UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO

POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE BIOLOGÍA

ECOLOGÍA

DIVERSIDAD FUNCIONAL Y ENSAMBLAJE DE LAS COMUNIDADES DE ANFIBIOS EN AMBIENTES CONTRASTANTES

TESIS

POR ARTÍCULO CIENTÍFICO

AMPHIBIAN COMMUNITIES IN TWO CONTRASTING ENVIRONMENTS: FUNCTIONAL DIVERSITY AND ENVIRONMENTAL FILTERS

QUE PARA OPTAR POR EL GRADO DE

MAESTRA EN CIENCIAS BIOLÓGICAS

PRESENTA

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MÉXICO, CIUDAD DE MÉXICO, AGOSTO, 2019

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M. en C. Ivonne Ramírez Wence
Directora General de Administración Escolar, UNAM

Presente

Me permito informar a usted que en la reunión ordinaria del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **13 de mayo del 2019** 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 **ÁLVAREZ GRZYBOWSKA ELIZA** con número de cuenta **517024863** por la modalidad de graduación de **tesis por artículo científico** titulado: **"Amphibian communities in two contrasting environments: functional diversity and environmental filters"**, que es producto del proyecto realizado en la maestría que lleva por título: **"Diversidad funcional y ensamblaje de las comunidades de anfibios en ambientes contrastantes"**, ambos realizados bajo la dirección del **DR. ANDRÉS GARCÍA AGUAYO**, quedando integrado de la siguiente manera:

Presidente:	DR. ALEJANDRO GONZALEZ VOYER
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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARA EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 25 de junio de 2019

DR. ADOLFO GERARDO NAVARRO SIGÜENZA
COORDINADOR DEL PROGRAMA

POSGRADO EN CIENCIAS BIOLOGICAS
COORDINACIÓN

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A los cachalotes, por aparecer en mi vida

Nicolás y Darío

"There is no organism without an environment, but there is no environment without an organism. […] Through their life activities, organisms are the active makers and remarkers of the milieu."

Richard Lewontin & Richard Levins

ÍNDICE

RESUMEN

Tradicionalmente con el fin de entender los cambios en la biodiversidad se han empleado enfoques que contemplan conceptos como riqueza, abundancia y diversidad en donde no se contempla la identidad de éstas ni su papel funcional en los ecosistemas. En ese sentido, la diversidad funcional reconoce la inmensa variedad de formas en las que los organismos utilizan los recursos y transforman el ambiente con su actividad, además de que nos permite entender las reglas a través de las cuales se ensamblan las comunidades biológicas a partir el conjunto regional de especies. Por ejemplo, de acuerdo al mecanismo de los filtros ambientales, las especies que coexisten en una comunidad serán funcionalmente más similares entre sí que lo esperado por el azar dado que las condiciones ambientales actúan como un filtro. En contraste, el mecanismo de similitud limitante promueve la dispersión de rasgos funcionales entre las especies y un uso compatible de recursos al reducir la competencia. En este estudio, evaluamos el efecto de ecosistemas contrastantes (bosque tropical caducifolio y bosque de pino-encino) y sus temporadas (lluviosa y seca) sobre la diversidad funcional y la estructura de la comunidad de anfibios en el occidente de México. Analizamos la estructura de grupos funcionales basada en once rasgos relacionados con: reproducción, flujo trófico y uso de hábitat. Siete grupos funcionales con características ecológicas distintas fueron detectados, cuatro de los cuales presentaron una alta redundancia funcional y dos representados por una especie. Las comunidades de anfibios estuvieron relacionadas con cambios en las variables ambientales de altitud, temperatura y humedad relativa. Nuestro estudio mostró que las asociaciones entre las diferentes métricas de diversidad (taxonómica y funcional) no son constantes a través de ecosistemas contrastantes. Aunque el bosque tropical caducifolio durante la temporada lluviosa obtuvo la mayor riqueza de especies, la riqueza y diversidad de grupos funcionales fueron significativamente menores que en las dos temporadas del bosque de pino-encino. Estos resultados sugieren que la sequía estacional en el bosque tropical caducifolio podría estar actuando como un filtro ambiental promoviendo la dominancia de rasgos funcionales que fueron similares en las especies, mientras que la similitud limitante podría estar actuando en el bosque de pino-encino ante condiciones hídricas relativamente estables permitiendo una alta diversificación funcional. Entender la relación entre la estructura de las comunidades, la biodiversidad y el funcionamiento de los ecosistemas es uno de los grandes retos que enfrenta la teoría ecológica y es necesario para emprender estrategias de conservación en sitios naturales.

ABSTRACT

Traditionally, in order to understand the changes in biodiversity classical approaches that contemplate concepts such as richness, abundance and diversity have been used, in which their identity is not contemplated nor their functional role in ecosystems. In this sense, functional diversity recognizes the immense variety of ways in which organisms use resources and with their activity transform the environment, as well as allowing us to understand the rules through which biological communities are assembled from the regional set of species. For example, according to the mechanism of environmental filters, the species that coexist in a community will be functionally more similar to each other than expected by chance given that the environmental conditions act as a filter. In contrast, the limiting similarity mechanism promotes the dispersion of functional traits between species and a compatible use of resources by reducing competition. In this study, we evaluated the effect of contrasting ecosystems (tropical dry forest and pine-oak forest) and their seasons (wet and dry) on the functional diversity and structure of the amphibian community in western Mexico. We analyze the structure of functional groups based on eleven traits related to: reproduction, trophic flow and habitat use. Seven functional groups with different ecological characteristics were detected, four presented a high functional redundancy and two represented by one species. The amphibian communities were related to changes in the environmental variables of altitude, temperature and relative humidity. Our study showed that associations between different diversity metrics are not constant across contrasting ecosystems. Although the tropical deciduous forest during the rainy season obtained the highest species richness, the richness and diversity of functional groups were significantly lower than in the two seasons of the pine-oak forest. These results suggest that the seasonal drought in the tropical dry forest could be acting as an environmental filter promoting the dominance of similar functional traits in the species, while the limiting similarity could be acting in the pine-oak forest in relatively stable hydrological conditions allowing a high functional diversification. Understanding the relationship between the structure of communities, biodiversity and the functioning of ecosystems is one of the great challenges of ecological theory and is necessary to undertake conservation strategies in natural sites.

INTRODUCCIÓN

Tradicionalmente con el fin de establecer prioridades de conservación en los sitios naturales se han realizado estudios que contemplan criterios tales como la riqueza, la abundancia y la presencia de especies endémicas o raras, entre otros (Moreno 2011; Morin 2011; Córdova-Tapia y Zambrano 2015), en donde se asumen las mismas funciones para cada una de las especies sin contemplar la identidad de éstas ni su papel funcional en los ecosistemas (Hooper et al. 2005; Morin 2011). No obstante, en la actualidad la diversidad funcional se reconoce que la variedad de formas en las que los organismos usan los recursos, son componentes esenciales de la diversidad biológica y son clave para entender los mecanismos de ensamblaje de las comunidades y los procesos de los ecosistemas, así como los servicios que ofrecen (Mason et al. 2005; Duffy et al. 2007; Villéger et al. 2008; Mason y de Bello 2013; Tilman et al. 2014; Orlandi et al. 2015). Por ello, la ecología funcional se ha propuesto como una herramienta para entender la biodiversidad porque describe a través del estudio de rasgos funcionales las diversas estrategias de vida de las especies en los ecosistemas, la estructura de las comunidades y los procesos ecosistémicos (Chapin et al. 2000; Tilman 2001; Duffy et al. 2007; Violle et al. 2007; Salgado-Negret 2015), además de la predicción de procesos importantes como la resistencia y resiliencia de los ecosistemas (Mason et al. 2005).

La diversidad funcional se define como el grado de diferencia de rasgos entre y dentro de las especies, o como la distribución de las especies en el espacio funcional de nicho (Mason et al. 2005; Villéger et al. 2010; Mason y de Bello 2013; Córdova-Tapia y Zambrano 2015). Los rasgos funcionales son entendidos como cualquier característica morfológica, bioquímica, fisiológica, estructural y de historia de vida que puede ser medida a nivel de individuo y que tiene un efecto en su adecuación (*sensu* fitness; Cadotte et al. 2011; Luck et al. 2012). Además, los rasgos proveen una conexión entre las especies y los múltiples procesos de los ecosistemas como la productividad primaria, los flujos de nutrientes y la resiliencia (Mason y de Bello, 2013). En ese sentido, la adición o pérdida de especies o grupos con ciertos rasgos funcionales puede tener un impacto diferencial en los ecosistemas (Tilman et al. 1997; Tilman 2001; Díaz y Cabido 2001; Petchey y Gaston 2002; de Bello et al. 2010) debido a que pueden existir especies que resulten clave y otras que se consideren redundantes respecto a un proceso ecosistémico en particular (Díaz y Cabido 2001). De esta manera, la abundancia, rango y distribución de los rasgos funcionales tienen influencia en el funcionamiento de los ecosistemas (*sensu* diversidad

funcional; Díaz y Cabido 2001; McGill et al. 2006; de Bello et al. 2010) y a su vez responden a filtros ambientales (Keddy 1992; Díaz et al. 2007).

Una forma de evaluar la diversidad funcional de una comunidad es separar a las especies en grupos funcionales discretos, entendidos como un conjunto de especies que explotan el mismo tipo de recursos y exhiben respuestas similares al ambiente (Blaum et al. 2011; Luck et al. 2012). También, la diversidad funcional puede medirse a escala continua como la distribución de las especies en el espacio funcional de nicho (Tilman 2001; Mason et al. 2005; Villéger et al. 2008; Laliberté y Legendre 2010). El estudio de la diversidad funcional a través de diferentes métricas ha resultado clave para entender los cambios en la biodiversidad, los mecanismos de ensamblaje de las comunidades y los procesos de los ecosistemas así como los servicios que ofrecen (Chapin et al. 2000; Duffy et al. 2007; Violle et al. 2007; Schleuter 2010; Mason y de Bello, 2013). De esta manera, el estudio de la diversidad funcional puede responder preguntas de investigación como ¿cuáles son los mecanismos que conducen al ensamblaje de comunidades?, ¿cuál es el efecto de las especies en el funcionamiento de los ecosistemas?, ¿cómo responden a cambios ambientales?, y ¿cuál es el impacto de las extinciones de especies en el funcionamiento de los ecosistemas? (Petchey y Gaston 2002; Mason y Bello 2013; Orlandi et al. 2015).

La diversidad funcional es una herramienta que puede ser utilizada para revelar las reglas a través de las cuales se ensamblan las comunidades biológicas (Díaz et al. 2007). Una regla de ensamblaje es entendida como los límites a través de los cuales las comunidades locales son seleccionadas a partir de la fuente regional de especies mediante el estudio de sus rasgos funcionales (Diamond 1975; Keddy 1989; Wilson y Stubbs 2012; Tilman et al. 2014). Existen varias reglas de ensamblaje, de acuerdo al mecanismo de los filtros ambientales, las especies que coexisten en una comunidad serán funcionalmente más similares entre sí que lo esperado por el azar dado que las condiciones ambientales actúan como un filtro, permitiendo que solo algunas especies con rasgos similares persistan (Díaz et al. 2007; Herben y Goldberg 2014). En este sentido, se espera que las especies dominantes en la comunidad local tengan nichos similares que les permitan tolerar los filtros ambientales que el ambiente les impone dado sus tolerancias fisiológicas, historia biogeográfica y procesos evolutivos involucrados (Díaz et al. 2007; Morin 2011; Kraft et al. 2015; Hooper et al. 2005; Cadotte y Tucker 2017). En contraste, el mecanismo de similitud limitante resulta en una restricción competitiva en la similitud de rasgos (MacArthur y Levins 1967; Herben y Goldberg 2014), es decir, que promueve la

dispersión de rasgos ya que estipula que especies con alta superposición de nicho deben tener bajas dominancias en el ensamblaje; mientras que las especies dominantes tendrán un bajo traslape de nicho, promoviendo un uso compatible de recursos (ej. mayor productividad) al reducir la competencia (Tilman et al. 2014).

Cada vez son más los estudios de vertebrados bajo el enfoque de la ecología funcional (Gómez y Moreno 2017), y más aun los que evalúan las reglas de ensamblaje (Bellwood et al. 2002; Spasojevic y Suding 2012; Córdova-Tapia y Zambrano 2016; Lechêne et al. 2018; Carvajal-Cogollo et al. 2019) y el potencial que tienen los anfibios para comprender los procesos ecosistémicos (Pineda et al. 2005; Strauß et al. 2010; Tobar-Suárez 2012; Corral-Gómez 2013; Trimble y van Aarde 2014; Tsianou y Kallimanis 2016; Cortés-Gómez et al. 2015; Riemann et al. 2017; Lemus-Mejía 2017; Díaz-García et al. 2017). En ese sentido, los anfibios son un excelente modelo para el estudio de la diversidad funcional debido a que: son i) organismos de baja movilidad, son ii) los vertebrados más abundantes de los ecosistemas tropicales y son iii) especialmente susceptibles a los cambios ambientales y por lo tanto valiosos bioindicadores de calidad ambiental (Whiles et al. 2006; Stuart et al. 2008; Cortés-Gómez et al. 2015).

Los anfibios son responsables de una considerable parte de flujo de energía en ecosistemas acuáticos y terrestres al influir en las interacciones bióticas de depredación y competencia. Durante su etapa adulta son los mayores consumidores de invertebrados de los ecosistemas terrestres, mientras que durante las primeras etapas de su desarrollo se alimentan de algas, detritos u otros animales pequeños (Whiles et al. 2006; Stuart et al. 2008). Además, los huevos, embriones, renacuajos y adultos representan una importante fuente de alimento para organismos como moluscos, crustáceos, arácnidos, insectos, peces, aves, mamíferos, reptiles e incluso otros anfibios (Cortés-Gómez et al. 2015). La capacidad de los anfibios de vivir en ambientes terrestres y acuáticos a lo largo de su ontogenia les confiere un papel único en los ecosistemas (Whiles et al. 2006), por lo que su adición o remoción podría llegar a tener impactos desproporcionados en la estructura de los mismos (Whiles et al. 2006; Stuart et al. 2008). No obstante, poco se conoce acerca de su rol en el mantenimiento y la regulación de las funciones en los ecosistemas, y por tanto, su valor potencial como soportadores de los servicios ecosistémicos (Cortés-Gómez et al. 2015).

Desafortunadamente, el aumento de las presiones antropogénicas sobre los ecosistemas ha conducido a la pérdida irreversible de especies, siendo los anfibios el grupo de vertebrados más amenazado a nivel global. Tan sólo en México sus poblaciones disminuyen a tasas mucho

más elevadas (57.97%) que las de otros vertebrados como las aves (5.01%), los reptiles (14.07%) y los mamíferos (19.35%) (Stuart et al. 2004; Frías-Alvarez et al. 2010; Ceballos et al. 2017). Ante este nuevo panorama de cambios se requieren soluciones que tomen en cuenta la complejidad estructural y funcional de las comunidades bióticas dentro de los ecosistemas y que nos permitan avanzar hacia una comprensión mucho más real de las propuestas de conservación.

En ese sentido, la evaluación de paisajes transformados en la conservación de la biodiversidad solo resulta útil si se compara con ecosistemas prístinos que sirvan como referentes ecológicos para entender cómo se estructuran las comunidades biológicas (Laurila-Pant et al. 2015). Por ello, la región de Cabo Corrientes en el occidente de México es un lugar ideal para el estudio de las comunidades de anfibios en sitios poco alterados, ya que alberga ecosistemas con una gran diversidad de especies y ha sido reconocida por su potencial biológico como zona terrestre con prioridad en investigación y conservación (Arriaga et al. 2000; Ceballos et al. 2010), así como sitio de alta prioridad para la conservación de los anfibios (Ochoa-Ochoa et al. 2011). Esta región se encuentra dividida en dos ambientes a lo largo de un gradiente altitudinal que va de 0 a los 1,920 m.s.n.m.: bosque tropical caducifolio y bosque de pino-encino (Fig. 1). Sin embargo, no se han realizado trabajos sistemáticos en esta región relacionados con anfibios y el conocimiento de la historia natural y ecología de la mayoría de las especies ha sido prácticamente inexplorado (Ceballos et al. 2010).

En México no se han estudiado las reglas de ensamblaje de las comunidades de anfibios en ecosistemas contrastantes desde el enfoque de la diversidad funcional. El municipio de Cabo Corrientes es una plataforma ideal para evaluar reglas de ensamblaje de las comunidades de anfibios en ambientes conservados. En ese sentido, este estudio podrá ser un referente para evaluar a futuro el efecto de los ecosistemas en la conservación de los anfibios, así como del funcionamiento de las especies y su relación con los procesos ecosistémicos. Finalmente, planteamos la hipótesis de que los filtros ambientales predominan como un mecanismo de estructuración en la comunidad de anfibios del bosque tropical caducifolio, promoviendo una mayor redundancia funcional debido a las condiciones estacionales de la sequía, mientras que la similitud limitante actúa en el bosque de pino-encino, lo que permite una mayor diversificación de funciones y un uso compatible de los recursos.
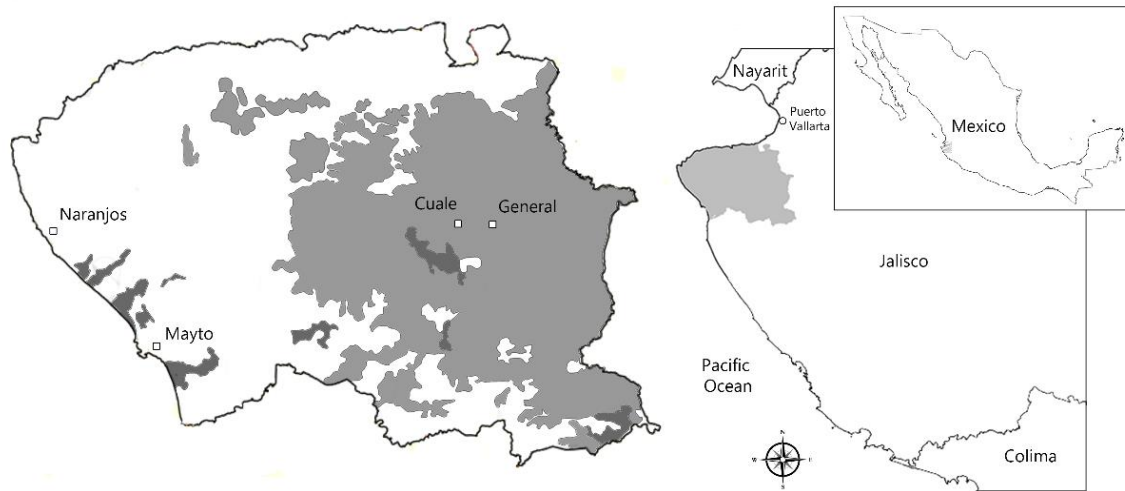
Fig 1. Ubicación geográfica de las localidades de muestreo en el municipio de Cabo Corrientes, México: Naranjos, Mayto, Cuale y General. Blanco = bosque tropical caducifolio, gris = bosque de pino-encino, negro = otras coberturas.

Cuadro 1. Especies de anfibios registradas durante el estudio.

Orden	Familia	Especie	Forma y talla*
Anura			
	Bufonidae		5 cm
		Incilius mazatlanensis (Taylor, 1940)	
		Incilius occidentalis (Camerano, 1879)	
		Rhinella horribilis (Linnaeus, 1758)	
	Eleutherodactylidae		
		Craugastor occidentalis (Taylor, 1941)	
		Craugastor pygmaeus (Taylor, 1937)	
		Eleutherodactylus modestus (Taylor, 1942)	
	Hylidae		
		Agalychnis dacnicolor (Cope, 1864)	
		Dryophytes arenicolor (Cope, 1866)	
		Exerodonta smaragdina (Taylor, 1940)	
		Smilisca baudinii (Duméril y Bibron, 1841)	
		Tlalocohyla smithii (Boulenger, 1902)	
	Leptodactylidae		
		Leptodactylus melanonotus (Hallowell, 1861)	
	Microhylidae		
		Hypopachus variolosus (Cope, 1866)	
	Ranidae		
		Lithobates forreri (Boulenger, 1883)	
		Lithobates neovolcanicus (Hillis y Frost, 1985)	
		Lithobates pustulosus (Boulenger, 1833)	

*La silueta se dibujó con base en fotografías digitales de los individuos observados en los sitios de muestreo; la talla corresponde al largo patrón promedio registrado durante todo el estudio.

OBJETIVOS

OBJETIVO GENERAL

Analizar la diversidad funcional y la estructura de la comunidad de anfibios en dos ecosistemas contrastantes (bosque tropical caducifolio y bosque de pino-encino) del Occidente de México.

OBJETIVOS PARTICULARES

- Comparar la diversidad y estructura de la comunidad de anfibios entre ecosistemas (bosque tropical caducifolio y bosque de pino-encino) y entre temporadas (lluviosa y seca).

- Caracterizar a la comunidad a partir de la determinación de grupos funcionales de acuerdo con su similitud de rasgos relacionados con la reproducción, flujo trófico y uso de hábitat.

- Evaluar los cambios en los grupos funcionales y los índices de diversidad funcional entre ecosistemas (bosque tropical caducifolio y bosque de pino-encino) y entre temporadas (lluviosa y seca).

- Identificar variables de paisaje que puedan estar asociadas con los patrones de la diversidad taxonómica de anfibios.

Amphibian communities in two contrasting environments: functional diversity and environmental filters

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Abstract

Functional diversity is a useful tool for understanding biological communities and the influence of environmental filters on the rules of assemblage. However, few studies explore the relationships of diversity metrics across contrasting ecosystems. We evaluated the effect of ecosystems (tropical dry forest and pine-oak forest) and seasons (wet and dry) on the functional diversity and community structure of amphibians in western Mexico. Our study showed that associations between different metrics of diversity are not constant across contrasting ecosystems. The amphibian communities were related to changes in the environmental variables of elevation, temperature and relative humidity. We analyzed the functional structure of the amphibian community based on eleven traits related to reproduction, trophic flow and habitat use. Seven functional groups with distinct ecological characteristics were detected, of which, four presented functional redundancy and two were represented by a single species. While the tropical dry forest during the wet season showed the highest species richness, the richness and diversity of functional groups were significantly lower than in the pine-oak forest in both seasons. These results suggest that the seasonal drought in the tropical dry forest could act as an environmental filter, promoting dominance of similar functional traits among the species, while limiting similarity could be acting in the pine-oak forest, in the face of relatively stable hydric conditions, allowing a

greater functional diversity. Analysis of the relationship between the community structure and ecosystem functioning is necessary to undertake conservation strategies in natural sites that allow us to protect biodiversity and thus human well-being.

Key words Tropical dry forest Pine-oak forest Mexico Assembly rules Limiting similarity

Introduction

Understanding the relationship between biodiversity, community structure and ecosystem functioning is one of the great challenges of ecological theory (Duffy 2002; Morin, 2011; Córdova-Tapia and Zambrano 2015). To evaluate changes in biodiversity, classical approaches have been used that contemplate concepts such as richness, abundance, diversity and evenness of species, among others (Moreno 2011; Morin 2011). These concepts assume the same possibilities of survival for the species without considering their identity or functional role within the ecosystems (Hooper et al. 2005; Morin 2011). However, it is currently recognized that the variety of forms in which organisms use resources, respond to changes and transform the environment with their activity are essential components of biodiversity and can be integrated through functional ecology (Duffy et al. 2007; Violle et al. 2007; Mason and de Bello 2013; Tilman et al. 2014; Orlandi et al. 2015).

Through the study of species traits, functional diversity allows us to determine the rules by which biological communities are assembled (Díaz et al. 2007). A rule of assembly represents limits to the understanding and prediction of how local communities are selected from a regional set of species (Diamond 1975; Keddy 1989; Wilson and Stubbs 2012; Tilman et al. 2014). According to the mechanism of environmental filters, the species that coexist in a community are functionally more similar to each other than could be expected by chance, since the environmental conditions act as a filter that enable only those species with similar traits to persist (Díaz et al. 2007; Herben and Goldberg 2014). Thus, it is expected that the dominant species in the local community will present similar niches that allow them to tolerate the conditions imposed upon them by the environment, given their particular physiological tolerances, historic factors and evolutionary processes (Hooper et al. 2005; Díaz et al. 2007; Morin 2011; Kraft et al. 2015; Cadotte and Tucker 2017). In contrast, the mechanism of limiting similarity produces a competitive restriction to trait similarity (MacArthur and Levins 1967; Herben and Goldberg 2014); i.e., it acts to promote functional diversification since it stipulates that species with high niche overlap must be of low dominance within the community, thus favoring a

compatible and efficient use of resources (e.g., greater productivity) by reducing competition (MacArthur and Levins 1967; Hubbell 2005; Tilman et al. 2014).

In this way, the abundance, range and distribution of functional traits have an influence on ecosystem functioning (*sensu* functional diversity; Díaz and Cabido 2001; McGill et al. 2006; de Bello et al. 2010) and, in turn, respond to environmental filters (Keddy 1992; Díaz et al. 2007). A functional trait is understood as any biological characteristic, be it morphological, biochemical, physiological, structural, phenological or behavioral, that can be measured at the individual level and affects its reproductive performance (*sensu* fitness; Cadotte et al. 2011; Luck et al. 2012). Functional traits can be related to ecosystem processes such as stability, resilience, biological interactions and habitat modification (Hooper et al. 2005; Villéger et al. 2010). For this reason, the addition or loss of species can have a differential impact on ecosystems (Tilman et al. 1997; Díaz and Cabido 2001; Petchey and Gaston 2002; de Bello et al. 2010) since some species may be key while others are considered redundant, in terms of a particular ecosystem process (Díaz and Cabido 2001). One way to evaluate the functional diversity of a community is to separate the species into discrete functional groups, understood as a set of species that exploit the same type of resources and exhibit similar responses to the environment (Blaum et al. 2011; Luck et al. 2012). On the other hand, functional diversity can be measured on a continuous scale such as the distribution of species in the functional niche space (Tilman 2001; Mason et al. 2005; Villéger et al. 2008; Laliberté and Legendre 2010). Study of functional diversity through different metrics has become key to understanding changes in biodiversity, the assembly mechanisms of communities and ecosystem processes as well as the services offered (Chapin et al. 2000; Duffy et al. 2007; Violle et al. 2007; Schleuter 2010; Mason and de Bello, 2013).

There are an increasing number of studies of functional diversity in vertebrates (Gómez and Moreno 2017); however, few evaluate the rules of assemblage (Spasojevic and Suding 2012; Córdova-Tapia et al. 2017; Lechêne et al. 2017; Carvajal-Cogollo et al. 2019) and the potential of amphibians to contribute to the understanding of the ecosystem processes (Pineda et al. 2005; Strauß et al. 2010; Tobar-Suárez 2012; Corral-Gómez 2013; Trimble and van Aarde 2014; Cortés-Gómez et al. 2015; Tsianou and Kallimanis 2016; Díaz-García et al. 2017; Lemus-Mejía 2017; Riemann et al. 2017). The capacity of amphibians to inhabit aquatic and terrestrial environments throughout their different stages of development makes them a key group in ecosystems (Whiles et al. 2006). On one hand, during their larval stage, they control algal growth and participate in the

bioturbation of water, while on the other, they are responsible for a considerable part of the energetic flow in aquatic and terrestrial ecosystems due to the biotic interactions of depredation and competition during their adult stage (Whiles et al. 2006; Stuart et al. 2008; Cortés-Gómez et al. 2015). Amphibians constitute an excellent model for the study of functional diversity because they are: i) organisms of low mobility, ii) the most abundant vertebrates in tropical ecosystems, and iii) particularly susceptible to environmental changes and are therefore valuable bioindicators of environmental quality (Waddle 2006; Whiles et al. 2006; Campos et al. 2017). Thus, amphibians can be an important tool for monitoring of landscape quality in little-changed environments (Hopkins 2007; Siqueira et al. 2014; Campos et al. 2017; Hernández-Ordóñez et al. 2019).

Studies of the rules of assemblage of biological communities in conserved environments serve as ecological references for the evaluation of transformed landscapes (Laurila-Pant et al. 2015). However, few studies compare the association between metrics of diversity across different ecosystems (Atauri and de Lucio 2001; Morelli et al. 2018). In this sense, the region of Cabo Corrientes in western Mexico is an ideal location for the study of amphibian communities in little-changed environments since it hosts ecosystems with a wide diversity of species and is recognized for its biological potential as a terrestrial priority zone for research and conservation (Arriaga et al. 2000; Ceballos et al. 2010), particularly as a site of high priority for conservation of amphibians (Ochoa-Ochoa et al. 2011). In Mexico, the rules of the assemblage of amphibian communities in contrasting ecosystems have not been studied with a focus on functional diversity. In this study, we characterized the amphibian community in the Cabo Corrientes region based on the taxonomic diversity, the relationship between the structure of community and changes in environmental variables, the calculation of functional diversity indices and the formation of functional groups. We analyzed functional traits of the species related to reproduction, trophic flow and habitat use, in order to: i) evaluate changes in functional diversity between ecosystems (tropical dry forest and pine-oak forest) and seasons (wet and dry), and ii) determine functional redundancy by defining functional groups. We hypothesized that environmental filters predominate as a structuring mechanism for the amphibian community in the tropical dry forest, promoting greater functional redundancy due to the seasonal conditions of drought, while limiting similarity acts in the pine-oak forest, permitting a greater diversification of functions and compatible use of resources.

Materials and methods

Study area

The municipality of Cabo Corrientes (1,454 km^2) is located on the Pacific coast in the northeast of the state of Jalisco in Mexico. The region is divided into two contrasting environments: the coastal zones and mountainous zones (Fig. 1). From West to East, the climate changes from warm sub-humid in the coastal region to semi-warm semi-humid in the mountainous region along a marked altitudinal gradient that ranges from 0 to 1920 m.a.s.l. Due to this gradient, the temperature of the region changes dramatically from a maximum of 36° C to a minimum of 13.3 °C, presenting a mean annual temperature of 24.6° C. Most of the territory is occupied by natural coverage (53.4% tropical dry forest and 37.4% mixed pine-oak forests) and, in a much lower proportion, areas of cultivation and human settlement (2.8 and 0.2%, respectively) (IIEG 2018). The mountainous zones in the eastern part present pine-oak forests, an ecosystem that is widespread in the mountains of Jalisco (Sierra Madre Occidental, Sierra Madre del Sur and the Transversal Neovolcanic Axis). In these forests, the trees measure between 8 and 25 m and mean annual precipitation ranges from 600 to 1000 mm, distributed over a period of 6 to 7 months, although this can vary and reach up to 2,882 mm in some regions of Mexico (Rzedowski 2006; Gómez-Tagle et al. 2015). In the western part, plant cover is dominated mainly by tropical dry forests, an ecosystem that is found throughout the Pacific coast and one that is characterized by its marked seasonality, with tree species that lose their leaves during the dry season. The trees measure between 8 and 12 m and mean annual precipitation ranges from 600 to 1200 mm, with 5 to 8 consecutive dry months (Trejo and Dirzo 2000; Rzedowski 2006) (Fig. 2).

The study was conducted in four localities: Mayto and Naranjos in the tropical dry forest coverage (20°14.55′–20°17.94′N and 105°33.49′–105°36.45′W) and Cuale and General in the pine-oak forest (20°21.60′–20°21.58′N and 05°17.54′–105°14.20′W) (Fig. 1). Plots were distributed from 30 to 105 m.a.s.l. in the tropical dry forest, and from 934 to 1151 m.a.s.l. in the pine-oak forest. Each vegetation type contains a water body; in the case of the tropical dry forest, this was found in the locality of Naranjos at a minimum distance of 0 m and maximum of 4 km from the sampling plots, while the water body in the pine-oak forest was found in the locality of Cuale at a minimum of 0 m and a maximum of 2 km from the sampling plots. In both ecosystems, distance to the edge of anthropogenic coverages (15 and 18.5 km for the tropical dry forest and

pine-oak forest, respectively) or highways (27 and 6 km for the tropical dry forest and pine-oak forest, respectively) was controlled in the sampling design in order to avoid possible edge effects on amphibian abundance (*sensu* Schneider-Maunoury et al. 2016) or on the environmental and plant structural gradients (*sensu* Laurance et al. 2002; Broadbent et al. 2008).

Sampling of amphibians

Two sampling trips were conducted in June and September 2017 to cover both the dry and wet seasons, respectively. In each ecosystem, 24 sampling plots each of 400 m^2 (20 x 20 m) were established at a distance of 250 m apart to avoid spatial pseudoreplication through migration between populations and to guarantee sample independence (Lips et al. 2001). In total, 48 sampling plots were delimited, representing a geographic area of 19,200 m^2. Each plot was sampled randomly during the day (7:00 to 12:00 hrs) and at night (19:00 to 24:00 hrs) by four people within a period of 15 minutes. The sampling effort, measured in time/person/site in each season, was 96 effective sampling hours. During the entire study, 192 sampling hours were accumulated between the two sampling trees. In each of the plots, visual inspections were conducted with manual capture, searching in typical amphibian microhabitats such as pools, galleries, vegetation, trunks and rocks (Crump and Scott 1994; Lips et al. 2001). Each captured individual was identified to species and morphometric measurements taken, along with information regarding the microhabitat in which it was found. All of the organisms were subsequently released in the same microhabitat in which they were originally collected.

Environmental variables

Five environmental variables were measured during each visit to the sampling plots: (1) mean elevation, which was determined with a GPS (this was only measured once since it does not vary temporally); (2) canopy coverage, measured through analysis of digital photographs (taken on clear bright days at a height of 1.50 m above ground level) using the software Image J and following the method proposed by Korhonen et al. (2006); and (3) environmental temperature, measured using a thermometer and (4) relative humidity, measured using a hygrometer.

Data analysis

Diversity of amphibian species

We evaluated the completeness of the inventory in both ecosystems and during both seasons to determine the magnitude of the variation in observed richness compared to the richness estimators Chao1 and Bootstrap, as well as to validate subsequent comparisons (Gotelli and Colwell 2011; Moreno et al. 2011; Chao and Jost 2012). We then calculated the three dimensions of diversity with the Hill numbers: species richness as the value of the estimator Chao1 ($q=0$) (Chao 1984), the diversity and evenness of species with the exponential of the index of entropy of Shannon ($q=1$) and the diversity of the inverse of Simpson ($q=2$) (Jost 2006). For each measurement of diversity, confidence intervals (CI) were calculated at 95% to determine whether there were significant differences between seasons and ecosystems (when the CI did not overlap, this implied the existence of significant differences. These analyses were conducted with the package iNEXT of the program R version 2.0.17 (Hsieh et al. 2016).

The composition and structure of the amphibian communities were compared between ecosystems and seasons using a range-abundance curve that considered the proportion of the number of individuals recorded for each species on a logarithmic scale (log10) (Feinsinger 2001; Jost 2010). This analysis was conducted with the package BiodiversityR of the program R Studio (Kindt 2019). Differences in the amphibian community structure between ecosystems and seasons were analyzed using a permutational multivariate analysis of variance (PERMANOVA) based on a Bray-Curtis similarity matrix with the partial sum of squares (type III). The experimental design had two factors: ecosystems (fixed), with two levels (tropical dry forest, pine-oak forest) and seasons (fixed), with two levels (wet, dry). The factors and their interactions were analyzed by applying an *a posteriori* paired comparison with PERMANOVA t-statistic and 9,999 permutations. These analyses were conducted with the software PRIMER 7.0.13 (Clarke et al. 2015).

Relationship between the amphibian community and the environmental variables

We identified the best-fitting model to the relationship between the structure of the amphibian community and the environmental variables and vegetation structure through a distance-based linear model (DistLM), applying the Akaike Information Criterion for small samples (AICc). Through a subsequent analysis of ordination, we

visualized the best-fitting model with a distance-based analysis of redundancy (dbRDA). These analyses were conducted with the software PRIMER v7.0.13 (Clarke et al. 2015).

Functional diversity of amphibians

In order to analyze the functional diversity, we selected eleven functional traits related to amphibian reproduction, trophic flow and habitat: reproductive mode, mouth width, eye diameter, period of activity, weight, preferred microhabitat, length of posterior extremity, interdigital membranes, disc terminals, skin type and dorsal pattern, from consultation of specialized literature (Table 1; Pineda et al. 2005; Tobar-Suárez 2012; Corral-Gómez 2013; Córdova-Tapia and Zambrano 2016; Cortés-Gómez et al. 2016; Tsianou and Kallimanis 2016; Díaz-García et al. 2017; Lemus-Mejía 2017; Riemann et al. 2017). The functional characterization was conducted with a maximum of 20 randomly selected adult individuals of each species, which were measured and then released in the same microhabitat in which they were originally collected.

We calculated the functional diversity between ecosystems and seasons on a continuous scale using three indices proposed by Villéger et al. (2008): 1) functional richness (FRic), which represents the quantity of functional space filled by the community, where low functional richness implies that some available resources are not being exploited, 2) functional evenness (FEve), which describes the distribution of abundances in a functional space of traits, where low functional evenness indicates that some parts of the functional niche are being underutilized, and 3) functional divergence (FDiv), which is a measure of functional similarity among the dominant species of a community (Mason et al. 2005; Córdova-Tapia and Zambrano 2015). These multitrait indices are independent of each other and provide complementary information in terms of the functional diversity of the species (Mouchet et al. 2010; Villeger et al. 2010). Subsequently, we searched for significant differences between the results for ecosystems and season with the non-parametric Kruskal-Wallis test. These analyses were conducted with the packages "FD" and "vegan", versions 1.0-12 and 2.5-4 of R Studio, respectively (Laliberté et al. 2015; Oksanen et al. 2019).

Also, we classified the species into discrete groups in terms of their functional similarities according to traits related to reproduction, trophic flow and habitat use, to obtain a broad and complementary characterization of the niche partition (Table 1) (Díaz and Cabido 2001; Villéger et al. 2010). Traits with categorical values were converted to dummy variables and, together with the traits with continuous values,

similarity among species was calculated with modified Gower distances, since it allows to work with categorical and continuous data together (Pla et al. 2012). For the classification of the functional groups, we constructed a regression and classification tree (LINKTREE) of the value of the functional traits for the amphibian species along a B% scale that calculates the mean dissimilarity between groups for each binary division (Clarke et al. 2008). The functional grouping was validated statistically through a similarity profile routine (SIMPROF), conducted with 9,999 permutations between the values of the traits per species. This allowed detection, with the *Pi* statistic, of the degree of deviation of the observed profile relative to the null distribution of the permuted profiles (Clarke et al. 2008). These analyses were conducted with the software PRIMER 7.0.13 (Clarke et al. 2015).

To compare the richness, diversity and evenness of functional groups between ecosystems and seasons, we applied the indices of taxonomic diversity (Schleuter et al. 2010). The richness of functional groups (FG-richness) represents the number of functional groups, the diversity of functional groups (FG-diversity) was estimated based on the exponential index of Shannon and the evenness of functional groups (FG-evenness) was evaluated using the Pielou´s index (Morin 2011). A Kruskal-Wallis test was subsequently conducted to examine differences in the indices of taxonomic diversity between ecosystems and seasons. Finally, we applied a *post hoc* comparison by pairs, utilizing the Tukey and Kramer (Nemenyi) test for independent samples. These analyses were conducted with the packages "vegan" and "PMCMR" of R Studio (Pohlert 2018; Oksanen 2019).

Results

Diversity of species of amphibians

During the sampling, 320 individuals of 16 species, 12 genera and six families were recorded. The tropical dry forest during the wet season presented the highest number of records (DFw = 140), followed by the pine-oak forest during the wet (TFw = 91) and dry (TFd = 89) seasons, while the tropical dry forest during the dry season presented no records (DFd = 0). No species were found across all of the ecosystems and seasons. The species with the highest number of records was *Eleutherodactylus modestus* (N = 91), while the species *Rhinella horribilis* only presented one record throughout the entire sampling (N = 1) (Table 2).

The completeness of inventory for ecosystems and seasons was 100% in all cases according to Chao1, and greater than 84% according to Bootstrap (DFw = 84.98%, TFd = 95.82%, TFw = 95.15%). We found the highest species richness in the tropical dry forest during the wet season (q0 = 12), followed by the pine-oak forest during the dry (q0 = 11) and wet (q0 = 10) seasons, while no species were found in the tropical dry forest during the dry season (q0 = 0). As a result, the diversity of species, expressed in the number of common and dominant species, was significantly lower in the tropical dry forest during the wet season (q1 = 4.13, q2 = 2.53) than in the pine-oak forest in the wet (q1= 8.32, q2 = 7.12) and dry (q1 = 7.82, q2 = 5.54) seasons (Fig. 3).

Species abundance presented wide variation between ecosystems and seasons. The species were homogeneously distributed in the pine-oak forest during both seasons, while extreme values were found in the abundance of species in the tropical dry forest during the wet season. In the tropical dry forest during the wet season, the species *E. modestus* was the most dominant and presented the highest abundance of the entire sampling. In contrast, the pine-oak forest was dominated by the species *Tlalocohyla smithii* and *Lithobates neovolcanicus* during the dry and wet seasons, respectively. The least abundant species of the entire sampling were *Incilius occidentalis* and *R. horribilis* in the tropical dry forest during the wet season, *Lithobates forreri* in the pine-oak forest in the dry season and, finally, *Incilius mazatlanensis* in the pine-oak forest during the wet season (Fig. 4).

The structure of the amphibian community presented significant differences between ecosystems (tropical dry forest and pine-oak forest: F = 10.37, p-perm = 0.0001) and seasons (wet and dry: F = 4.50, p-perm = 0.0007). Similarly, the *post hoc* or *pairwise* analysis between seasons showed that the differences were significant between ecosystems during both the dry and wet seasons (t = 3.15, p-perm = 0.0001 and t = 2.81, p-perm = 0.0001, respectively). The *post hoc* or *pairwise* analysis between ecosystems showed significant differences between seasons in both the tropical dry forest and pine-oak forest (t = 3.83, p-perm = 0.0001 and t = 1.51, p-perm = 0.0288, respectively).

Relationship between amphibian diversity and environmental variables

The best-fitted model explained, in the first two axes of the ordination of the dbRDA, 91.3% of the variation in the structure of the amphibian community throughout the entire sampling (AICc = 684.32, R^2 = 0.21). The ordination showed differences in the structure of the amphibian community across the sampling plots

between ecosystems and seasons (Fig. 7). Of the four environmental variables measured, three were significant to the best-fitted model: ambient temperature (pseudo-F = 2.4451, p = 0.0288), relative humidity (pseudo-F = 4.7511, p = 0.0007) and elevation (pseudo-F = 9.4244, p = 0.0001). The variable of canopy coverage was very close to the limit of significance (pseudo-F = 2.1101, p = 0.0508) (Fig. 5).

Functional diversity of amphibians

The indices of functional diversity showed no significant differences between seasons and ecosystems: functional richness (X^2 = 0.67, *p* = 0.72), functional evenness (X^2 = 0.58, *p* = 0.75) and functional divergence (X^2 = 2.52, *p* = 0.28). The tropical dry forest during the wet season presented the lowest values of richness and functional divergence, the pine-oak forest during the wet season presented the highest functional evenness, while the highest values of richness and functional divergence were presented by the pine-oak forest during the dry season (Fig. 6).

The tree of regression and classification (LINKTREE) enabled classification of the species into seven distinct ecological groups, of which four present greater functional redundancy and two are represented by a single species. (Fig. 7). The binary divisions revealed important values of functional traits that together explained the formation of the groups. The first and most important division, with 88% of explanation (R = 0.72), separated the species by arboreal mode of life and skin type (smooth), forming group G (*Agalychnis dacnicolor* and *Smilisca baudinii*). The next binary division, at 64% (R = 0.66), by skin type (smooth) and dorsal pattern (reticular), did not form groups but rather two large divisions: 47% (R = 0.89) separated the species forming the groups F (*L. forreri*, *L. neovolcanicus* and *Lithobates pustulosus*) by semiaquatic mode of life, diurnal-nocturnal activity, presence of interdigital membranes and greater energetic contribution to the trophic networks, and E (*T. smithii*, *Exerodonta smaragdina* and *Hypopachus variolosus*) by exclusively nocturnal activity; and 40% (R = 0.86) by pustulated skin type, from which was divided at 28% (R = 1) group D (*I. occientalis*, *I. mazatlanensis* and *R. horribilis*) for their pattern of exclusively nocturnal activity and higher corporal measurements (mouth width, eye diameter, body weight and body size) and group C (*Dryophytes arenicolor*) by the presence of terminal discs and diurnal-nocturnal pattern of activity. Beyond the division at 40% related to the presence of reticular skin, a new division arose at 14% (R = 1) separating group B (*Craugastor pygmaeus*, *Craugastor occidentalis* and *E. modestus*) by terrestrial mode of life and the fact that

these species do not deposit their eggs in water, and group A (*Leptodactylus melanonotus*) by aquatic mode of life and eggs with indirect development deposited in the water (Fig. 7).

Six groups were formed in the tropical dry forest during the wet season (A, B, D, E, F and G), and six in the pine-oak forest during the dry and wet seasons (B, C, D, E, F and G). Even though the ecosystems and seasons presented the same quantity of functional groups (apart from the tropical dry forest during the dry season, which presented no records), we found differences in the formation and distribution of functional groups. During the wet season, the tropical dry forest was dominated by group B (86 individuals), the species of which were terrestrial frogs of small size, of direct development, with eggs that are not deposited in the water, and with diurnal and nocturnal habits and tubercular skin (Eleutherodactylidae). In the pine-oak forest, the most dominant functional groups were group E (35 individuals) during the dry season, formed by species of medium size, nocturnal habits, indirect development and eggs deposited in the water (*T. smithii, E. smaragdina* and *H. variolosus*) and group F (46 individuals) during the wet season, formed by semiaquatic frogs of large size with eggs deposited in the water, smooth skin and interdigital membranes for swimming (Ranidae) (Fig. 8). Finally, the tropical dry forest during the wet season presented a richness and diversity of functional groups that were significantly lower relative to both seasons in the pine-oak forest (H = 8.75, p = 0.01; H = 8.77, p = 0.01, respectively) (Table 3).

Discussion

In this study, we showed that associations between metrics of diversity in the amphibian communities are not constant across contrasting ecosystems since changes in diversity are evident in the richness and composition of species, as well as the distribution of functional groups. Even though species richness was highest in the tropical dry forest during the wet season, the richness and diversity of functional groups were significantly lower than in the pine-oak forest in both seasons. Our results suggest that the seasonal drought in the tropical dry forest could be acting as an environmental filter for the amphibian community, promoting the dominance of similar functional traits among the species that enable them to tolerate the conditions imposed upon them by the environment. At the same time, in the pine-oak forest, limiting similarity could be the mechanism that is acting on the amphibian community in the face of the relatively more stable hydric conditions that promote greater diversification of functions among the species and compatible use of resources. However, further studies

are necessary that consider null models in order to determine the rules of assemblage that operate in these ecosystems.

The functional traits reveal the effect and the response of the species to environmental factors (Rosenfeld 2002; Violle et al. 2007) and their selection is the element that could influence studies of functional diversity to the highest degree (Petchey and Gaston 2006; Tsianou and Kallimanis 2015). Given that different processes may be affected by different species or functional groups, it is essential to consider various traits simultaneously, since different species could be redundant in some functional aspect while differing in others (Tilman et al. 1997; Rosenfeld 2002; Tsianou and Kallimanis 2015). To describe the most important aspects of the life history of the amphibians, we recognized traits related to reproduction (reproductive performance), trophic flow (position in the food web and antipredator strategies) and habitat use (habits, dependence on water and use of time and space) (Table 1). For example, the reproductive mode reflects the reproductive strategies of the species and the use of the habitat, for which reason it has been used by different authors as a critical aspect in the functional description of amphibian life history (Pineda et al. 2005; Tobar-Suárez 2012; Díaz-García et al. 2017). Since there is no detailed information regarding the diet of all of the species of the region, mouth width was used as a trait that indicates the size of prey items consumed by the amphibians (Corral-Gómez 2013; Cortés-Gómez et al. 2016; Lemus-Mejía 2017). Other traits, such as the presence of terminal discs, fingers terminating in a point and interdigital membranes reflect modes of life (arboreal, terrestrial and semiaquatic, respectively) and have been proposed for the functional study of this taxonomic group (Cortés-Gómez et al. 2016; Riemann et al. 2017). Finally, eye diameter was incorporated as a new trait for the functional analysis of the amphibians due to the influence of this parameter on the detection of prey (Córdova-Tapia and Zambrano 2016).

The structure of the amphibian communities in the contrasting ecosystems evaluated showed that 62.5% of the species that inhabit the tropical dry forest are also found in the pine-oak forest, while 18.75% of the species of the tropical dry forest (in the wet season) and 25% of the species of the pine-oak forest (6.25 and 6.25% in the wet and dry seasons, respectively) were recorded exclusively in their respective ecosystems. Contrary to expectation and even though the community in the pine-oak forest presented greater evenness, the amphibian abundance of was lower in this ecosystem, possibly indicating that its capacity to maintain large populations is limited, despite the relatively more stable hydric conditions (Fig. 4). For example, in the pine-

oak forest during the wet season, the most dominant (*L. neovolcanicus*) and the rarest (*I. mazatlanensis*) species presented the lowest difference of abundances of the entire sampling (22 and 2, respectively). In the dry season, the difference between the most dominant (*T. smithii*) and the rarest (*L. forreri*) species was similar (32 and 3, respectively), while in the tropical dry forest, the dominant (*E. modestus*) and rare (*I. occidentalis* and *R. horribilis*) species presented a greater difference in abundance (84 and 1, respectively) (Table 2). This may be due resources are shared more equally among the species in the pine-oak forest compared to the tropical dry forest.

We evaluated the effect of the microhabitat variables on the presence of species and demonstrated, in the contrasting ecosystems evaluated, that the composition of the amphibian community is mainly affected by changes in the environmental variables of elevation, temperature and relative humidity, as has been reported for other amphibian communities (Fig. 5; Pineda et al. 2005; Strauß et al. 2010; Santos-Barrera and Urbina-Cardona 2011; Tobar-Suárez 2012; Cortés-Gómez et al. 2013; Trimble and van Aarde 2014). The results suggests that the dominance of generalist species, such as *E. modestus* in the tropical dry forest, is due to the fact that these species are adapted to higher levels of temperature and humidity because of their indirect development and tubercular skin, which helps them to avoid desiccation and thus allows them to present diurnal and nocturnal activity even when faced with environmental conditions and a vegetation structure that changes dramatically over the course of the year. The pine-oak forest was dominated by specialist species such as *L. neovolcanicus* and *T. smithii*, which require stable hydric conditions and constant vegetation structure throughout the year in order to complete their life cycle, since these species are associated with environmental conditions that present little change (Fig. 4; Cabrera-Guzmán and Reynoso 2002; Klaus and Noss 2016).

The tropical dry forest is characterized by the presentation of extreme values of diversity (taxonomic and functional), given its condition of seasonal hydric stress. No records of amphibians were obtained during the dry season but, during the wet season, the highest species richness of the entire study was obtained, although their functional richness remained below that of both seasons in the pine-oak forest (Fig. 3). This indicates that, despite their large species richness, the species tend to resemble each other in terms of their functional traits, for which reason some of the potentially available ecological niches remained unoccupied by the species (Mason et al. 2005; Villéger et al. 2010; Córdova-Tapia and Zambrano 2015). The functional evenness of the tropical dry forest also presented the lowest values of the comparison, indicating that some niches occupied by

the species may be underutilized. As a consequence, this ecosystem could be associated with a high potential for invasion by exotic and translocated species with low resilience, compared to the pine-oak forest (Mason et al. 2005; Mouchet et al. 2010; Morelli et al. 2018). Finally, while the values are scattered, the highest functional divergence was found in the pine-oak forest during the dry season, reflecting the fact that the dominant species in this ecosystem differ among themselves according to the functions evaluated and could thus present lower competition and a more efficient use of resources through niche complementarity (Mason et al. 2005) (Fig. 6).

The generation of functional groups through systems of classification allows us to understand the level of niche partitioning within a community and is useful for determining functional redundancy, which is not necessarily linked to taxonomic identity (Rosenfeld 2002; Violle et al. 2007). For example, groups B, D, F and G were clustered into taxonomic families (Eleutherodactylidae, Bufonidae, Ranidae and Hylidae, respectively), while group E was formed by species of two different families (Hylidae and Microhylidae). In this way, our results show that the functions of the species are independent of their phylogeny, although those with similar traits frequently tend to be grouped by family or genus (Bellwood et al. 2002). The formation of functional groups showed greater redundancy in groups B (*C. occidentalis*, *C. pygmaeus* and *E. modestus*), D (*I. occidentalis*, *I. mazatlanensis* and *R. horribilis*), E (*H. variolosus*, *T. smithii* and *E. smaragdina*) and F (*L. forreri*, *L. neovolcanicus* and *L. pustulosus*), each formed by three species. Functional redundancy in local communities could indicate stability in the sense that the loss of one species could be compensated by another of similar function (Tilman et al. 1997). On the other hand, the formation of functional groups allows us to identify key species in the ecosystems. (Rosenfeld 2002); for example, the groups A (*L. melanonotus*) and C (*D. arenicolor*) were each formed by a single species, which could be fulfilling a unique ecological function according to the traits evaluated and therefore the loss of one of these species would represent the loss of a unique function in the tropical dry forest and pine-oak forest, respectively (Fig. 7).

The identity, abundance and distribution of the functional groups of amphibians between contrasting seasons and ecosystems presented a differential response (Fig. 8). The tropical dry forest was dominated by one group (B), comprised by frogs of terrestrial habits that play an important role in the maintenance of the trophic networks as biological controllers of small insects by day and night. The pine-oak forest during the dry season was dominated by one group (E) of frogs of nocturnal habits that form an important part of predator and prey interactions, mainly in micro-habitats on vegetation. In the pine-oak forest during the wet season, one group (F)

dominated, which comprised semi-aquatic frogs that have a considerable effect on the water bodies as controllers of algae and bioturbators during their larval stage, as well as presenting an important participation in the trophic networks of the water bodies by being predators and prey of vertebrates such as fish, reptiles, birds, amphibians and even mammals. Variation in the abundances of species could reflect different habitat needs, since some groups are stricter than others, in terms of micro-habitat requirements (Fig. 8; Duellman and Trueb 1986; Pough 2007).

Environmental filters restrict the abundance and occurrence of species, promoting trait similarity among the dominant species and allowing them to tolerate the conditions imposed by the environment (Hooper et al. 2005; Díaz et al. 2007; Mason et al. 2008). The tropical dry forest presented a lower richness and diversity of functional groups compared to the pine-oak forest, which could indicate that there is a lower diversification of functions, resources and micro-habitats in this ecosystem as a result of the effect of environmental filters. In this sense, our results suggest that environmental conditions of the tropical dry forest could be acting as environmental filters for the amphibian community, with a considerable effect on the functional group diversity (Table 3). In contrast, limiting similarity could be operating in the pine-oak forest in both seasons, promoting the occupation of different functional niches by the species in a relatively more stable ecosystem in hydric terms (Fig. 8; Tilman 1982; Hooper et al. 2005; Mason et al. 2007). However, these results must be treated with some caution since the results depend on the chosen trait type and the particular functional indices analyzed (Villéger et al. 2010; Mason and de Bello 2013).

The relationship between the classical approaches of diversity and the functioning of ecosystems remains unclear (Córdova-Tapia and Zambrano, 2015); however, studies related to functional diversity allow us to come close to answering certain questions. For example, what happens in communities in which the taxonomic and functional diversity do not concur? Are these values essentially related? What is the influence of the rules of assemblage on the different manifestation of diversity? (Villéger et al. 2012; Mason et al. 2013). Many studies have demonstrated dissimilar associations among the patterns of diversity observed (e.g., taxonomic, functional and phylogenetic diversity) (Farias and Jaksic 2009; Campos et al. 2017; Morelli et al. 2018). In general, there is a positive correlation between taxonomic and functional richness since it is expected that an increase in the number of species will tend to produce different functions and thus greater occupation of the niche space by the species (Morelli et al. 2018; Hernández-Ordóñez et al. 2019). However, at the same time,

this correlation decreases with an increased species number due to the effect of redundant species (Petchey and Gaston 2006). In this sense, the strength of association between these metrics is not gradual, universal or replicable, but rather depends on the community since it takes functional traits into account (Petchey and Gaston 2006; Villéger et al. 2008). For example, the tropical dry forest during the wet season presented the highest observed and estimated richness of the study (Fig. 3; Sobs = 12 and q = 12, respectively), while the index of functional richness as well as the richness and diversity of functional groups, was higher in the pine-oak forest during both seasons (Fig. 3, 6; Table 3). In this sense, our study shows that the relationship between taxonomic and functional richness is not linear between the contrasting ecosystems analyzed. For this reason, recent studies have explored the importance of conducting separate analyses of each component of diversity to describe different aspects of a given community or to calculate different functions of the ecosystem (Petchey and Gaston 2006; Morelli et al. 2018).

While associations among patterns of diversity are often assumed to be linear and analysis attempted at regional scales to model biodiversity patterns for conservation purposes, our results highlight the importance of considering the essential functional differences of the species related to the ecosystem type they inhabit. It is therefore important to consider conserved ecosystems as a model for future studies in which the effect of the ecosystems and their contrast on the conservation of amphibians can be evaluated, as well as the functioning of the species and their relationship with ecosystem processes. One future challenge will be to determine how environmental conditions influence the components of functional diversity and how these conditions interact with the ecosystem processes at different spatiotemporal scales (Loreau et al. 2002; Hooper et al. 2005; Chapin et al. 2010; Brose and Hillebrand 2016). In this way, relationships among the structure of the communities, diversity and functioning of the ecosystems, as well as their differences across contrasting ecosystems, must be fully understood in order to create integral conservation strategies that consider the functional role of the species in order to maintain resilient and resistant ecosystems (Díaz et al. 2006; Chapin et al. 2010; Midgley 2012; Tilman et al. 2014; Newbold 2015).

Conservation of amphibians and their ecosystems

Increased anthropogenic pressures on ecosystems have led to the irreversible loss of species and their functions, due mainly to habitat transformation (Keil et al. 2015), with the amphibians representing the most threatened

group of vertebrates at the global level (Ceballos et al. 2017). In Mexico alone, their populations are decreasing at much more elevated rates (57.97%) than those of other vertebrates, such as the birds (5.01%), reptiles (14.07%) and mammals (19.35%) (Stuart et al. 2004; Frías-Alvarez et al. 2010). In this study, we recorded species that are threatened according to the IUCN Red List, including *E. modestus*, *L. neovolcanicus* and *C. pygmaeus* (IUCN Group 2018). The presence of amphibian communities can contribute to important ecosystem processes related to the maintenance of trophic networks in aquatic and terrestrial environments, processes of bioturbation of the water, control of algae in water bodies and pests in terrestrial environments, among others (Valencia-Aguilar et al. 2012). On the other hand, while the tropical dry forest hosts a large proportion of the terrestrial vertebrates and endemism in the country (33 and 31%, respectively), it remains a vulnerable ecosystem that requires considerable conservation efforts since it faces one of the highest deforestation rates both in Mexico (Trejo and Dirzo 2000; Ceballos et al. 2010) and worldwide (Janzen 1988; Elmqvist et al. 2007; Portillo-Quintero and Sánchez-Azofeifa 2010; Bianchi and Haig 2012). For all of these reasons, it is necessary to understand the ecosystems as large reservoirs of biodiversity, in which the ecological functions and services they provide are vital to protect biodiversity and with it human well-being (Naeem et al. 1999; O´Connor and Crowe 2005; Díaz et al. 2006; Cadotte et al. 2011; Ceballos et al. 2017).

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Figures captions

Fig. 1 Geographic location of the sampling sites in the municipality of Cabo Corrientes, Mexico: Naranjos, Mayto, Cuale and General. White = tropical dry forest, grey = pine-oak forest, black = other land cover types

Fig. 2 Precipitation and temperatures: maximum, minimum and mean values from the study area (records from 1981 to 2010). El Tuito (20°19´11 and 105°19´34: 600 m.a.s.l.) (left) and Tomatlán (19°56´27 and 105°14´55: 50 m.a.s.l.) (right) as representations of the closest stations that present conditions similar to those of the sampled study locations (pine-oak

forest and tropical dry forest, respectively). The arrows represent the months in which sampling was conducted. Taken and modified from Ruiz-Corral et al. (2012)

Fig. 3 Diversity of amphibian species for each ecosystem and season in Cabo Corrientes, Jalisco, Mexico. DFw tropical dry forest during the wet season, DFd tropical dry forest during the dry season, TFw pine-oak forest during the wet season and TFd pine-oak forest during the dry season. We evaluated the diversities of order 0 (q0 species richness or Chao1), order 1 (q1 number of common species or exponential of Shannon-Wiener) and order 2 (q2 number of dominant species or inverse of Simpson), as well as their 95% confidence intervals (error bars)

Fig. 4 Range-abundance curve of the amphibian species between ecosystems and seasons in Cabo Corrientes, Jalisco, Mexico. DFw tropical dry forest during the wet season, DFd tropical dry forest during the dry season, TFw pine-oak forest during the wet season and TFd pine-oak forest during the dry season. The species are represented by letters (Table 1)

Fig. 5 The dbRDA analysis of the structure of the amphibian community between seasons and ecosystems, and its association with the environmental variables and vegetation structure. The first two axes explain 48.5 and 42.8%, respectively, of the variation outside of the fitted model. The structure of the amphibian community is represented by the different points: tropical dry forest during the dry season (black triangle), pine-oak forest during the dry season (white triangle), tropical dry forest during the wet season (gray square) and pine-oak forest during the wet season (black rhombus). The direction and strength of the association between the environmental variables and the axes of ordination are represented by their orientation and length

Fig. 6 Functional richness (a), functional evenness (b) and functional divergence (c) of amphibians between seasons and ecosystems in Cabo Corrientes, Jalisco, Mexico. DFw tropical dry forest during the wet season, DFd tropical dry forest during the dry season, TFw pine-oak forest during the wet season and TFd pine-oak forest during the dry season

Fig. 7 Tree of regression classification with Gower distances of the functional traits of the amphibian community of Cabo Corrientes, Jalisco, Mexico. The dotted lines show the functional groups recognized by the SIMPROF test. *R* is a nonparametric measure of multivariate differences among functional traits. *B%* is the absolute measure of the difference of groups calculated by the mean of ranges among groups as a percentage

Fig. 8 Relative abundance of the biomass of functional groups between ecosystems and seasons. Group A (*L. melanonotus*), group B (*C. occidentalis*, *C. pygmaeus* and *E. modestus*), group C (*D. arenicolor*), group D (*I. occidentalis*, *I. mazatlanensis* and *R. horribilis*), group E (*H. variolosus*, *T. smithii* and *E. samaragdina*), group F (*L. forreri*, *L. neovolcanicus* and *L. pustulosus*) and group G (*A. dacnicolor* and *S. baudinii*)
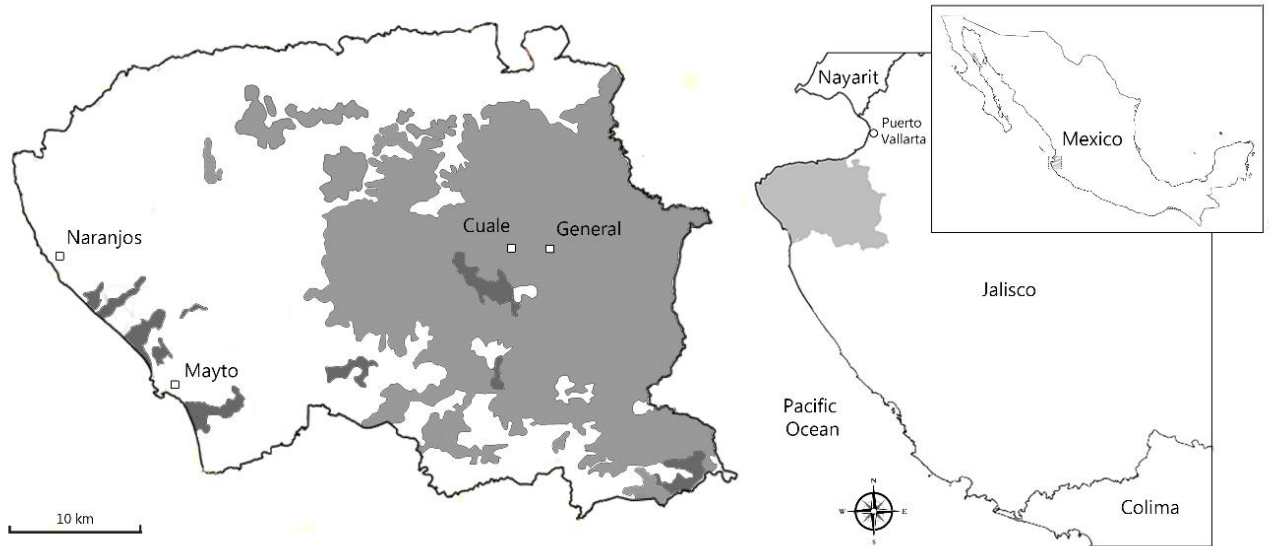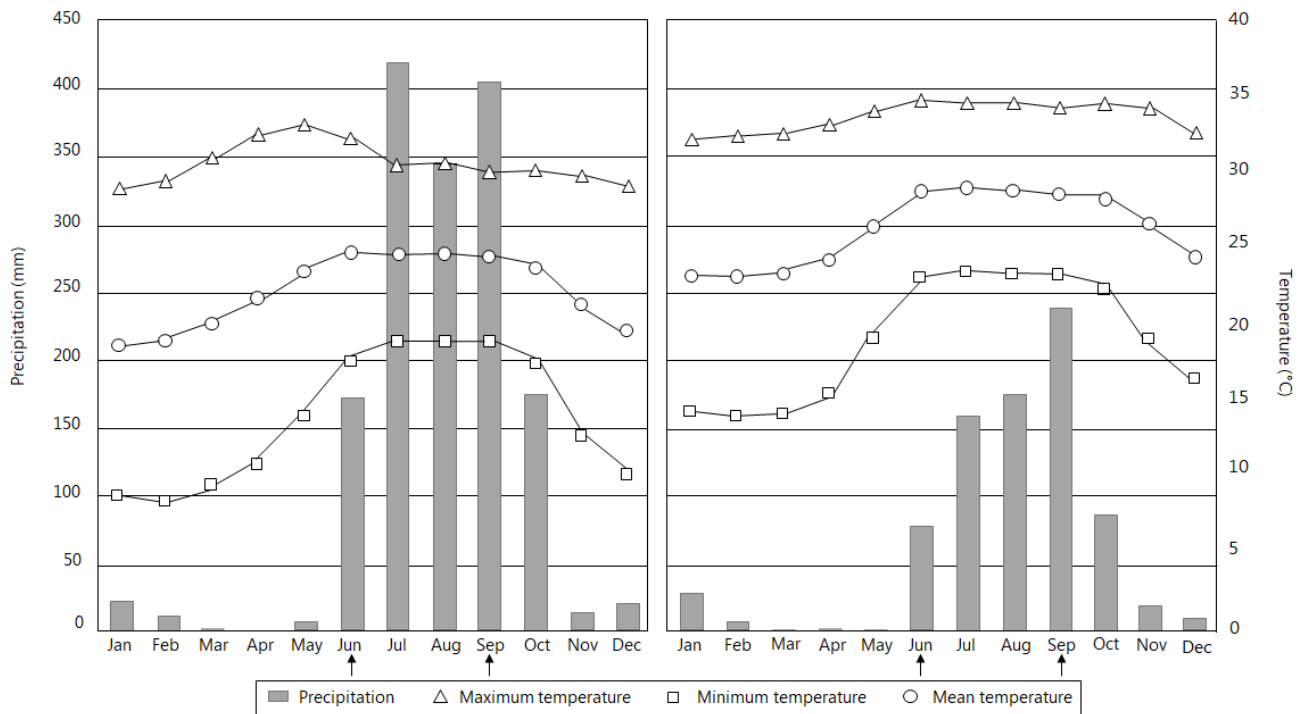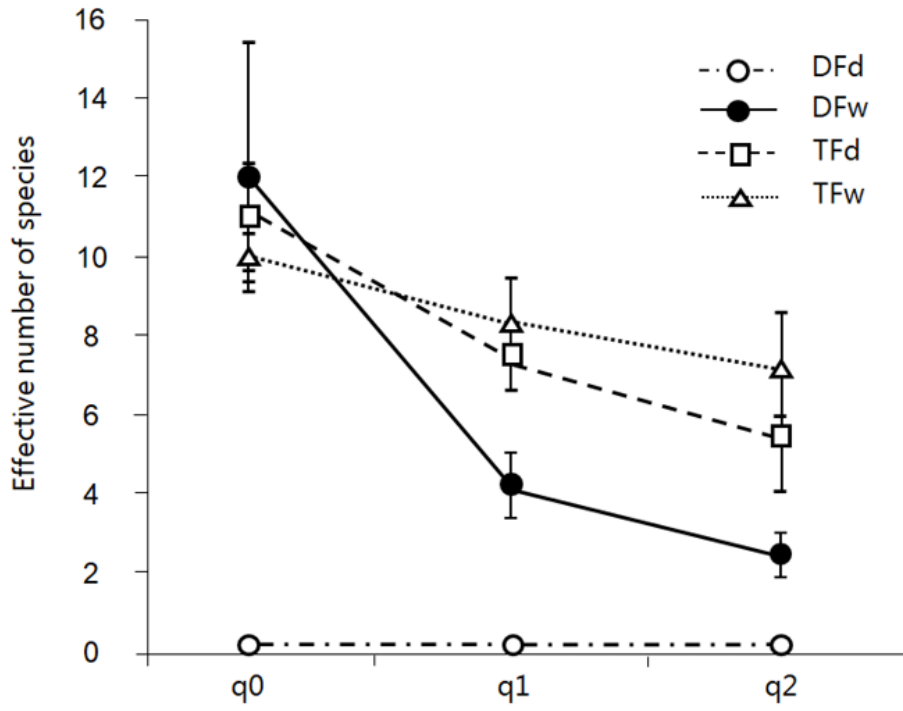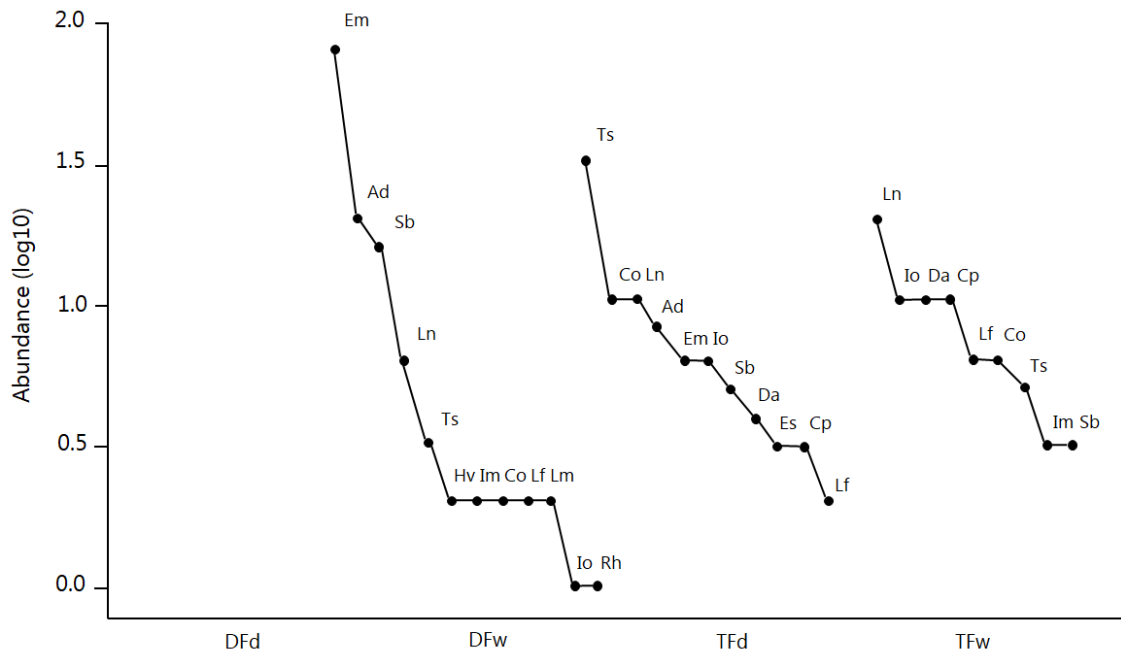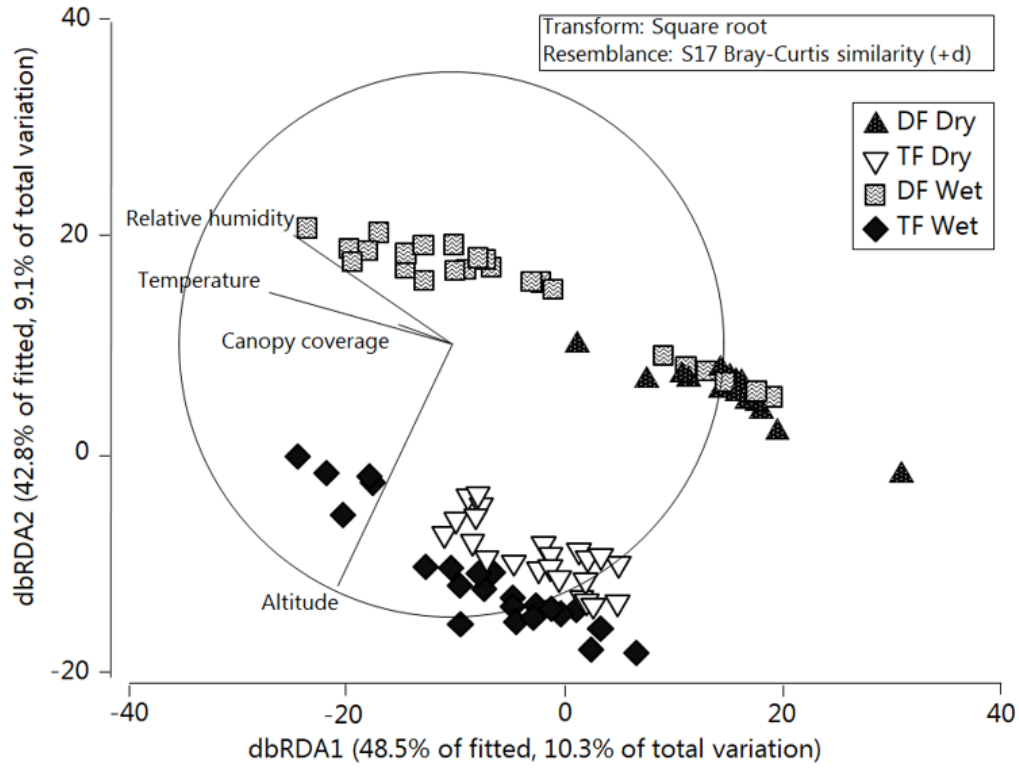
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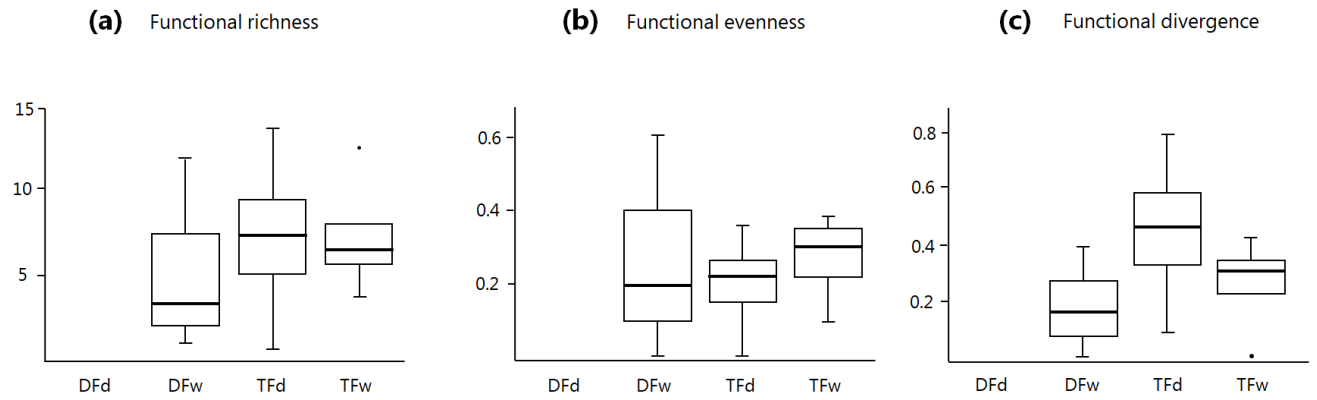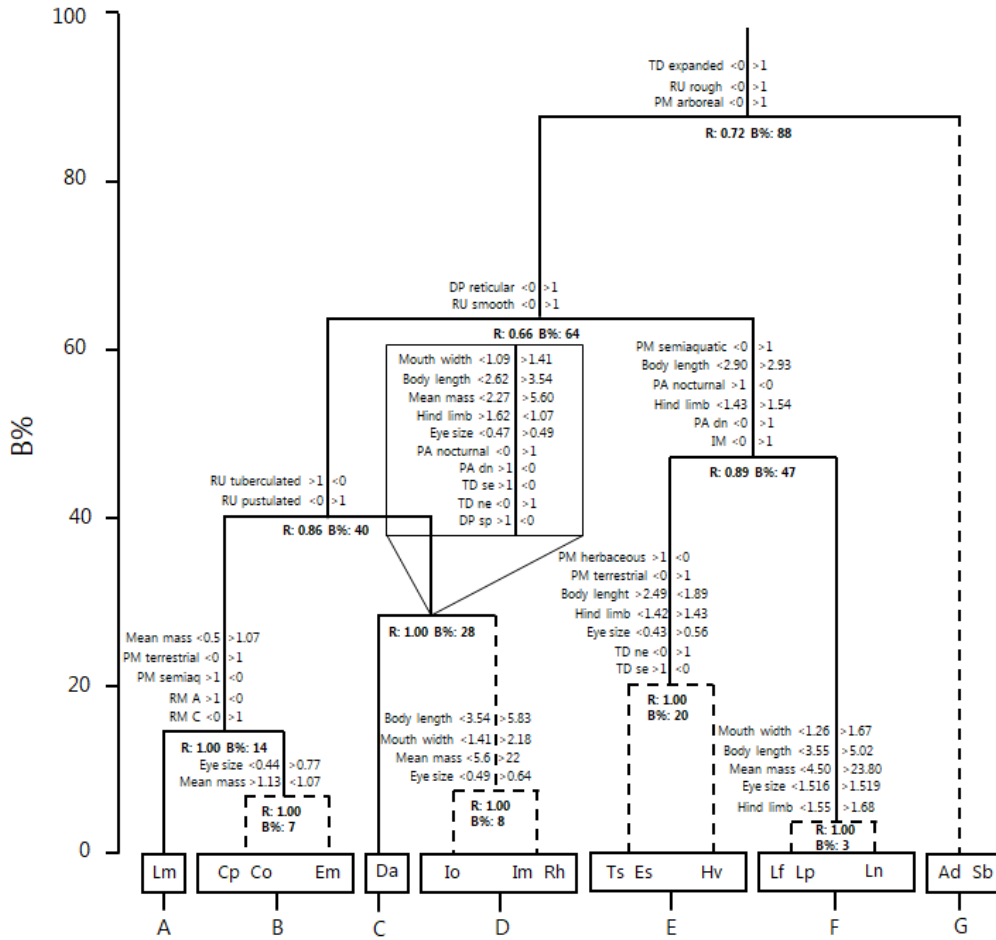Fig. 1

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Fig. 7

Fig. 8

Tables

Table 1 List of functional traits and their ecological meaning

Functional trait	Key	Description	Type of measure	Functional meaning	Reference
REPRODUCTIVE					
Reproductive mode	RM	Eggs laid in water and larvae develop in water; eggs laid in vegetation on water and larvae develop in water; eggs laid outside of the water and larvae develop within the egg	CA	Strategy and reproductive success and habitat use	1, 2, 7
TROPHIC FLOW					
Mouth width	MW	Mouth width	CO	Size of food items	3, 5, 8
Eye size	ES	Diameter of eye divided by head length	CO	Prey detection	4
Mass	MM	Mean mass	CO	Recycling of nutrients and energy flow through food webs as predator or prey	2, 5, 7, 8
Hind limb	HL	Body length divided by hind limb	CO	Predation and antidepredatory strategies	3, 5
HABITAT USE					
Period of activity	PA	Diurnal; nocturnal; diurnal-nocturnal	CA	Differential contribution of matter and energy in time	5, 8
Preferred microhabitat	PM	Arboreal; herbaceous-shrub; semiaquatic; terrestrial	CA	Differential contribution of matter and energy in time	7
Interdigital membranes	IM	Presence of interdigital membranes; ausence of interdigital membranes	CA	Swimming structures that reflect aquatic life	5
Terminal disks	TD	Not expanded; slightly expanded; expanded	CA	Climbing structures that reflect arboreal habits	9
Skin	SK	Rough; pustuated; smooth; tuberculated	CA	Resistance to drying and hydrodynamism	5
Dorsal pattern	DP	Spotted; reticular; homogeneus	CA	Differential use of space, predation and antidepredatory strategies	6

1 Pineda et al. (2005), 2 Tobar-Suárez (2012), 3 Corral-Gómez (2013), 4 Córdova-Tapia and Zambrano (2016), 5 Cortés-Gómez et al. (2016), 6 Tsianou and Kallimanis (2016), 7 Díaz-García et al. (2017), 8 Lemus-Mejía (2017), 9 Riemann et al. (2017). Type of data: CO continuous, CA categorical

Table 2 Species richness and abundance for amphibians in Cabo Corrientes, Jalisco, Mexico

Family	Species	Code	Ecosystem and season				Total
			DFw	DFd	TFw	TFd	
Bufonidae							
	Incilius mazatlanensis	Im	2	0	2	0	4
	Incilius occidentalis	Io	1	0	11	6	18
	Rhinella horribilis	Rh	1	0	0	0	1
Eleutherodactylidae							
	Craugastor occidentalis	Co	2	0	6	9	17
	Craugastor pygmaeus	Cp	0	0	9	3	12
	Eleutherodactylus modestus	Em	84	0	0	7	91
Hylidae							
	Agalychnis dacnicolor	Ad	18	0	0	8	26
	Dryophytes arenicolor	Da	0	0	9	4	13
	Exerodonta smaragdina	Es	0	0	0	3	3
	Smilisca baudinii	Sb	17	0	3	5	25
	Tlalocohyla smithii	Ts	3	0	5	32	40
Leptodactylidae							
	Leptodactylus melanonotus	Lm	2	0	0	0	2
Microhylidae							
	Hypopachus variolosus	Hv	2	0	0	0	2
Ranidae							
	Lithobates forreri	Lf	2	0	7	2	11
	Lithobates neovolcanicus	Ln	6	0	22	9	37
	Lithobates pustulosus	Lp	0	0	17	0	17
	Richness		**12**	**0**	**10**	**11**	**16**
	Abundance		**140**	**0**	**91**	**89**	**320**

DFw dry forest during the wet season, DFd dry forest during the dry season, TFw pine-oak forest during the wet season and TFd pine-oak forest during the dry season

Table 3 Diversity indices applied to functional groups between ecosystems and season. *Significant differences ($p < 0.05$)

Ecosystem and season	FG-richness	FG-diversty	FG-evenness
DFd	0	0	0
DFw	5±1*	3.35±1*	0.99±0.75
TFd	5±0	3.44±1.75	1±0.70
TFw	3±2	2.88±1.52	1±0.38

Biodiversity and Conservation

Amphibian communities in two contrasting environments: functional diversity and environmental filters

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Abstract:	Functional diversity is a tool for understanding biological communities and the influence of environmental filters on the rules of assemblage. However, few studies explore the relationships of diversity metrics across contrasting ecosystems. We evaluated the effect of ecosystems (tropical dry forest and pine-oak forest) and seasons (wet and dry) on the functional diversity and community structure of amphibians in western Mexico. Our study showed that associations between different metrics of diversity are not constant across contrasting ecosystems. The amphibian communities were related to changes in the environmental variables of elevation, temperature and relative humidity. We analyzed the functional structure of the amphibian community based on eleven traits related to reproduction, trophic flow and habitat use. Seven functional groups with distinct ecological characteristics were detected, of which, four presented functional redundancy and two were represented by a single species.

	While the tropical dry forest during the wet season showed the highest species richness, the richness and diversity of functional groups were significantly lower than in the pine-oak forest in both seasons. These results suggest that the seasonal drought in the tropical dry forest could act as an environmental filter, promoting dominance of similar functional traits among the species, while limiting similarity could be acting in the pine-oak forest, in the face of relatively stable hydric conditions, allowing a greater functional diversity. Analysis of the relationship between the community structure and ecosystem functioning is necessary to undertake conservation strategies in natural sites that allow us to protect biodiversity and thus human well-being.
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DISCUSIÓN

Las causas que explican las diferencias de diversidad de especies en las comunidades naturales constituyen uno de los problemas centrales de la ecología de comunidades (Wiens et al. 2010; Morin 2011). En este estudio mostramos que las asociaciones entre métricas de diversidad (taxonómica y funcional) en las comunidades de anfibios no son constantes a través de ecosistemas contrastantes, ya que los cambios fueron evidentes en la riqueza y composición de especies, así como en la distribución de grupos funcionales. Por ejemplo, en el bosque tropical caducifolio durante la temporada lluviosa la riqueza de especies fue la más alta, la riqueza y diversidad de grupos funcionales fue significativamente menor que en el bosque de pino-encino en las dos temporadas. Nuestros resultados sugieren que la sequía estacional en el bosque tropical caducifolio podría estar actuando como un filtro ambiental mientras que, en el bosque de pino-encino la similitud limitante podría ser el mecanismo que esté actuando sobre la comunidad de anfibios. Sin embargo, son necesarios más estudios que tomen en cuenta modelos nulos y la historia biogeográfica de las especies para determinar las reglas de ensamblaje que operan en estos ecosistemas.

La relación entre las aproximaciones clásicas de la diversidad y el funcionamiento de los ecosistemas aun no es clara. Sin embargo, se ha visto que la fuerza y el significado de las asociaciones entre la diversidad taxonómica y funcional pueden variar considerablemente según el tipo de entorno, debido a que múltiples procesos de ensamblaje pueden llevar al mismo patrón de dispersión de rasgos o el mismo proceso puede conducir a diferentes patrones de dispersión (Herben y Goldberg 2014; Córdova-Tapia y Zambrano 2015). Esta relación asimétrica entre las métricas de diversidad a menudo es tomado como un indicador de reglas de ensamblaje, por lo que es importante evaluar diversas medidas de diversidad simultáneamente para una mejor comprensión de las comunidades y los ecosistemas (Petchey y Gaston 2006; Villéger et al. 2012; Morelli et al. 2018).

El nicho funcional de una especie está influenciado no solamente por los procesos ecológicos que afecta de manera directa a través de su morfología y fisiología, sino también por sus respuestas a factores ambientales e incluso por sus atributos demográficos e interacciones entre especies (Rosenfeld 2002; Violle et al. 2007). También, el conservadurismo de nicho, entendido como la tendencia de las especies a retener rasgos ecológicos a través del tiempo, puede tener consecuencias importantes en la función de los ecosistemas (Wiens et al. 2010) pues determina qué condiciones ambientales pueden soportar los miembros de un clado (Wiens

y Donoghue 2004). De esta manera, el nicho de las especies es estudiado a través de los rasgos funcionales que revelan el efecto y la respuesta de las especies a factores ambientales (Rosenfeld 2002), siendo la conexión rasgo-ambiente sin importar las especies involucradas, la consecuencia del efecto de filtro de las condiciones ambientales (Keddy 1989; Morin 2011; Herben y Goldberg 2014). Así, cuando las especies miembros de una comunidad comparten rasgos comunes, a menudo se interpreta como el resultado del filtrado ambiental (Herben y Goldberg 2014). Este argumento se basa en el supuesto de que los valores de los rasgos están correlacionados con los nichos: cuanto más difieren las especies en algún rasgo, más probable es que ocupen un nicho diferente y, por lo tanto, puedan coexistir (MacArthur y Levins 1967; Herben y Goldberg 2014). Sin embargo, diferentes procesos pueden ser afectados por distintas especies o grupos funcionales por lo que es importante considerar distintos rasgos simultáneamente, pues diferentes especies podrían ser redundantes en algún aspecto funcional pero diferir en otros (Tilman et al. 1997; Rosenfeld 2002; Tsianou y Kallimanis 2015).

En ese sentido, los rasgos funcionales revelan el efecto y la respuesta de las especies a factores ambientales (Rosenfeld 2002; Violle et al. 2007) y su elección es el elemento que más puede influenciar los estudios de diversidad funcional (Petchey y Gaston 2006; Tsianou y Kallimanis 2015). Para describir los aspectos más relevantes de la historia de vida de los anfibios reconocimos rasgos relacionados con la reproducción (desempeño reproductivo), flujo trófico (posición en la red alimenticia y estrategias antidepredatorias) y uso de hábitat (hábitos, dependencia del agua y uso del tiempo y el espacio). Por ejemplo, el modo reproductivo refleja las estrategias reproductivas de las especies y el uso del hábitat, por lo que ha sido utilizado por distintos autores como un aspecto clave en la descripción funcional de la historia de vida de los anfibios (Pineda et al. 2005; Tobar-Suárez 2012; Díaz-García et al. 2017). Como no existe información detallada de la dieta de todas las especies de la región el ancho de boca fue utilizado como un rasgo que indica el tamaño de presas consumidas por los anfibios (Corral-Gómez 2013; Cortés-Gómez et al. 2016; Lemus-Mejía 2017). Otros rasgos como la presencia de discos terminales, dedos terminados en punta y membranas interdigitales reflejan modos de vida (arborícola, terrestre y semiacuático, respectivamente) y han sido propuestos para el estudio funcional de este grupo taxonómico (Cortés-Gómez et al. 2016; Riemann et al. 2017). Finalmente, se incorporó diámetro de ojo como un nuevo rasgo para el análisis funcional de los anfibios por su posible influencia en la detección de presas (Córdova-Tapia y Zambrano 2016).

La generación de grupos funcionales a partir de sistemas de clasificación nos permitió entender el nivel de partición de nicho dentro de una comunidad ya que es útil para determinar la redundancia funcional, que no necesariamente está ligada a la identidad taxonómica (Rosenfeld 2002; Violle et al. 2007). Por ejemplo, los grupos B, D, F y G se agruparon en familias taxonómicas (Eleutherodactylidae, Bufonidae, Ranidae e Hylidae, respectivamente), mientras que el grupo E estuvo conformado por especies de dos familias distintas (Hylidae y Microhylidae). Por ello, aunque frecuentemente especies con rasgos similares tienden a agruparse por familias o géneros (Bellwood et al. 2002), los resultados muestran que las funciones de cada especie no son estrictamente dependientes de su filogenia, pues otros factores como la especiación, extinción y dispersión biogeográfica, pueden influir en la distribución de especies y por lo tanto en su similitud funcional. Como ha sido demostrado en familias Hylidae y Ranidae en donde la riqueza de especies en zonas tropicales fue explicada más por el tiempo de colonización que por las diferencias de clima (Wiens et al. 2009).

La formación de grupos funcionales mostró una mayor redundancia en los grupos: B (*C. occidentalis*, *C. pygmaeus* y *E. modestus*), D (*I. occidentalis*, *I. mazatlanensis* y *R. horribilis*), E (*H. variolosus*, *T. smithii* y *E. smaragdina*) y F (*L. forreri*, *L. neovolcanicus* y *L. pustulosus*) conformados por tres especies cada uno. Siendo la redundancia funcional de las especies un componente crítico de los ecosistemas ya que puede aumentar su resiliencia (Díaz y Cabido 2001). Por otro lado, la formación de grupos funcionales nos permite identificar especies clave para los ecosistemas (Rosenfeld 2002), por ejemplo, los grupos A (*L. melanonotus*) y C (*D. arenicolor*) estuvieron conformados por una sola especie, que podría estar realizando una función ecológica única de acuerdo a los rasgos evaluados, y en ese sentido, la pérdida de una de ellas representaría la pérdida de una función única en el bosque tropical caducifolio y el bosque de pino-encino, respectivamente.

La identidad, abundancia y distribución de los grupos funcionales de anfibios entre temporadas y ecosistemas contrastantes mostraron una respuesta diferencial. En el bosque tropical caducifolio dominó un grupo (B) compuesto por ranas de hábitos terrestres que juegan un papel importante en el mantenimiento de las redes tróficas como controladores biológicos de pequeños insectos tanto de día como de noche. El bosque de pino-encino durante la temporada seca estuvo dominado por un grupo (E) de ranas de hábitos nocturnos que son parte importante de las interacciones como depredadores y presas principalmente en micro-hábitats sobre la vegetación. En el bosque de pino-encino durante lluvias dominó un grupo (F) compuesto por

ranas semiacuáticas, que tienen un efecto considerable en los cuerpos de agua como controladores de algas y bioturbadores durante su etapa larval, además de que participan de forma importante dentro de las redes tróficas en los cuerpos de agua al ser depredadores y presas de vertebrados como peces, reptiles, aves, anfibios e incluso mamíferos. La variación en las abundancias de especies puede reflejar necesidades distintas de hábitat, pues algunos grupos son más estrictos con los requerimientos de micro-hábitat que otros, producto de las reglas de ensamblaje que formaron las comunidades (Duellman 1999).

El bosque tropical caducifolio se caracteriza por tener valores extremos de diversidad (taxonómica y funcional) debido a su condición de estrés hídrico estacional. Durante la temporada seca no se obtuvieron registros de anfibios, mientras que durante la temporada lluviosa se registró la mayor riqueza de especies de todo el estudio, sin embargo, su riqueza funcional se mantuvo por debajo de las dos temporadas del bosque de pino-encino. Esto indica que a pesar del gran número de especies, éstas tienden a parecerse más en sus rasgos funcionales por lo que pocos nichos ecológicos están siendo ocupados por las especies (Mason et al. 2005; Villéger et al. 2010; Córdova-Tapia y Zambrano 2015). La equitatividad funcional del bosque tropical caducifolio también obtuvo los valores más bajos de la comparación, señalando que algunos nichos ocupados por las especies podrían estar siendo subutilizados, y como consecuencia, este ecosistema podría estar asociado con un alto potencial de invasión de especies exóticas y/o traslocadas y con una baja resiliencia en comparación con el bosque de pino-encino (Mason et al. 2005; Mouchet et al. 2010; Morelli et al. 2018). Por último, aunque los valores se encontraron dispersos la mayor divergencia funcional se encontró en el bosque de pino-encino durante la temporada seca lo que refleja que las especies dominantes en este ecosistema son distintas entre sí de acuerdo a las funciones evaluadas y por lo tanto podrían tener una menor competencia y un uso eficiente de los recursos a través de la complementariedad de nicho (Mason et al. 2005).

Los filtros ambientales restringen la abundancia y la ocurrencia de especies promoviendo la similitud de rasgos entre las especies dominantes que les permitan tolerar las condiciones que el ambiente les impone (Hooper et al. 2005; Díaz et al. 2007; Mason et al. 2008). El bosque tropical caducifolio mostró una menor riqueza y diversidad de grupos funcionales respecto al bosque de pino-encino, lo que podría indicar que en este ecosistema hay una menor diversificación de funciones, recursos y micro-hábitats. Por lo tanto, nuestros resultados sugieren que las condiciones ambientales del bosque tropical caducifolio podrían estar actuando como

filtros ambientales sobre la comunidad de anfibios, al ejercer un efecto considerable en la diversidad de grupos funcionales. Mientras que, la similitud limitante podría estar operando en el bosque de pino-encino en ambas temporadas al promover que las especies ocupen nichos funcionales distintos en un ecosistema relativamente más estable en términos hídricos (Tilman 1982; Hooper et al. 2005; Mason et al. 2007).

Por otro lado, los cambios en la abundancia de especies a lo largo de gradientes físicos, como la elevación, la temperatura o la humedad, pueden revelar información importante sobre la organización de las comunidades, ya que los ambientes ejercen una fuerte influencia sobre la ocurrencia y distribución de las especies (Morin 2011). Por ejemplo, el efecto de las variables de micro-hábitat en la presencia de especies de los ecosistemas contrastantes evaluados mostró que la composición de la comunidad de anfibios está principalmente afectada por cambios en las variables ambientales de altitud, temperatura y humedad relativa. Como se había reportado para otras comunidades de anfibios (Pineda et al. 2005; Strauß et al. 2010; Santos-Barrera y Urbina-Cardona 2011; Tobar-Suárez 2012; Cortés-Gómez et al. 2013; Trimble y van Aarde 2014). Sin embargo, a la hora de explicar los patrones de riqueza de especies, y en este caso funciones, la ecología tiende a establecer una fuerte correlación entre la riqueza de especies y el clima, pero la variación latitudinal o elevacional en el clima no son los únicos factores que generan un gradiente en la diversidad de especies de anfibios, sino que ésta también se determina por factores como: el nicho ecológico del clado ancestral, los niveles de especiación y extinción, las condiciones abióticas y bióticas, el tiempo desde que se originó el clado y la historia biogeográfica (Wiens et al. 2009; Morelli et al. 2018). Esto debe tomarse en cuenta en los estudios de diversidad funcional, puesto que muchos de los rasgos y patrones que se intentan explicar tienen raíces antiguas que no es posible ver a través de las condiciones actuales (Wiens et al. 2010).

Los anfibios tienen un papel importante en el mantenimiento de redes tróficas en ambientes acuáticos y terrestres, procesos de bioturbación del agua, control de algas en cuerpos de agua y plagas en ambientes terrestres, entre otros (Valencia-Aguilar et al. 2012). No obstante, las consecuencias del declive de la biodiversidad sobre el funcionamiento de los ecosistemas aún no han sido evaluadas. La extinción acelerada de las especies de anfibios desde una perspectiva funcional podría tener graves implicaciones en el funcionamiento de los ecosistemas debido a su condición bifásica larva-adulto, en donde perder una especie significaría, en términos funcionales, perder a dos (Whiles et al. 2006), aspecto que ha sido prácticamente ignorado en la conservación de los ecosistemas. Por ello, es preciso entender a los ecosistemas como grandes

reservorios de la biodiversidad, así como de las funciones y los servicios ecológicos que aportan (O´Connor y Crowe 2005; Díaz et al. 2006; Cadotte et al. 2011; Ceballos et al. 2017), para que a partir del estudio de la diversidad funcional entendamos el impacto de las extinciones de especies sobre el funcionamiento de los ecosistemas (Petchey y Gaston 2002).

Finalmente, comprender cómo cambian las asociaciones asimétricas de diversidad entre las comunidades a lo largo de diferentes entornos proporcionará nuevos conocimientos sobre las estrategias de planificación de la conservación a grandes escalas espaciales, además de que ayudará a mejorar las capacidades predictivas en la modelación de especies y comunidades (Morelli et al. 2018). Por ello, nuestros resultados enfatizan la importancia de considerar las diferencias funcionales intrínsecas de las especies relacionadas con el tipo de ecosistema que habitan. En ese sentido, es importante tomar en cuenta ecosistemas conservados como modelo para estudios futuros en los que se pueda evaluar el efecto de los ecosistemas y su contraste en la conservación de los anfibios, así como del funcionamiento de las especies y su relación con los procesos ecosistémicos. Un reto a futuro consiste en determinar cómo es que las condiciones ambientales influyen en los componentes de la diversidad funcional y cómo estos interactúan con los procesos ecosistémicos a través de distintas escalas espacio-temporales (Hooper et al. 2005; Chapin et al. 2010; Brose y Hillebrand 2016).

CONCLUSIÓN

Nuestro estudio muestra que las asociaciones entre las diferentes métricas de diversidad de anfibios (taxonómica y funcional) no son constantes a través de ecosistemas contrastantes. Aunque el bosque tropical caducifolio durante la temporada lluviosa obtuvo la mayor riqueza de especies, la riqueza y diversidad de grupos funcionales fueron significativamente menores que en las dos temporadas del bosque de pino-encino. Estos resultados sugieren que la sequía estacional en el bosque tropical caducifolio podría estar actuando como un filtro ambiental promoviendo la dominancia de rasgos funcionales similares entre las especies, mientras que la similitud limitante podría estar actuando en el bosque de pino-encino ante condiciones hídricas relativamente estables permitiendo una mayor diversidad funcional. Además, las comunidades de anfibios estuvieron relacionadas con cambios en las variables ambientales de altitud, temperatura y humedad relativa. Pocos trabajos examinan la relación de métricas de diversidad entre ecosistemas contrastantes, sin embargo, analizar la relación entre la estructura de las comunidades y el funcionamiento de los ecosistemas es necesario para emprender estrategias de conservación integrales para la protección de la biodiversidad.

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