub-province, and upper sectors of the depresión del Balsas separated by a sector with high cumulative human footprint values. However, high values of connectivity were more noticeable in the scenarios for group 1 and for all species (Figures 4a and 4b).

Regarding the effect of human footprint on connectivity, few differences were observed between scenarios (Figure 5). The scenario for group 4 (all species) had the largest surface area with a high degree of human footprint on connectivity (65%) relative to the three multi-species scenarios. As expected, a very small extension of the $\text{TMVS}_{\text{Mich}}$ was represented by low values of impact on connectivity (<7%) in all scenarios, and between 28% and 33% of the surface was dominated by a medium level of impact on connectivity.

In general, all pairwise comparisons of current flow maps depicted a high spatial agreement (>0.8). The comparison between scenario 2 and the all-species scenario depicted the highest relative rank value (0.87), indicating a high spatial similitude between the spatial effects of human footprint on connectivity in scenario 2 in relationship to the all-species scenario. In addition, the correlations between flow maps depicted a clear spatial relationship.

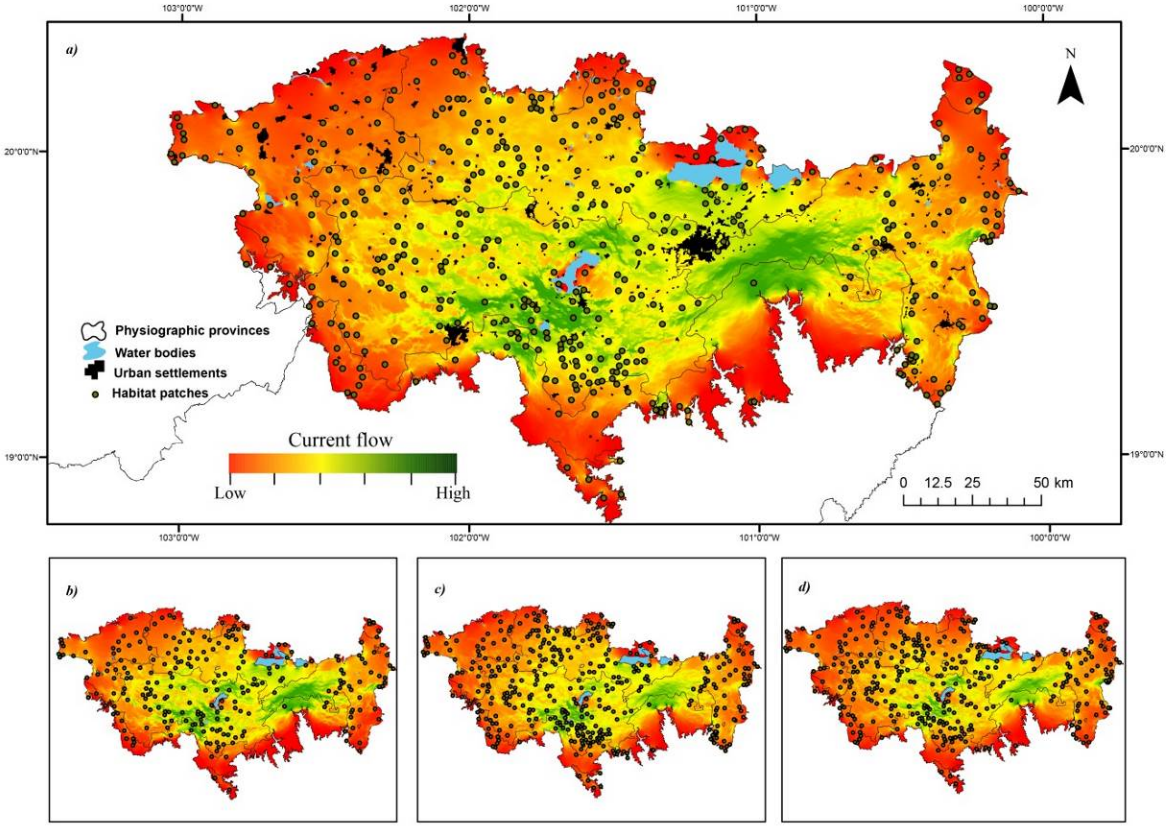

Figure 4. Maps of current flow based on circuit theory. The model can be interpreted under two assumptions: as a surface of probability of connectivity between all habitat patches in each multi-species scenario (b, c, and d) and in the scenario including all species (a); or as the degree of human impact on connectivity (inversely proportional to current flow) in which a high current flow is equivalent to a higher

probability of mobility through habitat patches (green dots), and, therefore, also to less human impact on connectivity.

The application of the relative rank test by categories (Table 4), shows that the spatial distribution of the human footprint effect is very similar in all the scenarios. Additionally, they are similitudes in the spatial distribution of the categories of the impact of human footprint on connectivity of particular groups of species and the group that include all species. For example, the comparison between scenario 2 and the all-species scenario has high values of a range above 0.81, indicating that the spatial distribution agreement of the impact levels is high. Particularly, the categories "low" and "very low" of impact of the human footprint presented the highest values of relative rank, which indicate a high level of spatial coincidence (>0.92). The impact categories that are more different in spatial terms, were high and low, nevertheless, the overlap values was above, 0.73.

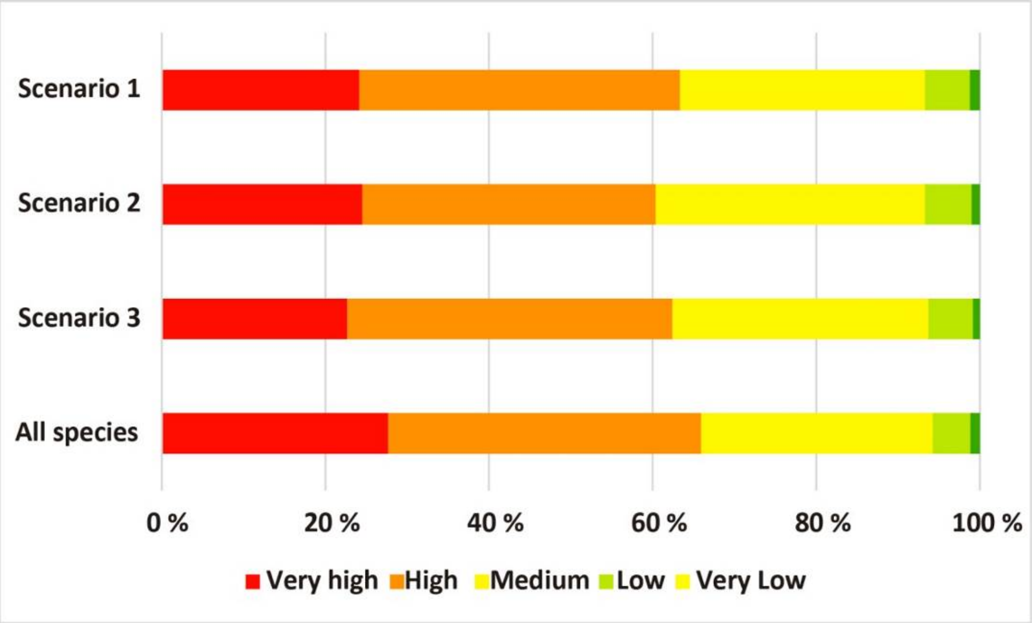

Figure 5. Distribution of the cumulative effect on landscape connectivity of the human footprint for each multi-species scenario and for the scenario including all species. Note: Colors correspond to the levels of current flow in Figure 4.

In general, all pairwise map comparisons showed high spatial correspondences (>0.80). The highest value of relative rank (0.87) was obtained when comparing scenario 2 with the all-species scenario, which indicates a close similarity in scenario 2 between the spatial distributions of the effects of the human footprint on connectivity, relative to that in the all-species scenario. Similarly, correlations between current flow maps in general show a direct relation with their spatial distributions (>0.87). The results from the relative rank test by category (Table 4) in general showed that the spatial distribution of the human footprint is very similar for all scenarios. We identified important similarities, though, in spatial distribution between the categories of human footprint impact on connectivity that relate to particular groups of species and the group containing all species. For instance, in the comparison between scenario 2 and the all-species scenario, all relative rank values were above 0.81, indicating a high correspondence between the spatial distributions of the different levels of impact. In particular, the “low” and “very low” categories of human footprint impact resulted in the highest relative rank values, showing high level of spatial overlapping (> 0.92). The categories of impact showing the highest differences were “high” and “low,” despite that their overlapping value was above 0.73.

3.3 Relationship of the effect of human footprint on habitat loss and inter-patch connectivity

We considered the effect on connectivity of the landscape matrix by using the different resistance surfaces derived from the SHFI by single-species and in the multi-species groups. We assumed that the landscape has become more resistant to mobility of species because of the effect of the human footprint. According to our results of the *ECA* index, the human footprint has generated a substantial change in habitat availability of the multi-species groups and particularly in the general connectivity of the landscape. We found that an average 54% of the habitat of all the studied species has been transformed. The relative variation in terms of connectivity (*dECA*), however, was higher, with an average 84% of the general connectivity along the $\text{TMVS}_{\text{Mich}}$ being lost (Figure 6). When considering the effect of the landscape matrix on the four scenarios by means of cost distances between patches of habitat, we found that the *ECA* is considerably diminished in comparison with the same when only Euclidean distances between patches of habitat are considered and the landscape matrix is not taken into account. Similarly, the groups of species with short dispersal distances (groups 2 and 3) have the lowest *ECA* index value (<430,000 ha), indicating a higher impact on connectivity, which diminishes as dispersal distances become longer (Figure 6).

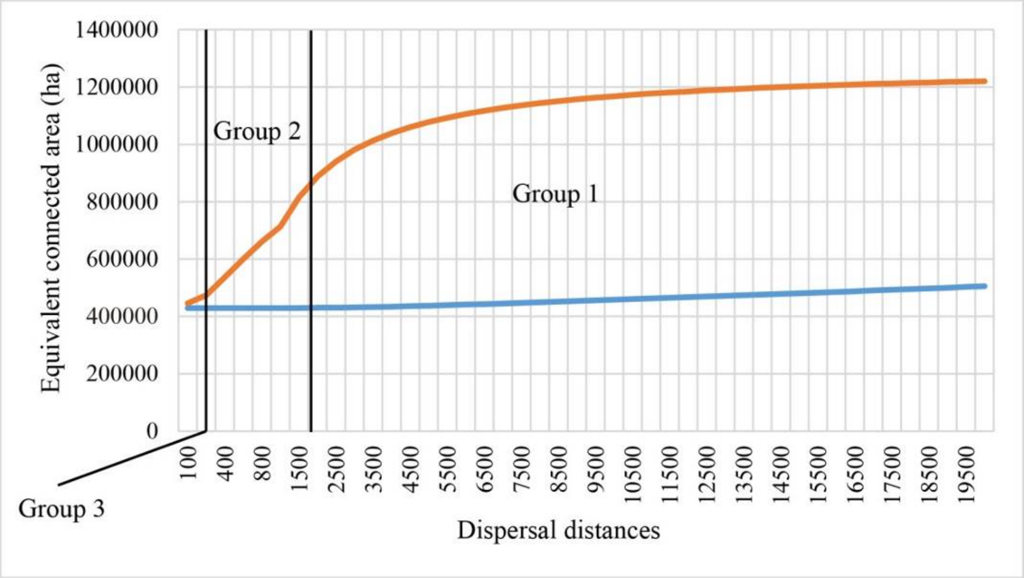

Figure 6. Values of *ECA* index based on Euclidean distances between habitat patches (orange line) and considering the effect of the landscape matrix based on cost distances between habitat patches in the multi-species scenarios (blue line). The characteristics of each group are explained in Methodology.

4. DISCUSSION

We applied a comprehensive SHFI in terms of conservation planning (Etter et al., 2011), adjusting it by the addition of a new component, which include habitat loss and fragmentation for evaluating cumulative human impact on the probability of connectivity in groups of species with similar spatial requirements. We mapped such an effect and its distribution across common habitat patches to each multi-species scenario. The incorporation of potential habitat models for multi-species groups (relative to individual species) was key for our study as a reference for modeling the distribution of the remnant habitat (Fuller et al., 2006; Baldwin, 2009; Kuemmerle et al., 2011; Mendoza et al., 2013) and the subsequent analysis of the anthropogenic impact on dispersal flow and inter-patch connectivity (Saura et al., 2011).

4.1 Spatial human footprint in habitat scenarios

In general, our results showed that a strong anthropic impact predominates over the habitat of all studied species and identified large areas within the $\text{TMVS}_{\text{Mich}}$ which are dominated by high values of SHFI (Figure 2a). According to González-Abraham et al. (2015), the TMVS is one of the ecoregions in Mexico with the highest anthropic impact in areas characterized by high agricultural productivity, geographic accessibility, and high population density. Within the $\text{TMVS}_{\text{Mich}}$, the Bajío Michoacano, in particular the center of the Cuitzeo lake basin is one of the areas with the highest habitat suitability for all the species and is the most impacted by the human footprint. This area has been widely transformed for agriculture (e.g., maize, wheat, chickpeas, oats, etc.) and concentrates 35% of the population in the $\mathrm{TMVS}_{\mathrm{Mich}}$. About 20% of the population is in the city of Morelia (INEGI, 2010), which has the highest urban growth rates both within the region (López et al., 2001; Mendoza et al., 2011) and the state of Michoacán (Bocco et al., 2001). We found, however, other less impacted areas in the southern part of the $\mathrm{TMVS}_{\mathrm{Mich}}$, such as the Neovolcánica Tarasca sub-province (in particular in the Pico de Tancítaro and in the high basins of the Lakes Cuitzeo and Zirahuén), the Mil Cumbres sub-province, and the Monarch Butterfly Biosphere Reserve. Before being transformed by human activities, these regions formed a habitat corridor throughout the TMVS in Mexico (Correa et al., 2016).

In the low impacted areas, low values of human footprint predominate in all multi-species scenarios (Figures 2b, 2c, and 2d). This condition may be explained by the remnant suitable habitat patches represented by fragmented primary and secondary land covers (mostly temperate forests with stands of mountain cloud forest), indicating that historical human activities have generated a heterogeneous spatial pattern of these remnants (Etter et al., 2011). However, the predominant anthropic matrix shows very high values of SHFI in the sub-provinces of the Neovolcánica Tarasca, Mil Cumbres, depresión del Balsas, and the Monarch Butterfly Biosphere Reserve, which is largely caused by the expansion of avocado plantations and the industrial exploitation of forests (Mendoza et al., 2011; Barzinmantov and Antezana, 2012; Garibay and Bocco, 2012; Bravo-Espinosa et al., 2014).

The observed concordance between human impact levels and the multi-species habitat scenarios is partly related to the high degree of overlap (94%) between the spatial distribution of highly suitable habitat patches of the species being considered. In terms of conservation planning, we think that this habitat overlap can be positive because actions aimed at highly impacted areas can favor multiple species or serve as surrogate areas for other species with an imminent need for conservation (Favreau et al., 2006). In addition, the identification of habitat areas with low impact that are coincident for the three multi-species scenarios can be useful for localizing and prioritizing effective climate change refuges allowing for better long-term protection of species (Carrol et al., 2010; Garden et al., 2015).

The differences in sensitivity to habitat fragmentation of the analyzed species is largely determined by their particular dispersal characteristics and spatial requirements (Fahrig, 2003; Crooks et al., 2011; Gibson et al., 2013; Haddad et al., 2015). By applying the SHFI to inform habitat scenarios about habitat quality results in differences in impact value, which largely depend on the following: a) the spatial distribution of habitat suitability, and b) the spatial coincidence of environmentally similar habitats (Alagador et al., 2012; Di Marco et al., 2013). For example, the multi-species scenario 3 (Figure 2d) that considers terrestrial mammals with relatively short dispersal ranges and small habitat had the largest proportion of surface dominated by a high cumulative anthropic impact –coincident with units of habitat offering low habitat quality for the species (Correa et al., 2014)– and high values of human footprint for the F_{frag} component. The identification of the anthropic impacts across environmentally similar habitats is important for maintaining connectivity, because it helps to maintain (and restore) connections between habitats for a group of species by identifying the optimal connection routes (Alagador et al., 2012; Bras et al., 2013; Mimet et al., 2013; Krosby et al., 2015).

4.2 Effect on habitat connectivity of the cumulative human footprint

We estimated the anthropic impact on habitat connectivity for groups of species based on the spatial effect of the SHFI by introducing the variable F_{frag} for each species, and then we aggregated the impact of the SHFI in the probability of connectivity between all habitat units. The model was set to identify areas with lower human footprints that are assumed to be less resistant to species mobility and, therefore, more relevant for conservation (Theobald, 2010; Theobald et al., 2012). Our study identified important areas with high probability of connectivity for all the analyzed species (e.g., in the Cuitzeo lake basin and the Bajío Michoacano; Figure 4a) despite showing high disturbance levels, which underlies the importance of multi-species groups approach that supports habitat complementarity. This contrasts with the previous study made in the same area (Correa et al. 2014), which found low to medium probability of connectivity when analyzing individual species of terrestrial mammals (using individual models for *Lynx rufus escuinapae* and for *Bassariscus astutus*). This shows how our present approach is more comprehensive by better representing the mobility needs of the biota of a region (Krosby et al., 2015), offering a more integrated view of conservation by assigning priority to areas important for habitat connectivity for multiple species (e.g., habitat networks for short- and long-range connectivity; Cushman and Landguth, 2012; Koen et al., 2014; Rayfield et al., 2015).

Our study identified areas with low anthropic impact and a high degree of connectivity, where scattered habitat remnants located in between the three largest natural protected areas in the $TMVS_{Mich}$, mainly in the Neovolcánica Tarasca sub-province (Pico de Tancítaro, Insurgentes José María Morelos Park, and Monarch Butterfly Biosphere Reserve; Figure 4), which can help increase the regional probability of connectivity. Based on this, landscape managers could consider conservation strategies based on inter-patch connectivity in areas with high human impact (e.g., restoration of riparian vegetation and mountain cloud forests) to favor dispersal flow across the three natural protected areas with remnant patches, functioning as stepping-stone habitats restoring appropriate spatial thresholds for species mobility (Bodin et al., 2006; Saura et al., 2013).

We identified several levels of spatial overlap and extent between the multi-species scenarios and the all-species scenarios in terms of habitat distribution and availability, cumulative human footprint, and dispersal probabilities. In this regard, the results based on a multi-species approach and their respective habitat scenarios can help in identifying threats to species with similar habitats, but with different dispersal capabilities and spatial requirements, which complement methodologies previously applied in the $\text{TMVS}_{\text{Mich}}$ for prioritization of conservation areas and identifying dispersal corridors (Fuller et al., 2006; Correa et al., 2014). Our results can show which groups of species are more sensitive to the spatial human footprint and establish similarities in impact on the habitat of species with different ecological characteristics. For example, scenarios 1 and 3, which group species with long and short dispersal ranges, respectively, displayed the largest surface area with high values of human impact on habitat connectivity. This suggests that despite the differences in dispersal capabilities and spatial requirements, the actual habitat availability can show similarities in susceptibility to human impact. Furthermore, the increase of levels of human disturbance close or above the dispersal thresholds and minimum habitat requirement can negatively affect the habitat connectivity of multi-species groups (as in Section 4.3 below), making them more susceptible to eventual future increment in habitat loss and fragmentation. In contrast, species in the multi-species scenario 2 (intermediate dispersal thresholds) would be less susceptible to such impacts (Cushman et al., 2012; Hand et al., 2014).

The spatial overlap analysis allowed the visualization of which species or group of species can be used as estimated surrogates for conservation protocols (Margulis and Sarkar, 2007). For example, the group of species we included in scenario 2 (see Methods) seems to be a good surrogate, having a high spatial agreement with the all-species scenario. That means that the group of species in scenario 2 simultaneously represents the relationship between the human footprint and its spatial effect on connectivity; it might also be useful for identifying areas important for dispersion at the multi-species level. Nevertheless, it is important to test this conclusion by incorporating other taxa into the analysis (e.g., amphibians and reptiles), as well as less common species (Breckheimer et al., 2014) that we were unable to include in our analysis.

4.3. Relationship of the effect of the spatial footprint on habitat loss and inter-patch connectivity

The relative variation in habitat area (*dA*) between scenarios was similar (54%), but when comparing the results of *dECA* based on Euclidean distances between habitat units and *dECA* which incorporates the resistance resulting from the SHFI (Figure 6), the differences increased greatly. This highlights the impact on the assessment of connectivity when considering not only the structural changes in the landscape and the spatial configuration of the habitat remnants, but also the effects of the anthropic matrix (Baldwin, 2010; Saura et al., 2011; Alagador et al., 2012; Theobald et al., 2012).

When we integrated the effect of the landscape matrix, values of the*ECA* index were much smaller. In addition, the trend of *ECA* through multi-species groups was similar. Connectivity was low when an *ECA* index was applied at short dispersal distances and gradually increased as dispersal distances are longer (Figure 6). This allows us to estimate possible differences in human impacts on habitat connectivity of species with different dispersal distances. i.e., the species with relatively limited mobility (group 3) are potentially more sensitive to changes in the spatial patterns and permeability loss of the landscape matrix (Saura et al., 2011).

The equivalent connected area greatly diminishes when considering its variation relative to the original (*dECA*) in the scenario including all species. The comparison between *dECA* (-84%) and *dA* (-54%) indicates that connectivity losses are higher than losses of habitat availability ($dECA<dA<0$). This suggests that the accessible habitat units for the different analyzed species in the $\text{TMVS}_{\text{Mich}}$ have lost their capacity for providing inter-patch connectivity. In other words, the human impact has affected the potential of habitat units to promote connectivity in terms of connectors or stepping-stones between patches and as providers or receptors of dispersal flows (Gurrutxaga et al., 2011; Saura and Rubio, 2010; Bodin and Saura, 2010; Saura et al., 2014).

The ecological restoration of small patches (>*dA*) and its strategic relocation within the landscape would improve the connectivity performance. The increase in connectivity would be above the increase in the habitat area ($dECA>dA>0$). This strategy would be ideal for returning connectivity among small habitat patches characteristic of the Volcánica Tarasca sub-province and located between protected areas; patches mostly corresponding to mountain cloud forests with high biological value (Santana et al., 2014).

To test and validate our results, we recommend: a) the compilation of current telemetry data about the wildlife in order to locate movement trends b) and habitat preferences therefore reinforcing connectivity models and obtaining new data about the occurrence of species for improving habitat suitability models, and c) expanding the range of studied species, which usually is limited to most common ones.

CONCLUSIONS

Our assessment shows that the connectivity in the $\text{TMVS}_{\text{Mich}}$ has been strongly altered through human land uses, by concentrating in critical sectors coincident with high habitat suitability for multi-species groups. The interaction between land use intensity, time of anthropic intervention, biophysical vulnerability, and the degree of isolation and habitat loss of terrestrial mammals in the $\text{TMVS}_{\text{Mich}}$ has caused the loss of 80% of connectivity and the transformation of over half the accessible habitat in areas with high resistance to species movement. Our analysis, however, identified areas with high values of “naturalness,” which promote connectivity along the system. In particular, areas that although being ineffective in terms of conservation because of their current extension, can favor multiple species and would form important dispersal corridors between protected areas in the $\text{TMVS}_{\text{Mich}}$ with an adequate restoration plan.

The adjusted SHFI applied in our study provided an integrated assessment of the magnitude of the human impact on connectivity, which we detected by means of current flow models of the four scenarios as a reduction in the probability of connectivity through the landscape. We believe that the applied multi-species approach could lead to conservation strategies that contribute to the maintenance of viable wild populations of most or many species of terrestrial mammals in the TMVS in Mexico. In this sense our results represent a significant advance in identifying critical habitat units and areas with high or low habitat quality; furthermore, they also provide a more comprehensive characterization of the dispersal patterns of focal species in a highly biodiverse landscape. The methodology we adopted substantially contributes to conservation planning and natural resource monitoring.

ACKNOWLEDGEMENTS

The authors acknowledge CONACYT for financing the project *Evaluación de la importancia relativa de bosque húmedo de niebla bajo un enfoque de paisaje* (*clave* 179386). The main author thanks CONACYT for the scholarship granted to him for pursuing a PhD in Geography studies at UNAM. We also want to thank Dr. Sergio Zárate and Miss Mary Ann Hall for his support in revising the English version of the manuscript. We additionally thank two anonymous reviewers for their suggestions and constructive comments that improved the manuscript.

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Supplementary Material.

Table s1. Multi-species groups and information about home ranges and dispersal distances used to evaluate the human footprint on habitat connectivity

Multi-species group	Scientific name	Order	Average Home Range (ha)	Median dispersal distance (m)	Reference
1	*Bassariscus astutus*	Carnivora	74	6022	Jones et al. (2009)
1	*Didelphis virginiana*	Didelphimorphia	58	5331	Jones et al. (2009)
1	*Lynx rufus*	Carnivora	560	5331	Burton et al. (2003); López-González et al. (1998)
1	*Mephitis macroura*	Carnivora	280	11713	Jones et al. (2009)
1	*Mustela frenata*	Carnivora	21	3208	Jones et al. (2009)
1	*Odocoileus virginianus*	Artiodactyla	206	10047	Bello et al. (2005); Gallina & Bello (2014)
1	*Procyon lotor*	Carnivora	463	15062	Jones et al. (2009)
1	*Spilogale putorius*	Carnivora	29	3770	Jones et al. (2009)
1	*Urocyon cinereoargenteus*	Carnivora	135	8133	Servin et al. (2014)
2	*Baiomys musculus*	Rodentia	0.6	542	Nowak (1999); Schnell et al .

					(2008)
2	*Baiomys taylori*	Rodentia	0.6	542	Nowak (1999); Eshelman & Cameron (1987)
2	*Cryptotys parva*	Insectivora	0.17	289	Withaker (1974)
2	*Neotoma mexicana*	Rodentia	0.23	336	Cranford (1977)
2	*Oryzomys couesi*	Rodentia	1	700	Medellín & Medellín (2006); Hofmann et al. (1990)
2	*Osgoodomys banderanus*	Rodentia	1	700	Dominguez et al. (2007); Pointdexter et al. (2013);
2	*Peromyscus aztecus*	Rodentia	1	700	Witmer & Moulton (2012)
2	*Peromyscus melanophrys*	Rodentia	1	700	Witmer & Moulton (2012)
2	*Peromyscus spicilegus*	Rodentia	1	700	Witmer & Moulton (2012)
2	*Peromyscus truei*	Rodentia	1.3	798	Ribble et al. (2002)
2	*Reithrodontomys megalotis*	Rodentia	0.3525	416	Webster y Jones (1982)
2	*Reithrodontomys microdon*	Rodentia	0.8994	664	Reid (1997)
2	*Reithrodontomys sumichrasti*	Rodentia	1	700	Webster y Jones (1982)
2	*Sigmodon alleni*	Rodentia	0.247	348	Cameron & Spencer (1985)
2	*Sigmodon fulviventer*	Rodentia	0.247	348	Cameron & Spencer (1985)
2	*Sigmodon hispidus*	Rodentia	0.247	348	Cameron & Spencer (1985)
2	*Sigmodon mascotensis*	Rodentia	0.5	495	Schnell et al. (2010)
2	*Sorex saussurei*	Insectivora	0.17	289	Withaker (1974)
2	*Spermophilus variegatus*	Rodentia	3	1212	Jones et al. (2009)
2	*Sylvilagus cunicularis*	Lagomorpha	3.62	1332	Vázquez et al. (2013)
2	*Sylvilagus floridianus*	Lagomorpha	2.5	1107	Jones et al. (2009)
3	*Cratogeomys gymnurus*	Rodentia	0.03	111	Feldhamer et al. (2003)
3	*Cratogeomys tylorhynus*	Rodentia	0.03	111	Feldhamer et al. (2003)
3	*Liomys irroratus*	Rodentia	0.0126	79	Santiago & Santos

					(2009)
3	*Microtus mexicanus*	Rodentia	0.035	131	Hayne (1950)
3	*Neotomodon alstoni*	Rodentia	0.127	249	Rojas-Martínez et al. (2012)
3	*Peromyscus maniculatus*	Rodentia	0.0372	135	Wood et al. (2010)
3	*Peromyscus melanotis*	Rodentia	0.042	143	Álvarez-Castañeda (2005)
3	*Reithrodontomys fulvescens*	Rodentia	0.0843	203	Spencer & Cameron (2008)
3	*Thomomys umbrinus*	Rodentia	0.025	111	Feldhamer et al. (2003)
3	*Zygogeomys trichopus*	Rodentia	0.025	111	Feldhamer et al. (2003)

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CAPITULO IV

EFECTO DE LA MATRIZ DEL PAISAJE PARA LA PRIORIZACIÓN DE LA CONSERVACIÓN DE LA CONECTVIDAD MULTI-ESPECIE EN UN PAISAJE ALTAMENTE BIODIVERSO DEL CENTRO DE MÉXICO

EFFECT OF THE LANDSCAPE MATRIX CONDITION FOR PRIORITIZING MULTI-SPECIES CONNECTIVITY CONSERVATION IN A HIGHLY BIODIVERSE LANDSCAPE OF CENTRAL MEXICO

Artículo en revisión en Biodiversity and Conservation

Effect of the landscape matrix condition for prioritizing Multi-Species Connectivity Conservation in a Highly Biodiverse Landscape of Central Mexico

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Date of the manuscript draft: Month Day, Year

Manuscript word count: XXX

ABSTRACT

Implementing and monitoring long-term conservation strategies demands identifying priorities for preserving landscape connectivity. Our main goal was the identification of priority areas for preserving habitat connectivity of the landscape matrix in central-western Mexico that functionally connect habitat patches for a suite of different terrestrial organisms. We aggregated three multispecies connectivity models in a composite corridor model. To evaluate which corridors were most important to multi-species connectivity, we used the composite corridor model based on two ways: 1) the contribution of habitat patches that the corridor connects to overall connectivity and 2) the corridor capability to facilitate movement across network. Landscape was classified according to their value for conservation of multispecies connectivity by means of an approach hybridizing circuit based models and spatial prioritization for conservation connectivity. For that, we developed current flow models for each species (*n*=40) and combined in four prioritization models corresponding to the three multispecies groups and all species group. We found that the corridors having the highest accumulated importance (CI<70) are located along the protected areas of Pico de Tancítaro and the Monarch Butterfly Biosphere Reserve, which have relatively similar spatial distribution than areas with priority for conservation (relative rank test= 0.6). Within that area, permeable sectors with high connectivity retention values remain to exist that could optimize their ecological function by means of multispecies corridors. Our approach is applicable to different scales and landscapes and it additionally allows for identifying priorities for connectivity conservation integrating landscape elements outside habitat patches.

Key words: spatial conservation planning, habitat connectivity, multispecies, corridors, Mexico

5. INTRODUCTION

The capacity of ecosystems for preserving biodiversity and environmental services in the present scenario of fast environmental transformation depends on availability and quality of habitat provided by remnant landscape patches, their degree of connectivity, and their resilience against disturbances such as climate change or invasive species (Haddad et al. 2015). Conservation strategies have been proposed for counteracting the negative effects of habitat loss and fragmentation, such as establishing corridors to facilitate the dispersal of species across suitable habitat patches to ensure the viability of populations (Beier, 1993; Rabinowitz & Zeller, 2010; Cushman & Landguth, 2013; Brodie et al. 2015; Belote et al. 2016). The more common approaches to model landscape connectivity are based on least-cost analysis (Correa et al. 2016), which assumes that the degree of connectivity can be calculated from the characteristics of the landscape matrix that enable or impede species mobility (Adriaensen et al. 2003). Although least-cost paths (LCP) allow to estimate the shortest and less difficult path between habitat patches (Bunn et al. 2000; Adriaensen et al. 2003), the result from such analyses are straight lines with little resemblance to real corridors (Rudnick et al. 2012; Theobald et al. 2012). In order to overcome this limitation, least-cost corridors (LCC) are increasingly being represented by an accumulated cost gradient that is more similar to an area communicating habitat patches (Beier et al. 2009), and are more realistic representations for the goals of conservation (Correa et al. 2016). Complementing the above-mentioned models, the circuit theory allows to design flow models that integrate all possible routes between all habitat patches instead of finding a single optimal path between pairs of patches (McRae & Beier, 2007). Because flow models predict the probabilities of dispersal between all habitat patches, they can be used for identifying the corridors or areas of the landscape matrix in which focal organisms have of the best dispersal chances between habitat patches (McRae et al. 2008; Dickson et al. 2013).

The approaches for exploring the potential of corridors for optimizing connectivity of landscapes are commonly based on the responses to landscape changes of single species, frequently, a charismatic mammal species, or species with long dispersal ranges that are assumed to also benefit other species (Atwood et al. 2011; Morato et al. 2014; Rodríguez-Soto; 2013; Correa et al. 2014). Focusing on single species may be useful for providing detailed information about conservation, but is limited by only addressing species of interest (Lindenmayer et al. 2007) or, in terms of connectivity, areas suitable for the dispersal of one species may constitute dispersal barriers for other species, which implies restrictions for management of corridors (Alagador et al. 2012; Bras et al. 2013; Mimet et al. 2013; Krosby et al. 2015). Contrastingly, multispecies-based strategies can identify effective management priorities for the simultaneous conservation of many species or for multiple conservation goals (Lindenmayer et al. 2007; Brodie et al. 2015). The complexity of ecological requirements of multiple species, added to the ongoing transformation of the landscapes in which they disperse, implies that developing habitat networks is currently imperative (Mimet et al. 2013). However, multispecies based approaches may result in less effective strategies for a given species than a strategy tailored for that species in particular (Brodie et al. 2015), or because of the lack in detailed information affecting the effectiveness of conservation strategies for a specialist species for example, can be undervalued (Lindenmayer et al. 2007). Despite these caveats, the multispecies approach for studying connectivity is being increasingly applied for identifying areas having high probability of connectivity for multiple species, or for selecting the most efficient corridors between protected areas (Mimet et al. 2013; Koen et al. 2014; Brodie et al. 2015).

Beyond the tasks involved in planning multi-purpose corridors, researchers continue to be challenged by attempting to identify the most efficient strategies for optimizing connectivity. To this end Rayfield et al. (2015) developed a methodology that combines graph theory and circuit theory for obtaining landscape connectivity models (Saura et al. 2011, McRae et al. 2008), based on spatial prioritization for conservation (Moilanen et al. 2005; Lehtomäki & Moilanen, 2013) and focusing on the identification of habitat patches with multiple connectivity functions. However, Rayfield et al. (2015) limited their analysis to forest patches, disregarding the landscape matrix as a whole, which neglects “inter-patch” areas which may be pertinent to maximize the retention of connectivity for multiple species (Breckheimer et al. 2014). McRae et al. (2012) also underscored the potential of implementing a mixed approach incorporating current flow models of single species as inputs for spatial prioritization of conservation (Breckheimer, 2012), aggregating the connectivity criteria of single species to identify optimal areas for multi-species connectivity, for instance through restoration.

The purpose of this was to identify the portions of the landscape matrix that are most important for allowing the movement across habitat patches of multiple species and prioritize the areas with highest value for conserving or restoring landscape connectivity. First, we model least-cost corridors in three multi-species scenarios and in a composite corridor scenario combining all species, and we afterwards prioritized these corridors based on patch contribution to connectivity and to their capacity for facilitating dispersal across the whole network (Brodie et al. 2015; Brodie et al. 2016). Finally, we built models of current flow for single species and combined them in four spatial prioritization models (three multispecies scenarios, and one scenario combining all species), classifying pixels according to their connectivity conservation value across all species (Moilanen et al. 2005; Breckheimer, 2012). This novel approach advances the current spatial conservation prioritization methods by including connectivity optimization using multi-species criteria in the inter-patch matrices.

6. METHODS

2.1 Study area

The study area corresponds to the portion of the central Trans Mexican Volcanic System (TMVS) located in the north of the state of Michoacán ($\text{TMVS}_{\text{Mich}}$; Figure 1) including the physiographic sub-provinces of Chapala, Bajío guanajuatense, Bajío michoacano, Llanuras y Sierras de Querétaro e Hidalgo, Cordillera Costera del sur, Subprovincia Neovolcánica Tarasca, Depresión del Balsas, Mil Cumbres, and Depresión del Tepalcatepec. The central TMVS zone establishes a biogeographic transition between the Nearctic and the Neotropical regions (Gámez et al. 2012). The $\text{TMVS}_{\text{Mich}}$ has an extension of 28,100 km^2 and an altitudinal range between 1,000 and 3,800 m a.s.l. The study area includes eight protected areas mostly located in the higher areas of the the mountainous sector, and covering only 2.4% of the $\text{TMVS}_{\text{Mich}}$ (Bezaury-Creel et al. 2009). The main natural land covers in the area are temperate forests (conifer forest, mixed conifer and oak forest, and mountain cloud forest), and to a lesser extent low tropical deciduous forests and aquatic vegetation (INEGI, 2013). Gámez et al. (2012) and Escalante et al. (2007) consider the central TMVS as a highly biodiverse landscape with an average land mammal species richness of 105 species.

Anthropic land covers dominate 70 % of the $\text{TMVS}_{\text{Mich}}$ and the population density is very high, mostly in the state capital city of Morelia (INEGI, 2010) having the highest urban growth rates in the region (López et al. 2001; Mendoza et al. 2011) and the state of Michoacán (Bocco et al. 2001). A dense road network is distributed throughout the $\text{TMVS}_{\text{Mich}}$ including conserved sectors, which potentially limits land mammal species dispersal (Correa et al. 2014).

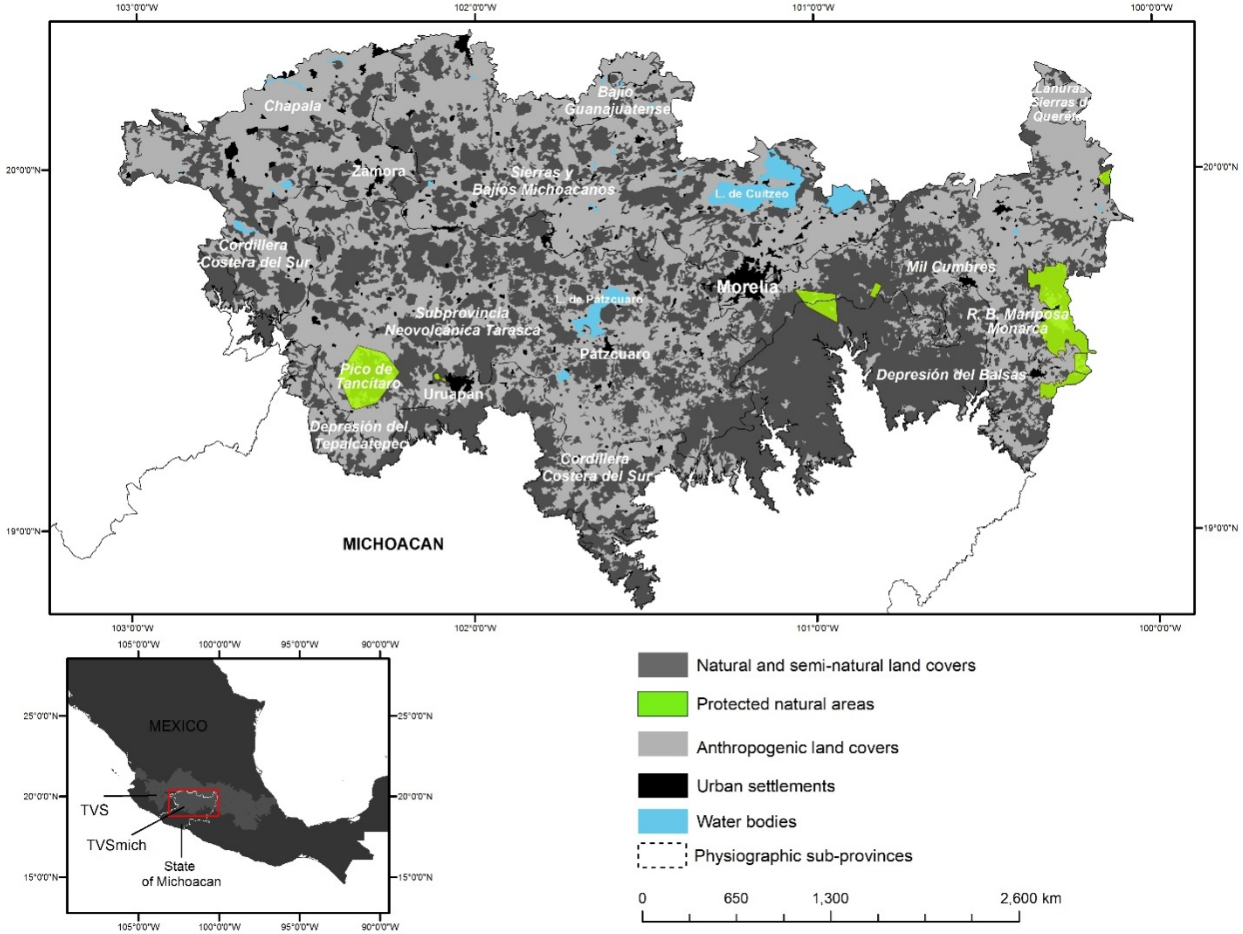

Figure 1. Location of the study area showing the spatial distribution of natural, semi-natural (including secondary vegetation) and anthropic land covers. Source: Land cover and land use map series V (INEGI, 2013).

2.2 Building of multispecies scenarios

We selected 40 focal species of terrestrial mammals (Appendix 1) based on previous studies of connectivity in the TMVS (Fuller et al. 2006; Correa et al., in review). Focal species were selected based on data availability on occurrence and geographic representativeness in the $\text{TMVS}_{\text{Mich}}$ (Krosbie et al. 2015). For selecting the habitat patches at the multispecies level we used the potential and actual habitat of single species established by Correa et al. (in review).

Models of potential habitat were created based on the principle of maximum entropy (Philips et al. 2006) and actual habitat models, by overlapping natural land covers with models of potential habitat and excluding transformed areas (Fuller et al. 2006). Models of habitat for single species were unified in three multispecies habitat scenarios (Correa et al., in review). Each scenario represents the habitat patches common to each group of species based on geographical distribution, availability of remnant habitat, and minimal spatial requirements. Scenario 1 groups terrestrial species with long dispersal range (>3000 m) and large minimum habitat area (>350 ha) including seven species in the order Carnivora, one species in the order Didelphimorphia, and one species in the order Artyodactila. Scenario 2 groups 21 species with medium dispersal range (250-1,500 m) and minimal size of patches of between 3 and 350 ha and it includes three species in the order Lagomorpha, two species in the order Insectivora, and 17 species in the order Rodentia. Scenario 3 contains species with short dispersal ranges of less than 250 m and minimal habitat patches smaller than 3 ha, including ten species in the order Rodentia (Appendix 1; McShea & Madison, 1992; Bowman et al. 2002; Saura et al. 2011; Santini et al. 2013; Saura et al. 2014).

To estimate the cost of movement for single species we built a friction/resistance surface for each one of them based on a multi-dimensional human footprint index (Etter et al. 2011) modified for assessing anthropic impact on landscape connectivity (Correa et al., in review). We assumed that the areas with higher human footprint index values have lower permeability for species dispersal (Baldwin et al. 2010; Alagador et al. 2012). The areas lying outside the optimum habitat of single species but within the limits of the $\text{TMVS}_{\text{Mich}}$, were considered movement restriction areas (Resistance=100), but not absolute barriers for all species of the multispecies groups. To obtain cumulative resistance models, we added the surface of resistance of all species in each multispecies scenario (sum of human footprint of species in scenarios 1, 2, and 3), and rescaled the resulting three models to a 0 to 100 range (Cushman & Landguth, 2012; Brodie et al. 2015).

2.3. Connectivity models and prioritization of least-cost corridors

To generate three corridor models (suitable to each scenario), we used the multispecies habitat scenarios and their corresponding resistance surfaces obtained as described above. We based on the least-cost corridor approach (Pinto & Keitt, 2009; Krosby et al. 2015), using the Linkage Mapper software (McRae & Kavanaugh, 2011). We first used least-cost corridors for identifying thresholds of cumulative cost ideal for connecting each pair of habitat patches for each multispecies scenario, thereafter constructing a new “all species scenario” following Belote et al. (2016), by combining each corridor map to identify common areas with high degree of spatial agreement. For that, we first reclassified the values of corridors in deciles, assigning a value of

10 to the lower decile (low values of normalized cost distance), of 9 to the next decile, of 8 to the following decile, etc. Corridors with the lowest cost (better corridors) received higher importance values and vice versa (Figure 2). The three reclassified models were then summed to produce a composite corridor model (all species scenario) with values between 3 and 30 (Belote et al. 2016). Finally, we selected the top 20% of pixels for identifying the corridors having the highest spatial congruence and the lowest cost distance values.

Thereafter, the importance of selected corridors was evaluated based on the cumulative value of three criteria: a) importance of corridor for connecting habitat patches; b) contribution to landscape connectivity of connected patches by a given corridor; and c) capability of a given corridor for easing dispersal through the patches it connects. Criterion *a* was assessed based on the number of patches it connects (*NP*) and criterion *b* was established by weighting the number of patches each corridor connects by the average value of *dPC* ($NP * \overline{dPC}$), *dPC* assessing the contribution to general landscape connectivity of each patch and quantifying the percentage of connectivity loss when each habitat patch is systematically removed from the network (Saura & Pascual-Hortal, 2007). *dPC* takes into account the variation inside patches of the connected area (availability of habitat determining the inter-patch connectivity), the estimated dispersal flow between patches, and patch contribution as stepping stones (Saura & Rubio, 2010; Saura et al. 2011). Values of *dPC* were calculated in the software Conefor (Saura & Torné, 2009). The average weighted importance of patches connected by a corridor was indicated by *WIP* (Weighted Importance of Patch).

For evaluating criterion *c* we used the centrality index “current flow betweenness centrality” derived from circuit theory (McRae et al. 2008; Newman 2005; Newman, 2010; Carrol et al. 2012) which measures the expected frequency (averaged over all patches) of a random walk occurs between patch *i* and patch *j* (McRae, 2006). The value of current flow betweenness centrality was added to each least-cost path in order to map them in the software Linkage Mapper (McRae, 2012). We used the average of current flow betweenness centrality values of patches connected by the corridor. The importance of corridor based on current flow betweenness centrality values was indicated by *CFC*. The *CFC* and *WIP* values of each corridor were added to obtain a final “corridor importance” value (*CI)*. Finally, the *CI* values were normalized in a 0 to 100 scale.

2.4. Spatial prioritization for connectivity conservation

The prioritization of high value areas of multispecies connectivity in the $\text{TMVS}_{\text{Mich}}$ was approached by combining circuit theory (McRae et al. 2008) and spatial prioritization of conservation (Moilanen et al. 2005; Lehtomäki & Moilanen, 2013). First we created current flow models of the 40 focal species in the software Circuitscape 4.0 (McRae et al. 2013). Current flow models were parameterized using the remnant habitat patches of each species as nodes, and the human footprint maps adapted for the habitat of each species as resistance surfaces (Correa et al., in review) (Figure 2). The outputs of the individual current flow models were then merged into four maps (one for each scenario) classifying the landscape in terms of value for multispecies dispersal (Rayfield et al. 2015). To identify the more important areas in the landscape for connectivity conservation (Breckheimer, 2012), we used the Zonation algorithm (Moilanen et al. 2005) in the software CONNECT (Breckheimer & Milt, 2012). The Zonation algorithm iteratively eliminates from the whole landscape the pixels with the lowest multispecies connectivity value advancing from the periphery of the spatial database, then comparing again the connectivity values from the new periphery removing the pixels with the lowest connectivity values, the process stopping when all pixels have been classified. For each pixel in the periphery of the spatial database, Zonation sums the connectivity value of each single species weighted by the total connectivity in the rest of the landscape (Moilanen et al. 2005; Early, 2007; Lehtomäki & Moilanen, 2013). The output models provide prioritization of conservation measure for multispecies connectivity.

Finally, in order to evaluate the spatial similarities in terms of importance for connectivity in the different multispecies scenarios, the relative rank test (Warren et al. 2011) was applied between pairs of spatial prioritization for conservation models and between spatial least-cost corridors models using the software ENM tools 1.4 (Warren et al. 2010). The values of relative rank closer to 1 indicate higher spatial similarity between two distributions (Warren et al. 2011). Additionally, the Pearson correlation test was applied to evaluate the differences between pairs of models, and measure the relation between scenarios.

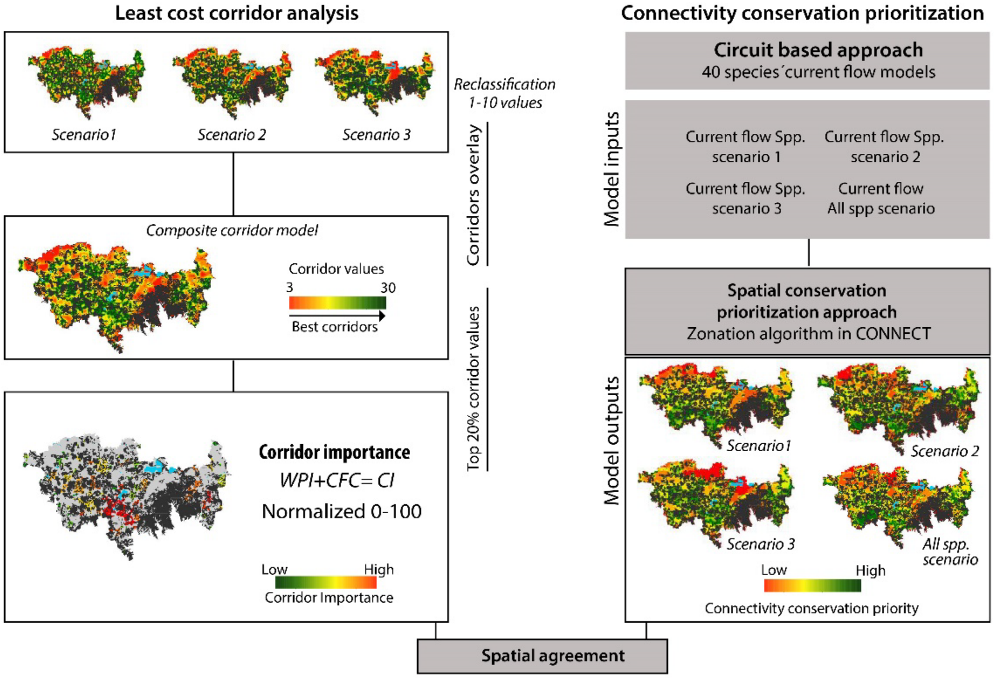

Figure 2. Flow diagram synthesizing the procedures followed for identifying the corridors and sectors in the $\text{TMVS}_{\text{Mich}}$ with most importance for conservation of multispecies connectivity.

7. RESULTS

3.1 Comparison of spatial congruence of least-cost corridors

The relative rank test revealed that the spatial distributions of the least-cost corridors were similar in all scenarios (Figure 2). However, the spatial differences between corridors (relative rank values between 0.51 and 0.78) indicated that relationships between landscape resistance, dispersal ranges, and distribution of habitat patches affect the distribution of movement cost across landscape. The highest congruence between corridors was observed between scenario 2 and the all species scenario (relative rank value=0.78), while the lowest relative value (0.52) occurred between scenarios 1 and 3. Likewise, scenario 2 and all species scenario had the highest observed pairwise correlation value (0.88) indicating high resemblances in their distributions. Conversely, the distributions of corridors in scenarios 1 and 3 showed the lowest observed correlation value (0.51) (Figure 4).

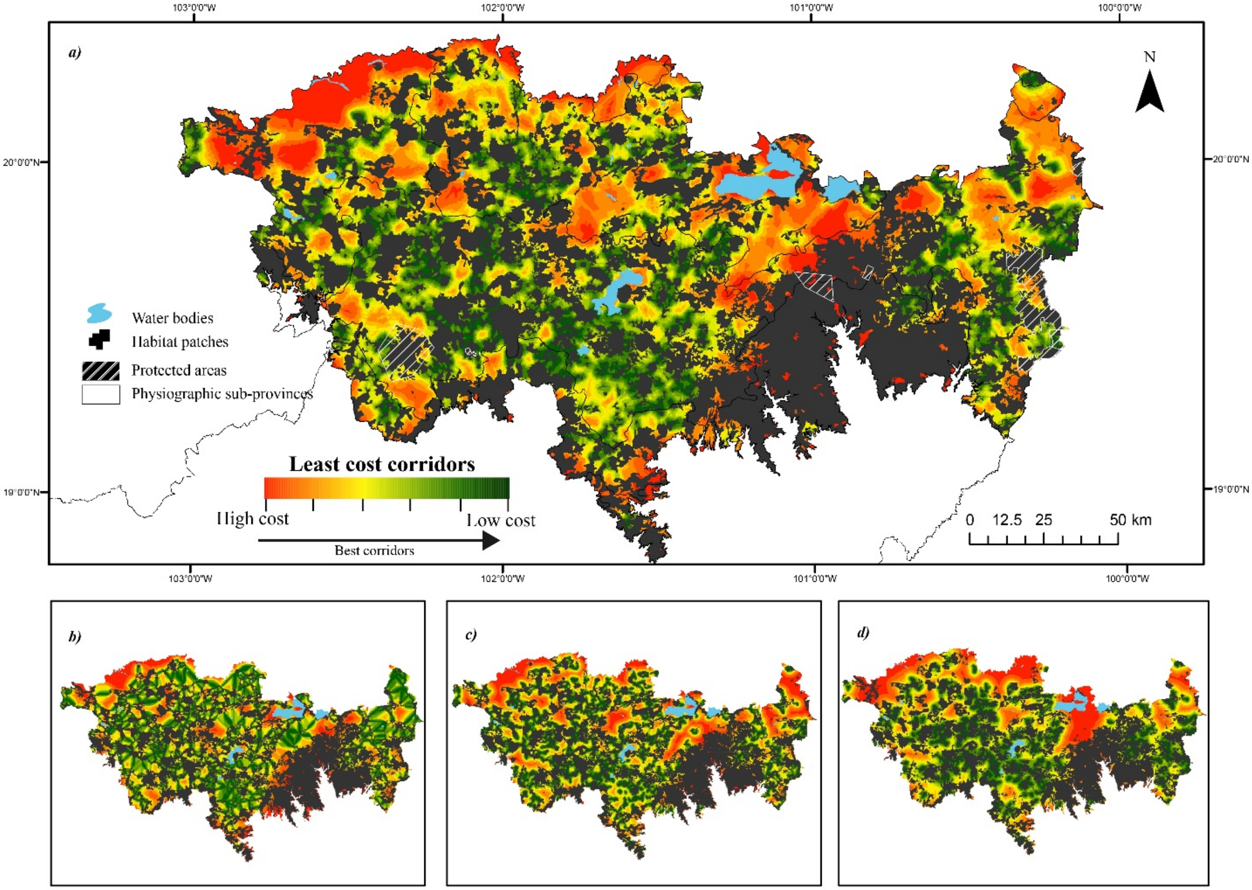

Figure 3. Distribution of least-cost corridors identified by their sum and reclassification of the normalized cost distance values in four different multispecies scenarios (*b*, *c*, and *d*): *a*) all species scenario showing corridors with the highest degree of spatial agreement and lowest distance cost values (green color) than the three multispecies scenarios (*b*, *c*, *d*). Red color areas represent areas with high distance cost values between habitat patches common to all 40 studied species; *b*) scenario 1 species groups with wide dispersal ranges (see supplementary material); *c*) scenario 2 species groups with intermediate dispersal ranges; *d*) scenario 3 species groups with short dispersal ranges.

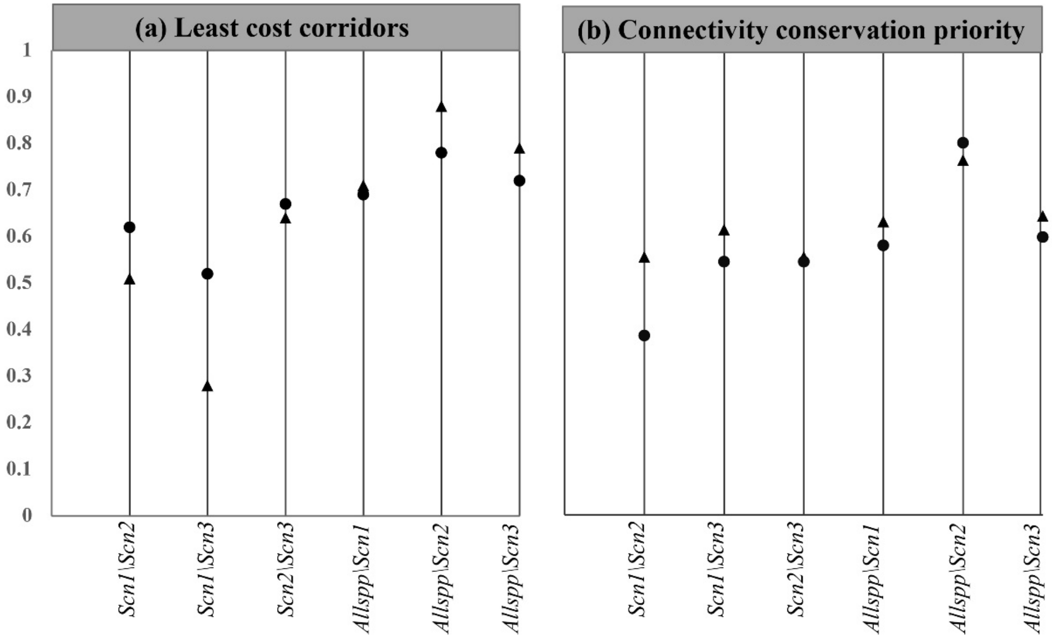

Figure 4. Results of the pairwise comparison of multispecies scenarios. Panel a) shows pairwise comparisons of least-cost corridors scenarios (see Figure 3) and panel b) corresponds to pairwise comparison between scenarios of areas of connectivity conservation priority (see Figure 7). Solid circles indicate the degree of spatial overlap of each pair of scenarios determined by the relative rank test of Warren (Warren & Seifert, 2010) and solid triangles show the results of the Spearman correlation test.

3.2 Prioritization of least-cost corridors

The selected corridors correspond to the 20% of the lowest cost-distance values for the all species scenario (Figure 3b) synthesized in 93 corridors connecting 404 habitat patches common to all focal species. Four main groups of corridors were identified (Figure 6) based on their values for the three criteria used for assessing the importance of individual corridors: one group includes corridors 1 and 2, characterized by having the highest values of *CI* (100 and 94, respectively); the second group is represented by corridors 3, 4, and 5 with high values of *WIP* (75 to 70) and intermediate values of *CFC* (60 to 38); the third group is made up of corridors 6, 7, 8, and 9 with high values of *CFC* (91 to 97), but with a low value of *WIP* (14 to 7); and the fourth group is represented by corridor 10 with high values of *WIP* (81) and low values of *CFC* (21).

In general, selected corridors had a heterogeneous distribution along the $\mathrm{TMVS}_{\mathrm{Mich}}$. The contributions to the *CI* value of *WIP* and *CFC* of corridors were not uniform, i.e., the more important corridors did not always had the highest values of *WIP* and *CFI*, indicating each corridor might contribute to connectivity in different ways. For example, our results show a main corridor in the center of the $\mathrm{TMVS}_{\mathrm{Mich}}$ connecting the largest patch of habitat with other smaller habitat patches (Figure 5a; Label 2); however, the *CI* value of this corridor (94) is the second highest such value, because its value of *CFC* is lower than that of other corridors (Figure 5). This results indicate that this main corridor is highly important in connecting multiple patches that are key for general connectivity because of having high values of dPC_k (it has the highest value of *WIP*; Figure 5b), but less important in terms of its capacity for facilitating current flow between patches (*CFC*=68; Figure 4c). The most important corridor (*CI*=100; Label 1) was located in the western sector of the $\mathrm{TMVS}_{\mathrm{Mich}}$ connecting a large portion of the Monarch Butterfly Biosphere Reserve (Figure 1) with a series of patches that have high multispecies habitat suitability located in the sub-province of Mil Cumbres and in part of the sub-province of Bajo Balsas. The *CI* value of this corridor is the highest for similar reasons as for corridor 2, but with a higher value of *CFC* (the highest among all other selected corridors: *CFC*=100; Figure 6) and a lower value of *WIP* (77), suggesting that its importance is due to its capacity to facilitate dispersal, despite connecting a lower number of habitat patches than corridor 1.

Prioritization revealed that the ten potential corridors with the highest values of *CI* (≥58; Figure 6) are mainly distributed in the three largest protected areas of the $\mathrm{TMVS}_{\mathrm{Mich}}$, which indicates the persistence of permeable sectors in the study area that are capable of maintaining movement between areas with high habitat suitability (Figure 5). For example, corridor 2 plays a key role as a central connector between the Pico de Tancítaro and Monarch Butterfly Biosphere Reserve protected areas, facilitating connectivity throughout the landscape matrix in a sector with relatively low distance cost values (Figure 3a). Corridor 2 was the most important potential corridor regarding the number of patches it connects (Figures 5b and 6) and because it connects small patches with high values of dPC_k relevant for acting as stepping stones (Figures 5c and 6) between the main protected areas. Likewise, corridors 7, 2, 10, and 1 particularly show the potential for integrating a connected network of protected areas.

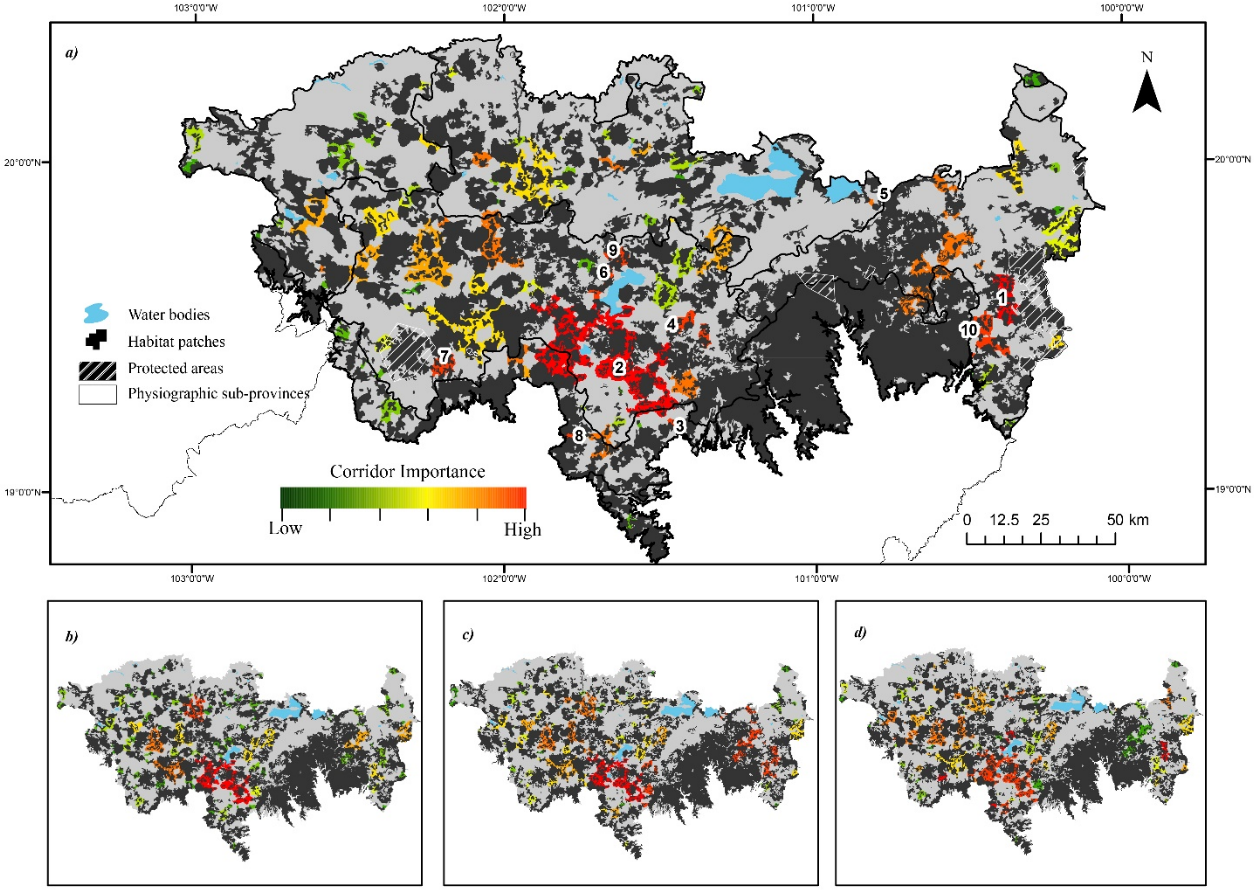

Figure 5. Results of least-cost corridor prioritization. a) Shows the more important corridors identified by 20% of the lowest cost distance values in the all species scenario (see Figure 3a). Numbered labels identify in ascending order the ten most important corridors (*CI*) by the sum of *WIP* and *CFC* (see Methods, section 2.3). b) Most important corridors by the number of patches they connect (*NP*). c) Most important corridors based on their average *dPC* values weighted by the number of patches (*WIP*). d) Most important corridors in terms of the value of current flow betweenness centrality (*CFC*) of their corresponding least-cost paths.

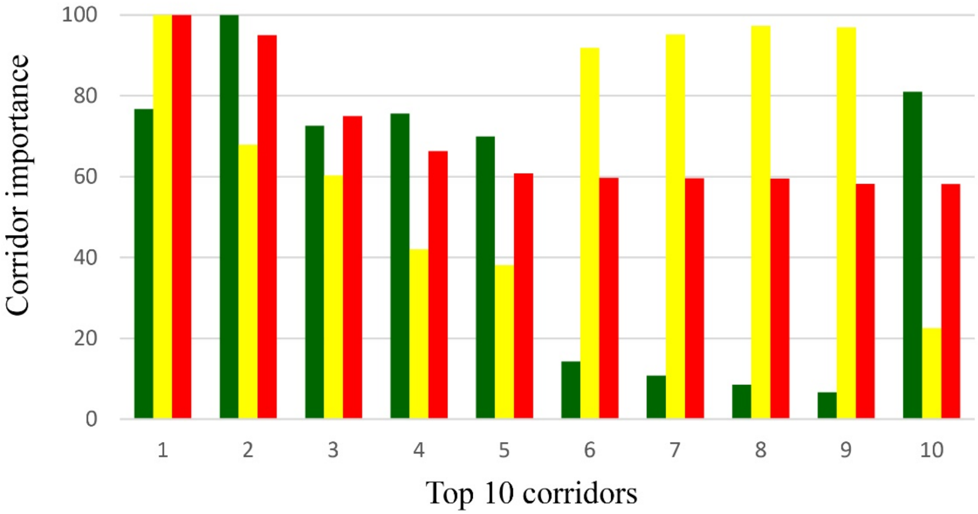

Figure 6. Values of corridors importance. Green bars represent the importance of corridors based on *WIP*. Yellow bars indicate the importance of corridors in terms of the values of current flow betweenness centrality of their corresponding least-cost path (*CFC*). Red bars indicate the cumulative importance of corridors. The spatial distribution of the ten corridors is shown in Figure 5.

7.3 Identification of priority areas for conservation of connectivity

We combined the current flow models based on the 40 focal species in order to identify important areas for multispecies connectivity. We represented these areas for each scenario and generated four models of spatial prioritization of connectivity in the $\mathrm{TMVS}_{\mathrm{Mich}}$. Figure 7 shows the prioritization for connectivity conservation derived from each multispecies scenario, indicating the portions of the landscape matrix that should be conserved for optimizing connectivity in the $\mathrm{TMVS}_{\mathrm{Mich}}$. We found that 60% of the potentially more important corridors in the all species scenario (20% of pixels with the lowest normalized distance cost values; Figure 3) spatially overlap the areas with high priority for connectivity conservation (20% of pixels with the highest values). The more important potential corridors (Figure 5) are mainly distributed between the Pico de Tancítaro and Monarch Butterfly Biosphere Reserve protected areas, suggesting spatial similarities exist between the sectors with high connectivity conserving capacity and inter-patch sectors with the lowest distance cost values for multiple species. Likewise, we observed a positive, but weak, correlation value (0.13) between the distribution of certain corridors and areas with high priority. This indicates that despite a reasonable spatial agreement that exists between potential corridors and the distribution of priority areas for connectivity conservation, these attributes are independent from each other.

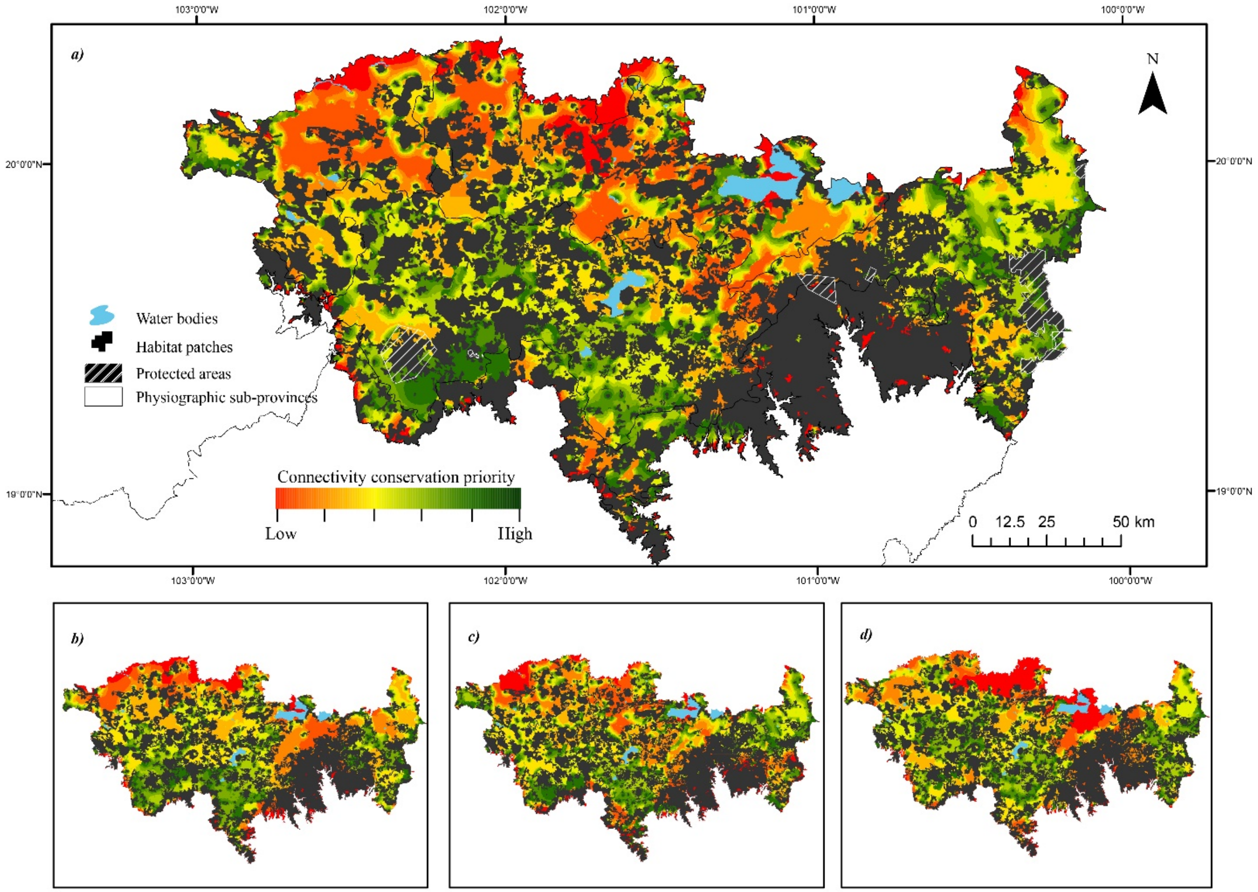

Figure 7. Prioritization of areas for connectivity conservation in the TMVS$_{\text{Mich}}$. The red to green colored scale indicates areas with lesser to greater priority, respectively. *a*) Prioritization map for all species. *b*), *c*), and *d*) correspond to priority areas for connectivity conservation based on the group of species of scenarios 1, 2, and 3, respectively.

The highest priority values for connectivity conservation cover 19% of the TMVS$_{\text{Mich}}$ and are located in the southwestern part of the study area, concentrating in the Neovolcánica Tarasca sub-province, mostly between the Pico de Tancítaro protected area and the mountainous landscapes of lake Pátzcuaro, linking a series of patches or stepping stones embedded in an agricultural matrix, connecting the eastern sector of the TMVS$_{\text{Mich}}$ in the Mil Cumbres sub-province, which is characterized by large patches of temperate forests and, in its eastern portion of stands of mountain cloud forests and the Monarch Butterfly Biosphere Reserve (Figure 7). These remnant patches concentrate high habitat suitability for most of the focal species. In contrast, the areas having the lowest values of priority are located in the Bajío Michoacano and Chapala sub-provinces (mostly in the lowlands surrounding lakes Cuitzeo and Chapala, respectively), areas where agroindustrial land uses are dominant, despite including a few small habitat patches with high conservation value.

The pairwise comparison of the spatial distribution of high priority connectivity conservation areas (20% of the zone with the best values of the landscape) in the multi-species scenarios, showed high spatial agreement (relative rank value >0.58) between all of them. Scenarios with highest agreement in priority areas were the *All Species Scenario* and *Scenario 2* (Figure 4b) containing species of intermediate spatial requirements (relative rank value =0.80). The lowest agreement (0.58) corresponds to the comparison of *Scenario 1* (wide dispersal ranges) and *Scenario* 3 (very narrow dispersal ranges). In the relative rank test applied to the general distribution of prioritization importance the highest value (>0.77) resulted from the comparison of scenarios 2 and all species, suggesting that the spatial distribution of ranks of importance for multispecies connectivity conservation are the most congruent in this combination relative to other pairwise comparisons. Likewise, the correlation test made between the 2 and all species scenarios showed a general direct relation between their distributions (r=0.80). Conversely, the comparison between scenarios 1 and 2 had both the lowest value in the relative rank test (0.65) and the lowest correlation (r=?). These results were essentially similar to those of the prioritization of potential corridors (see Section 3.2).

8. DISCUSSION

Our study demonstrates the importance of taking into account the landscape matrix condition to prioritize the connection routes between patches in a highly fragmented landscape, by functionally connecting habitat patches common to a number of terrestrial mammals, and their priority rank in terms of connectivity conservation. We addressed the process of connectivity assessment in two stages: one for identifying potential corridors with the highest cumulative importance for multispecies connectivity (Brodie et al. 2015; Brodie et al. 2016); and a second, combining spatial models of current flow based on circuit theory (McRae et al. 2008) with a spatial prioritization approach for classifying the landscape according to its value for multispecies connectivity (Moilanen et al. 2005; Breckheimer et al. 2014; Rayfield et al. 2015).

Matrix condition and connectivity design

In general, the similarity in the individual contributions of corridors to each one of the criteria of importance allowed their grouping, underscoring the different ways in which corridors may contribute to connectivity and at the same time differentiating possible management strategies.

For example, corridors in group 1 (corridors 1 and 2) could be the most effective for optimize connectivity between the protected natural areas of Pico de Tancítaro and Monarch Butterfly Biosphere Reserve, having the highest *CI* values and a strategic central location for connecting these two areas. However, corridors of group 2 (3, 4, and 5) are short, but have a high capacity for connecting a large number of habitat patches with high relevance for general connectivity, which is indicative of the utility of these corridors for optimizing connectivity for species with narrow dispersal ranges (Brodie et al. 2016), such as species in multispecies scenarios 1 and 2. Group 3 represented by corridors 6 to 9, might be optimal to produce or receive fluxes between high dispersal probability areas, thus increasing the permeability of the landscape matrix for finding patches with high habitat suitability because of their high *CFC* values and low *WIP* values. The single corridor 10 of group 4 could be useful as connector areas or bridges between large patches due to their location, and connect these large patches with small, stepping stones habitats encouraging inter-patch connectivity because of their high *WIP* and low *CFC* values.

Individual assessment of the importance rank of least-cost corridors showed that the potential of the landscape matrix for maintaining inter-patch connectivity depends on the capability of connections for simultaneously enhancing the dispersal between all habitat patches in the landscape (i.e., high *CFC* values; Carrol et al. 2012), but also on the different ways in which the patches being connected might contribute to landscape connectivity (i.e., high dPC_k values; Saura & Rubio, 2010). In that context, we identified the areas in which conservation actions should be concentrated in order to maintain valuable connections between patches having high habitat quality for multiple species (Carranza et al. 2012). For example, we found that the connectivity between the protected areas of Pico de Tancítaro and Monarch Butterfly Biosphere Reserve could potentially be optimized in an effort of regional planning of conservation. At least five of the high importance corridors (Figure 4b, corridors 1, 2, 4, 7, and 10) connect these protected areas throughout the $\mathrm{TMVS_{Mich}}$. We believe that improving connections in this sector would return part of the lost connectivity to the state, but talking into account that before being transformed these areas formed a continuous corridor along the whole TMBS and that this region is highly biodiverse, it would also significantly contribute to conservation of connectivity at the national level (Fuller et al. 2011; Correa et al., in review). The high importance of corridors in this region was mainly due to the high degree of current flow betweenness centrality (*CFC*) of the patches being connected (particularly in corridors 1 and 7; Figure 6), added to their capability for inter-patch connection, mainly provided by the more important patch for connectivity in the $\mathrm{TMVS_{Mich}}$, which has relevant intrinsic characteristics such as large size and strategic topological location within the study area

According to a recent study of Brodie et al. (2016), the more relevant links for connectivity join large patches and are generally short. Despite that we did not directly evaluate Euclidean distances for prioritizing corridors, we did observe that relatively short corridors are highly important and that their *CI* values increases when they connect large patches (e.g., corridors 1 and 7 in Figure 6a). This property was evaluated when calculating average *dPC* values of patches being connected by the corridors, a value that not only measures the importance of patches due to their area, but also estimates the contribution of patches as connectors and emitters/receivers of current flows (Saura & Rubio, 2010). These findings are important for conservation because in the event of increased connectivity the probability of survival of populations in large patches would also be increased, as would their expansion between previously isolated areas of suitable habitat (Carranza et al. 2012; Brodie et al. 2016).

Our analysis also allowed for differentiating the importance of corridors in terms of their capacity for connecting patches and to weight such importance based on the contribution of patches to the general landscape connectivity (*WIP*). *WIP* can be useful for establishing conservation priorities of sectors of the landscape matrix where multiple small patches are distributed (areas of low inter-patch connectivity), but that despite their size, they significantly contribute to connectivity by acting as stepping stones, bridging patches. An example of this is corridor 1 (Figure 6b) located between the Pico de Tancítaro protected area that is the largest corridor of habitat in the $\mathrm{TMVS_{Mich}}$, displays a high value of dPC_k, and has the highest importance values in terms of *WIP* (Figure 6b), i.e., it may connect many (40) small patches having relatively high importance for inter-patch connectivity (Saura & Rubio, 2010). Correa et al. (in review) highlighted the importance of these areas for their contribution to connectivity by being stepping stones capable of generating a functional link that reaches the western extreme of the $\mathrm{TMVS_{Mich}}$ where the Monarch Butterfly Biosphere Reserve is located.

We compared the spatial congruence of the potential corridor models for species having different dispersal ranges (Cushman & Landguth, 2012) grouped in three multispecies scenarios (Figures 5b, 5c, and 5d) and a scenario including all species (Figure 5a). In general, the spatial distribution of corridors was relatively similar in all scenarios; however, corridors of scenario 2 (species with dispersal ranges between 250 and 1500 m) were the more similar to corridors in the all species scenario (*Allspp\scn2*; Figure 4a), suggesting that corridors modeled for species in scenario 2 may act as spatial proxies or surrogate estimates of a more ample group of species, and be of use for guiding conservation actions in areas important for dispersal of species for which little information is available, or of species threatened by human impact (Mimet et al. 2013; Breckheimer et al. 2014). Likewise, potential corridors modeled for the all species scenario could be useful as a conservation strategy for reducing human impact in the connectivity of the $\mathrm{TMVS_{Mich}}$, further corroborating previous results of Correa et al. (in review) who using the same multispecies scenarios modeled the effect of the human footprint on connectivity finding a high degree of spatial overlapping between the level of the human impact in the 2 and all species scenarios.

Our spatial prioritization for connectivity conservation (Figure 7) identified sectors of the landscape matrix important for preserving multispecies connectivity and that could form part of a more detailed conservation protocol (Moilanen et al. 2005). The highest values of connectivity conservation priority have a trend for locating in the southern part of the $\mathrm{TMVS}_{\mathrm{Mich}}$ (Figure 7b), concentrating in the protected area of Pico de Tancítaro, distributing along the areas surrounding the lakes of Zirahuén and Pátzcuaro, and reaching the western portion of the study area in the Monarch Butterfly Biosphere Reserve. In that sense, we found a relative spatial congruence (relative rank value=0.6) between the compound (all species) corridor model (Figure 3a) and the model of priorities for conservation of connectivity (Figure 7a). This result signifies that, despite distributions being different, they have a certain degree of congruence with the landscape matrix, which has low distance cost values for multiple species and areas with high connectivity conservation value. According to Morato et al. (2014), the role of established protected areas and proposals of priority conservation areas could be complemented with multispecies corridors, therefore enhancing ecological functionality by linking areas of the landscape matrix with high values of retention of connectivity. In landscapes like the $\mathrm{TMVS}_{\mathrm{Mich}}$ having few protected areas, but a high potential for dispersal of organism, such actions might be useful for regaining the spatial role of small patches with high conservation value –such as mountain cloud forests– that are key for optimizing inter-patch connectivity in the study area.

We also compared the spatial congruence of the distribution of connectivity conservation priority across the multispecies and all species scenarios, finding the pairwise comparison with more spatial overlap was that between scenarios 2 and all species, which means that the species with intermediate dispersal ranges that we studied could be effective indicators of connectivity for many other species with impending need for conservation (Favreau et al. 2006). Nevertheless, we excluded species of reptiles or amphibians that could have expanded the threshold of retention of connectivity (Franco et al. 2009), more so if these species are sensitive to human impact (e.g., amphibians such as *Exerodonta smaragdina, Ambystoma amblycephalum*, or *Ambystoma andersoni*; Frias et al. 2010; Flores-Villela & Canseco Márquez, 2007). Identifying important connectivity conservation areas coincident throughout all scenarios is the key for facilitating the proposal of multispecies conservation areas (Early, 2007; Mimet et al., 2013; Breckheimer et al., 2014), as for example, in the design of extensions of protected areas (Venter et al. 2014), in the location and identification of climatic change refugees for better long-term protection of species (Carrol et al. 2010; Garden et al. 2015), and in places in which working with land owners needs to be prioritized in order for preventing land use change and maintain the forest cover.

The approach we developed in this study integrated the identification of high multispecies connectivity conservation value areas (Breckheimer, 2012; Rayfield et al. 2015) with a classification of potential dispersal corridors based both on their capacity for enhancing dispersal and on the contribution of patches networking the general connectivity (Creech et al. 2014; Brodie et al. 2016). Following the recommendations of Rayfield et al. (2015) and of McRae et al. (2012), our approach allowed for an extended prioritization of the landscape matrix outside the habitat patches that includes the probability of dispersal of multiple species. Therefore, our approach can help to address multiple conservation goals. On one side, the model of importance of corridors might guide regional conservation protocols towards ecologic restoration and optimization of the network of protected areas (McRae et al. 2012), on the other side, spatial prioritization of connectivity conservation could provide a practical instrument for identifying landscapes that could be objects of more detailed planning (Moilanen et al. 2005) and for establishing which parts of the landscape matrix are capable for retaining connectivity simultaneously for most terrestrial species in the $\text{TMVS}_{\text{Mich}}$ (Rayfield et al. 2015).

CONCLUSION

We demonstrate the use of landscape elements external to the habitat patches. Integration of connectivity models and spatial conservation planning allowed for the inclusion of different spatially explicit criteria for valuing sectors of the landscape having potential for optimizing present connectivity to identify potential corridors and important areas for connectivity conservation across the $\text{TMVS}_{\text{Mich.}}$ In practice, results highlight the importance of implementing actions for conservation of connectivity between the strategic $\text{TMVS}_{\text{Mich}}$ protected areas of Pico de Tancítaro and the Monarch Butterfly Biosphere Reserve, where the most spatially congruent areas with priority corridors facilitating the simultaneous mobility of multiple species were found. Despite that our approach is only a partial initiative for conservation of biodiversity it may be useful for public policies regulating land use in areas with priority for connectivity. Likewise, we expect that future studies made in the region may supplement the information gathered here with the economic costs of conservation and other studies of prioritization of conservation in specific patches having high socioecological value, such as valuing of the mountain cloud forests in the region, which are key for the maintenance of ecological flows.

ACKNOWLEDGEMENTS

The authors acknowledge CONACYT for financing the project “*Evaluación de la importancia relativa de bosque húmedo de niebla bajo un enfoque de paisaje*" (*clave* 179386). The first author thanks CONACYT for granting him a scholarship for obtaining a PhD degree in Geography in UNAM. We also acknowledge. for his(her) aid in …... Thanks are due to the two

anonymous reviewers for their suggestions and constructive comments aiding us to improve the manuscript.

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CONCLUSIONES GENERALES

En general, la aplicación de los modelos de conectividad del paisaje permitió identificar las áreas más importantes para la conservación de la conectividad en el SVT_{Mich}. Los resultados generales de este estudio no solo resaltan la importancia de los parches de hábitat remanentes sino también de la matriz del paisaje. El sector ubicado entre el área protegida del Pico de Tancítaro y la Reserva de la Biósfera Mariposa Monarca es el de mayor importancia para la conservación de la conectividad en el área de estudio (Capítulo 2, 3 y 4). Este sector concentra las áreas con mayor aptitud de hábitat para múltiples especies y elementos del paisaje de alto valor de conservación como los bosques de niebla (Capítulo 2); así mismo la resistencia del paisaje permite la movilidad de los organismos (Capitulo 3) a través de los hábitats de paso para conectar las dos áreas protegidas. La importancia de este sector resalta la necesidad de alternativas de manejo que pueden ser optimizadas por medio de un protocolo de conservación que fomente la implementación de elementos conectores (como los corredores prioritarios identificados en este estudio) que en gran medida favorecerían las condiciones para la movilidad simultanea de múltiples especies (Capítulo 4).

El estado de la conectividad en el SVT_{Mich} no solo está afectada por el cambio del paisaje y la intensidad del uso del suelo sino también por los patrones espaciales de las coberturas naturales que ofrecen alta aptitud de hábitat. En el capítulo 2, los resultados muestran que el área potencial de los bosques de niebla y su distribución espacial tienen en la actualidad una pobre contribución a la conectividad general del área de estudio comparada con la original y con otras coberturas más abundantes como los bosques de coníferas. Sin embargo, su conservación es clave para el mantenimiento de la dispersión de flujos ecológicos y como elementos conectores entre otras unidades de hábitat. Estos resultados destacan que la importancia de dichas áreas para la conservación no sólo debe ser considerada por las características ecológicas intrínsecas de cada parche (p.e. calidad de hábitat y tamaño) sino también por su ubicación o posición en el paisaje. Esto puede ser útil para la planeación estratégica de sitios para restauración. En este sentido, reducir la resistencia de la matriz antrópica es clave para conformar corredores de dispersión que favorezcan a múltiples especies entre las áreas protegidas del $\mathrm{SVT}_{\mathrm{Mich}}$ que por su tamaño y aislamiento no son eficientes en términos de conservación, esto puede ser una alternativa a largo plazo teniendo en cuenta que las actividades humanas han causado la pérdida de más del 80% de la conectividad en el área de estudio, así como la transformación de más de la mitad del hábitat accesible en áreas sumamente resistentes a la movilidad de las especies (Capítulo 3). La integración entre modelos de corredores y planificación espacial de la conservación desarrollada en este estudio (Capítulo 4), permite incluir diferentes criterios espacialmente explícitos para valorar partes del paisaje con potencial para optimizar la conectividad actual.

El presente estudio permitió valorar el impacto de la perdida en la conectividad de aquellas áreas que en su mayoría han sido actualmente transformadas por el establecimiento de coberturas antrópicas. Así mismo, por medio del índice de huella espacial humana ajustado en este estudio se logró una medida integral y robusta de la magnitud del impacto antrópico sobre la conectividad, el cual se manifiesta en una reducción de la probabilidad de movilidad a través del paisaje. Por otro lado, la identificación de prioridades para la conservación proporcionó una definición preliminar de los corredores potenciales y áreas de importancia para la conservación de la conectividad teniendo en cuenta elementos del paisaje externos a los parches de hábitat.

Los resultados presentados en esta tesis representan un paso importante en la identificación de unidades de hábitat crítico, áreas con alta o baja calidad de hábitat y aporta una caracterización más completa de los patrones de dispersión de especies en un paisaje altamente biodiverso. El enfoque presentado aquí es un aporte sustancial para la planificación de la conservación y el monitoreo de los recursos naturales y puede ser útil en las políticas gubernamentales para regular el uso del suelo en las áreas prioritarias para la conectividad. Así mismo, los resultados pueden servir para solucionar múltiples objetivos de conservación. Por una parte, el modelo de importancia de corredores presentado en el capítulo 4 podría guiar los protocolos de conservación regionales hacia la restauración ecológica y la optimización de la red de áreas protegidas y la priorización espacial de la conservación de la conectividad podría proporcionar un medio práctico para identificar los paisajes que podrían ser objeto de una planificación más y para determinar qué partes de la matriz antrópica son mejores para optimizar la conectividad de forma simultánea para la mayoría de especies en el SVT_{Mich}.

ANEXOS

MODELACIÓN ESPACIAL DEL TIEMPO DE INTERVENCIÓN ANTRÓPICA SOBRE EL PAISAJE: UN CASO DE ESTUDIO EN EL SISTEMA VOLCÁNICO TRASNVERSAL DE MICHOACÁN, MÉXICO

Artículo publicado en *"Geografía y Sistemas de Información Geográfica"*

GESIG *Geografía y Sistemas de Información Geográfica (GEOSIG)*. Revista digital del Grupo de Estudios sobre Geografía y Análisis Espacial con Sistemas de Información Geográfica (GESIG). Programa de Docencia e Investigación en Sistemas de Información Geográfica (PRODISIG). Universidad Nacional de Luján, Argentina. http://www.gesig-proeg.com.ar (ISSN 1852-8031)

Luján, Año 8, Número 8, 2016, Sección I: Artículos. pp. 183-205

MODELACIÓN ESPACIAL DEL TIEMPO DE INTERVENCIÓN ANTRÓPICA SOBRE EL PAISAJE: UN CASO DE ESTUDIO EN EL SISTEMA VOLCÁNICO TRANSVERSAL DE MICHOACÁN, MÉXICO

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RESUMEN

En este estudio se presenta un modelo espacial del tiempo de intervención humana sobre el paisaje (TI), construido como componente integral de un índice de huella espacial humana aplicado al Sistema Volcánico Transversal de Michoacán (SVT_{Mich}). Para elaborar el modelo espacial de TI se llevó acabó una recopilación de datos históricos georreferenciados acerca del proceso de ocupación del territorio y las actividades humanas principalmente antes del periodo prehispánico. Estos datos se incorporaron a un modelo de uso potencial del suelo relativo a la topografía (Pendiente, elevación, sistema hídrico y distancia a cuerpos de agua) como limitante de las actividades humanas en el pasado. El modelo se

clasificó según el tiempo de intervención antrópica en 6 categorías de acuerdo a los años de duración de las actividades humanas sobre el paisaje (0 años, 0-40 años, 40-200 años, 200-500 años, 500-1500 años, >1500 años). Según los resultados, el 53% del SVTMich ha estado sujeto continuamente a la influencia humana durante más de 500 años, mientras que un 43% ha sido intervenido desde hace 40 años. La estimación de la duración en años en que el paisaje ha estado sometido a la actividad humana es crucial para entender el nivel de impacto antrópico sobre el mismo y de esta forma mejorar las decisiones sobre su manejo.

1. INTRODUCCIÓN

Las actividades humanas sobre los paisajes han trasformado a través del tiempo su estructura y composición provocando una drástica reducción de la biodiversidad en todo el mundo (Lindenmayer y Fischer, 2006). Así mismo, el tiempo en que el hombre ha usado su territorio y la intensidad de dicho uso afectan la capacidad de recuperación de los sistemas naturales y son factores que determinan la magnitud del efecto antrópico acumulado sobre el paisaje (Folke et al., 2002; Erb et al., 2013). La interacción entre el tiempo de intervención antrópica (TI) y la sobre explotación de los elementos del paisaje (p.e. deforestación) puede generar un efecto irreversible sobre los sistemas naturales al no alcanzar a ajustarse a la escala temporal necesaria para que haya una recuperación de dichas modificaciones (Gingrich et al., 2015). TI se define como la duración en años en que los paisajes y ecosistemas han estado sometidos al disturbio humano (Etter et al., 2011). TI se ha aplicado en estudios del impacto humano sobre el paisaje como una variable espacial para cuantificar e identificar los patrones espaciales de la huella humana y su efecto sobre los sistemas naturales. Con base en dicho conocimiento se pueden mejorar las decisiones en cuanto a la planificación y conservación de la biodiversidad (Ocampo-Peñuela, 2015; Qiu et al., 2015) y las políticas públicas sobre el uso del suelo (Etter et al., 2008; Etter et al., 2011).

Etter et al. (2011) calcularon el tiempo de intervención humana en Colombia como parte de un índice de huella espacial que integra dos componentes más, la intensidad del uso del suelo y la vulnerabilidad biofísica. En conjunto, estas tres dimensiones espaciales ayudan a una cuantificación más precisa del grado de impacto humano, con respecto a otros índices que se basan solo en el efecto del tipo de uso del suelo y la infraestructura (Hanna et al., 1999; Sanderson et al., 2002). En México, González-Abraham et al. (2015) aplicaron un índice de huella espacial humana basado en la metodología de Sanderson et al. (2002), para identificar las regiones ecológicas más afectadas por las actividades humanas e integraron la distribución espacial de los asentamientos humanos pasados (dimensión histórica) como un factor que ha direccionado la trasformación antrópica sobre el paisaje. Uno de las principales conclusiones de dicho trabajo fue que el grado de huella humana en México depende de la influencia de su complejo entorno geográfico el cual en mayor o menor medida influye en el desarrollo humano, y dentro de ese entorno, la influencia de una compleja historia de ocupación del territorio y su modificación. Así mismo, señalan que el Sistema Volcánico Transversal es una de las ecorregiones de México con mayor valor de huella espacial humana, sin embargo sus efectos sobre los procesos ecológicos en el nivel de paisaje han sido poco estudiados (Correa et al., sometido 2015).

El objetivo de este artículo es presentar el procedimiento metodológico utilizado para la modelación espacial del tiempo de intervención antrópica sobre el paisaje. TI se integró como parte de un índice multi-dimensional de huella espacial humana (Etter et al. 2011). Dicho índice se aplicó en el Sistema Volcánico Transversal de Michoacán (SVT_{Mich}) en el marco de un estudio sobre el efecto humano en la conectividad el paisaje (Correa et al., sometido 2015). El SVT_{Mich} se caracteriza por tener una gran riqueza biocultural y un legado histórico particular que lo hace especialmente relevante en el contexto de estudio, sobre todo en lo referente al proceso de ocupación del territorio. El modelo que se presenta puede ser aplicable a otros paisajes y regiones y puede ser adaptado a diferentes escalas espaciales.

2. METODOLOGÍA

a. Área de estudio

El Sistema Volcánico Transversal (SVT) presenta una superficie aproximada de 160000 km^2, se localiza en el centro de México y se extiende desde el océano Pacífico hasta el golfo de México (Ferrari et al., 2012). Se distingue por su amplia riqueza biológica y cultural, existen comunidades humanas que han aprovechado por generaciones los recursos de su entorno como por ejemplo los indígenas Purépechas y la comunidad Mazahua-Otomí (Toledo ,2001; Toledo y Barrera-Bassols, 2009). La porción central del SVT que abarca la parte norte del estado de Michoacán corresponde al área de estudio del presente trabajo ($\mathrm{SVT}_{\mathrm{Mich}}$; Figura 1).

El $\mathrm{SVT}_{\mathrm{Mich}}$ presenta una superficie de 28,100 km^2 y un rango altitudinal entre 1,044 m.s.n.m a 3,800 m.s.n.m, se encuentra localizado en el norte del estado de Michoacán entre los 18°47´ y 20°30´ latitud norte y 100°4´y 103°3´ longitud oeste. El 70 % de su extensión se encuentra dominado por coberturas antrópicas lo que indica una fuerte influencia antrópica sobre el paisaje. El $\mathrm{SVT}_{\mathrm{Mich}}$ se distingue por poseer una de las regiones indígenas más importantes de México, la Purépecha, distribuida en 14 municipios del $\mathrm{SVT}_{\mathrm{Mich}}$. Existen ocho áreas naturales protegidas dentro del área de estudio ubicadas en su mayoría en el sector montañoso (Figura 1), abarcando el 2.4% del área de estudio (Bezaury-Creel et al., 2009).

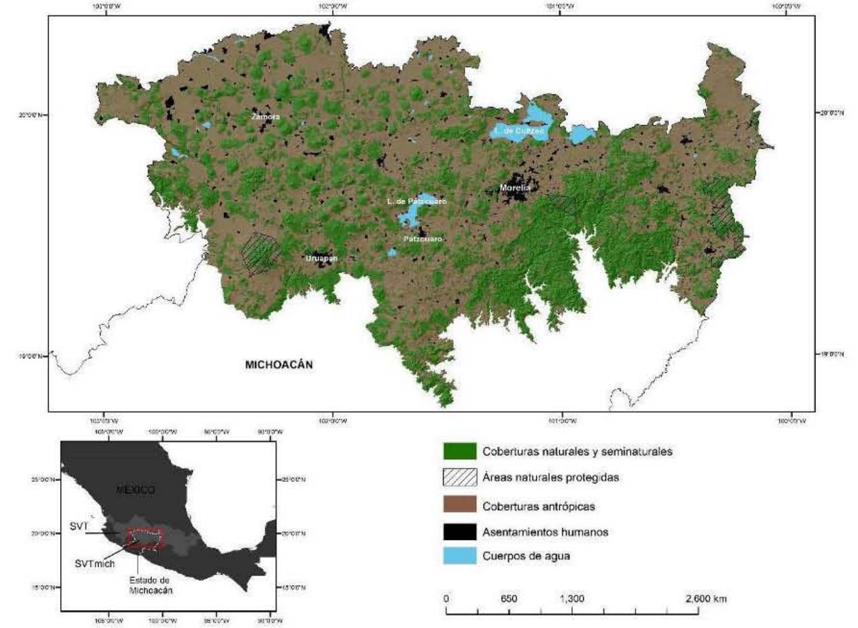

Figura 1. **Situación relativa del área de estudio**

b. Elaboración del mapa de coberturas naturales de referencia

Se elaboró un mapa de coberturas potenciales para identificar la distribución espacial de los principales tipos de vegetación madura en ausencia de intervención humana en el $\mathrm{SVT}_{\mathrm{Mich}}$ (Hardtle, 1995). Este mapa sirvió como punto de partida para cartografiar el tiempo de intervención antrópica sobre el paisaje y para buscar una asignación práctica a las unidades de cobertura natural que se desarrollan bajo condiciones ecológicamente homogéneas (Loidi et al., 2010). La leyenda del mapa actual de cobertura y uso del suelo, serie V (INEGI, 2013), se generalizó con base en las coberturas de tipo natural en 5 clases: Bosque templado, bosque de latifoliadas, selva baja sub y caducifolia, vegetación hidrófila, cuerpos de agua (natural).

Se elaboraron modelos de distribución potencial de especies diagnósticas de cada tipo de cobertura con base en un enfoque MaxEnt (Philips et al., 2006; Philips & Dudik, 2008) utilizando 19 variables ambientales (Cuervo et al., 2014) y 7 topográficas derivadas de un DEM de 30 m de resolución (ASTER GDEM) que abarca el área de estudio, siguiendo la metodología de Correa et al. (Manuscrito sometido, 2015). Con base en un umbral logístico se extrajo el área óptima de cada tipo de cobertura y posteriormente se generó un mapa de cobertura "unificado" mediante sobre posición de las coberturas potenciales individuales. Los límites y áreas con vacíos de cada cobertura se ajustaron con base en criterios fisiográficos (p.e rangos altitudinales, Rendowsky, 1990; topoformas, INEGI, 2001); y la vegetación natural remanente (INEGI, 2013).

2.3 Fuentes de datos históricas

Se llevó a cabo una revisión de fuentes históricas con el fin de recabar información referente a los procesos de ocupación del territorio y de las actividades humanas en el paisaje, especialmente en el pasado (Tabla 1). Los documentos consultados corresponden a crónicas, libros de síntesis históricas, artículos científicos especializados en arqueología y mapas históricos. De la información recopilada solo se utilizó la que pudiera ser georreferenciada para construir modelos espaciales que permitieran la posterior asignación puntual del tiempo de intervención humana en el paisaje (Ver numeral 2.4.). La información histórica georreferenciada preliminarmente se agrupó en periodos históricos propuestos para las culturas de Mesoamérica (López-Austin & López-Luján, 2000) para facilitar el análisis y la asignación del tiempo de intervención antrópica (Tabla 1). Posteriormente los periodos de tiempo fueron reclasificados en 6 categorías tal como se explica en el numeral 2.4 y la tabla 2.

Tabla 1. Fuentes de datos históricas, localidades georreferenciadas y periodos históricos para la elaboración de los modelos espaciales. Nota: Para ver la ubicación relativa de cada localidad seleccionada ver figura 2.

No de localidades georreferenciadas	Fuente	Autores/año	Periodo histórico		Localidades
1	Acambaro: Frontier Settlement on the Tarascan-Aztec Border	GORENSTEIN, S. 1985	Postclásico Tardío	1200-1521 d.C	Tuzantla
1	Apuntes para la Historia de la Villa de Tangancicuaro	SAMANO-MAGAÑA, M. 1987	Clásico-Postclásico Tardío	400-1521 d.C	Tangancicuaro
1	Arqueología de las Lomas en la cuenca lacustre de Zacapu, Michoacán, México	ARNAULD, CH., CAROT, P., FAUVET-BERTHELOT, M.F. 1993	Preclásico Tardío	100 a.C-100 d.C	Loma alta
3	Arqueología en el norte de Michoacán. Investigación de salvamento en una carretera	PULIDO MÉNDEZ, S., ARAIZA, L. A & GRAVE TIRADO, L. A. 1996	Clásico Temprano-Postclásico Tardío	200-1521 d.C	Valle de Churintzio, Maravatio y de Atotonilco
1	Boletín Conaculta	CONACULTA. 2013	Clásico Temprano-Postclásico Temprano	350-900 d.C	Tiripatillo
1	Cueva de los Portales: un sitio arcaico del norte de Michoacán, México	FAUGÈRE, B. 2006	Protoneolítico-Postclásico Tardío	5200 a.C - 1500 d.C	Cueva de los Portales
2	El antiguo occidente de México. Nuevas perspectivas sobre el pasado prehispánico	WEIGAN, P. C., WILLIAMS, E., LÓPEZ MESTAS, L. & GROVE, D. 2005	Preclásico Tardío-Epiclásico-Postclásico Temprano	400 a.C-1200 d.C	Ucareo, Puraguita
1	El Bajío, la cuenca de Cuitzeo y el estado teotihuacano. Un estudio de relaciones y antagonismos	FAUGÈRE, B. 2010	Clásico-Postclásico Tardío	400-1521 d.C	Quiringuicharo
1	El Opeño, Jacona, Michoacán. En: Arqueología Méxicana. Vol. XXI. Num. 123	OLIVEROS, J. A. 2013	Preclásico Temprano	1800-1500 a.C	Jacona
2	El Valle de Toluca. Época prehispánica y siglo XVI	HERNANDEZ RODRÍGUEZ. R. 2013	Clásico Temprano-Postclásico Tardío	200-1521 d.C	Epitacio Huerta, Contepec
13	Enciclopedia de los municipios de México	Centro Nacional de Desarrollo Municipal. 1986	Clásico-Postclásico Tardío-Colonia-Presente	400-1200-1521-2015 d.C	Tanhuato, Ixtlán, Angamacutiro, Senguio, Ocampo ,Angangueo, Madero, Tzitzio ,Tacámbaro ,Susuapato , Jungapeo ,Ario ,Tinguindi
1	Historia General de Michoacán. Vol 2	FLORESCANO, E. 1989	Clásico Tardío-Postclásico Tardío	600 d.C-1250 d.C	Yurécuaro
5	Las cuencas del occidente de México: Época prehispánica	WILLIAMS, E., WEIGAND, P.C. 1996	Clásico Tardío-Postclásico Tardío	450-600-1250 d.C	Tizapán, Cojumatlán , San Gregorio ,Valle de Maravatio ,Tinganio Jiquilpán
1	Las Pinturas en los Riscos de Parangaricutiro, Michoacán, México	BABANY-GUERRERO, T. 2005	Clásico	400 d.C	La Alberca
1	Les Mines-Ateliers D'Obsidienne de La Région de Zinaparo-Prieto, Michoacan, Mexique	DARRAS, V. 1994	Clásico Tardío-Postclásico Tardío	800-1200 d.C	Zináparo
6	Lugares del más antes, el Cerro y el pueblo en la historia purepecha	MUÑOZ MORÁN, O. 2009	Clásico-Postclásico Tardío	400-1521 d.C	Sevina, Comachuen ,Turicuaro ,Pichátaro ,Cherán ,Paracho
1	Recent research in western Mexican archeology	POLLARD, H. P. 1997	Clásico Tardío-Postclásico Tardío	750-1250 d.C	Perales
2	Red de zonas arqeuológicas del INAH	INAH. 2015	Clásico-Postclásico Tardío	400-900-1200-1521 d.C	San Felipe los Alzati, Zaragoza
34	Relación de Michoacán	Fray Jerónimo de Alcalá. (aprox 1540)	Preclásico Medio-Preclásico Tardío-Clásico Temprano-Clásico Tardío-Postclásico Temprano-Postclásico Tardío	1200 a.C-600 a.C-350 d.C-600-900-1200-1530 d.C	Huaniqueo de Morales, Cerro el Chivo, Zacapu, Pátzcuaro, Capacuaro, Capula, Chahueto, Chucándiro, Zinapecuaro, Taximaroa, Comanja, Condémbaro, Cuitzeo, Erongaricuaro, Araro, Yziparamucu, Hurecho, Uricho, Indaparapeo, Iramuco, Jeruco, La Huacana, Naranjan, Parácuaro, Puco, Ucareo, Puruaguita, Cueva de los portales, Santa Maria, Huiramangaro, Zipiajo, Zirahuén, Tancítaro, Tarimbaro, Tzintzimeo, Ziracuaretiro, Zurumucapio.
1	The Ethnoarchaeology of Salt Production at Lake Cuitzeo, Michoacán, Mexico	WILLIAMS, E. 1999.	Clásico-Postclásico Tardío	200-1521 d.C	Yácatas (Puruándiro)
1	The Political Economy of Prehispanic Tarascan Metallurgy.	POLLARD, H. P. 1987	Postclásico tardío	1250-1521 d.C	Tarécuato

2.4 Elaboración del mapa de usos del suelo potenciales

El paisaje se clasificó en términos de aptitud para la agricultura como base para cartografiar la distribución espacial del uso del suelo en el pasado. Se elaboró un modelo relativo a la topografía (Pendiente, elevación, sistema hídrico y distancia a cuerpos de agua), apoyándonos en la premisa que el terreno es una variable condicionante para la transformación del paisaje, el cual limita o favorece ciertos usos en el territorio (Verhagen, 2007; Uriarte-González, 2008; Verhagen y Withley, 2012; Yu et al., 2012) y que no cambia significativamente durante miles de años al presente (Banks et al., 2006; Yu et al., 2012). El modelo se clasificó preliminarmente en 3 categorías (Uriarte-González, 2008): No cultivable, cultivable (humedad) e intermedio. La categoría no cultivable corresponde a las áreas donde las condiciones topográficas de pendiente y altura no permiten la agricultura a partir de la tecnología prehispánica. De acuerdo a una revisión rigurosa de literatura asumimos que dichas áreas deben cumplir dos condiciones: 1) pendiente >30%; 2) altitud > 2800 m (Pollard y Gorestein, 1980; Judge y Sebastian, 1988; Fischer et al., 2003; Garibay y Bocco, 2011, Ullah, 2011). La presencia de cuerpos de agua, humedales y ciénagas en el $\mathrm{SVT}_{\mathrm{Mich}}$ ha facilitado la implementación de prácticas agrícolas que aprovechan la humedad del suelo y retención de agua en las zonas inundables y/o cercanas a los lagos (INEGI, 2014) las cuales fueron ampliamente desarrolladas en la época prehispánica sobre todo en las cuenca lacustres del lago Cuitzeo y Pátzcuaro, en las ciénagas del lago de Chapala y el lago de Zacapu antes de que fuera desecado (Arnauld, 1996; Boehm, 2005; Williams, 2009). Para definir estos espacios con aptitud para la agricultura de humedad se generó un modelo de distancia costo a partir de la cercanía a las corrientes y cuerpos de agua. Como superficie de fricción se utilizó un modelo condicional donde asumimos que toda la superficie mayor a 5% de pendiente no es apta para este tipo de uso (Uriarte-González, 2008; Williams, 2009). El resultado es un modelo binario con la distribución espacial de las áreas aptas y no aptas para cultivos de humedad. La categoría intermedia corresponde a las áreas que no han sido asignadas a ninguna de las dos categorías y también corresponde a un modelo binario (intermedio-no intermedio).

Los 3 modelos se unificaron y se reclasificaron en un nuevo modelo binario (Cultivable-no cultivable) de la siguiente forma:

Intermedio + cultivable (humedad)= Cultivable
No cultivable (humedad) + No Intermedio=No cultivable
No cultivable (humedad) + intermedio= Cultivable
Cultivable (humedad) + No cultivable= No cultivable

2.5 Asignación de los años de intervención antrópica sobre el paisaje

Se clasificó el tiempo de intervención antrópica en 6 categorías de acuerdo a los años de duración de las actividades humanas sobre el paisaje (Tabla 2), con base en el escalamiento aplicado en Etter et al. (2011), donde se asume que un mayor tiempo de intervención antrópica puede generar un mayor impacto humano sobre el paisaje al interactuar con la intensidad de las actividades humanas y la vulnerabilidad del sistema biofísico.

Tabla 2. Categorías asignadas a los años de intervención antrópica (TI) y tipos de fuentes de datos.

Contribución al impacto humano	Años de intervención antrópica	Tipos de datos utilizados para la asignación de años de intervención
0- Nula	0	Cartográfico (Cobertura y uso de la tierra actual)
1- Muy poca	0-40	Cartográfico (Cobertura y uso de la tierra serie I + Mapa binario de uso potencial
2- Poca	40-200	Cartográfico (Cobertura y uso de la tierra serie I + Mapa binario de uso potencial), Crónicas y síntesis históricas
3- Moderada	200-500	Crónicas y síntesis históricas
4- Alta	500-1500	Arqueológico, Crónicas y síntesis históricas
5- Muy Alta	>1500	Arqueológico

0 años de intervención antrópica: A esta categoría corresponde la vegetación primaria remanente (INEGI, 2013) que no ha sido transformada a coberturas antrópicas (Bosques primarios de latifoliadas, coníferas y mixtos (coníferas y latifoliadas), selvas bajas). El mapa de usos potenciales binario se actualizó con esta información y se generó un nuevo mapa (TI preliminar_1) con tres categorías (0) Cultivable, (1) No cultivable, (2) 0 años de intervención.

0-40 años de intervención antrópica: Se generaron dos modelos preliminares: 1) corresponde a los bosques y matorrales que fueron transformados recientemente y se recuperaron (entre 0 y 40 años). Es producto de la intersección entre la vegetación secundaria y la categoría no cultivable del modelo de uso potencial. 2) Vegetación natural que cambió en los últimos 40 años. Se elaboró mediante una intersección entre la vegetación natural del mapa de cobertura de la tierra de 1976 y la actual y se eliminaron las áreas que se sobreponen. Posteriormente los dos modelos se unificaron y se actualizó con el modelo TI preliminar_1 y se generó un nuevo mapa (TI preliminar_2) con cuatro categorías: (0) Cultivable, (1) No cultivable, (2) 0 años de intervención, (3) 0-40 años de intervención.

40-200 años de intervención antrópica: A esta categoría corresponden las áreas que cambiaron de vegetación natural a asentamientos humanos dentro de ese periodo de tiempo y a otras actividades humanas exceptuando la ganadería y la agricultura (p.e. Minería). Se utilizó información secundaria correspondiente a síntesis históricas relacionadas con el establecimiento de los asentamientos y de áreas mineras (entre 1976 y 1776) y con base el mapa de cobertura serie I se ajustaron los límites preliminares. Se actualizó el modelo TI prelimanar_2 y se generó uno nuevo (TI preliminar_3), con cinco categorías: (0) Cultivable, (1) No cultivable, (2) 0 años de intervención, (3) 0-40 años de intervención, (4) 40-200 años de intervención.

200-500 años de intervención antrópica: Este intervalo se calculó mediante la intersección entre los pastizales artificiales e inducidos actuales y la categoría no cultivable del mapa de uso potencial. El modelo se ajustó con información secundaria y corresponde a las áreas no cultivables que pudieron ser transformadas a ganadería después de la conquista, teniendo en cuenta el establecimiento de áreas ganaderas en el SVT_{Mich} aproximadamente a principios del siglo XVI (Leonard, 1993; García, 1994; Dávila, 2014). Las áreas no cultivables en la época prehispánica pero que se transformaron en cultivos actualmente también fueron incluidas en esta categoría bajo el supuesto que en dicho intervalo de tiempo algunas áreas catalogadas como no cultivables podrían ser cultivadas por la llegada de nuevas tecnologías, sin embargo en las áreas no cultivables habría mayor aptitud para el establecimiento de la ganadería. Se actualizó el modelo TI prelimanar$_3$ y se generó uno nuevo (TI preliminar$_4$), con 6 categorías: (0) Cultivable, (1) No cultivable, (2) 0 años de intervención, (3) 0-40 años de intervención, (4) 40-200 años de intervención, (5) 200-500 años.

>500 años de intervención humana: Se dividió en dos categorías basadas en el mismo proceso metodológico: Un intervalo de tiempo de 500-1500 años de intervención y otro > 1500 años (Tabla 2). Con base en 81 datos arqueológicos georreferenciados (Tabla 1 y Figura 2) e información histórica se estimaron los años de intervención dentro de los dos intervalos de tiempo (Ver numeral 2.3). Los años se asignaron a la categoría "cultivable" del mapa de usos potenciales y posteriormente se ajustaron los límites con base en criterios fisiográficos utilizando un mapa de topo formas y el mapa de cobertura vegetales potenciales. Se actualizó el modelo TI preliminar$_4$ y se generó el mapa de tiempo de intervención final (TI), compuesto por 6 categorías: (1) 0 años de intervención, (2) 0-40 años de intervención, (3) 40-200 años de intervención, (4) 200-500 años, (4) 500-1500, (6) > 1500 años.

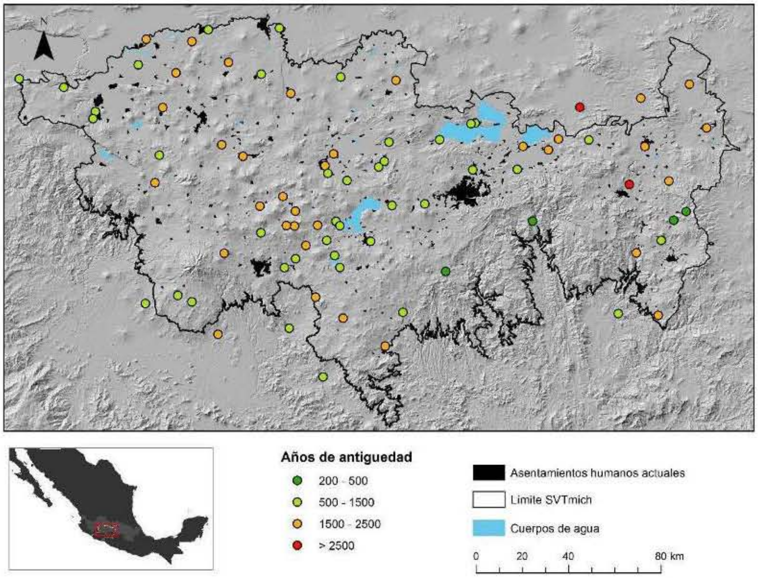

Figura 2. Ubicación de los 81 datos basados en hallazgos arqueológicos y bibliografía histórica en el SVTMich. Los datos fueron utilizados como insumo para cartografiar el tiempo de intervención humana sobre el paisaje en su mayoría para el periodo prehispánico.

Finalmente, se aplicó la prueba de rango relativo (Warren y Seifert, 2010) para corroborar el grado de similaridad entre el modelo de uso potencial binario (Cultivable-No cultivable) y las áreas cultivadas actuales. La prueba del rango relativo se calcula entre valores de 0 a 1, los valores cercanos a 1 significan mayor probabilidad de que dos categorías sean la misma para los dos modelos (Warren y Seifert, 2010).

3 RESULTADOS Y DISCUSIÓN

3.1 Similaridad del modelo de uso potencial con el actual

La comparación entre el modelo de uso potencial binario en la época prehispánica (Cultivable-No Cultivable) con las áreas cultivadas actuales muestra un buen ajuste entre los dos modelos con un valor de (0.74), lo que significa que en general existe una alta probabilidad de que las áreas clasificadas como potencialmente cultivables en la época prehispánica correspondan a áreas cultivadas en la actualidad (Figura 3). Sin embargo, se encontraron algunos desacuerdos en el sector noroccidental del SVT_{Mich} que pueden deberse a áreas con cobertura arbórea o arbustiva que fueron en un momento transformadas a coberturas antrópicas pero que en la actualidad se recuperaron y corresponden a vegetación secundaria o que pertenecen en la actualidad a pastos inducidos.

En total, el 46% de la superficie del SVT_{Mich} en la época prehispánica potencialmente corresponde a áreas aptas para cultivar y el 40 % actualmente se encuentra cultivado. Solo un 6% de las áreas simuladas no corresponden a las actuales, lo que indica que el uso potencial presenta un acuerdo razonable con el observado.

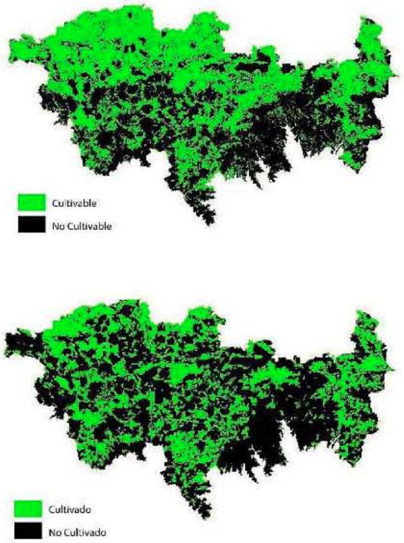

Figura 3. Comparación entre el mapa de uso potencial binario (Cultivable-No Cultivable), arriba y el mapa de uso actual (Cultivado-No Cultivado)

3.2 Distribución espacial y representatividad del tiempo de intervención antrópica en el SVT$_{\text{Mich}}$

En general, los resultados indican que más de la mitad de la superficie del SVT$_{\text{Mich}}$ ha estado sujeta a actividades humanas desde la época prehispánica, teniendo en cuenta que los rangos de intervención antrópica entre 500-1500 y >1500 años se encuentran ampliamente representados en el SVT$_{\text{Mich}}$ y dominan el 53 % de la superficie total (Figura 4). Desde el punto de vista espacial, las áreas con actividades humanas más antiguas se distribuyen en su mayoría en lugares con pendientes poco pronunciadas (<10%) y cercanas a los lagos y sus áreas de influencia, como por ejemplo las áreas aledañas al lago de Cuitzeo, Chapala, Pátzcuaro y la cuenca lacustre de Zacapu (Figura 5). Sitios que se han caracterizado por una actividad humana milenaria relacionada con la agricultura de humedad donde se han aprovechado las fluctuaciones de las áreas cenagosas principalmente para prácticas hortícolas intensivas y también para el aprovechamiento agrícola sobre campos drenados con un alto nivel de productividad (Arnauld, 1996).

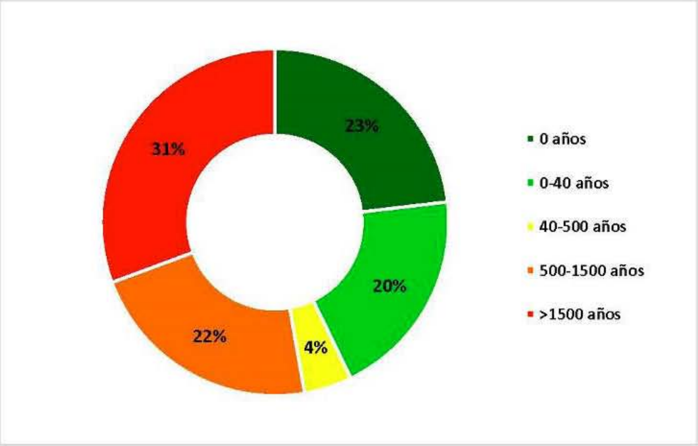

Figura 4. Representatividad del tiempo de intervención antrópica en la superficie total del SVTMich.

Las áreas restantes en su mayoría presentan una intervención antrópica más reciente (entre 40 y 0 años) con una representatividad del 43% de la superficie total del SVT$_{\text{Mich}}$, y se encuentran distribuidas en las partes altas de las cuencas lacustres (Cuitzeo y Pátzcuaro) y en general con alto porcentaje de pendiente (>20%). Las áreas correspondientes a cero años de intervención en general pertenecen a bosques templados, de latifoliadas y mixtos, maduros y en menor proporción a selvas bajas, que han permanecido poco intervenidos tal vez por las limitaciones impuestas por la heterogeneidad del terreno relacionado con el difícil acceso para su extracción y la lejanía a vías de transporte y a asentamientos humanos. Otras razones pueden estar relacionadas con la baja productividad y capacidad de los suelos para la agricultura (González-Abraham, 2014). Los lugares donde la actividad humana se ha llevado a cabo en los últimos 40 años corresponden a las coberturas boscosas que existían en la década de los años setenta y que se transformaron actualmente, y se encuentran dentro de las áreas potenciales no cultivables. Además, corresponden a áreas transformadas en la década de los años setenta que por eventos de recuperación se transformaron a vegetación secundaria en la actualidad (Etter et al., 2011). Así mismo, la distribución de dichas áreas está relacionada con el recurso maderable que pudo ser extraído en sitios con mayor acceso, terrenos más homogéneos y pendientes menos pronunciadas (<15%).

El 4% restante correspondió a las áreas intervenidas por el hombre entre 40 y 500 años. Nosotros asumimos que la llegada de la ganadería durante la Colonia fue un instrumento que permitió que las áreas con potencial no cultivable (Hasta comienzos del siglo XVI) fueran finalmente intervenidas en años posteriores, modificando el uso del paisaje y su espacio geográfico. Su asociación con las prácticas agrícolas impulsó la trasformación del entorno y el establecimiento de otras estrategias de apropiación del territorio (p.e. Grandes haciendas en la ciénaga de Chapala) permitiendo su expansión en la mayoría del SVT_{Mich} (Figura 5) (Leonard, 1993; Dávila, 2014). Así mismo, las áreas correspondientes entre los 40 y 200 años de intervención antrópica (se fusionaron en un solo intervalo de 40-500 años para la descripción de resultados), se distribuyen en la región oriental del SVT_{Mich}, en la cual, durante el siglo XVIII se desarrolló la minería, sobre áreas dominadas por bosques templados y mixtos que se extendían en la región (Uribe-Salas, 2006). Por medio del mapa de coberturas de referencia (Ver numeral 2.1) identificamos las áreas de bosque templado que se transformaron en dicho sector y las anexamos a este intervalo, así como las áreas transformadas por los asentamientos que fueron fundados o rápidamente expandidos a partir de los últimos 200 años al presente (p.e. Angangueo después de 1792 por el auge minero; CEDEMUD, 1986).

4. CONCLUSION

El propósito de este artículo se concentró en describir el proceso para obtener la distribución espacial del tiempo de intervención antrópica en el SVTMich, como insumo para un estudio paralelo sobre el efecto del impacto humano en los procesos ecológicos en el nivel de paisaje. Por esta razón no se profundizó en los resultados acerca del tiempo de intervención sobre las coberturas naturales. Sin embargo, este enfoque al ser considerado con la intensidad del uso del suelo y la vulnerabilidad biofísica, permite evaluar y dar seguimiento a los impactos antrópicos y su magnitud. Así mismo, puede servir como una herramienta de planificación del paisaje que ayude al entendimiento de los efectos de las transformaciones del entorno de una forma más contundente y detallada que solamente los análisis de cambio de cobertura y uso del suelo.

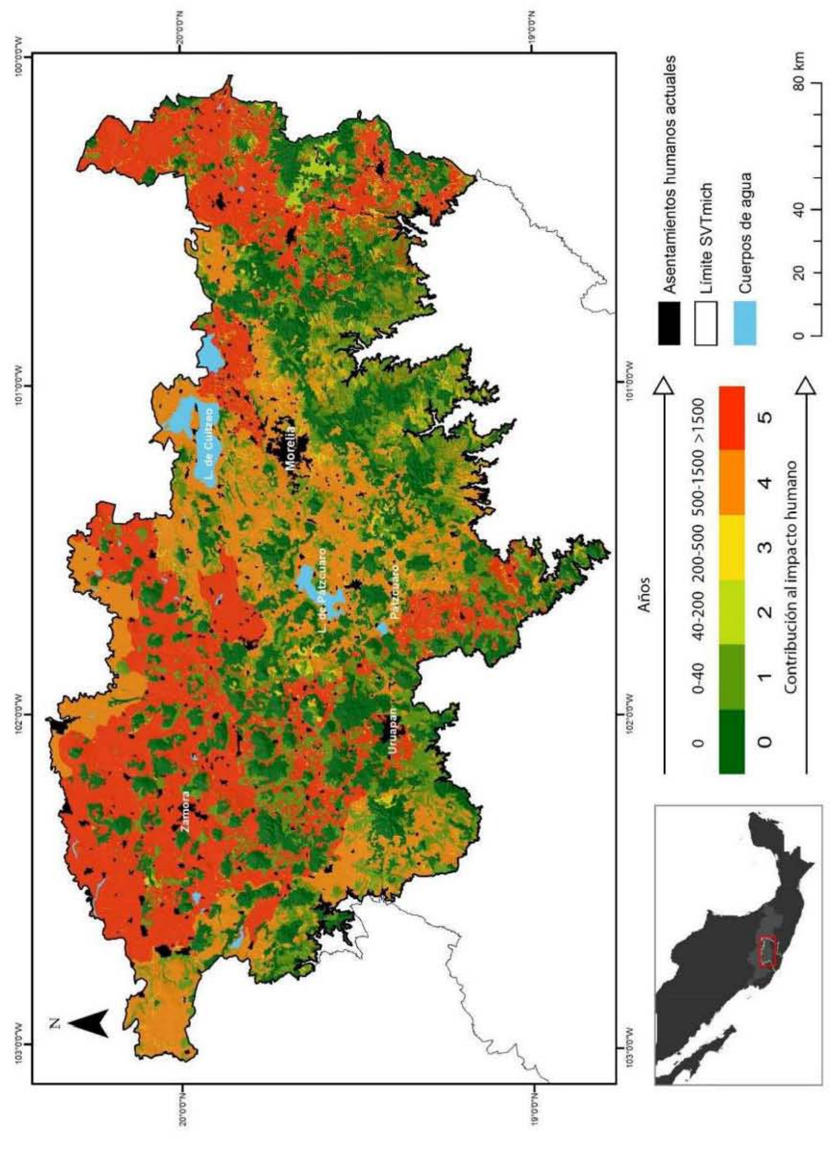

Figura 5. Mapa de la distribución espacial del tiempo de intervención antrópica en el $\mathrm{SVT}_{\mathrm{Mich}}$.

AGRADECIMIENTOS

Los autores agradecen al proyecto “Evaluación de la importancia relativa de bosque húmedo de niebla bajo un enfoque de paisaje”, financiado por DGAPA-PAPIIT. El autor principal agradece a CONACYT por la beca otorgada para realizar los estudios de Doctorado en Geografía de la UNAM.

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Recibido: 11 de noviembre de 2015

Aprobado: 15 de diciembre de 2015