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

PATRONES GEOGRÁFICOS ACTUALES Y FUTUROS DE LAS DIMENSIONES DE LA BIODIVERSIDAD DE AVES PRESENTES EN LA PENÍNSULA DE YUCATÁN Y SU REPRESENTATIVIDAD EN ÁREAS PROTEGIDAS

TESIS

(**POR ARTÍCULO CIENTÍFICO**)

Current and future geographic patterns of bird diversity dimensions of the Yucatan Peninsula and their representativeness in Natural Protected Areas

QUE PARA OPTAR POR EL GRADO DE:

MAESTRA EN CIENCIAS BIOLÓGICAS

PRESENTA:

NELLY JAZMÍN ESCOBAR LUJÁN

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Ciudad Universitaria, CD. MX. , Agosto   2020

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M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM
P r e s e n t e.

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 **ESCOBAR LUJÁN NELLY JAZMÍN** con número de cuenta **518494092** por la modalidad de graduación de **tesis por artículo científico** titulado: **"Current and future geographic patterns of bird diversity dimensions of the Yucatan Peninsula and their representativeness in Natural Protected Areas",** que es producto del proyecto realizado en la maestría que lleva por título **"Patrones geográficos actuales y futuros de las dimensiones de la biodiversidad de aves presentes en la Península de Yucatán y su representatividad en Areas Protegidas"** ambos realizados bajo la dirección del **DR. CARLOS ALBERTO YÁÑEZ ARENAS**, quedando integrado de la siguiente manera:

Presidente:	DR. ADOLFO GERARDO NAVARRO SIGÜENZA
Vocal:	DR. ANDRÉS LIRA NORIEGA
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Suplente:	DR. LUIS DANIEL ÁVILA CABADILLA

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

A T E N T A M E N T E
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Cd. Universitaria, Cd. Mx., a 24 de agosto de 2020

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

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En memoria de mi padre Ramiro Escobar, mi tío Gabriel Luján, Arya y de Tobías.

ÍNDICE

RESUMEN

Los patrones geográficos de la biodiversidad y sus mecanismos subyacentes se encuentran entre los temas más interesantes en la ecología. Si bien se espera que la diversidad taxonómica esté relacionada con la diversidad funcional y filogenética, la forma de estas relaciones puede variar espacialmente. La desviación de las relaciones esperadas puede informar sobre algunos procesos (especiación, extinción, competencia y migración) responsables de los patrones de biodiversidad actuales. En este estudio, se evaluó la relación entre diferentes dimensiones de la diversidad de aves (taxonómica - TD, filogenética - PD y funcional – FD, por sus siglas en inglés) de la Península de Yucatán (PY) en un contexto de cambio climático futuro. Se esperaba que la TD, la PD y la FD se correlacionen positivamente y que la configuración espacial de estas relaciones permita comprender los procesos históricos y ecológicos que determinan las comunidades de aves en esta región. Además, se evaluó la efectividad del sistema de áreas protegidas (APs) de la PY en la conservación de las dimensiones de diversidad de aves. Se utilizaron modelos de nicho ecológicos para predecir la distribución potencial de las especies de aves del PY y estimar la TD, la PD y la FD. Los patrones espaciales de congruencia y discrepancia entre las dimensiones de diversidad se analizaron mediante los coeficientes de correlación de Pearson y los residuales de regresiones locales con suavizado no paramétrico (LOESS). Finalmente, se evaluó la efectividad del APs comparando los valores de diversidad observados en cada AP versus lo que se espera de un modelo nulo en el que se aleatorizó la posición de la AP dentro del PY. Se encontró una correlación positiva entre la PD y la TD, y una correlación negativa entre la FD y la TD en el presente y en los escenarios futuros. Los patrones espaciales de las relaciones derivadas de LOESS indicaron desajustes espaciales entre las dimensiones de la biodiversidad en todos los escenarios analizados. Finalmente, ninguna de las AP protege más diversidad (en cualquiera de las dimensiones evaluadas) de las aves que la esperada por un modelo nulo. Los resultados encontrados sugieren que los procesos macroevolutivos han desempeñado un papel importante en la composición de los actuales conjuntos de

aves de la PY. La evaluación de la efectividad de las APs en la protección de las dimensiones de la diversidad de aves sugiere la necesidad de adoptar un enfoque integrador para la conservación de la biodiversidad en la PY.

ABSTRACT

The geographical patterns of biodiversity and its underlying mechanisms are among the most interesting topics in ecology. While taxonomic diversity (TD) is expected to be related to functional (FD) and phylogenetic (PD) diversities, the form of these relationships may vary spatially. The deviation of expected relationships between TD, PD, and FD may inform about the processes of speciation, extinction, competition and migration, which are responsible for current biodiversity patterns. We study the relationship between TD, PD, FD of birds that distribute in the Yucatan peninsula (YP) under a context of future climate change. We hypothesized that TD, PD and FD would correlate positively, and spatial configuration of these relationships would allow us to understand historical and ecological processes that determine bird communities throughout this region In addition, we evaluated the effectiveness of the protected areas (PA) of the YP to represent the three bird dimensions of diversity. We used ecological niche models to predict the potential distribution of bird species of the YP and estimate TD, PD, and FD. Spatial patterns of congruence and discrepancy between diversity dimensions were analyzed via Pearson correlation coefficients and residuals of local regressions with non-parametric smoothing (LOESS). Also, we evaluated the effectiveness of the system of PA comparing the observed diversity values in each PA versus what is expected for a null model in which we randomized the position of the PA within the YP. We found a positive correlation between PD and TD, and a negative correlation between FD and TD in the present and future scenarios. Spatial patterns of the relationships derived from LOESS indicated spatial mismatches between biodiversity dimensions in all scenarios analyzed. Finally, we found that none of the PAs protect more diversity (in any of the evaluated dimensions) of birds than the expected by a null model. Our results suggest that macroevolutionary processes have played an important role in the composition of the current Yucatan Peninsula avian assemblages. Our assessment of the effectiveness of the PAs in

protecting the dimensions of bird diversity suggests the need to adopt an integrative approach to biodiversity conservation in the YP.

INTRODUCCIÓN GENERAL

El concepto de biodiversidad comprende muchos aspectos de la variación biológica integrando las diferencias genéticas, taxonómicas y funcionaless entre las especies (Magurran, 2004). Se piensa que las diferentes dimensiones de la biodiversidad están relacionadas, afectando las interacciones biológicas que modulan los patrones de coexistencia de las especies (Safi et al., 2011) y además, que las distribuciones de las especies y, en última instancia los patrones de biodiversidad están modulados por la interacción de procesos evolutivos, biológicos y antropogénicos (Ricklefs, 1987).

Los patrones geográficos a gran escala de la biodiversidad y sus mecanismos subyacentes se encuentran entre los temas centrales de la ecología (Currie, 1991; Francis & Currie, 2003). El patrón geográfico mayormente estudiado es el de la diversidad taxonómica (TD), debido a que entre las distintas dimensiones de la biodiversidad ésta es la más sencilla de cuantificar e interpretar (Cadotte & Jonathan Davies, 2010). Por ende, los esfuerzos de conservación con frecuencia se centran en la TD, teniendo en cuenta por lo general sólo esta medida en la priorización de sitios de conservación (Gotelli & Colwell, 2001; Fuller et al., 2010). Sin embargo, la diversidad taxonómica ignora las diferencias entre las especies en términos de las características funcionales y evolutivas, (Cardoso et al 2014), por lo que la priorización para la conservación basada exclusivamente en esta métrica a menudo no logra captar todas las facetas que componen a la biodiversidad (Brooks et al., 2006).

Actualmente existen métricas que incluyen la historia evolutiva y la función de las especies dentro de los ecosistemas (Buckley et al., 2010; Cadotte & Jonathan Davies, 2010) en aras de poder realizar evaluaciones más precisas e integrales de los problemas ecológicos y de conservación relacionados con la diversidad a través de escalas espaciales y temporales (Hadly & Maurer, 2001; Cadotte, Carscadden, & Mirotchnick, 2011). Una de las medidas de biodiversidad propuestas es la

diversidad filogenética (PD), que mide las relaciones evolutivas entre especies, es decir, la cantidad de historia evolutiva (Faith, 1992; Hardy & Senterre, 2007). La PD puede ser utilizada para cuantificar la singularidad de las especies en términos de historia evolutiva (Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011) y además proporciona información sobre el potencial evolutivo ante futuros cambios ambientales (Dalerum, Cameron, Kunkel, & Somers, 2009). En contraste, la diversidad funcional (FD) puede entenderse como la representación las distribuciones de las especies en el espacio a partir de la cuantificación de rasgos morfológicos, fisiológicos y ecológicos para una comunidad determinada (Petchey & Gaston, 2006). Esta medida es un proxy (o sustituto) del funcionamiento de los ecosistemas (Díaz & Cabido, 2001), su resiliencia y servicios ambientales (Tilman et al., 1997; Díaz et al., 2013).

A pesar de que se espera que la diversidad taxonómica esté relacionada con la PD y la FD (Zupan et al., 2014), la forma precisa de estas relaciones pueden variar espacialmente (Forest et al., 2007). Comunidades que presenten un valor similar de TD pueden diferir tanto en las relaciones filogenéticas de las especies como consecuencia de las diferencias en sus historias evolutivas (PD), así como en sus características funcionales (FD), posiblemente debido a la existencia de condiciones ambientales contrastantes (Stevens, Cox, Strauss, & Willig, 2003). La desviación de las relaciones esperadas entre PD, FD y TD, puede informar sobre algunos procesos (especiación, extinción, competencia y migración) responsables de los patrones de biodiversidad actuales (Davies Jonathan & Buckley, 2011; Fritz & Rahbek, 2012).

Regiones con alta TD y baja PD puede indicar áreas donde han ocurrido radiaciones adaptativas recientes (Fritz & Rahbek, 2012; Zupan et al., 2014). De manera inversa, áreas con baja TD y alta PD podrían ser el resultado de la presencia de linajes antiguos que pueden resultar de un proceso de especiación con poca radiación, o de la extinción de otras especies en los mismos clados (Rodrigues, Brooks, & Gaston, 2005; Voskamp, Baker, Stephens, Valdes, & Willis, 2017). Por su parte, la FD

puede ser mayor que la esperada por la TD cuando los recursos son limitados, presentándose una sobredispersión en los rasgos funcionales; y en caso contrario la FD sería menor de la esperada por la TD, en presencia de filtros ambientales fuertes que podría implicar redundancia funcional (Safi et al., 2011). Adicionalmente, las relaciones entre PD y FD permiten investigar cómo se relaciona el tiempo evolutivo con la diversificación de los rasgos, y de esta manera comprender la coexistencia de especies funcional y filogenéticamente diferentes dentro de las comunidades (Safi et al., 2011).

Desde la perspectiva de la conservación, la FD y la PD fueron promovidos como dos facetas importantes de la diversidad, respectivamente, para garantizar la permanencia de servicios ecosistémicos (Díaz et al. 2007) y para representar algún linaje de interés para la conservación (Knapp, Kühn, Schweiger, & Klotz, 2008; Mace, Gittleman, & Purvis, 2003). En teoría, la preservación de varios componentes de la biodiversidad simultáneamente podría lograrse maximizando la protección de la TD. Por ejemplo, una red complementaria de áreas protegidas que abarque a todas las especies de un lugar capturará la FD y la PD en general. Sin embargo, esta estrategia es metodológicamente y económicamente inviable, por lo que los planes de conservación se han enfocado en proteger la rareza y el endemismo (Kier et al., 2009; Myers, Mittermeler, Mittermeler, Da Fonseca, & Kent, 2000). Además, las estrategias efectivas para la conservación de la biodiversidad requieren no solo la inclusión de especies, funciones o linajes individuales en áreas protegidas, sino también conjuntos de especies que interactúan en grandes áreas (Devictor et al. 2010).

Adoptar una visón integrada de la biodiversidad es también un desafío para la planeación de la conservación, dado que los cambios globales podrían tener un efecto específico sobre las distintas expresiones de diversidad (Taylor, Flecker, & Hall, 2006; Díaz et al., 2007; Flynn et al., 2009). De manera particular, se ha encontrado que el cambio climático entendido como la variación significativa en las condiciones del clima promedio (Walther et al., 2002), ha alterado la demografía y el éxito

reproductivo de algunas especies de aves (Barbraud & Welmerskirch, 2001; Stenseth et al., 2002), o incluso modificando sus rangos de distribución en otras especies (Pounds, Fogden, & Campbell, 1999; Thomas & Lennon, 1999; Parmesan et al., 2005). Si la tasa de cambio excede el ritmo de la respuesta biológica de las especies, especialmente la capacidad de las poblaciones para emigrar o experimentar cambios adaptativos evolutivos, los impactos sobre la distribución de las especies, la estructura de las comunidades y la función de los ecosistemas pueden ser severos (Lawler et al., 2010).

Actualmente se usan los modelos de nicho ecológico (MNE) como estrategia para la aproximación hacia las distribuciones geográficas, a partir de los cuales es posible generar inferencias en cuanto a los ámbitos de distribución de las especies en diferentes escalas temporales. Las proyecciones geográficas de estos modelos se pueden utilizar para predecir la cantidad de especies potencialmente presentes en un lugar (Ferrier & Guisan, 2006), incluso en el futuro (Peterson et al., 2002). Esto permite estudiar los patrones geográficos de la diversidad frente a un ambiente cambiante, y específicamente por cambio climático dado que usualmente esto modelos son alimentados con variables climáticas o bioclimáticas que guardan estrecha relación con las tolerancias fisiológicas de las especies. Generalmente los trabajos que tienen como objetivo inferir los patrones espaciales de la riqueza de especies, o de la FD o PD a grandes escalas (Fritz & Rahbek, 2012; Safi et al., 2011; Zupan et al., 2014) parten del uso de mapas de distribución basados en polígonos para los cuales se asume un área ambientalmente idónea constante. Una alternativa sería el uso de ENMs que tienen en cuenta la variación en la idoneidad ambiental en el área de distribución, con base en las tolerancias fisiológicas de las especies (Peterson et al., 2002). Adicionalmente, para maximizar los esfuerzos de conservación de la biodiverisdad, es importante integrar los procesos de dispersión de las especies como respuesta al cambio climático, por lo que Debido a que las especies podrían desplazarse a lo largo del paisaje a medida que el clima cambian (Tingley, Monahan, Beissinger, & Moritz, 2009), integrar esta dinámica

temporal, junto con las diferentes dimensiones de la biodiversidad, podría maximizar los esfuerzos por la conservación, frente al actual cambio climático (Flynn et al, 2009).

La comprensión de los patrones espaciales de la diversidad es crucial tanto para el conocimiento como para la conservación de estos en países megadiversos como México. Dentro del país, la Península de Yucatán (PY) es una de las áreas de alta diversidad de aves ya que en esta se distribuyen ~38% de las aves de México (Navarro-Sigüenza et al., 2014); además es considerado un centro de endemismo ornitológico (Paynter 1955), y lugar de paso de aves migratorias (Lynch 1989). La PY ha sido definida como provincia biógeográfica gracias a sus características bióticas y físicas (Espadas-Manrique et al., 2003; Morrone & Márquez, 2003; Ramírez-Barahona et al., 2009), en su interior se sugiere la existencia de cuatro zonas bióticas distintivas en el avifauna. La primera, al norte definida por una mayor aridez y donde se presenta el bosque tropical seco y áreas de dunas costeras. La segunda incluye la zona de bosques caducifolios y subcaducifolios. La tercera se distingue por presentar mayor humedad y precipitación, donde predomina el bosque perennifolio. Y por último, la cuarta corresponde a la isla de Cozumel que comporte elementos con la segunda área, pero contiene elementos antillanos (Cortés-Ramírez et al., 2012).

Este trabajo tiene como objetivo estudiar las distribuciones geográficas y evaluar la relación entre las diferentes dimensiones de la biodiversidad (taxonómica, filogenética y funcional) de las aves presentes en la Península de Yucatán en un contexto de cambio climático. Se espera que la TD, la PD y la FD se correlacionen positivamente, siendo la relación entre PD y FD la más alta bajo el supuesto de que las especies estrechamente relacionadas podrían potencialmente compartir características como los rasgos funcionales (Faith, 1992). Se prevé que el patrón espacial de la diversidad taxonómica siga el gradiente de precipitación, presentándose mayor riqueza de especies en las áreas más húmedas y además, con mayor complejidad topográfica (Rahbek & Graves, 2001). En cuanto a la diversidad

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funcional se espera que las áreas con mayor variabilidad ambiental y diversidad en los tipos de coberturas contengan una mayor FD (Schoener, 1974; Barbaro et al., 2014). Por otra parte, en las zonas de contacto entre las áreas bióticas dentro de la PY se prevé que se encuentren ubicadas las áreas de mayor PD (Voskamp, Baker, Stephens, Valdes, & Willis, 2017) y que la configuración espacial de la diversidad funcional y filogenética permita la comprensión de procesos históricos y ecológicos. Se propone además, que se podrían observar diferencias potenciales entre las relaciones de las diferentes dimensiones de la biodiversidad por la potencial contracción de los rangos geográficos de las especies a causa del cambio climático. Finalmente, se pretende evaluar la efectividad del sistema de áreas protegidas en la conservación de las facetas de la biodiversidad, donde se espera qué sólo la diversidad taxonómica se encuentre bien representada en la Península. La ejecución de este proyecto podría servir como base en el desarrollo de estrategias que tengan el propósito la selección de áreas prioritarias para su conservación.

Sobretiro de artículo científico enviado

Current and future geographic patterns of bird diversity dimensions of the Yucatan Peninsula and their representativeness in Natural Protected Areas

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ABSTRACT

Aim

To study the relationship between different dimensions of bird diversity (taxonomic – TD, phylogenetic – PD, and functional – FD) of the Yucatan peninsula (YP) in a context of future climate change. We hypothesized that TD, PD and FD would correlate positively and spatial configuration of these relationships would allow us to understand historical and ecological processes that determine bird communities throughout this region. Also, we evaluated the effectiveness of the system of protected areas of the YP in the conservation of bird diversity dimensions.

Location

The biotic province of the Yucatan peninsula.

Taxon

Birds.

Methods

We used ecological niche models to predict the current and future potential distribution of bird species of the YP and estimate their TD, PD, and FD. Spatial patterns of congruence and discrepancy between diversity dimensions were analyzed via Pearson correlation coefficients and residuals of local regressions with non-parametric smoothing (LOESS). In addition, we evaluated the effectiveness of the system of protected areas (PA) comparing the observed diversity values in each PA versus what is expected for a null model in which we randomized the position of the PA within the YP.

Results

We found a positive correlation between PD and TD, and a negative correlation between FD and TD in the current and future scenarios. Spatial patterns of the relationships derived from LOESS indicated spatial mismatches between biodiversity dimensions in all scenarios analyzed. Finally, we found that none of the PAs protect more diversity (in any of the evaluated dimensions) of birds than the expected by a null model.

Main conclusions

Our results suggest that macroevolutionary processes have played an important role in the composition of the current Yucatan Peninsula avian assemblages. Our assessment of the effectiveness of the PAs in protecting the dimensions of bird diversity suggests the need to adopt an integrative approach to biodiversity conservation in the YP.

Keywords: Birds diversity, climate change, conservation, functional diversity, phylogenetic diversity, Yucatan Peninsula**.**

INTRODUCTION

Biodiversity is the most important determinant of communities and ecosystems dynamics and functioning (Tilman, Reich, & Knops, 2006). The concept of biodiversity comprises many aspects of biological variation by integrating genetic, taxonomic and phenotypic differences between species (Magurran, 2004). The interrelation of these biodiversity dimensions affects biological processes that end-up modulating the co-existence patterns of species at multiple levels (Ricklefs, 1987; Safi et al., 2011).

Large-scale geographical patterns of biodiversity and the exploration of the underlying mechanisms that structure them are central topics to ecology and biogeography (Currie, 1991; Francis & Currie, 2003). Among the different dimensions of biodiversity, taxonomic diversity (TD) is by far the most recurrently studied pattern, given its ease of quantification and understanding (Cadotte & Davies, 2010). Therefore conservation efforts often focus exclusively on TD as the only measure in prioritizing conservation areas (Fuller et al., 2010; Gotelli & Colwell, 2001). Despite its relevance and value at representing biodiversity patterns, TD ignores differences between species in terms of other key features for representing diversity of the living world, such as functional and evolutionary characteristics of species (Cardoso, Rigal, Borges, & Carvalho, 2014). Thus, not only prioritization for conservation based exclusively on TD fails to capture several biodiversity dimensions (Brooks et al.,

2006), but the incorporation of other features of biodiversity in setting conservation goals is necessary for properly identifying key differences among them (Devictor et al., 2010).

Currently there are metrics that include evolutionary history and functioning of species within ecosystems (Buckley et al., 2010; Cadotte & Davies, 2010), in order to be able to carry out more accurate and comprehensive assessments of ecological and conservation problems related to diversity through spatial and temporal scales (Cadotte, Carscadden, & Mirotchnick, 2011; Hadly & Maurer, 2001). For instance, phylogenetic diversity (PD) incorporates the amount of evolutionary history among species (Faith, 1992; Hardy & Senterre, 2007) so it can be used to quantify uniqueness of species in terms of evolutionary history (Flynn, Mirotchnick, Jain, Palmer, & Naeem, 2011). It also provides information on the evolutionary potential for future environmental changes (Dalerum, Cameron, Kunkel, & Somers, 2009). In contrast, functional diversity (FD) denotes morphological, physiological and ecological traits within communities (Petchey & Gaston, 2006). This measure gives an account of ecosystems functioning (Díaz & Cabido, 2001), and is useful to understand current dynamics of ecosystems, their resilience and environmental services (Díaz et al., 2013; Tilman et al., 1997).

Although TD is expected to be related to PD and FD (Zupan et al., 2014), the precise form of these relationships may vary spatially (Forest et al., 2007). Communities with a similar TD value may differ in the phylogenetic relationships of species as a result of differences in their evolutionary histories (PD) as well as in their functional characteristics (FD) due to the existence of contrasting environmental conditions (Stevens, Cox, Strauss, & Willig, 2003). The deviation of expected relationships between TD, PD, and FD may inform about some processes (speciation, extinction, competition and migration) responsible for current biodiversity patterns (Davies & Buckley, 2011; Fritz & Rahbek, 2012). Regions with high TD but low PD may indicate areas where recent adaptive radiation has occurred (Fritz & Rahbek, 2012; Zupan et al., 2014). Conversely, areas with low TD associated with high PD could be the outcome of the presence of ancient lineages that may result from

a process of speciation with low radiation, or from the extinction of other species in the same clades (Rodrigues, Brooks, & Gaston, 2005; Voskamp, Baker, Stephens, Valdes, & Willis, 2017). On the other hand, FD may be higher than expected by TD when resources are limited, presenting an overdispersion in the functional traits; in the opposite scenario, FD would be lower than expected by TD in the presence of strong environmental filters that could imply functional redundancy (Safi et al., 2011). Also, PD-FD relationships allow us to investigate how evolutionary time is related to diversification of traits, and thus understand coexistence of functional and phylogenetically different species within communities (Safi et al., 2011).

Adopting an integrated vision of biodiversity dimensions is also a challenge for conservation planning since global changes can have a specific effect on different expressions of diversity (Diaz et al., 2007; Flynn et al., 2009; B. W. Taylor, Flecker, & Hall, 2006). In particular, it has been found that Climate Change (CC), understood as long-term variation in the average climate (Walther et al., 2002), has altered demography, reproductive success and the geographic distribution of many bird species (Barbraud & Welmerskirch, 2001; Parmesan et al., 2005; Pounds, Fogden, & Campbell, 1999; Stenseth et al., 2002; Thomas & Lennon, 1999). Predicting demographic attributes in the future is challenging, however modeling species' distributions and transferring these models to climatic conditions of other times is a common practice to assess potential deviations between climatic scenarios (Araújo, Thuiller, & Pearson, 2006; Peterson et al., 2002; Thomas et al., 2004). Estimated distributional changes could be used to anticipate potential turnover in biodiversity (Thuiller, Lavorel, Araújo, Sykes, & Prentice, 2005).

Ecological niche models (ENM) are increasingly being used to predict the potential effects of future CC on species geographic ranges (Warren, Wright, Seifert, & Shaffer, 2014). This represents the possibility of studying the geographical patterns of diversity in the face of a changing environment. ENMs correlate the presence of species to environmental conditions, in order to estimate their physiological tolerances (Peterson et al., 2002). Because species could move throughout the landscape

as the climate changes, thus modifying their distribution ranges (Tingley, Monahan, Beissinger, & Moritz, 2009), integrating this temporal dynamic, together with the different dimensions of biodiversity, could maximize conservation efforts in the face of current climate change (Flynn et al., 2009).

Understanding the spatial patterns of diversity is crucial for both understanding and conserving them in megadiverse countries like Mexico. Within the country, the Yucatan Peninsula (YP) is one of the areas of high diversity of birds since ~ 38% of the birds of Mexico are distributed in it (Navarro-Sigüenza et al., 2014); it is also considered a center of ornithological endemism (Paynter 1955), and a place of passage for migratory birds (Lynch 1989). The PY has been defined as a biogeographic province due to its biotic and physical characteristics (Espadas-Manrique et al., 2003; Morrone & Márquez, 2003; Ramírez-Barahona et al., 2009), in its interior the existence of four distinctive biotic zones in the avifauna. The first, to the north, is defined by greater aridity and where the dry tropical forest and coastal dune areas occur. The second includes the zone of deciduous and sub-deciduous forests. The third is distinguished by presenting higher humidity and precipitation, where the evergreen forest predominates. And finally, the fourth corresponds to the island of Cozumel that contains elements with the second area but contains Antillean elements (Cortés-Ramírez et al., 2012).

Here we used ENMs to study the relationship between different dimensions of bird diversity (taxonomic, phylogenetic and functional) of the Yucatan Peninsula in a context of future climate change. We expect that TD, PD and FD correlate positively, with the relationship between PD and FD being the highest under the assumption that closely related species could share characteristics such as functional traits (Faith, 1992). Spatial configuration of these relationships will allow us to understand historical and ecological processes that determine bird communities throughout the region. We also anticipate that TD will be higher in areas of high precipitation and with topographic complexity (Rahbek & Graves, 2001) , also that FD is associated with the areas with greater environmental variability and diversity in the types of coverage (Schoener, 1974; Barbaro et al., 2014), and that the

contact zones between the biotic areas within the PY present the highest PD (Voskamp, Baker, Stephens, Valdes, & Willis, 2017). Finally, we evaluated the effectiveness of the system of protected areas (PAs) of the Yucatan Peninsula in the conservation of bird diversity dimensions, where we expect that only TD is well represented.

MATERIALS AND METHODS

Study area

We conducted this study in the Yucatan Peninsula (YP), which is located in the southeast of Mexico separating the Gulf of Mexico from the Caribbean Sea. Predominant climate is warm and subhumid, however across the region there is a gradient that goes from warm-dry to cold-wet from the northwest corner to the southeast corner (Ramamoorthy, 1994). It also present a marine climatic influence due to lack of mountains and its recent emergence of the sea (Vázquez-Domínguez & Arita, 2010). This results in frequent offshore winds, tropical storms, and occasionally hurricanes (Morrone, 2005). The predominant vegetation of the YP includes humid and dry tropical forests, as well as flood grasslands (Morrone, 2005) (Fig. 1).

Presence data

We obtained geo-referenced presence records for bird species of the YP from the Global Biodiversity Information Facility database (GBIF, 2017) and the VertNet portal (VertNet, 2017). Only birds that are resident throughout the year in the YP were included in this study, since we consider that they are the ones that compose the regional pool and therefore need to be prioritized in the conservation schemes of the region (Cooper & Soberón, 2018; Guisan et al., 2006). Each presence record was verified with the purpose of having the greatest certainty about its identification and geographical position with respect to the distribution ranges reported in online databases (BirdLife International, 2018; Cornell Lab of Ornithology, 2018). We also filtered environmentally presence records of each species in order to reduce sampling bias and model overfitting (Varela, Anderson, García-Valdés, & Fernández-González,

2014). Filtering was carried out using the first two principal components with the 'gridSample' function of the 'raster' package (Hijmans et al., 2015). We used the function 'chekerboard1' of the ENMeval package (Muscarella et al., 2014) to divide the resulting databases were divided into training and testing)

Environmental data

We downloaded 15 bioclimatic variables from WorldClim v1.4 (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) at a spatial resolution of 2.5' (~5 km^2). These represent annual trends, seasonal trends, and limiting predictors of temperature and precipitation for the period 1950-2000. We obtained future analogous variables from projections of global circulation models (GCM) for the 2050 and 2070 periods (CMIP5) (K. E. Taylor, Stouffer, & Meehl, 2012). Two GCM were selected (CCSM4 and MIROC5) to include variation and uncertainty between predictions (Diniz-Filho et al., 2009). In addition, for each GCM we choose two representative concentration pathways (RCP); one optimistic (RCP45) and other pessimistic (RCP85).

We performed a principal component analysis (PCA) to reduce multicollinearity and dimensions of environmental variables using the 'PCARaster' function of the 'ENMGadgets' package (Barve & Barve, 2013). The resulting components were projected to the future variables applying the 'iPCAProjection' function of the same package. We selected the first five components that explained 97% of the total variance, as predictors to build niche models. Finally, components were cropped with a polygon that represents a hypothetical area of historical accessibility of each species (area M of the BAM diagram, Soberón & Peterson, 2005). Calibration of models in this M prevents the algorithms to predict in regions inaccessible to the species, and also prevents the evaluation metrics from inflating (Barve et al., 2011; Cooper & Soberón, 2018). For each species, the M was generated from the join of the WWF terrestrial ecoregions (Olson et al., 2001) in which at least one presence record intersect.

Ecological niche modeling

We built ecological niche models (ENMs) for each species using Maxent (Phillips, Anderson, & Schapire, 2006) in the 'kuenm' package (Cobos, Peterson, Barve, & Osorio-Olvera, 2019) in R (R Development Core Team, 2018). This package was designed to calibrate, evaluate and select models in Maxent varying the algorithm settings by an automated process. Four regularization multipliers (1, 2, 3 and 4) and the "basic" combination of features were defined as arguments while calibrating models. In order to evaluate the performance of the candidate models and select the ones that had the best ability we specified in 'kuenm' a hierarchically protocol of three steps: 1) significance of each model was estimated via the partial receiver operating characteristic (ROC) technique (Peterson, Papeş, & Soberón, 2008) by analyzing the proportion of bootstrap replicates with area under the curve (AUC) ratios > 1 (bootstrap was performed by randomly splitting the evaluation data in half 100 times). In this first step only significant models were retained. 2) Among the significant models we chose those that presented a permitted omission rate (E) of less than 5%; thus, presence records that may have resulted from unidentified errors (particularly occurrences from sink populations) in the cleaning phase were included in this percentage and were not predicted by our distribution maps. 3) Based on the Akaike information criterion for small samples (AICc) we selected those models with least complexity (Warren & Seifert, 2011). Models that met the evaluation criteria were built again using the bootstrap functionality (five replicates were created) of Maxent and were transferred to future scenarios by applying two transfer procedures: clamping and truncation.

For each future period and RCP scenarios we used the medians of the medians of the replicates obtained by each GCM and transfer procedure. Finally, we estimated the potential distribution of each species by applying a threshold of 5% of allowed omission in the training presences. To carry out the mentioned operations we used the 'raster' package (Hijmans et al., 2015) in R (R Development Core Team, 2018).

Diversity measures

We computed presence-absence matrices (PAM) using potential distribution models as inputs. Based on PAMs we estimated TD, PD, and FD with the 'lets.presab' function of the 'LetsR' package (Vilela & Villalobos, 2015) in R (R Development Core Team, 2018). Dissimilarity and distance matrices required to estimate PD and FD, respectively, were generated as follows: for the first, we used cophenetic distances of 100 trees derived from the phylogeny of birds published by Jetz, Thomas, Joy, Hartmann, & Mooers, (2012) to account for phylogenetic uncertainty. And in the case of FD, we used the Gower distance to estimate the paired functional dissimilarity matrix between all species, based on the following traits: body mass, trophic guild, forage stratum, habit, laying size and egg size. These functional traits include ecological, life history and morphological characteristics, and were downloaded from the EltonTraits database (Wilman et al., 2014).

We used the Rao's quadratic entropy index (QE; Rao, 1982) to measure PD and FD per cell. This index indicates the average of all dissimilarities in the dissimilarity matrix, including the diagonal, which represents the dissimilarity between a species and itself (De Bello, Carmona, Lepš, Szava-Kovats, & Pärtel, 2016; De Bello, Lavergne, Meynard, Lepš, & Thuiller, 2010). Rao indices for PD and FD were estimated with the melodic function (De Bello et al., 2016) in R (R Development Core Team, 2018).

In order to ensure that all indices (TD, PD and FD) were comparable in a biological sense (De Bello et al., 2010), we transformed the values of PD and FD to equivalent numbers (Jost, 2007). We applied the corrections PDj = 1/(1-PD) and FDj =1/(1-FD) resulting in PD and FD in terms of the effective number of species needed to obtain the given value of the diversity index per cell (Jost, 2007).

Spatial congruence of diversity dimensions

To analyze spatial patterns of congruence and discrepancy between TD, FD and PD we obtained the Pearson correlation coefficients and the residuals of local regressions with non-parametric smoothing (LOESS) between the PD-TD and FD-TD relationships (rPD and rFD, respectively). Then, we

employed quantiles to generate a three level discrete variable from the residual values; those below the first quantile were assigned -1, values greater than the last quantile 1, and values that fit the model 0. In this way, we identified areas in which PD and/or FD were higher or lower than which is expected by TD (Daru et al., 2019; Forest et al., 2007; Fritz & Rahbek, 2012; Voskamp et al., 2017).

Effectiveness of Protected Areas

We compared the estimated values of TD, rPD and rFD in each PA of the YP versus what is expected for a null model. We fix the values of diversity and randomize the position of the PAs within the YP based on the protocol described by Ferro, Lemes, Melo, & Loyola, (2014) and Ribeiro, Sales, De Marco, & Loyola, (2016) in which it is possible to maintain the size, shape and orientation of the PAs. We carried out 1000 randomizations and a PA was considered effective when the observed TD, rPD or rFD was higher than expected in at least 95% of the randomizations (p-value ≤ 0.05).

RESULTS

The regional pool of the YP birds consisted of 257 species. At current the highest values of TD were found in the south and the eastern region of the peninsula between the states of Campeche and Quintana Roo. The highest PD was located towards the south-central part, extending eastward, also including the island of Cozumel. The areas with the highest FD corresponded to the center of the YP (Fig. 2). When comparing the spatial distribution of diversities in future scenarios regarding to the present, there would be a potential increase of species up to 8.3% towards the coast of the YP and reductions towards the center that range from 29.6% to 98.7%. The areas of highest TD would be restricted to the north and south of the state of Quintana Roo. The increase of PD is expected to be higher in the southeast and center of the YP, conversely there would be areas of reduction of up to 41% of PD in the north and west of the state of Quintana Roo. The areas of PD potential increase would be dispersed concentrically in the YP, with an increase of up to 45% in the west (Fig. 2).

We found a positive correlation between PD and TD, and a negative correlation between FD and TD under current climatic conditions (Table 1), in which about 57% and 76% of the variation of PD and FD, respectively, is not explained by TD. For the future scenarios, the dynamics of these relationships were variable, the relationship between TD and PD decreased regarding to the present, while the relationship between TD and FD increased. On the other hand, PD and FD in all cases showed a positive correlation, being higher in the present (Table 1).

The spatial patterns of the relationships between PD, FD and TD, derived from LOESS indicated spatial mismatches and congruence's between biodiversity measures in the scenarios analyzed. At current, rPD and rFD presented a spatial pattern with areas grouped in positive and negative residues, which indicates a divergence between PD and FD regarding TD. In both, rPD and rFD most of the cells with positive values are located inside the YP (although the area with more positive rPD is located in the center-south zone, and the region with more positive rFD in the center-north), in areas adjacent to Laguna de Términos, in the east of Chetumal Bay and on Cozumel Island. On the contrary, most of the cells with negative values are bordering the YP, although this pattern is more marked in rPD (Fig. 3).

In the future scenarios, the areas with positive rPD would expand to the northeast of the peninsula, while on the coast of the state of Yucatan most of the areas with negative rPD would be presented. In addition, there would be a dispersion of the positive rFD values towards the ends of the peninsula, leaving the negative rFD at the base in greater proportion. Although the spatial patterns of rPD and rFD were variable in the different scenarios the proportion of cells in both categories was very similar between them (Fig. 3).

Finally, we found that, both in present and in future scenarios, none of the PAs protect more diversity (in any of the evaluated dimensions) of birds than expected by a null model (Table S2).

DISCUSSION

This study is the most complete analysis of current and future geographical patterns of bird diversity in the YP. Our results suggest that macroevolutionary processes have played an important role in the composition of current avian assemblages. Areas where PD and FD are higher or lower than the expected by TD, could be indicating that other biological processes modulate the composition of the set and coexistence of species. In this sense, identifying specific factors that potentially shape communities is critical to better understand biodiversity patterns and assess conservation priorities.

Our predictions of higher TD in the south of the YP is consistent with the peninsularity effect previously observed among other taxonomic groups in this region (Vázquez-Domínguez & Arita, 2010). On the other hand, the high TD east of the peninsula coincides with the region with the highest rainfall, where dominant vegetation corresponds to evergreen tropical forest, thus fulfilling the spatial prediction of the distribution of TD. The structural complexity, both horizontal and vertical, of this type of vegetation allows the coexistence of many birds, as it offers them shelter and food resources (Graham & Blake, 2001; McIntyre, 1995).

According to Arita, (1997) current fauna of the north of the YP is of recent origin, and it is suggested that these would have originated largely by the dispersal of species from the base of the peninsula (Arita, 1997). This idea supports the high PD found at the south of this region, indicating that bird communities in these areas have a high singularity in terms of evolutionary history (Faith, 1992), and also contain a subset of species with high evolutionary potential (Winter, Devictor, & Schweiger, 2013). It is also highlighted that some areas with a higher PD agree with the contact areas of the second and third biotic zones proposed for the PY (Cortés-Ramírez et al., 2012), suggesting possible dispersal events of different groups of species between these zones (Voskamp et al., 2017).

In the areas with the highest FD of birds it predominates sub-deciduous forests. This type of vegetation is characterized by intermediate communities of tropical evergreen and deciduous forest (Miranda & Hernández-X., 1963; Palacios-Wassenaar, Castillo-Campos, Vázquez-Torres, & Del Amo-

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Rodríguez, 2014). Structural variation of these vegetation communities could facilitate the presence of different food guilds and foraging strategies, agreeing with the prediction that the variable environments in the vegetation admit a higher FD in the birds (Barbaro et al., 2014). This heterogeneity in plant structure could also differentially influence the success of bird nesting, promoting the existence of species with different reproductive strategies (Powell & Steidl, 2000).

The positive relationship between TD and PD observed here coincides with previous studies carried out at continental and global scales (Devictor et al., 2010; Voskamp et al., 2017; Zupan et al., 2014). However, the negative relationship between TD and FD differs from what it has been previously reported in literature (Safi et al., 2011; Voskamp et al., 2017). The low environmental heterogeneity of the YP might not be limiting the functional similarity between the species (Ding, Feeley, Wang, Pakeman, & Ding, 2013), thus allowing species with very similar traits to coexist.

Positive residuals of PD (that is, phylogenetically dispersed assemblages) observed in the center and east of the YP, may be indicating that this are areas where the speciation rate has been low over time and lineages that occur there are ancient (Rodrigues et al., 2005; Voskamp et al., 2017). Positive values on the island of Cozumel are consistent with Voskamp et al., (2017), who reported high rPD values in islands and isolated areas. On the other hand, areas with negative rPD and rFD, would correspond to areas with more recent speciation events and that have very similar functional species (Davies & Buckley, 2011; Devictor et al., 2010). Positive rFD values were observed in the north-central part of the YP indicating signs of high dispersion in the functional traits of the communities that occur in that region. Among the factors that could generate high FD values are competition, high environmental heterogeneity and rapid evolution of traits (Safi et al., 2011).

The potential reduction in TD in future scenarios agree with that reported by Jetz, Wilcove, & Dobson, (2007), who suggested that birds in tropical countries would face a complicated panorama due to habitat loss. Also, our future projections do not predict a large increase or decrease of FD in the YP, but they suggest a future spatial restructuring of species distributions, resulting for example in the

confluence of phylogenetically close species on the coasts of the north of the YP. Potential changes in

FD under CC scenarios would be determining the level of redundancy or functional distinction that

species added or lost in an assemblage (cell) have with respect to those that remained there (Barbet-

Massin & Jetz, 2015).

In addition, potential shifts in the geographic configuration of the residuals allow us to speculate

which are the processes that influence dynamics of bird communities in this region. For instance, today

in the northeast of the YP there is a higher FD than the expected by the TD, but under future conditions

this pattern shows a reverse pattern. The potential loss of functionally unique species, if they are also

key species (for example, pollinators), could have cascading effects on the functioning of the

ecosystem (Power et al., 1996), even if TD is high (Taylor et al., 2006).

Our results have implications for conservation of birds in the YP, because the estimated values

of rPD and rFD could help us to understand the historical patterns of evolution, extinction and

colonization that modulate current diversity. In addition, the rPD and the rFD could be a useful metric

to highlight areas of high phylogenetic or functional irreplaceability in terms of conservation (Voskamp

et al., 2017), since they indicate a high evolutionary potential of a community compared to the

communities that present a similar taxonomic diversity. It also could help as a basis to inform decisions

regarding the large infrastructure projects that will take place in this region (*e.g.,* the Mayan train, and

various solar power and wind energy stations). Finally, our assessment of the effectiveness of the PAs

in protecting the dimensions of bird diversity clearly suggests that it is necessary to include other

unprotected regions in the conservation schemes of the YP.

TABLES

Table 1. Pearson correlation coefficients with Dutilleul correction between taxonomic (TD), phylogenetic (PD) and functional (FD) diversities for the different scenarios. $p<0.001$***, $p<0.01$**, $p<0.05$*

	TD-PD Correlation	**TD-FD Correlation**	**PD-FD Correlation**
Present	0.432***	-0.238*	0.482***
2050 rcp45	0.247*	-0.306***	0.367***
2050 rcp85	0.117	-0.335***	0.371***
2070 rcp45	0.054	-0.446***	0.424***
2070 rcp85	0.074	-0.384***	0.437***

FIGURE LEGENDS

Figure 1. Study area. Mexican portion of the Yucatan Peninsula with the ecoregions and protected areas present in the place.

Figure 2. Change in time of the spatial configuration of diversities. The columns show TD, PD and FD. The first row is the current scenario. In the remaining rows is the change of the future scenarios regarding the current one on the large map and on the small one the diversity map for each scenario. Abbreviations: TD: taxonomic diversity, PD: phylogenetic diversity, FD: functional diversity.

Figure 3. Residual maps derived from LOESS regressions and histograms. 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 and Expected relationship: 0.

FIGURES

Figure 1.

Figure 2.

Present

TD 252 — 1
PD 3,56 — 1
FD 1,76 — 1

2050 rcp-45

Percentage 8,33 — -29,6   TD 240 — 1
Percentage 8,08 — -9,70   PD 3,62 — 1
Percentage 45,66 — 0   FD 1,79 — 1

2050 rcp-85

Percentage 8,33 — -98,75   TD 238 — 1
Percentage 7,92 — -41,14   PD 3,72 — 1
Percentage 45,44 — 0   FD 1,79 — 1

2070 rcp-45

Percentage 8,33 — -98,75   TD 236 — 1
Percentage 8,54 — -41,14   PD 3,73 — 1
Percentage 45,99 — 0   FD 1,80 — 1

2070 rcp-85

Percentage 8,33 — -98,75   TD 233 — 1
Percentage 8,83 — -41,14   PD 3,72 — 1
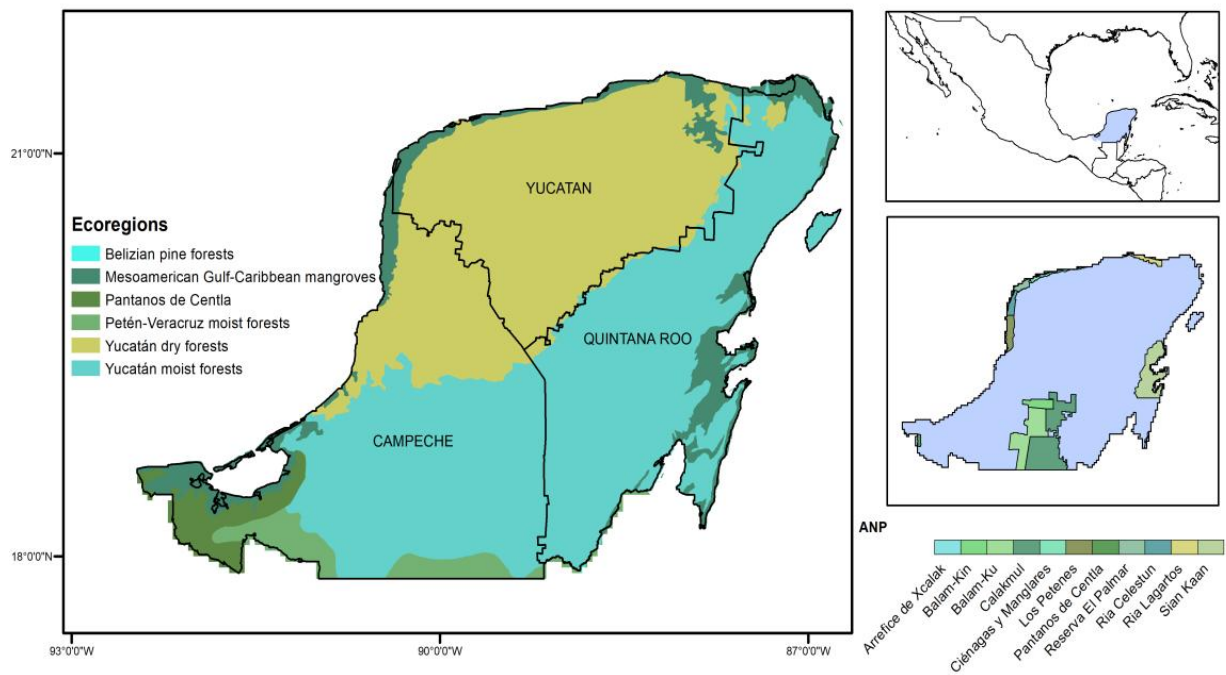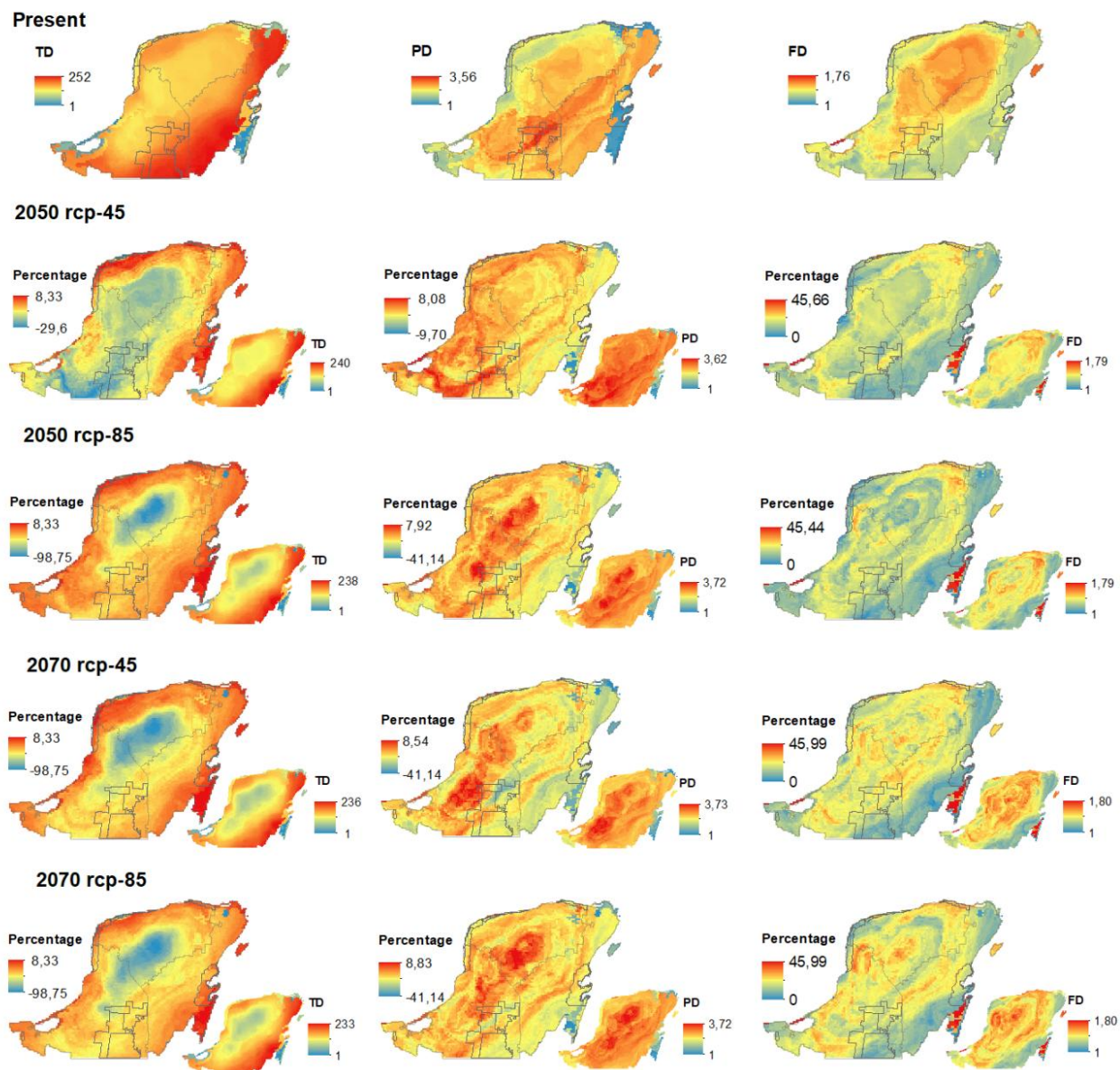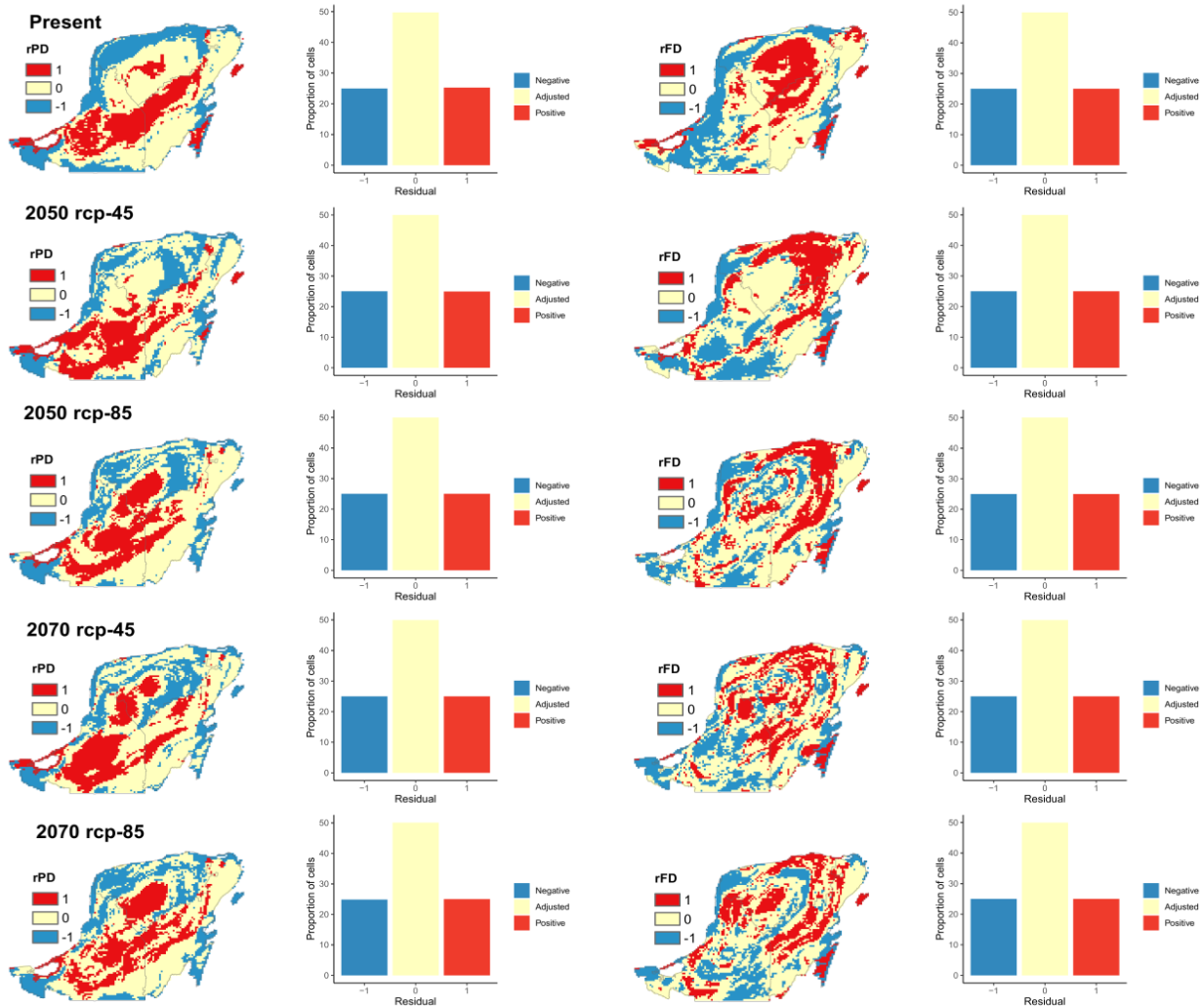Percentage 45,99 — 0   FD 1,80 — 1

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Figure 3.

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BIOSKETCH

Jazmín Escobar is interested in ecology, biogeography and conservation of vertebrates, especially birds.

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SUPPORTING INFORMATION

Table S1. Protected Areas in categories Ia to IV of the UICN present in the Yucatan Peninsula.

PA name	Designation	Designation type	Designation Year
Ciénagas y Manglares de la Costa Norte de Yucatán	State Reserve	State	2010
Balam-Ku	Area subject to conservation	State	2003
Reserva El Palmar	Area subject to conservation	State	2006
Balam-Kin	Area subject to conservation	State	1999
Ría Lagartos	Biosphere Reserve	National	1999
Ría Celestun	Biosphere Reserve	National	2000
Los Petenes	Biosphere Reserve	National	1999
Sian Kaan	Biosphere Reserve	National	2000
Calakmul	Biosphere Reserve	National	1989
Arrefice de Xcalak	Natural Park	National	2000
Pantanos de Centla	Biosphere Reserve	National	1992

Table S2. Effectiveness of the PAs. p values resulting from randomization of PAs. Abbreviations: TD: Taxonomic diversity, rPD: Positive (+), negative (-) and expected (0) residuals from the regression between phylogenetic and taxonomic diversity, rFD: Positive (+), negative (-) and expected (0) residuals of the regression between functional and taxonomic diversity. Scenarios: a) Present, b) 2050-rcp45, c) 2050-rcp85, d) 2070-rcp45, e) 2070-rcp85.

a)

PAs	TD	rPD			rFD		
		(+)	(-)	(0)	(+)	(-)	(0)
Ciénagas y Manglares de la Costa Norte de Yucatán	0.49	1.00	0.46	0.93	0.81	0.48	0.96
Balam-Ku	0.16	0.95	0.65	1.00	0.97	0.61	1.00
Reserva El Palmar	0.37	1.00	0.35	0.86	0.58	0.39	0.85
Balam-Kin	0.45	0.64	1.00	0.96	0.79	0.45	0.95
Ría Lagartos	0.27	0.68	0.48	0.99	1.00	0.41	0.98
Ría Celestun	1.00	1.00	0.42	1.00	1.00	0.41	1.00
Los Petenes	0.43	1.00	0.45	0.99	1.00	0.41	0.97
Sian Kaan	0.09	0.97	0.60	1.00	0.93	0.55	1.00
Calakmul	0.13	1.00	0.76	1.00	0.99	0.65	1.00
Arrefice de Xcalak	0.97	1.00	0.25	1.00	1.00	0.28	1.00
Pantanos de Centla	0.34	1.00	0.29	1.00	0.40	0.34	0.75

b)

PAs	TD	rPD			rFD		
		(+)	(-)	(0)	(+)	(-)	(0)
Ciénagas y Manglares de la Costa Norte de Yucatán	0.48	0.54	0.69	1.00	0.74	0.58	0.98
Balam-Ku	0.22	0.83	0.91	1.00	0.97	0.81	1.00
Reserva El Palmar	0.28	1.00	0.51	0.93	1.00	0.48	0.92
Balam-Kin	0.70	0.60	1.00	1.00	1.00	0.62	0.98
Ría Lagartos	0.20	1.00	0.69	0.98	0.76	1.00	0.97
Ría Celestun	0.73	1.00	0.53	1.00	1.00	0.50	1.00
Los Petenes	0.44	1.00	0.67	0.98	1.00	0.63	1.00
Sian Kaan	0.07	0.86	0.88	1.00	0.96	0.86	1.00
Calakmul	0.16	0.98	0.96	1.00	1.00	1.00	1.00
Arrefice de Xcalak	0.97	1.00	0.29	1.00	1.00	0.26	1.00
Pantanos de Centla	0.33	1.00	0.37	1.00	1.00	0.34	0.79

c)

PAs	TD	rPD			rFD		
		(+)	(-)	(0)	(+)	(-)	(0)
Ciénagas y Manglares de la Costa Norte de Yucatán	0.35	1.00	0.68	0.98	0.89	0.79	1.00
Balam-Ku	0.17	0.95	0.87	1.00	1.00	0.99	1.00
Reserva El Palmar	0.27	1.00	0.44	0.91	1.00	0.61	0.95
Balam-Kin	0.64	0.68	1.00	1.00	0.89	0.82	1.00
Ría Lagartos	0.27	1.00	0.65	0.99	0.91	1.00	0.99
Ría Celestun	0.69	1.00	0.48	1.00	1.00	0.69	1.00
Los Petenes	0.50	1.00	0.54	0.98	1.00	0.79	1.00
Sian Kaan	0.06	1.00	0.80	1.00	1.00	0.97	1.00
Calakmul	0.13	1.00	0.97	1.00	1.00	1.00	1.00
Arrefice de Xcalak	0.96	1.00	0.31	1.00	1.00	0.32	1.00
Pantanos de Centla	0.25	1.00	0.34	1.00	1.00	0.45	0.81

d)

PAs	TD	rPD			rFD		
		(+)	(-)	(0)	(+)	(-)	(0)
Ciénagas y Manglares de la Costa Norte de Yucatán	0.43	0.66	0.76	0.99	0.92	0.78	1.00
Balam-Ku	0.19	0.96	0.93	1.00	1.00	1.00	1.00
Reserva El Palmar	0.24	1.00	0.53	0.89	0.76	0.65	0.97
Balam-Kin	0.65	0.69	1.00	0.98	0.92	0.82	1.00
Ría Lagartos	0.23	1.00	0.80	0.99	0.93	0.81	1.00
Ría Celestun	0.62	1.00	0.55	1.00	1.00	0.69	1.00
Los Petenes	0.33	0.77	0.70	0.97	0.91	0.87	1.00
Sian Kaan	0.09	0.97	0.93	1.00	0.99	1.00	1.00
Calakmul	0.13	1.00	1.00	1.00	1.00	1.00	1.00
Arrefice de Xcalak	0.97	1.00	0.32	1.00	1.00	0.28	1.00
Pantanos de Centla	0.24	1.00	0.40	1.00	1.00	0.42	1.00

e)

PAs	TD	rPD			rFD		
		(+)	(-)	(0)	(+)	(-)	(0)
Ciénagas y Manglares de la Costa Norte de Yucatán	0.44	1.00	0.70	0.99	0.90	0.76	1.00
Balam-Ku	0.19	0.97	0.82	1.00	1.00	0.98	1.00
Reserva El Palmar	0.24	1.00	0.47	0.90	1.00	0.57	0.98
Balam-Kin	0.60	0.74	1.00	0.98	1.00	0.74	1.00
Ría Lagartos	0.20	0.79	0.69	0.99	0.90	1.00	1.00
Ría Celestun	0.66	1.00	0.46	1.00	1.00	0.65	1.00
Los Petenes	0.42	0.79	0.61	0.99	0.89	0.77	1.00
Sian Kaan	0.10	0.98	0.83	1.00	1.00	0.99	1.00
Calakmul	0.11	1.00	0.98	1.00	1.00	1.00	1.00
Arrefice de Xcalak	0.97	1.00	0.28	1.00	1.00	0.27	1.00
Pantanos de Centla	0.23	1.00	0.33	1.00	1.00	0.36	0.85

DISCUSIÓN GENERAL Y CONCLUSIONES

Este trabajo es, hasta el momento, el análisis más completo sobre patrones espaciales actuales y futuros de las distintas expresiones de biodiversidad de aves de la PY. Los resultados obtenidos sugieren que los procesos macroevolutivos han desempeñado un rol importante en la composición de los ensamblajes de aves actuales. Asimismo, las áreas donde la PD y la FD se alejan de la TD, pudieran estar indicando que otros procesos biológicos modulan la composición del conjunto y la coexistencia de las especies. En este sentido, conocer cuáles serían los factores que moldean o potencialmente podrían modelar las comunidades en el futuro, resulta prioritario, en el contexto de pérdida de la biodiversidad que se enfrenta actualmente.

El patrón espacial de mayor TD al sur de la PY, es consistente con el efecto de peninsularidad antes registrado para otros grupos taxonómicos en la región donde la riqueza de especies disminuye de la base a la punta (Vázquez-Domínguez & Arita, 2010). Por otro lado, la elevada TD al este de la península coincide con la región de mayor precipitación, en donde la vegetación dominante corresponde a la selva perennifolia, cumpliéndose así la predicción espacial de la distribución de TD. La complejidad estructural, tanto horizontal como vertical, de este tipo de vegetación permite la coexistencia de un gran número de aves (Blake & Loiselle, 1991; Bojorges Baños & López-Mata, 2005), ya que estas requieren cobertura para obtención de refugio y recursos alimenticios (McIntyre, 1995; Graham & Blake, 2001).

Se estima que las faunas actuales presentes en la parte norte de la península son de origen geológico reciente, y se sugiere que estas se habrían originado en gran medida por la dispersión de especies desde la base de la península (Arita, 1997). Esta idea soporta la alta PD encontrada al sur de la península, indicando que las comunidades de aves en estas áreas podrían tener alta singularidad en

términos de historia evolutiva (Faith, 1992) además, podrían contener un subconjunto de especies con alto potencial evolutivo (Winter, Devictor, & Schweiger, 2013). Se resalta también, que algunas áreas mayor PD concuerdan con las áreas de contacto de la segunda y tercera zona biótica propuestas para la PY (Cortés-Ramírez et al., 2012), sugiriendo posibles eventos de dispersión de diferentes grupos de especies entre estas zonas (Voskamp et al., 2017).

En las áreas con mayor FD de aves predominan las selvas subcaducifolias, siendo este un tipo de vegetación que agrupa comunidades intermedias entre la selva perennifolia y la selva caducifolia (Miranda & Hernández-X., 1963; Palacios-Wassenaar, Castillo-Campos, Vázquez-Torres, & Del Amo-Rodríguez, 2014), la variación estructural podría facilitar la presencia de diferentes gremios alimentarios y estrategias de forrajeo, concordando con la predicción de que los entornos variables en la vegetación admiten una mayor FD en las aves (Barbaro et al., 2014). Esta heterogeneidad en la estructura vegetal, también podría influir de manera diferencial en el éxito de anidación de las aves, promoviendo la existencia de especies con diferentes estrategias reproductivas (Powell & Steidl, 2000).

Al igual que otros estudios a escalas globales y continentales (Devictor et al., 2010; Zupan et al., 2014; Voskamp et al., 2017) se observó una correlación positiva entre la TD y la PD. Sin embargo, contrario a lo que sugieren diferentes trabajos (Safi et al., 2011; Voskamp et al., 2017) se encontró una relación negativa entre la TD y la FD, indicando que al aumentar el número de especies es posible que se estén incluyendo especies funcionalmente muy similares. La baja heterogeneidad ambiental de la PY podría no estar limitando la similitud funcional entre las especies (Ding, Feeley, Wang, Pakeman, & Ding, 2013), permitiendo así que especies con rasgos muy similares puedan coexistir.

Los patrones de congruencia o no congruencia entre las medidas de la biodiversidad sugieren que las especies que se presentan localmente pueden derivar tanto de grupos regionales de especies con

historias biogeográficas y evolutivas similares, como diferentes (Webb, Ackerly, McPeek, & Donoghue, 2002; Losos, 2008; Cumming & Child, 2009; Devictor et al., 2010). En el caso de la PD la mayoría de los residuales positivos (es decir, ensamblajes filogenéticamente dispersos) se ubicaron en el centro y al este de la PY, indicando que podrían ser áreas donde la tasa de especiación ha sido baja a través del tiempo y es probable que los linajes allí presentes sean antiguos (Rodrigues et al., 2005; Voskamp et al., 2017). Los valores positivos en la isla de Cozumel, son consistentes con los encontrados por Voskamp et al., (2017), quienes han documentado valores altos de rPD en islas y áreas aisladas. Por otro lado, las áreas con rPD y rFD negativos, corresponderían a áreas con eventos de especiación más recientes y que presentan especies muy similares funcionalmente (Devictor et al., 2010; Davies & Buckley, 2011). Los valores de rFD positivos se presentaron en la parte centro-norte de la PY indicando que estas comunidades presentan signos de alta dispersión en los rasgos funcionales. Entre los factores que podrían generar valores altos en FD se encuentra la competencia, la alta heterogenidad ambiental y la rápida evolución de rasgos (Safi et al., 2011).

La potencial reducción en la TD coincide con lo reportado por Jetz et al., (2007), quienes sugieren que las aves en los países tropicales enfrentan un panorama complicado. No obstante, las proyecciones futuras en este estudio no predicen un gran aumento o disminución en la FD de la región, pero si sugieren futuras reestructuraciones espaciales de las distribuciones de las especies, resultando por ejemplo en la confluencia de especies filogenéticamente cercanas en las costas del norte de la PY. Los cambios potenciales en la FD bajo escenarios de CC estarían determinando el nivel de redundancia o distinción funcional que las especies agregadas o perdidas en un ensamblaje (celda) tienen con respecto a las que permanecieron allí (Barbet-Massin & Jetz, 2015).

Además, los cambios potenciales en la configuración geográfica de los residuales permiten especular sobre procesos determinantes en la dinámica de las comunidades de aves. Por ejemplo, en

regiones hacia el noreste de la PY, donde en el presente se ubicaron áreas de mayor FD de la esperada por la TD se predice que ocurra lo contrario en el futuro. La pérdida de especies funcionalmente únicas, si además son especies clave (por ejemplo, polinizadoras), podría tener efectos en cascada en el funcionamiento del ecosistema (Power et al., 1996), incluso si la TD en éste es alta (Taylor et al., 2006).

Los resultados son importantes para la conservación de las aves en la PY, debido a que los valores de rPD y rFD encontrados, podrían ayudar a comprender los patrones históricos de evolución, extinción y colonización que modulan la diversidad actual. Además, la rPD y la rFD podría ser una métrica útil para resaltar áreas de alta irremplazabilidad filogenética o funcional en términos de la conservación (Voskamp et al., 2017), ya que indican un alto potencial evolutivo de una comunidad en comparación con las comunidades que presenten una diversidad taxonómica similar. Dado que las áreas protegidas son la base de las estrategias de conservación actuales y por tanto desempeñan un papel vital en la protección de las especies frente al cambio climático, los hallazgos de este estudio muestran que la red actual de APs no es efectiva en la protección de las facetas de diversidad de aves evaluadas, por lo que representa una primera aproximación en la evaluación de la vulnerabilidad de las especies y podría tenerse como guía en las decisiones de conservación, con el objetivo de minimizar los efectos negativos del cambio climático en la diversidad de aves presentes en la PY.

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