



UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
FACULTAD DE CIENCIAS
ECOLOGÍA

**PATRONES ACTUALES Y FUTUROS DE LA DIVERSIDAD TAXONÓMICA, FUNCIONAL Y
FILOGENÉTICA DE ANFIBIOS EN LA PENÍNSULA DE YUCATÁN Y SU REPRESENTACIÓN
EN ÁREAS PROTEGIDAS**

TESIS

POR ARTÍCULO CIENTÍFICO

**Current and future patterns of taxonomic, functional and phylogenetic diversity of
amphibians in the Yucatan Peninsula and their representation in Protected Areas**

QUE PARA OPTAR POR EL GRADO DE:

MAESTRA EN CIENCIAS BIOLÓGICAS

PRESENTA:

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Presente.

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **24 de febrero de 2020** se aprobó el siguiente jurado para el examen de grado de **MAESTRA EN CIENCIAS BIOLÓGICAS** en el campo de conocimiento de **Ecología** de la alumna **CASTAÑO QUINTERO SANDRA MILENA** con número de cuenta **518494102** por la modalidad de graduación de **tesis por artículo científico** titulado: **"Current and future patterns of taxonomic, functional and phylogenetic diversity of amphibians in the Yucatan Peninsula and their representation in Protected Areas"**, que es producto del proyecto realizado en la maestría que lleva por título **"Patrones actuales y futuros de la diversidad taxonómica, funcional y filogenética de anfibios en la Península de Yucatán y su representación en Áreas Protegidas"** ambos realizados bajo la dirección del **DR. CARLOS ALBERTO YAÑEZ ARENAS**, quedando integrado de la siguiente manera:

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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, Cd. Mx., a 24 de agosto de 2020

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RESUMEN

Desde la revolución industrial (1880), la temperatura promedio de la Tierra ha aumentado en aproximadamente 1.1 °C y se espera que entre 2030 y 2052 aumente en 1.5 °C respecto a los niveles preindustriales. Como respuesta a los cambios en el ambiente, las especies residentes pueden colonizar nuevas áreas con condiciones ambientales óptimas, aclimatarse a las nuevas condiciones de su ambiente natural o bien, sufrir extinciones locales. Dichas respuestas pueden generar cambios en la distribución espacial de las facetas de la diversidad como la diversidad taxonómica, diversidad filogenética y diversidad funcional (TD, PD y FD, respectivamente por sus siglas en inglés) que, en conjunto, arrojan información acerca de los patrones y procesos que originan y mantienen la biodiversidad.

En grupos como el de los anfibios con capacidad de dispersión baja y distribuciones reducidas, los cambios acelerados del clima pueden traer consecuencias más graves que en otros grupos de vertebrados. Además, en lugares como la Península de Yucatán (PY) donde se desconocen los patrones geográficos de diversidad de anfibios, sus posibles cambios en la geografía en el marco de escenario futuros de cambio climático y su representatividad a largo plazo en el sistema actual de áreas protegidas, no podrían identificarse sitios en los que la pérdida de diversidad podría ser máxima. Dicho esto, la posibilidad de plantear estrategias de conservación y mitigación más efectivas sobre los ecosistemas y las especies sería nula. En este sentido, el objetivo de este trabajo fue estimar los patrones espaciales actuales y futuros de la TD, PD y FD de los anfibios de la Península de Yucatán y evaluar la relación entre estas facetas de la diversidad y su representación en las áreas protegidas (AP). Para esto, estimamos las distribuciones potenciales actuales y futuras de anfibios por medio de modelos de nicho ecológico en la PY. Luego, apilamos los modelos de distribución para estimar la diversidad taxonómica, y con base a la filogenia de anfibios más reciente y nueve rasgos funcionales, estimamos la PD y FD, respectivamente. La congruencia espacial entre las tres facetas de la diversidad se evaluó mediante los coeficientes de correlación de Pearson y los residuales se obtuvieron de las regresiones

locales con suavizado no paramétrico (LOESS, por sus siglas en inglés). Por último, evaluamos la representatividad de las diferentes facetas de diversidad en el sistema de AP en el escenario presente y cuatro escenarios futuros de cambio climático producto de la combinación de dos trayectorias de concentración de gases de efecto invernadero (RCP 45 y 85) y dos años futuros (2050 y 2070).

Las facetas de la diversidad presentaron correlaciones positivas, pero más fuertes entre PD y FD. En los escenarios de cambio climático se prevé una disminución general de todas las facetas de la diversidad con respecto al presente. Por otra parte, ninguna de las AP evaluadas fue efectiva protegiendo las diferentes facetas de la diversidad, ni en el presente ni en los escenarios futuros respecto a un modelo nulo. Encontramos que para el presente las diversidades están ampliamente acopladas en el espacio geográfico, probablemente llenando todo el espacio ecológico disponible y para escenarios futuros se pronostica un desacoplamiento debido a extirpaciones aleatorias y masivas de especies, es decir, disminución de TD. No obstante, a pesar de la pérdida de TD, algunos sitios puntuales mantendrían altas PD y FD debido a la coexistencia de especies estrechamente emparentadas y funcionalmente redundantes. Finalmente, el hecho de que las AP evaluadas no cubren significativamente las zonas de diversidad de los anfibios, subraya la necesidad de incrementar la cobertura del sistema de AP existente.

ABSTRACT

Since the Industrial Revolution (1880), the average temperature of the Earth has increased approximately 1.1 °C and is likely that it reaches 1.5 °C increase above pre-industrial levels between 2030 and 2052. In response to environmental changes, resident species can colonize new areas with optimal environmental conditions, acclimatize to the new conditions or suffer local extinctions. These responses can generate alterations in the spatial distribution of the facets of diversity such as taxonomic diversity (TD), phylogenetic diversity (PD) and functional diversity (FD), which together can give insights on the main causal processes of the origin and maintenance of biodiversity.

In groups such as amphibians, with low dispersion capacity and narrow distribution ranges, accelerated climate change can depict more severe consequences than for other vertebrate groups. Furthermore, in places such as the Yucatan Peninsula (YP) where the geographic patterns of amphibian diversity are unknown, as their possible changes in geography in the context of future climate change scenarios and their long-term representativeness in the current system of protected areas, it could not be possible to identify where the loss of diversity could be greatest. That said, the possibility of proposing more effective conservation and mitigation strategies on ecosystems and species would be null. Consequently, we aimed to estimate current and future spatial patterns of TD, PD and FD of amphibians in the Yucatan peninsula (YP); evaluate relationship between these diversity facets, and asses their representation in the Protected Areas (PA) of this region. We used ecological niche modeling to predict current and future potential distributions of amphibians in the YP. Then, we stacked distribution models to estimate TD, and based on the most recent amphibian phylogeny and nine functional traits we measured PD and FD. Then, we used Pearson's correlation coefficients and the residuals of local regressions with non-parametric smoothing (LOESS) to assess the spatial congruence between the three diversity dimensions. Finally, we evaluated the representativity of the different expressions of diversity in the PA system under present and future scenarios.

We found positive correlations between the different diversity facets, but it was stronger between PD and FD. Climate change may reduce all facets of diversity compared to the present. Lastly, none current PA system does not cover any of the amphibian diversity facets adequately, neither in the present nor in future scenarios. Overall, diversity dimensions showed a spatial congruence in the present, Filling all the available ecological space. This congruence may decouple under future scenarios, as a consequence of random and massive extirpations of species. Still, since given the redundancy between PD and FD, these two diversity expressions could be higher than expected by the remaining TD. Finally, we stress out the necessity to increase the current coverage of the existing PAs system to improve the protection of the amphibians now and in the future.

INTRODUCCIÓN GENERAL

La biodiversidad, como característica de un sitio, incluye las especies que lo componen, la variación genotípica y fenotípica dentro de cada especie, y la variabilidad espacial y temporal en las comunidades y ecosistemas que estas especies conforman (Tilman, 2001). A menudo las estrategias de conservación y caracterización de la biodiversidad han estado enfocadas en la diversidad taxonómica (TD por sus siglas en inglés, o riqueza de especies) y abundancia de especies (Véron, Saito, Padilla-García, Forest, & Bertheau, 2019). Sin embargo, TD ignora que las comunidades se componen de especies con historias evolutivas diferentes y una amplia gama de funciones ecológicas (Cardoso, Rigal, Borges, & Carvalho, 2014). Descripciones más profundas de los ensamblajes de especies (definido como el conjunto de especies relacionadas filogenéticamente que ocupan un mismo espacio, Fauth et al., 1996) incluyen facetas complementarias de la biodiversidad como la diversidad filogenética y diversidad funcional (PD y FD, por sus siglas en inglés), que representan la historia evolutiva (Faith, 1992) y la diversidad de rasgos ecológicos o funcionales de un grupo de especies (Tilman, 2001), respectivamente. En conjunto, TD, PD y FD pueden informar acerca de los principales procesos causales del origen y mantenimiento de la biodiversidad (Cadotte, Albert, & Walker, 2013)

La PD provee información acerca de las relaciones evolutivas de las especies, aportando información sobre los procesos evolutivos que moldean los ensamblajes contemporáneos de especies y gradientes geográficos de la biodiversidad (Tucker et al., 2017). No obstante, aunque la PD y la TD exhiben una correlación positiva, ésta puede variar espacialmente e informar sobre procesos en parte responsables de los patrones actuales de biodiversidad (Fritz & Rahbek, 2012). En este sentido, áreas con mayor PD de lo esperado por su TD (residuales positivos de un modelo lineal donde TD predice PD) podrían ser el producto de: i) la presencia de un gran número de linajes junto con una alta diversificación *in situ*; ii) inmigración de múltiples linajes (Fritz & Rahbek, 2012); iii) zonas donde la tasa de especiación ha sido baja a través del tiempo y los linajes presentes en aquellas regiones probablemente sean pocos, antiguos y con información evolutiva única (Voskamp, Baker, Stephens,

Valdes, & Willis, 2017); iv) áreas donde han tenido lugar diversificaciones antiguas y v) altas tasas de extinción (Davies & Buckley, 2011). Por otra parte, los residuales negativos de dicho modelo PD ~ TD indicarían radiaciones *in situ* de pocos linajes evolutivamente cercanos después de eventos iniciales de inmigración (Fritz & Rahbek, 2012).

Por su parte, la FD es el componente de la biodiversidad que determina las dinámicas, estabilidad, productividad, balance de nutrientes y otros aspectos del funcionamiento de los ecosistemas (Tilman, 2001). La FD puede ser estimada a partir del agrupamiento de rasgos que componen el fenotipo de un organismo y afectan potencialmente su desempeño (fitness en inglés) (Cadotte, Carscadden, & Mirotnick, 2011) al tiempo que influyen el funcionamiento de los ecosistemas (Petchey & Gaston 2006). Los rasgos pueden ser de carácter físico (*e.g.*, morfología de los dientes de un depredador, apertura bucal), bioquímico (*e.g.*, presencia de metabolitos secundarios), de comportamiento (*e.g.*, forrajeo nocturno vs. diurno, canibalismo de hembras sobre machos) o fenológico (*e.g.*, tiempo de floración, duración de la etapa larval) (M. W. Cadotte, Carscadden, & Mirotnick, 2011). Al igual que la PD, la FD presenta una relación positiva con la TD que puede variar espacialmente y permite identificar zonas donde operan procesos como límite a la similitud (las especies que coexisten son funcionalmente diferentes) y filtros ambientales (las especies que coexisten son funcionalmente similares) (Holdaway & Sparrow, 2006). Asimismo, comparando las relaciones espaciales entre la PD y la FD, se podría investigar cómo se relaciona el tiempo evolutivo con la evolución de rasgos (Safi et al., 2011).

La mayoría de estudios donde se han estimado TD, PD y FD han tomado como distribuciones hipotéticas de las especies, polígonos mínimos convexos donde, por lo general, se sobreestima el área que realmente alberga condiciones idóneas para las especies (Fritz & Rahbek, 2012; Safi, et al., 2011; Zupan et al., 2014). No obstante, a través de la modelación de nicho ecológico (MNE) se pueden obtener modelos de distribución de especies (MDS) donde se hace posible discriminar entre áreas

idóneas y no idóneas dentro de los límites geográficos que se presume han estado históricamente al alcance de las especies (Peterson, 2002; Solano & Feria, 2007).

Si los enfoques que combinan diferentes facetas de la biodiversidad permiten hacer inferencias más sólidas sobre los posibles procesos ecológicos y evolutivos que afectan la composición de los ensamblajes (Pavoine y Bonsal 2011), adoptar este tipo de aproximaciones en un contexto de cambio climático (CC), podría ser relevante en el desarrollo de estrategias que permitan la conservación a una escala temporal más amplia. En escenarios futuros de CC, se espera que las especies sufran cambios en sus distribuciones geográficas producto de las dinámicas demográficas asociadas a los cambios geográficos en las condiciones del ambiente (Tingley, Koo, Moritz, Rush, & Beissinger, 2012), incluyendo extinciones locales y totales (Berg et al., 2010); con ello, los patrones espaciales de TD, PD y FD, podrían cambiar. Si bien las Áreas Protegidas (AP) funcionan como medio para la protección de la biodiversidad, la mayoría de estas proceden de propuestas que ignoran los posibles cambios a futuro en la distribución de las especies (Cabeza & Moilanen, 2003), y debido a que por lo general sólo consideran maximizar el número de especies o TD (Margules & Pressey, 2000), existe un alto grado de incertidumbre respecto a su papel actual y futuro en la protección de las diferentes facetas de la diversidad.

Desde la Revolución Industrial (1880), la temperatura promedio de la tierra ha aumentado en aproximadamente 1.1 °C (Walther et al., 2002) y se espera que entre 2030 y 2052 aumente en 1.5 °C respecto a los niveles preindustriales (IPCC, 2020). Cuando el cambio en el clima es acelerado, las respuestas de las especies pueden verse limitadas o exacerbadas (Welch, 2005), particularmente para aquellas con distribuciones restringidas (N. Cooper, Bielby, Thomas, & Purvis, 2008). Entre los vertebrados, los anfibios exhiben los rangos de distribución más estrechos y podrían sufrir procesos de extinción más acelerados (Pounds et al., 1997, 1999; Stuart et al., 2004; Cooper et al., 2008). La pérdida y fragmentación del hábitat, contaminación ambiental, especies invasoras y enfermedades emergentes, podrían esbozar un panorama aún más grave para los anfibios (Ackerly et al., 2010;

Blaustein et al., 2010; Hof et al., 2011; Ochoa-Ochoa et al., 2012; Li et al., 2013). Además, se ha sugerido que aspectos importantes de la biología de los anfibios, como el crecimiento, el desarrollo, la alimentación y las temporadas de hibernación y reproducción, podrían verse afectados por el clima (Li et al., 2013).

En México residen más de 372 especies de anfibios de las cuales más del 65% son endémicas (Ochoa-Ochoa et al., 2012) y cerca del 43% están amenazadas (Parra-Olea et al., 2014). La porción mexicana de la Provincia Biótica Península de Yucatán (PY) alberga 24 especies nativas, siendo una de estas endémica regional (Gonzalez-Sanchez et al., 2017). Al ser una región que actualmente es bastante cálida, donde la disponibilidad de agua es un factor limitante y se prevén aumentos en la temperatura y disminución en las precipitaciones a causa del cambio climático (Sáenz-Romero et al., 2010), en la PY los anfibios podrían ser más vulnerables respecto los grupos de vertebrados restantes teniendo en cuenta su estrecha relación con estos parámetros climáticos (Islebe, Calmé, León-Cortés, & Schmook, 2015). A pesar de que se cuenta con un inventario reciente de la composición de especies de anfibios (Gonzalez-Sanchez et al., 2017) y el número de especies por estado de la PY (Islebe et al., 2015), se desconocen los patrones espaciales actuales y futuros, bajo escenarios de CC, de las tres facetas de la diversidad de este grupo, así como la representación de las mismas en el sistema actual de AP.

En este trabajo, se describen los patrones y relaciones geográficas entre las diversidades taxonómica, filogenética y funcional de los anfibios de la porción mexicana de la PY en un contexto de cambio climático. Se espera que el patrón espacial de la TD siga un gradiente de disponibilidad de agua, presentándose la mayor diversidad en áreas más húmedas. Asimismo, se espera que la estructuración espacial de las PD y FD permita inferir señales de procesos evolutivos y ecológicos y que, debido a la relación intrínseca entre éstas, se puedan encontrar patrones espacialmente congruentes. Se presume que, bajo escenario de cambio climático, se encuentren diferencias en las relaciones espaciales de las diferentes facetas de la biodiversidad, debido a los cambios potenciales en la distribución de las especies. Finalmente, se evalúa la representatividad de las tres facetas de la

diversidad de anfibios en el sistema de áreas protegidas de la región en la actualidad y bajo escenarios de cambio climático. Se espera que la TD esté bien representada, no así las FD y PD.

Sobretiro artículo científico enviado

Current and future patterns of taxonomic, functional and phylogenetic diversity of amphibians in the Yucatan Peninsula and their representation in Protected Areas

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Running head: Diversity patterns of amphibians in the Yucatan Peninsula.

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ABSTRACT

Aim

To estimate current and future spatial patterns of taxonomic (TD), phylogenetic (PD) and functional diversity (FD) of the amphibians of the Yucatan peninsula (YP); evaluate relationship between these facets of diversity, and asses their representation in Protected Areas (PA) of this region.

Location

Yucatan peninsula.

Taxon

Amphibians.

Methods

We used ecological niche modeling to predict current and future potential distributions of amphibians in the YP. Then, we stacked distribution models to estimate TD, and based on the most recent amphibian phylogeny and nine functional traits we also measured PD and FD, respectively. Spatial congruence between the three diversity facets were assessed through Pearson's correlation coefficients and the residuals of local regressions with non-parametric smoothing (LOESS). Finally, we evaluated the representativity of the different expressions of diversity in the PA system in the present and future scenarios.

Results

We found positive correlations between the different facets of diversity, but stronger between PD and FD. A general decrease of all diversity facets is predicted under climate change scenarios respect to the present. Lastly, none of the PAs evaluated were effective protecting the different facets of diversity, neither in the present nor in future scenarios.

Main conclusions

Overall, diversities have evolved altogether, probably in order to fill all the available ecological space. For future scenarios, a decoupling of the diversities due to random and massive extirpations of species

is predicted, but since there is a redundancy in PD and FD, there would be more PD and FD than expected by the remaining TD. Also, the fact that PAs evaluated were not effective, stress out the need to complete the existing PAs system.

Keywords: amphibians, biodiversity patterns, climate change, functional diversity, phylogenetic diversity, protected areas, taxonomic diversity.

INTRODUCTION

Biodiversity as a characteristic of a site includes the species that compose it, the genotypic and phenotypic variation within each species, and the spatial and temporal variability in the communities and ecosystems that these species shape (Tilman, 2001). Often biodiversity conservation and characterization strategies have been focused on taxonomic diversity (TD, or species richness) and abundance of species (Véron, Saito, Padilla-García, Forest, & Bertheau, 2019). However, TD ignores that communities are composed of species with different evolutionary histories and a wide range of ecological functions (Cardoso, Rigal, Borges, & Carvalho, 2014). Deeper descriptions of community assemblages (set of phylogenetically related species that occupy the same space and time, Fauth et al., 1996) include complementary facets of biodiversity such as phylogenetic diversity (PD) and functional diversity (FD), which represent the evolutionary history (Faith, 1992) and the diversity of ecological or functional features of a group of species (Tilman, 2001), respectively. Together, TD, PD and FD can give insights on the main causal processes of the origin and maintenance of biodiversity (Cadotte, Albert, & Walker, 2013)

The PD provides information about the evolutionary processes that shape contemporary assemblages of species and geographical gradients of biodiversity (Tucker et al., 2017). However, although PD and TD exhibit a positive correlation, it can vary spatially and, thus, enlighten about processes partly responsible for current biodiversity patterns (Fritz & Rahbek, 2012). In this sense,

areas with higher PD than expected by TD (positive residuals) could be the product of: i) the presence of many lineages together with high *in situ* diversification; ii) immigration of multiple lineages (Fritz & Rahbek, 2012); iii) areas where the speciation rate has been low over time and the lineages present in those regions are probably few, old and with unique evolutionary information (Voskamp, Baker, Stephens, Valdes, & Willis, 2017); iv) areas where old diversifications have taken place and v) high, phylogenetically spread, extinction rates (Davies & Buckley, 2011). Otherwise, negative residuals would indicate *in situ* radiation from few evolutionarily close lineages after initial immigration events (Fritz & Rahbek, 2012).

FD is the component of biodiversity that determines the dynamics, stability, productivity, balance of nutrients and other aspects of the functioning of ecosystems (Tilman, 2001). FD can be estimated from the grouping of life history traits of the species phenotype and potentially affect its fitness (Cadotte, Carscadden, & Mirotnick, 2011) while influencing the functioning of ecosystems (Petchey & Gaston, 2006). The traits can be physical (e. g. size, weight, tooth morphology), biochemical (e. g. presence of secondary metabolites), behavioral (e. g. night vs. day activity, female cannibalism over males) or phenological (e. g. flowering time, larval stage duration) (Cadotte et al., 2011). Like PD, FD has a positive correlation with TD that varies spatially and allows identifying areas where processes operate as a limit to similarity (presence of functionally-different species) and environmental filters (presence of highly functionally-similar species) (Holdaway & Sparrow, 2006). Also, comparing the spatial relationships of PD and FD, one could investigate how evolutionary time is related to traits evolution (Safi et al., 2011).

Evidence shows that combine different facets of biodiversity allow for stronger inferences about possible ecological and evolutionary processes that affect the composition of communities (Pavoine & Bonsall, 2011). Therefore adopt this type of approach in a context of climate change (CC), could be relevant for developing strategies that allow the conservation of the patterns and processes that maintain and originate biodiversity at broader time scales. In future CC scenarios, species are expected

to change their distribution ranges in search of adequate climatic conditions (Tingley, Koo, Moritz, Rush, & Beissinger, 2012), or become locally extinct (Berg et al., 2010), thereby, spatial patterns of TD, PD and FD, could change. Although Protected Areas (PA) serve as a means to protect biodiversity, most of these come from proposals that ignore possible future changes in the distribution of species (Cabeza & Moilanen, 2003), and because, in general, it was only considered species richness as the criterion for selecting areas to protect, in order to maximize the number of species or TD conserved (Margules & Pressey, 2000). However, nowadays conservation planning has become more integrative (Pressey, Cabeza, Watts, Cowling, & Wilson, 2007). Despite this, there is a high degree of uncertainty regarding their current and future role in protecting the different facets of diversity.

In the last century, the average temperature of the earth has increased by approximately 0.6° C (Walther et al., 2002). In response to environmental changes, resident species can migrate in search of optimal areas, acclimatize to the new conditions or suffer local extinctions (Berg et al., 2010; Peterson et al., 2002). However, these responses can be compromised when the change in climate is accelerated (Welch, 2005), particularly in organisms with restricted distributions and/or limited dispersal capabilities (Cooper, Bielby, Thomas, & Purvis, 2008). Among vertebrates, amphibians exhibit the narrowest distribution ranges and could suffer more severe extinction processes (Cooper et al., 2008; Pounds, Fogden, & Campbell, 1999; Pounds, Fogden, Savage, & Gorman, 1997; Stuart et al., 2004). Habitat loss and fragmentation, environmental pollution, invasive species and emerging diseases could act synergistically, depicting an even worse scenario for amphibians (Ackerly et al., 2010; Blaustein et al., 2010; Hof, Araújo, Jetz, & Rahbek, 2011; Li, Cohen, & Rohr, 2013; Ochoa-Ochoa, Rodríguez, Mora, Flores-Villela, & Whittaker, 2012). In addition, it has been suggested that important aspects of amphibian biology, such as growth, development, foraging, hibernation and reproduction seasons, could be affected by changes in climate (Li et al., 2013).

In Mexico, more than 400 species of amphibians currently occur (Frost, 2019) of which more than 65% are endemic (Ochoa-Ochoa et al., 2012) and about 43% are threatened (Parra-Olea, Flores-

Villela, & Mendoza-Almeralla, 2014)). The Mexican portion of the Biotic Province of the Yucatan Peninsula (YP) is home to 24 native species, one of which is regionally endemic (Gonzalez-Sanchez et al., 2017). Being a region that is currently quite warm where water availability is a limiting factor and increases in temperature and decrease in rainfall due to climate change are expected (Sáenz-Romero et al., 2010), in the YP the amphibians could be more vulnerable compared to other vertebrate groups considering their close relationship with these climatic parameters (Islebe, Calmé, León-Cortés, & Schmook, 2015). Although, different inventories have been performed for the YP, including a recent inventory about the composition, conservation status and patterns of distribution of herpetofaunal species (Gonzalez-Sanchez et al., 2017) and the state distribution on the YP (Islebe et al., 2015), the current and future (under CC scenarios) spatial patterns of the different diversity facets of this group are unknown, as well as their representation in the current system of PAs.

Here, we described the spatial patterns and geographical relationships between TD, PD and FD of amphibians of the Mexican Yucatan Peninsula in a CC context. As hypotheses, we expect that 1) the spatial pattern of TD follows a gradient of water availability, presenting the greatest diversity where the highest amount of water is available; 2) that the spatial structure of PD and FD, would allow us to infer evolutionary and ecological processes. 3) It has been shown that, as a result of CC, a decoupling of the different facets of biodiversity could occur due to the potential changes in the distribution of the species (Mendez-Guerrero et al. 2019), thus changes in the relationships among the different facets of diversity would be observed. Lastly, 4) we evaluated the representativity of the different facets of diversity (TD, PD and FD) in the governmental protected areas system currently and throughout future CC scenarios, where the TD is expected to be represented, but not the FD and PD.

MATERIALS AND METHODS

Study area

The Mexican Yucatan Peninsula (YP) is located in the southeast end of Mexico and includes the states of Campeche, Yucatán and Quintana Roo (Fig. 1). YP consist of a relatively flat platform of calcareous rock and hard limestone soil; there are no mountain systems in the YP and the maximum elevation barely reaches 250 m a.s.l. (Pérez-Sarabia et al., 2017). As a result of the lack of reliefs and its recent emergence of the sea (Vázquez-Domínguez & Arita, 2010), in the YP the marine climatic influence is accentuated to a greater extent, being located in the path of the Caribbean winds and cyclones (Morrone, 2005). The predominant vegetation consists of deciduous forest, sub-deciduous forest, evergreen forest and spiny forest (INEGI, 2018) distributed in five ecoregions: Mesoamerican Gulf-Caribbean mangroves, Pantanos de Centla, Petén-Veracruz moist-forests, Yucatan dry forests and Yucatan moist forests (Morrone, 2005). The annual mean temperature is between 25 and 28° C while the annual mean rainfall on the Peninsula is 1100 mm (White & Hood, 2004), presenting a gradient in precipitation that decreases from the southeast to the northwest (Pérez-Sarabia et al., 2017). Another characteristic that stands out in the YP is that rivers are superficially absent, and instead they travel below ground, opening outwards to form the so-called ‘cenotes’. Permanent lagoons and bodies of water are also scarce in the YP, being mainly located at its base (Islebe et al., 2015).

Presence Records

We obtained presence records of the 24 native amphibian species reported for YP (Gonzalez-Sanchez et al., 2017) from the databases of the Global Biodiversity Information Facility (GBIF, 2017) and VertNet (2017). Duplicate data, poorly georeferenced (located at sea) and possible error in determination were deleted, using as reference the book *Amphibians of Central America* (Köhler, 2011), *Amphibiaweb* (<https://amphibiaweb.org>, accessed October 2017) and the online resource *Amphibian Species of the World* (Frost, 2018; <https://research.amnh.org/vz/herpetology/amphibia>, accessed January 2018).

For each species we generated an area that represented a hypothesis of historical accessibility (area M of the BAM diagram; Soberon & Peterson, 2005), which has important implications in constructing robust ecological niche and species distribution models with reliable evaluations (Barve et al., 2011; Cooper & Soberón, 2018). The Ms were generated from the intersection of the presence records with the WWF terrestrial ecoregions (Olson et al., 2001) using the raster (Hijmans, 2018) and rgdal packages (Bivand, Keitt, & Rowlingson, 2018) of R (R Core Team, 2018). It is well known that presence records are clustered around roads and human settlements, thus avoid over-adjustment in the ENMs (Boria, Olson, Goodman, & Anderson, 2014) an environmental filter was applied on the presence records (Varela, Anderson, García-Valdés, & Fernández-González, 2014). This was done taking into account the first two main components of the environmental predictors (Environmental Data Section) with the ‘gridSample’ function of the raster package (Hijmans, 2018) in R (R Core Team, 2018). Then, the presence data were divided into two sets, training and evaluation, using the ‘chekerboard1’ function with an aggregation factor of 10 from the ENMeval package (Muscarella et al., 2014).

Environmental data

The environmental variables were obtained from the WorldClim database version 1.4 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005; <http://www.worldclim.org>, accessed January 2018) at a resolution of 2.5' (~ 5 km²) and datum WGS-84. The variables BIO8 (average temperature of the wettest quarter), BIO9 (Average temperature of the driest quarter), BIO18 (precipitation of the warmest quarter) and BIO19 (precipitation of the coldest quarter) were eliminated from the set because they contained previously identified artifacts (Ashraf et al., 2017). For future predictions, analogous variables to those of the present were downloaded but that simulate future climate behavior (2050 and 2070). Two general circulation models (CCSM4 and MIROC5) of CMIP5 (Taylor Stouffer, & Meehl, 2012) were chosen to take into account the variation and uncertainty between their predictions of the

future (Diniz-Filho et al., 2009; Yañez-Arenas, Townsend Peterson, Rodríguez-Medina, & Barve, 2016). In addition, for each GCM, two greenhouse gas concentration models were selected, one plausible optimistic (RCP45) and one pessimistic (RCP85).

In order to eliminate the multicollinearity and reduced number of dimensions of the environmental variables cut to the extension of the union of the Ms of all species, we performed a principal component analysis (PCA). The first four axes that explained $\geq 95\%$ of the total variance were taken into account to run the models. This procedure was performed with the ‘iPCAProjection’ function of the ENMGadgets package (Barve & Barve, 2013) in R (R Core Team, 2018).

Ecological niche modeling

The calibration, evaluation and selection of ENMs were performed using the Kuenm package (Cobos, Peterson, Barve, & Osorio-Olvera, 2019). Using the maxent algorithm this package executes the calibration and run the models (Phillips, Anderson, & Schapire, 2006) through the dismo package in R (R Core Team, 2018). The selection of the models was done in a hierarchical way, taking into account first the statistical significance via partial ROC (Peterson, Papeş, & Soberón, 2008), second the allowed omission rate ($E = 5\%$) and finally, the complexity through the Akaike Information Criterion corrected for the sample size (AICc; Warren and Seifert, 2011; but see Velasco & González-Salazar, 2019). Once the best models were selected, they were thresholded, taking as a threshold the allowed omission rate to generate geographical distributions (extents of occurrence, Gaston 2003). Further details of the modeling process and projections to the future are shown in the supporting information. In sum, we generated SDMs of 24 species for “present” distribution, and future for 2050 and 2070, with two greenhouses scenarios each.

Diversity Measurements

At regional or global scales, TD can be estimated per pixel by stacking species distribution maps (SDMs) derived from the ENM of each species. In this case, TD of each scenario was estimated from the presence / absence matrices (PAM) based on the thresholded SDMs at a resolution of 2.5' (~ 5 km²) using the 'lets.presab' function of the letsR package (Vilela & Villalobos, 2015). This procedure is based on the assumption that communities are constituted from the coincident assemblages of the individual ecological responses of the species (D'Amen et al., 2018).

We used Rao quadratic entropy index (QE; Rao, 1982) to measure PD and FD per pixel. QE can be understood as the mean distance between pairs of species in the distance matrix, including the diagonal, which represents the dissimilarity between a species and itself (de Bello, Carmona, Lepš, Szava-Kovats, & Pärtel, 2016). The Rao index is given by the formula:

$$QE = \sum_{i=1}^N \sum_{j=1}^N d_{ij} p_i p_j$$

where N is the number of species in a pixel, d_{ij} is the dissimilarity between each pair of species i and j , and p_i and p_j are the proportions of each species i and j (de Bello, Lavergne, Meynard, Lepš, & Thuiller, 2010), in this case given by PAM. Rao indices for PD and FD were estimated with the 'melodic' function (de Bello et al., 2016) in R (R Core Team, 2018).

We estimated PD by calculating standardized cophenetic distances between 0 and 1 from 100 trees derived from the phylogeny of Jetz and Pyron (2018). To account for the phylogenetic uncertainty, the values of the median on all trees are reported. Likewise, we estimated FD, using the Gower distance (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009), paired functional dissimilarity matrix was estimated among the 24 species, standardized between 0 and 1. The traits used were: body size, habit (e. g. Arboreal, terrestrial, aquatic), fertilization type, reproductive cycle, reproductive type, presence of larvae, spawn site, site of larval development and parental care. These traits comprehend a wide variety of ecological, life history and morphological features of the species (Sodhi et al., 2008).

To obtain the information of traits we used the database of Sodhi et al. (2008). The missing data were completed with the AmphibiBio database (Oliveira, São-Pedro, Santos-Barrera, Penone, & Costa, 2017).

The PD and FD Rao indices were transformed to equivalent numbers (Jost, 2007) to ensure that all indices (TD, PD and FD) could be compared directly and that these comparisons made biological sense (de Bello et al., 2010). Thus, PD and FD were expressed in terms of the effective number of species needed to produce the given value of the diversity index (Jost, 2007) per pixel. All subsequent analyses were performed based on these transformations to equivalent numbers of PD and FD.

Spatial congruence between diversity patterns

The spatial congruence between the PD, FD and TD patterns was evaluated by Pearson's correlation coefficients (Fritz & Rahbek, 2012) by applying the modified *t* test (Dutilleul, 1993), implemented in the R SpatialPack package (Osorio & Vallejos, 2019). This test takes into account spatial autocorrelation when estimating statistical significance. Then, we extracted the residuals of the local regressions (PD vs. TD and FD vs. TD) with non-parametric smoothing (LOESS), rPD and rFD, respectively. This was done in order to identify areas in which the phylogenetic and / or functional diversity was higher or lower than expected by TD (Forest et al., 2007; Fritz and Rahbek, 2012; Voskamp et al., 2017; Daru et al., 2019). In this sense, residuals with values lower than the first quantile or negative residuals were reclassified as -1; those higher than the last quantile or positive residuals were reclassified as 1. To better visualize the results, we mapped the changes (in percentage) per facet of diversity and per climate change scenario. We also mapped the resulting frequency values of the TD and, PD and FD, RAO indices for each time frame and scenario. This was done in order to rapidly visualize the central tendency of the resulting values. We carried out Wilcoxon test to compare the median diversity values observed in each future scenario against those observed in present scenario by applying `wilcox.test` function in R (R Core Team, 2018).

Effectiveness of Protected Areas

The PAs of categories Ia up to IV of the IUCN present in the YP were taken as a reference (Figure S1, Table S1), which includes only PAs with specific conservation objectives (Nori, Villalobos, & Loyola, 2018). A total of eleven PAs were evaluated. A pixel was considered protected when an area higher than or equal to 50% of it was included in a PA. The effectiveness of the current system of PAs was evaluated by comparing TD and residuals of PD and FD within each PA across all scenarios, with respect to the values expected by a null model. In the null model, the PAs were spatially randomized only on unprotected areas but keeping the shape, size and orientation (Ferro, Lemes, Melo, & Loyola, 2014; Lemes, Melo, & Loyola, 2014; Ribeiro, Sales, De Marco, & Loyola, 2016). We performed 1000 randomizations of the null model. A PA was considered effective when the observed diversity value (TD, rPD or rFD) was higher than expected in at least 95% of the runs, that is, $p \leq 0.05$ (Ribeiro et al., 2016).

RESULTS

Spatial patterns of PD and FD do not faithfully resemble the species richness pattern (Fig. 2). At present, the highest values of TD are found in the base of the peninsula and at the east, along the state of Quintana Roo. The lowest values of TD are found in part of the state of Yucatán and the north of Campeche. However, the PD and FD patterns present high spatial congruence (Fig. 2). Not surprisingly zones with the highest values of PD and FD overlap with the areas of high TD, at the base and east of the YP. However, it is interesting to note that areas with high PD and FD are located in the north-central zone of the YP, between the states of Yucatán and Campeche, where low values of TD predominate.

It is pertinent to highlight the contractions of the ranges of more or less diverse areas and their displacements on the peninsula, since they reflect the potential changes in the ranges of distribution of the species that are derived from the ENMs.

As a general trend models show that there would be a contraction of the areas of high TD through the different time frames towards the eastern zone of the peninsula along the state of Quintana Roo. A maximum loss of TD, between 43% and 61%, can be observed in future scenarios with respect to the present. Zones with maximum TD gain showed only 33% more, in small areas on the northern of YP (Fig. 2). Likewise, phylogenetic and functionally diverse areas would be reduced and located on the northern zone of the YP and on the southeast. Like TD, areas with the highest losses of PD (25-28%) and FD (21-24%) in future scenarios would be significantly larger than areas with gains (Fig. 2).

Throughout the scenarios, PD and FD presented positive correlations, the correlation being higher in the present and fluctuating in future scenarios (Table 1, Fig. 3). In the present scenario, PD and FD were moderately correlated with TD (Table 1, Fig. 3). This suggests that approximately 32% and 50% of the spatial variation of PD and FD, respectively, is not explained by TD. In the models projected to the future the dynamics of these relationships varied. In both scenarios for 2050, there was a reduction in the percentage of variation of PD and FD explained by TD. On the contrary, in the 2070-rcp45 scenario the correlations between PD and FD with TD reached their highest values and but in the 2070-rcp85 scenario about 48% and 94% of the PD variation and FD, respectively, is not explained by TD.

In general, negative residuals of both r_{PD} and r_{FD} were located mainly on the west of the peninsula, between the states of Campeche and Yucatán, as well as in some small parts on the east and on the north coast (Fig. 4). Positive residuals of r_{PD} and r_{FD} were essentially located on the central part of the peninsula. Likewise, discontinuous zones with positive residuals were observed on the northeast, south and on the north coast (Fig. 4). The number of cells of the positive residuals of r_{PD} and r_{FD} , increased (in two and one scenario, respectively) and decreased (in two and three scenarios, respectively) compared to the residuals of the present (Supplementary material FIG). The negative residuals of r_{PD} showed similar fluctuations to the positive r_{PD} and the negative r_{FD} s fluctuated slightly between scenarios. In figure 5 and table S2, it is possible to observe a clear and significant

displacement from relatively high values to lower values of all diversities measured from present to future scenarios, a clear consequence of range contractions and species extinctions.

Finally, according to the models none of the eleven existing PAs evaluated proved to be effective in protecting the different evaluated diversities, neither in the present nor in future scenarios (Table S3).

DISCUSSION

Due to the intrinsic properties of TD, PD and FD, an increase or decrease in species richness (TD) can only mean an increase or decrease in PD and FD, or rarely cause no change (Devictor et al., 2010; Safi et al., 2011). As expected, positive relationships were observed between TD and the remaining diversities. Although it is not expected that PD always reflects FD because functional traits may be the result of convergence processes (Faith, 1992) we did find that PD and FD obtained the highest correlations. Furthermore, although TD losses of up to 61% are observed, the loss of PD and FD is not even a half of this percentage, indicating that there is a phylogenetic and functional redundancy between species.

In the present scenario, the highest values of TD were found both, on the basis of the YP, exhibiting a peninsularity effect described above (Vázquez-Domínguez & Arita, 2010), and also on the east of the YP. The increase in TD from west to east has also been previously identified in the YP in forest communities, where it is suggested that is a consequence of increased rainfall in this direction (White & Hood, 2004). In the eastern region of the YP precipitation more frequent and there is higher availability of water which has a positive effect on the amphibians given their ecophysiological characteristics and their form of reproduction (Buckley & Jetz, 2007; Lion et al., 2019). In addition, it has been found that reduction in water availability is particularly important in areas that are already under hydrological stress as limiting factor for amphibian species distribution (Araújo, Thuiller, & Pearson, 2006).

The historical processes reflected by the spatial pattern of PD in the present, suggest that where more phylogenetic diversity is observed than expected by TD (center, northeast and base of the YP) are the result of local migration and extinction events that derive in the presence of ancient lineages that harbor unique evolutionary information. In contrast, along the west of the peninsula, small portions of southeast and north, less PD is recorded than expected by TD. This pattern may be the result of the grouping of highly related species, possibly due to recent radiation in situ, or migrations where only species with similar characteristics, given by a common and recent evolutionary history possibly along with environmental filtering effects, have been able to settle.

It would be expected that, because the ecological characteristics would apparently be restricting the spatial organization of the TD, FD would follow a similar spatial configuration. However, although high values of FD are located on the east of the peninsula in accordance with TD, the highest values of functional diversity are located over the central zone, where ecological processes could be acting as limits to the similarity possibly due to interspecific competition promoting niche partitioning (Holdaway & Sparrow, 2006).

In general, the consistency observed in the spatial arrangement of PD and FD could suppose, to some degree, a strong phylogenetic signal of shared traits that broadly could be the result of two processes. First, the YP has a relatively recent origin, which implies that, its biota also have it (Vázquez-Domínguez & Arita, 2010) and second, the lack of reliefs in the YP offers a relatively homogeneous environmental space which could have allowed closely related species that share advantageous traits exclude distant species and therefore, being the ones that have, so far, succeeded in the YP.

According to the residuals of both, rPD and rFD (Fig. 4), in the vast majority of sites diversities have evolved altogether probably trying to fill all the available ecological space in all the facets. Future scenarios show, that there will be a decoupling of these diversities. But, in the extreme scenario (2070-rcp85) the decoupling will be general, because there will be a massive random extinction of species,

but since phylogenetic lineages (PD) and functions (FD) are equally diverse with the particularity that there is redundancy in both of them. Thus, in the future residuals show a general pattern where there will be more PD and more FD than expected by the number of species remaining.

For example, substantial extinctions of amphibians by 2050 have been predicted over the YP, with approximately one species remaining in the northwest (Ochoa-Ochoa et al., 2012). Although is worth noting that climate change scenarios have been better modelled and now climate scenarios are not as severe as the ones used in that study. Nonetheless, our results show great changes in the spatial pattern of the relationships. This could have sever implications in the maintenance of the new formed communities, with low redundancy in functions and phylogenetic history, making this communities, possibly, even more vulnerable.

It has been suggested that one facet of diversity could be a good surrogate of another facet, depending on the available data, the objectives and the areas of study considered (Devictor et al., 2010). However, because species can change their distribution ranges, those congruencies observed in a reference time frame may change gradually when evaluated at another time as shown here (i. e. the variation in the relationship between PD and FD at throughout the different scenarios). Therefore, as shown in this paper, it is important to consider several future scenarios when evaluating the relationships and spatial arrangements of the different facets of diversity. In the case of YP, TD would not be a good surrogate of the different facets of diversity. In general, rPD and rFD, both positive and negative, present a spatial mismatch with respect to TD; and only PD or FD would be a good surrogate of each other, in some scenarios.

Like the PA system at a global level (Nori et al., 2015), the PA system of the YP constitutes an inefficient protection network for amphibians since they do not protect any facet of diversity better than a set of randomly located PAs on the YP would do. Seeking an alternative in the Permanent Forest Areas (AFPs) system in Mexico, between 1 and 6 AFPs of 94 proved to be effective in protecting TD throughout all scenarios (data not shown). However, most of these AFPs cover areas of approximately

5 to 10 Km². By not protecting the variation contained in the different facets of diversity, areas that harbor species with ancient evolutionary histories are put at risk (Zupan et al., 2014); areas occupied by species with recent evolutionary histories that constitute evolutionary potential, under the assumption that they will continue to evolve at rates similar to those of the past (Forest et al., 2007); areas that harbor communities that have multiple responses to environmental change and areas where communities could respond better to extirpation events, because they are composed of functionally redundant species. Finally, we highlight the importance of taking into account the temporal dynamics of the ranges of distribution of the species in conservation planning, since they should be aimed not only at conserving as much as possible of the facets of diversity in the present, but also in the long term.

Table 1. Pearson correlations between TD, PD and FD. Applying the Dutilleul method (1993), spatial autocorrelation was taken into account prior to the estimation of statistical significance (p-value). In each column the correlation value between pairs of diversities is presented. *** p <0.001; ** p <0.01; * p <0.05.

Scenario	TD-PD	F-stat	TD-FD	F-stat	PD-FD	F-stat
Present	0.616***	0.611	0.500***	0.334	0.910***	4.812
2050-rcp45	0.508***	0.349	0.319*	0.113	0.813***	1.952
2050-rcp85	0.565***	0.469	0.352**	0.142	0.784***	1.594
2070-rcp45	0.790***	1.660	0.569***	0.479	0.856***	2.747
2070-rcp85	0.519***	0.370	0.056	0.003	0.633***	0.668

Figure legends

Figure 1. Mexican portion of the Yucatan Peninsula.

Figure 2. Changes in time of the diversity patterns. Values of TD, PD and FD for the present are presented in the first row. In the remaining rows the percentage of loss and gain of each diversity per scenario is presented. In a smaller size, for each case, row values are shown for each diversity. TD (left), PD (middle) and FD to the right.

Figure 3. Models of local regressions between diversities. The regression between taxonomic diversity (TD) and phylogenetic diversity (PD) is shown in the upper panel; in the lower panel, the regression between TD and functional diversity (FD).

Figure 4. Maps of residuals derived from LOESS regressions for each scenario. Abbreviations: rPD: Residuals of the local regression between PD and TD, and rFD: Residuals of the local regression between FD and TD. Positive residuals: 1, negative residuals: -1, expected ratio: 0.

Figure 5. Histogram of the values of TD, PD and FD by scenario.

Figure 1.

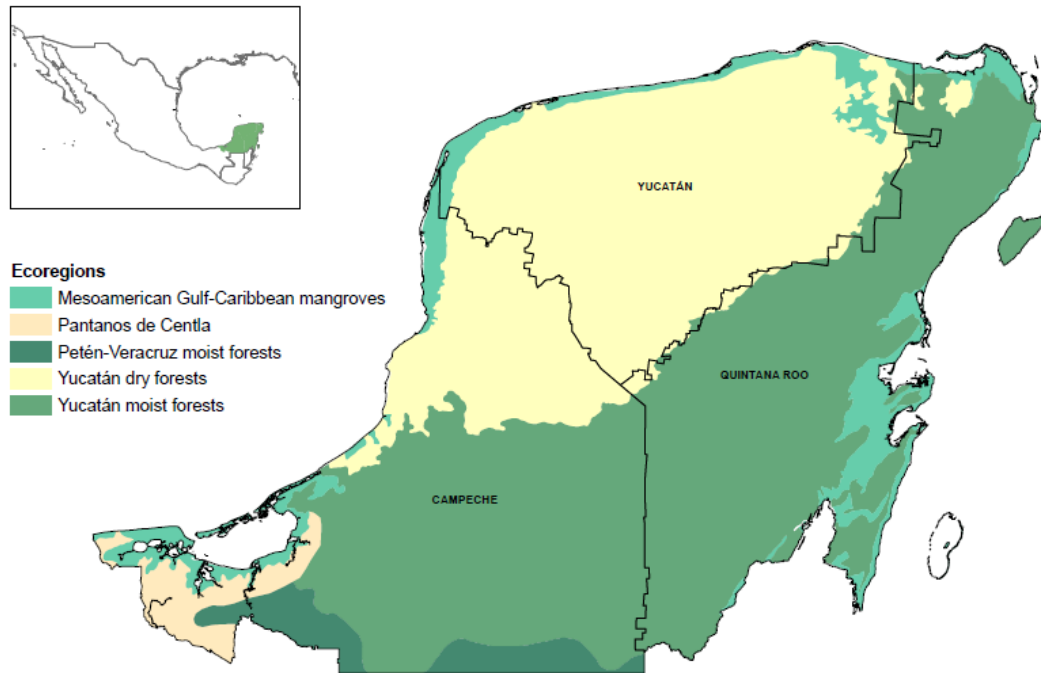


Figure 2.

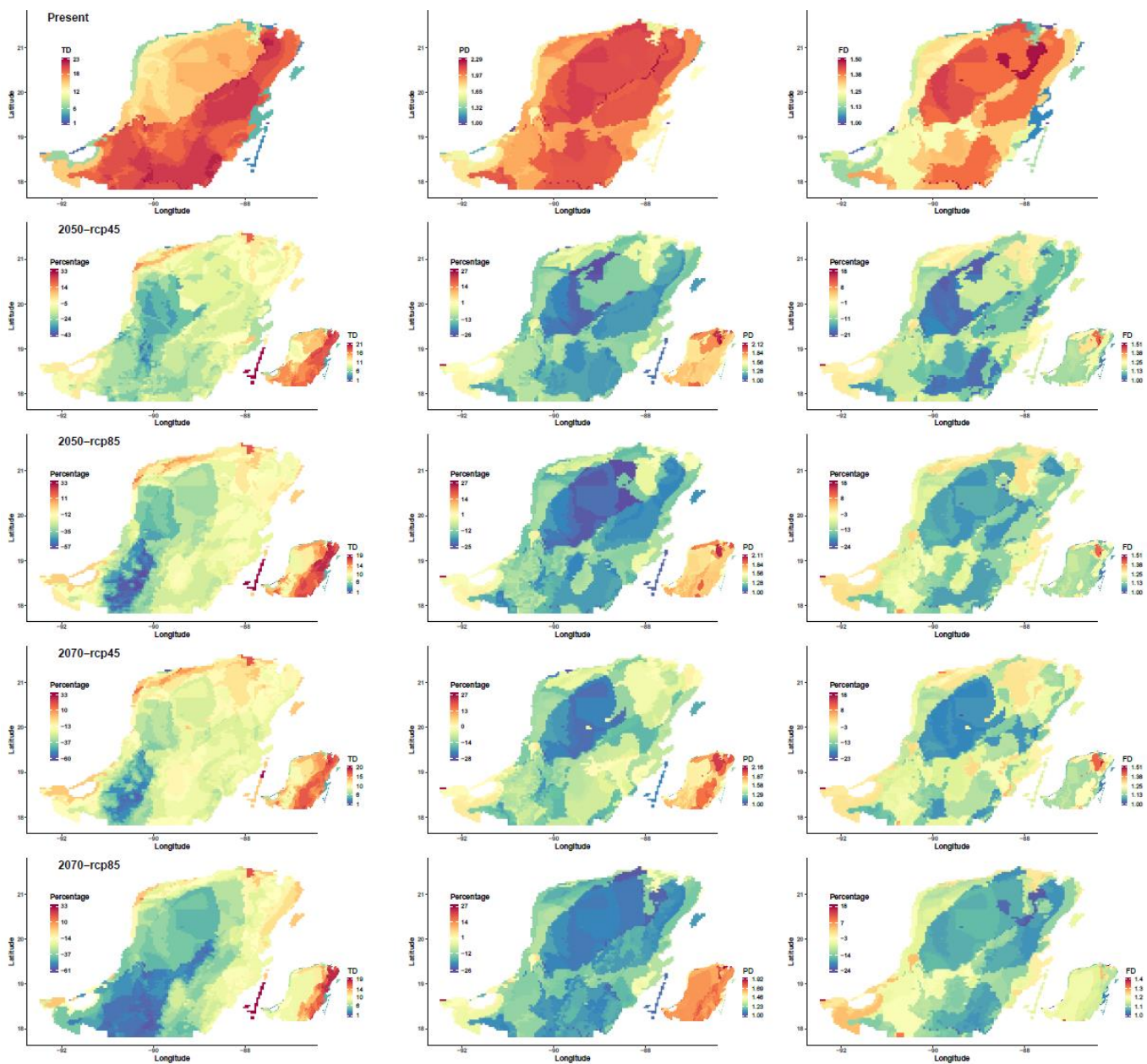


Figure 3.

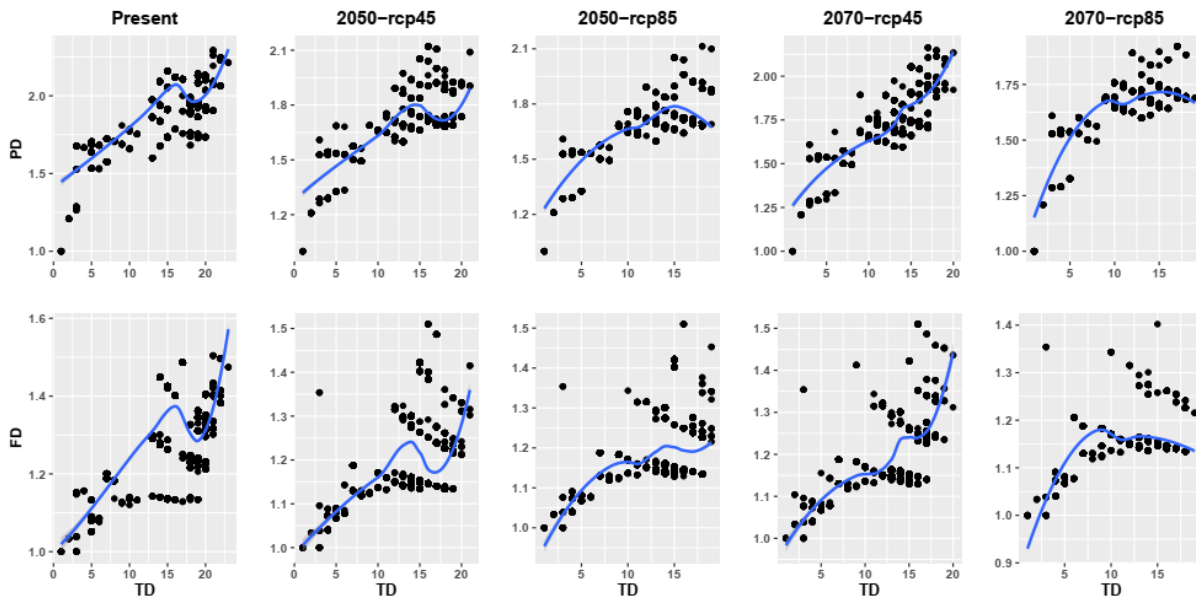


Figure 4.

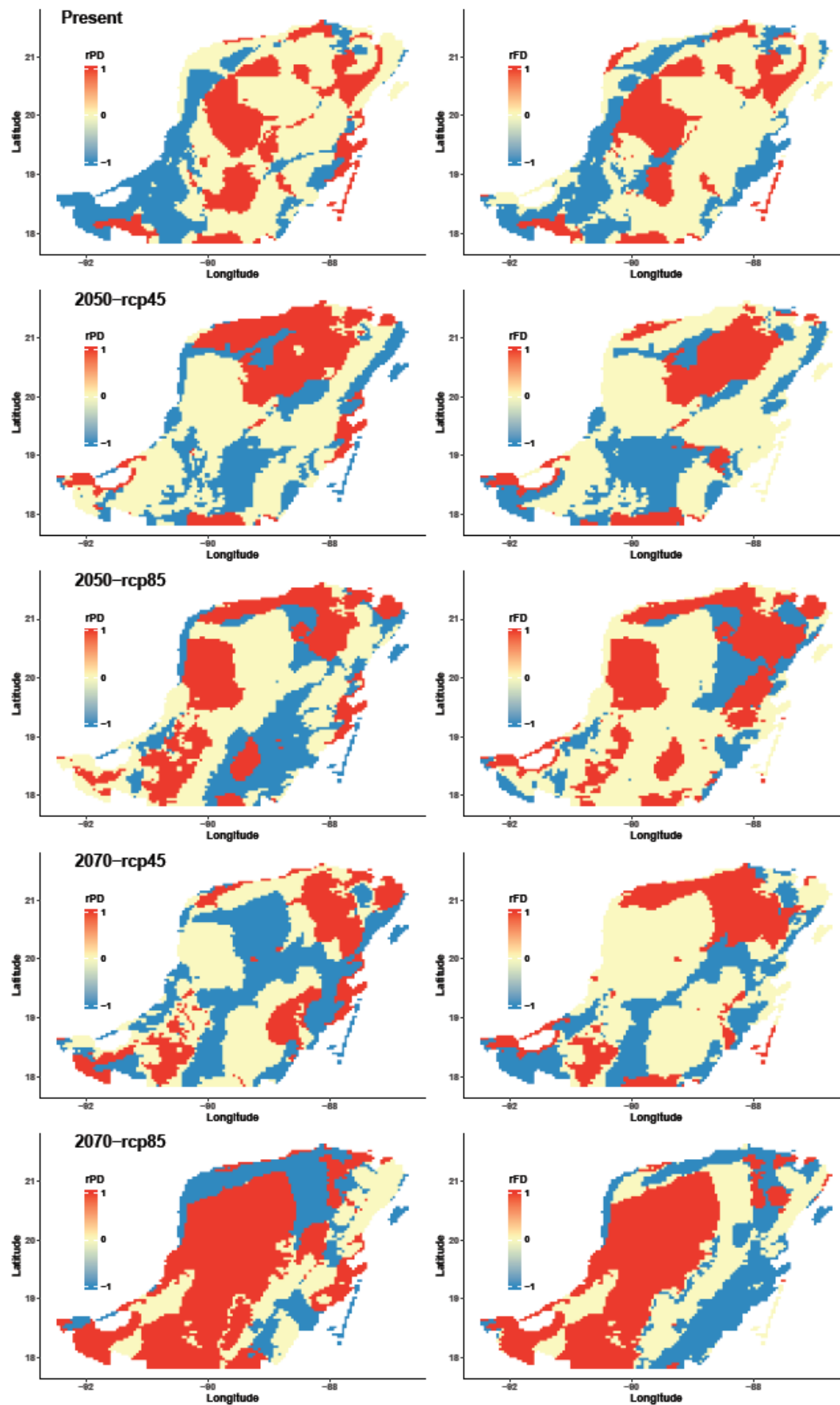
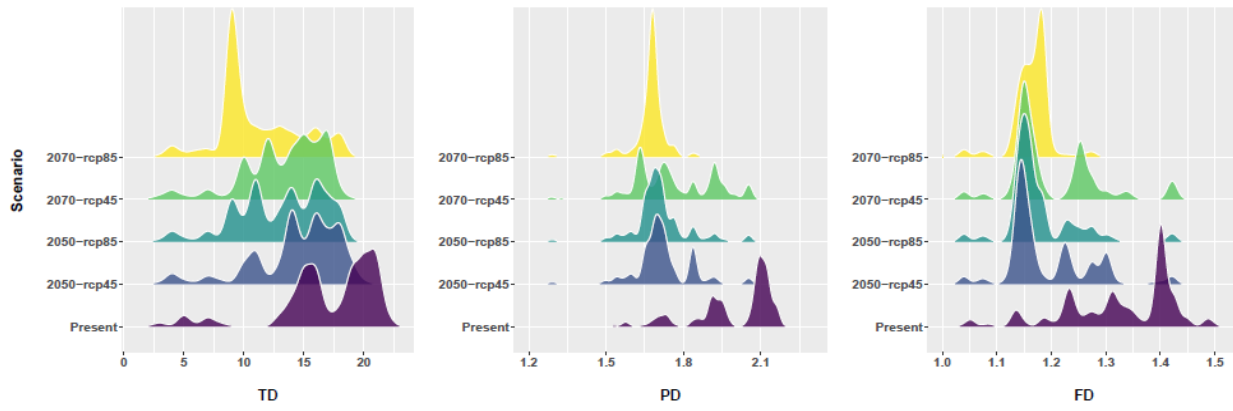


Figure 5.



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Biosketch

Sandra Castaño-Quintero is interested in studying the factors that determine the distribution and abundance of species, biogeography, conservation, biodiversity patterns of terrestrial vertebrates and the processes that determine such patterns.

Author contributions: C.Y.A. and F.V. designed the study. L.M.O.O. helped refining the study framework. S.C.Q. compiled the data. S.C.Q. and J.E.L. conducted all analyses. S.C. wrote the paper with contribution from the other authors.

Supporting Information

Appendix1

Ecological niche modeling process

Ecological niche modeling (ENM) was carried out through the Kuenm package (Cobos, Peterson, Barve, & Osorio-Olvera, 2019) in R. Models were calibrated with 'Kuenm_cal' function combining regularization multipliers one by one up to four, 10,000 background points and establishing the "basic" option for the argument of 'features' to be taken into account (see Kuenm's help in R).

A list of candidate models was obtained, which were evaluated with the 'Kuenm_ceval' function. First, the best models by species were selected from the set candidate models in a hierarchical manner, initially choosing those with significant statistical performance via Partial ROC (Peterson, Papeş, & Soberón, 2008), with bootstrap of 50% of the training data 100 times. Then those that met the allowed omission rate ($E = 5\%$) were taken, which was determined to leave out presences that could represent sink populations (Peterson et al. 2008). Finally, the resulting models were classified and selected according to their complexity through the Akaike Information Criterion corrected by the sample size (AICc; Warren and Seifert, 2011). In those cases where at the end of the three filters, more than one set of modeling configurations were selected, the model with the best statistical performance (highest AUC-ratio in partial roc) was chosen. The models selected in Kuenm were transferred to future scenarios. In this last step, five replicas were created in bootstrap mode, applying clamping and truncation as transfer procedures.

In each transfer procedure to the future, a model of the present is generated. So that the final model of the present, corresponds to the median among the medians of the models of the present generated by each transfer procedure. The models for the future, for each year-CPR combination (i.e. scenario 2050-rcp45) were the medians of the medians of the models generated by each GCM and each type of transfer. Subsequently, the binarization of the models was established from threshold E , where all the pixels that obtained suitability with values less than or equal to 5% of the presences with the

lowest suitability were classified as 0 and the remaining pixels were classified as 1 This was done in R (R Core Team, 2018) with the raster packages (Hijmans, 2018) and rgdal (Bivand, Keitt, & Rowlingson, 2018).

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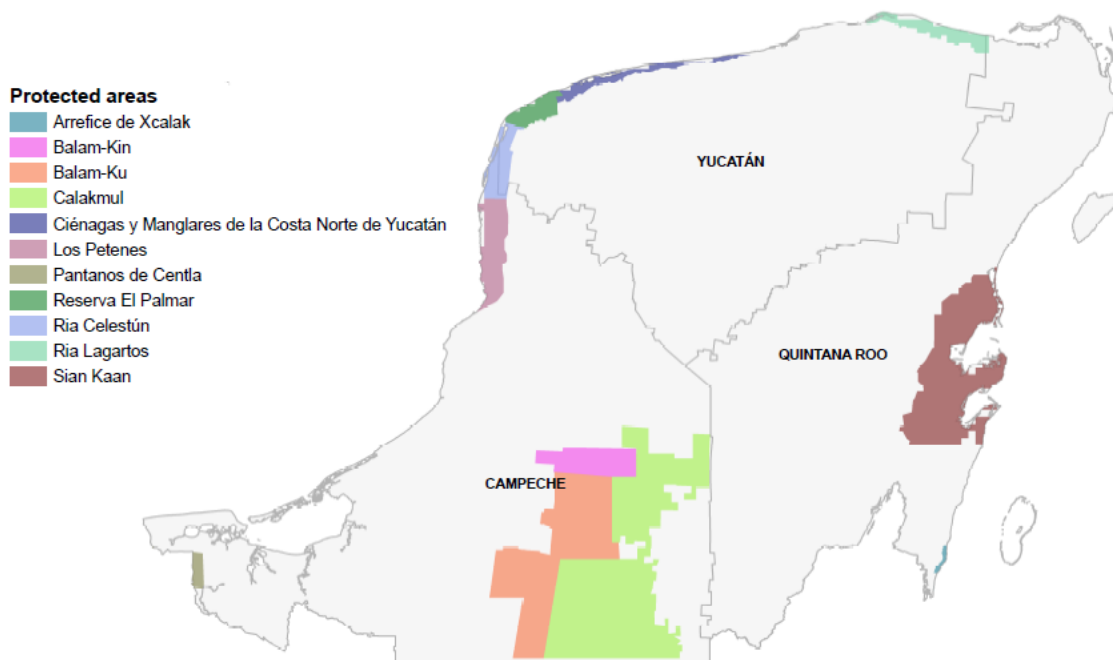


Figure S1. Protected areas of Yucatan Peninsula

Table S1. List of APs evaluated in terms of effectiveness to protect TD, rPD and rFD. CAT_UICN = Category in IUCN, CAT_MAN = Management category.

Name	Estate	CAT_UICN	CAT_MAN
Ciénagas y Manglares de la Costa Norte de Yucatán	Yucatán	Ia, VI	Reserva Estatal
Balam-Ku	Campeche	Ia, VI	Zona Sujeta a Conservación Ecológica
Reserva El Palmar	Yucatán	Ia, VI	Zona Sujeta a Conservación Ecológica
Balam-Kin	Campeche	Ia, VI	Zona Sujeta a Conservación Ecológica
Ria Lagartos	Yucatan	Ia, VI	Reserva de la Biósfera
Ria Celestún	Yucatan y Campeche	Ia, VI	Reserva de la Biósfera
Los Petenes	Campeche	Ia, VI	Reserva de la Biósfera
Sian Kaan	Quintana Roo	Ia, VI	Reserva de la Biósfera
Calakmul	Campeche	Ia, VI	Reserva de la Biósfera
Arrefice de Xcalak	Quintana Roo	IV	Parque Natural
Pantanos de Centla	Tabasco y Campeche	Ia, VI	Reserva de la Biósfera

Table S2. Wilcoxon statistic between future and present diversity values. *** p <0.001.

Comparison	TD	PD	FD
Present vs 2050rcp45	3.40E+07***	4.27E+07***	3.95E+07***
Present vs 2050rcp85	3.72E+07***	4.32E+07***	4.08E+07***
Present vs 2070rcp45	3.71E+07***	4.04E+07***	3.79E+07***
Present vs 2070rcp85	4.04E+07***	4.48E+07***	4.28E+07***

Table S3. P- value obtained from the comparison of the null models and the values observed in the spatial distribution of the diversities by PA and scenario. Positive = positive residuals, Negative = negative residuals.

PA	Present				
	TD	PD		FD	
		Positive	Negative	Positive	Negative
Ciénagas y Manglares de la Costa Norte de Yucatán	1.000	0.806	1.000	0.719	1.000
Balam-Ku	0.336	0.974	0.628	0.935	0.543
Reserva El Palmar	0.998	1.000	1.000	0.470	1.000
Balam-Kin	0.541	0.725	0.488	0.664	0.474
Ria Lagartos	0.571	0.748	0.464	0.674	0.464
Ria Celestun	1.000	1.000	1.000	0.581	1.000
Los Petenes	1.000	1.000	0.481	1.000	0.424
Sian Kaan	0.648	0.953	0.562	0.895	0.573
Calakmul	0.579	1.000	0.640	0.996	0.737
Arrefice de Xcalak	1.000	0.300	1.000	0.283	1.000
Pantanos de Centla	0.773	1.000	0.316	1.000	0.346

PA	2050-rcp45				
	TD	PD		FD	
		Positive	Negative	Positive	Negative
Ciénagas y Manglares de la Costa Norte de Yucatán	0.957	0.653	0.630	0.641	1.000
Balam-Ku	0.446	0.730	0.901	0.831	0.928
Reserva El Palmar	0.886	0.406	1.000	0.363	1.000
Balam-Kin	0.586	1.000	0.614	1.000	0.573
Ria Lagartos	0.522	0.625	1.000	0.642	0.598
Ria Celestun	1.000	1.000	0.541	1.000	1.000
Los Petenes	0.994	1.000	0.651	1.000	1.000
Sian Kaan	0.502	0.675	0.894	1.000	0.910
Calakmul	0.597	0.911	1.000	0.941	1.000
Arrefice de Xcalak	0.999	1.000	0.326	1.000	1.000
Pantanos de Centla	0.613	1.000	1.000	1.000	0.385

PA	2050-rcp85				
	TD	PD		FD	
		Positive	Negative	Positive	Negative
Ciénagas y Manglares de la Costa Norte de Yucatán	0.805	0.733	0.623	0.794	1.000
Balam-Ku	0.551	0.822	0.774	0.904	1.000
Reserva El Palmar	0.757	0.552	0.459	0.611	1.000
Balam-Kin	0.420	0.614	0.601	0.693	1.000
Ria Lagartos	0.359	0.638	0.629	0.713	1.000
Ria Celestun	1.000	1.000	0.528	1.000	1.000
Los Petenes	1.000	0.619	0.561	0.730	1.000
Sian Kaan	0.411	0.776	0.751	0.870	0.708
Calakmul	0.591	0.962	0.839	0.983	0.861
Arrefice de Xcalak	1.000	1.000	0.332	1.000	1.000
Pantanos de Centla	0.575	0.455	1.000	1.000	0.256

PA	2070-rcp45				
	TD	PD		FD	
		Positive	Negative	Positive	Negative
Ciénagas y Manglares de la Costa Norte de Yucatán	0.835	0.593	0.867	0.544	1.000
Balam-Ku	0.470	0.805	0.971	0.852	0.728
Reserva El Palmar	0.741	0.495	0.565	0.428	1.000
Balam-Kin	0.376	0.564	0.747	1.000	0.457
Ria Lagartos	0.417	0.569	1.000	0.588	0.519
Ria Celestun	1.000	1.000	0.667	1.000	1.000
Los Petenes	0.939	1.000	0.702	1.000	1.000
Sian Kaan	0.529	0.766	0.967	1.000	0.684
Calakmul	0.461	0.884	1.000	0.912	0.838
Arrefice de Xcalak	1.000	1.000	0.402	0.279	1.000
Pantanos de Centla	0.670	0.372	0.470	1.000	0.333

PA	2070-rcp85				
	TD	PD		FD	
		Positive	Negative	Positive	Negative
Ciénagas y Manglares de la Costa Norte de Yucatán	0.444	0.928	0.556	0.835	0.437
Balam-Ku	0.479	0.988	1.000	0.857	0.555
Reserva El Palmar	0.658	1.000	0.377	1.000	0.404
Balam-Kin	0.488	0.882	1.000	0.783	0.471
Ria Lagartos	0.189	0.917	0.517	0.831	0.495
Ria Celestun	1.000	1.000	0.434	1.000	0.399
Los Petenes	1.000	0.872	0.498	0.704	0.492
Sian Kaan	0.216	0.977	0.626	1.000	0.588
Calakmul	0.509	1.000	1.000	0.919	0.778
Arrefice de Xcalak	0.998	1.000	0.295	1.000	1.000
Pantanos de Centla	0.503	0.645	1.000	0.540	1.000

DISCUSIÓN GENERAL Y CONCLUSIONES

Debido a la propiedad intrínseca de las tres facetas de la biodiversidad (taxonómica [TD], filogenética [PD] y funcional [FD]), el incremento o decremento de la riqueza de especies solo puede significar un incremento o decremento de las otras facetas de la diversidad, o raramente no causar cambio alguno (Devictor et al., 2010; Safi et al., 2011). Como se esperaba, se observaron relaciones positivas entre TD y las otras facetas de la diversidad. Asimismo, aunque algunas veces la PD pudiera no reflejar la FD debido a que los rasgos funcionales pueden ser el resultado de procesos de convergencia (Faith, 1992), otras veces los rasgos evaluados pueden estar altamente conservados a lo largo de los linajes evolutivos y es posible observar, como en este trabajo, correlaciones altas entre la PD y la FD (Safi et al., 2011; Ouchi-Melo et al., 2018). Además, aunque se observen pérdidas de TD de hasta el 61%, la pérdida de PD y FD no es ni la mitad de este porcentaje, es decir, existe una redundancia filogenética y funcional entre especies.

En el escenario del presente, los valores más altos de TD se encontraron en parte sobre la base de la PY, exhibiendo un efecto de peninsularidad (definido por Cook (1969) como la disminución de la riqueza de especies desde la base hasta la punta de las penínsulas) descrito anteriormente (Vázquez-Domínguez & Arita, 2010) y también sobre el este de la península. El aumento de TD de oeste a este también ha sido identificado previamente en la PY en comunidades de bosques, donde se sugiere que es por el incremento de la precipitación en esta dirección (White & Hood, 2004). En la región este de la PY las lluvias son más frecuentes y hay mayor disponibilidad de agua lo cual tiene un efecto positivo en los anfibios dadas sus características ecofisiológicas y su forma de reproducción (Buckley & Jetz, 2007; Lion et al., 2019). Además, se ha encontrado que la reducción en la disponibilidad de agua es particularmente importante para los anfibios en áreas que ya están bajo un estrés hidrológico (Araújo, Thuiller, & Pearson, 2006).

Los procesos históricos reflejados por el arreglo espacial de la PD en el presente, sugieren que los ensamblajes donde se observa más diversidad filogenética de lo esperado por TD (centro y algunas

zonas del noreste y base de la PY) son el resultado de eventos de migración y extinciones locales que derivan en la presencia de linajes posiblemente antiguos que albergan información evolutiva única (Davis & Buckley, 2011; Fritz & Rahbek, 2012). En cambio, a lo largo del oeste de la península, pequeñas porciones al sureste y al norte, se registra menos PD de lo esperado por TD. Este patrón puede ser el resultado del agrupamiento de especies altamente emparentadas posiblemente por radiaciones recientes *in situ* o migraciones (Fritz & Rahbek, 2012), en donde solo han podido establecerse especies con características similares dadas por una historia evolutiva común y reciente, posiblemente en conjunto con filtros ambientales.

Se esperaría que, debido a que las características ecológicas aparentemente estarían restringiendo la organización espacial de la TD, la FD siguiera una configuración espacial similar. No obstante, si bien parte de la mayor FD se ubica sobre el este de la península en concordancia con la TD, los valores más altos de diversidad funcional se ubican sobre la zona centro, donde podrían estar actuando procesos como límites a la similitud debido posiblemente a la competencia interespecífica y, por lo tanto, estar promoviendo la separación de nichos (Holdaway & Sparrow, 2006).

En general, la consistencia observada en el arreglo espacial de las PD y FD podría suponer, en algún grado, una fuerte señal filogenética, donde los rasgos funcionales son rescatados en la filogenia, que a grandes rasgos toma dos connotaciones. Primero la PY tiene un origen relativamente reciente (Vázquez-Domínguez & Arita, 2010), lo que implica que sus biotas también lo tengan y hayan tenido menos tiempo para diferenciarse filogenética y funcionalmente y segundo, la carencia de relieves en la PY ofrece un espacio ambiental relativamente homogéneo, lo que tendría implicaciones en que las especies más emparentadas, por ende, ecológicamente más similares, sean las que hayan logrado, hasta ahora, tener éxito en la Península de Yucatán.

De acuerdo con los residuales de ambas diversidades, filogenética y funcional (Fig. 4), en la gran mayoría de los sitios, la diversidad ha evolucionado en conjunto, probablemente sus tres facetas ocupando todo el espacio ecológico disponible. Los escenarios futuros sugieren que podría haber un

desacoplamiento de estas diversidades. Pero, en el escenario extremo (2070-rcp85), el desacoplamiento podría ser generalizado, como consecuencia de una posible extinción masiva y aleatoria de especies, donde al ser los linajes filogenéticos (PD) y las funciones (FD) igualmente diversas con la particularidad de que hay redundancia en ambas facetas, en el futuro los residuales sugieren un patrón general donde podría existir más PD y más FD de lo esperado por el número de especies restantes.

Por ejemplo, se sugieren extinciones sustanciales de anfibios para 2050 sobre el YP, con aproximadamente una especie restante en el noroeste (Ochoa-Ochoa et al., 2012). Sin embargo, vale la pena señalar que ahora se cuentan con mejores modelos de escenarios de cambio climático que no son tan severos como los utilizados en ese estudio. No obstante, nuestros resultados muestran que podría haber grandes cambios en el patrón espacial de las relaciones, lo cual traería graves consecuencias en el mantenimiento de las nuevas comunidades formadas, con baja redundancia en las funciones y la historia filogenética, lo que hace que estas comunidades, posiblemente, sean aún más vulnerables.

Se ha sugerido que una faceta de la diversidad es un buen subrogado de otra faceta, dependiendo de los datos disponibles, los objetivos y las áreas de estudio consideradas (Devictor et al., 2010). No obstante, debido a que los rangos de distribución de las especies podrían cambiar, en parte por el cambio climático, esas congruencias observadas en un marco de tiempo de referencia, pueden cambiar de forma gradual al ser evaluados en otro tiempo (i.e., la variación de la relación entre PD y FD bajo diferentes escenarios). Por lo que, como se muestra en este trabajo, la escala de tiempo importa al momento de evaluar las relaciones y arreglos espaciales de las diferentes facetas de la diversidad. Para el caso de la Península de Yucatán, la TD no sería un buen subrogado de las diferentes facetas de la diversidad. En general, los residuales de las diversidades filogenética y funcional, tanto positivos como negativos, presentan un desajuste espacial respecto a la TD; y solo la PD o la FD serían un buen subrogado uno del otro, en algunos escenarios.

Al igual que el sistema de áreas protegidas a nivel global (Nori et al., 2015), el sistema de áreas protegidas de la Península de Yucatán es insuficiente para la protección de los anfibios, puesto que no

abarcan adecuadamente ninguna de las facetas de la diversidad mejor de lo que haría un conjunto de áreas protegidas ubicadas al azar sobre la PY. Buscando una alternativa en el sistema de Áreas Forestales Permanentes (AFPs) de México, entre 1 y 6 AFPs de 94 resultaron estar ubicadas adecuadamente para la protección de la TD a lo largo de todos los escenarios (datos no presentados). No obstante, la mayoría de estas AFPs cubren áreas aproximadamente de 5 a 10 Km². Al no protegerse la variación contenida en las diferentes facetas de diversidad, se ponen en riesgo áreas que albergan especies con historias evolutivas antiguas (Zupan et al., 2014), así como áreas ocupadas por especies con historias evolutivas recientes que constituyen un potencial evolutivo, bajo el supuesto de que continuarán evolucionando a tasas similares a las del pasado (Forest et al., 2007), áreas que albergan comunidades que poseen múltiples respuestas al cambio ambiental y áreas donde las comunidades pudieran ser resilientes a los eventos de extirpación, debido a que se componen de especies funcionalmente redundantes. Además, se pone en evidencia la importancia de tener en cuenta la dinámica temporal de los rangos de distribución de las especies en los planes de conservación, puesto que deberían estar encaminados no solo a conservar la mayor cantidad posible de las facetas de la diversidad en el presente, sino también en el futuro.

El mantenimiento a largo plazo de las comunidades podría lograrse si se conservan las funciones clave de los ecosistemas en lugar de solo las especies o sitios elegidos al azar o mediante criterios de rareza (Ouchi-Melo et al., 2018). Un primer paso radica en la identificación de los patrones geográficos actuales de las facetas de diversidad, sus posibles cambios en el tiempo y la estimación de qué tan representadas o protegidas están por los sistemas actuales de áreas protegidas. No obstante, si bien valdría la pena explorar al menos otras tres dimensiones de la composición filogenética y funcional como divergencia, uniformidad y originalidad, este trabajo podría representar un punto de partida para el planteamiento de soluciones, propuestas y estrategias que puedan ser efectivas en la conservación de los anfibios.

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