UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO
POSGRADO EN CIENCIAS BIOLÓGICAS
INSTITUTO DE INVESTIGACIONES EN ECOSISTEMAS Y SUSTENTABILIDAD
ECOLOGÍA

PATRONES DE DISTRIBUCIÓN Y RIQUEZA DE ANFIBIOS ASOCIADOS A VARIABLES AMBIENTALES EN ZONAS RIBEREÑAS ANTROPIZADAS

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

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MORELIA, MICHOACÁN. ENERO. AÑO 2022

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ASUNTO: Oficio de Jurado

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 **20 de septiembre de 2021,** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS,** del estudiante **OROPEZA SÁNCHEZ MARCO TULIO,** con número de cuenta **518009133,** con la tesis titulada, **"PATRONES DE DISTRIBUCIÓN Y RIQUEZA DE ANFIBIOS ASOCIADOS A VARIABLES AMBIENTALES EN ZONAS RIBEREÑAS ANTROPIZADAS**", realizada bajo la dirección de la **DRA. IRERI SUAZO ORTUÑO**, quedando integrado de la siguiente manera:

Presidente:	DRA. ELLEN ANDRESEN
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Sin otro particular, me es grato enviarle un cordial saludo.

ATENTAMENTE
"POR MI RAZA HABLARÁ EL ESPÍRITU"
Ciudad Universitaria, Cd. Mx., a 24 de noviembre de 2021

COORDINADOR DEL PROGRAMA

DR. ADOLFO GERARDO NAVARRO SIGÜENZA

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Índice

RESUMEN GENERAL

El cambio de uso de suelo representa la principal amenaza para el mantenimiento de la biodiversidad, ya que genera la disminución en la abundancia de individuos, la desaparición de poblaciones y la extinción local de especies. Para enfrentar esta crisis ambiental, las estrategias de conservación pueden establecerse con el propósito de proteger áreas, o regiones, con una mayor riqueza de especies nativas (hotspots) o áreas que incluyan la distribución de especies focales. Sin embargo, si no se considera que los datos de abundancia e incidencia de especies pueden ser resultado de su probabilidad de detección, pueden generarse reportes poco confiables e inventarios incompletos que comprometen el éxito de los planes de conservación.

En México la proporción de anfibios amenazados (60%) supera la cifra mundial (41%) y el cambio de uso de suelo es su principal amenaza. Por el ciclo de vida complejo de los anfibios, la vegetación ribereña representa una fuente de recursos alimentarios, refugio para evadir la desecación y sitios de reproducción. En el noreste de Michoacán, México, colindan las provincias biogeográficas Eje Neovolcánico y Depresión del Balsas, reconocidos centros de diversificación y endemismo de anfibios. En esta región residen 51 especies de anfibios y, entre las 26 especies en riesgo se distingue *Ambystoma ordinarium* por ser endémica a las zonas ribereñas de la región y por estar amenazada por el cambio de uso de suelo.

Esta tesis tuvo el objetivo general de evaluar el potencial de *A. ordinarium* como especie focal para la conservación de anfibios en ambientes ribereños del noreste de Michoacán. Teniendo en cuenta el objetivo general se plantearon los siguientes objetivos particulares: i) evaluar cómo varía la probabilidad de detección y de ocupación de *A. ordinarium* frente a características ambientales de escala local y de paisaje; ii) evaluar la respuesta de la probabilidad de detección y de ocupación de las especies que integran el ensamble de anfibios del noreste de Michoacán a características del paisaje; iii) comparar la riqueza de anfibios y número de especies en riesgo entre localidades en las que se ha detectado y en las que no la incidencia de *A. ordinarium*, y; iv) estimar la respuesta de diferentes facetas de la diversidad de anfibios al cambio de uso de suelo y comparar los valores de diversidad con relación a la incidencia de *A. ordinarium*.

Con los objetivos particulares definidos en el *Capítulo 1* comencé por describir los efectos negativos del cambio de uso de suelo sobre la biodiversidad y sus diferentes facetas, así como las ventajas y limitaciones de implementar las especies focales como estrategia de conservación.

Para lograr el objetivo de contar con una estimación precisa de la distribución de *A. ordinarium*, en el *Capítulo 2* se evaluaron sus probabilidades de detección y de ocupación y su respuesta a características ambientales en diferentes escalas espaciales. Para esto, se colectaron datos de detección-no-detección de *A. ordinarium* en 60 secciones de arroyo (unidades de muestreo) durante dos temporadas de 2018 (estiaje y lluvias), con tres eventos de muestreo cada una. Para cada unidad de muestreo se registró su elevación, se estimó la proporción de cada tipo de cobertura un radio de 500 m (cultivos, pastizal inducido, bosque primario y secundario) y variables fisicoquímicas del agua en cada evento de muestreo (temperatura, pH, oxígeno disuelto, conductividad eléctrica). Los resultados obtenidos mostraron que las probabilidades de ocupación y de detección de *A. ordinarium* fueron definidas por distintas variables según la temporada del año. La probabilidad de ocupación fue afectada por la proporción de cultivos en el paisaje y la elevación en temporada de secas, y tanto el oxígeno disuelto como la conductividad eléctrica cobraron importancia en lluvias. En cuanto a la detección de *A. ordinarium* fue afectada por la temperatura y profundidad de los arroyos únicamente en temporada de secas. Asimismo, la distribución estimada de *A. ordinarium* resultó menor en comparación con las proyecciones más recientes, las cuales no incluyen la probabilidad de detección.

Una vez identificadas las localidades donde habita *A. ordinarium*, el *Capítulo 3* estuvo enfocado en dos aspectos. El primero fue definir la distribución del resto de anfibios que habitan ambientes ribereños del noreste de Michoacán y su respuesta al cambio de uso de suelo. El segundo aspecto fue comparar la riqueza de anfibios y especies en riesgo en relación con la incidencia de *A. ordinarium*. Para lograr esto se utilizaron datos de detección-no-detección de 12 eventos de muestreo realizados entre 2018 y 2019 en las 60 secciones de arroyos seleccionadas previamente. Se evaluó el efecto de cuatro tipos de cobertura de uso de suelo y la elevación en la probabilidad de ocupación de los anfibios, así como el efecto de la temperatura, humedad ambiental y la fecha de cada evento de muestro sobre la probabilidad de detección. Los resultados mostraron que la variable más importante para explicar la distribución de anfibios en la región fue la proporción de cultivos, en un radio de 500 m. Asimismo, se estimó una mayor cantidad de especies amenazadas en los ensambles que incluyeron a *A. ordinarium*, lo que da soporte a la propuesta de *A. ordinarium* como especie bandera para proteger especies de anfibios en paisaje modificados.

Con la incidencia de los anfibios definida en cada una de las 60 secciones de arroyo, en el *Capítulo 4* se evaluó la respuesta de la diversidad beta, funcional y filogenética de ensambles de anfibios a la proporción de cultivos y comparar sus valores con relación a la incidencia de *A. ordinarium*. Para esto, se utilizaron estimaciones de incidencia de cada especie de anfibio producto del *Capítulo 3*, ya que consideran la probabilidad de detección de las especies. Los rasgos funcionales utilizados para estimar la diversidad funcional de los ensambles estuvieron asociados con el uso del hábitat, estrategia de reproducción y la biomasa. Para estimar la diversidad filogenética se utilizó una filogenia regional que sólo incluye las especies detectadas. Los resultados indicaron una respuesta lineal de segundo orden a la proporción de cultivos para las diferentes facetas de biodiversidad. La propuesta de *A. ordinarium* como especie bandera encontró soporte en que dicha especie forma parte de ensambles con una mayor diversidad funcional y filogenética.

Finalmente, en el *Capítulo 5* sinteticé y discutí los resultados más relevantes de los anteriores capítulos. Se reconoce que el cambio de uso de suelo no disminuyó de manera general la incidencia de los anfibios en la región. Asimismo, ni las propiedades funcionales ni las relaciones filogenéticas de los ensambles se vieron reducidas en los paisajes más modificados. La propuesta de *A. ordinarium* como especie bandera es sustentada por el número de especies amenazadas con las que coincide, así como los valores de diversidad funcional y filogenética de los ensambles que integra. Para promover la conservación de los anfibios a la par de los ambientes ribereños es necesario llevar a cabo acciones como: programas de educación ambiental, pago por servicios ambientales y adoptar usos de suelo de menor impacto. Asimismo, es necesario evaluar los beneficios para los anfibios que tiene proteger el área ribereña designada como zona federal en México, hasta 10 metros contiguos al cauce, espacio que podría ser insuficiente para conservar sus poblaciones.

GENERAL ABSTRACT

Land-use change represents the main threat to the maintenance of biodiversity, as it generates a decrease in the abundance of individuals, the disappearance of populations and the local extinction of species. To face this environmental crisis, conservation strategies can be established with the purpose of protecting areas, or regions, with a greater richness of native species (hotspots) or areas that include the distribution of focal species. However, if it is not considered that species abundance and incidence data may be the result of their probability of detection, unreliable reports and incomplete inventories may be generated, compromising the success of conservation plans.

In Mexico, the proportion of threatened amphibians (60%) exceeds the world amount (41%), and land-use change is their main threat. Because of the complex life cycle of amphibians, riparian vegetation represents a source of food resources, refuge from desiccation, and breeding sites. In northeastern Michoacan, Mexico, the biogeographic provinces of the Neovolcanic Axis and the Balsas Depression, recognized centers of amphibian diversification and endemism, are adjacent to each other. This region is home to 51 species of amphibians and, among the 26 species at risk, *Ambystoma ordinarium* stands out because it is endemic to the riparian zones of the region and because it is threatened by land-use change.

The general objective of this thesis was to evaluate the potential of *A. ordinarium* as a focal species for amphibian conservation in riparian environments of northeastern Michoacan. Taking into account the general objective, the following particular objectives were proposed: i) to evaluate how the probability of detection and occupancy of *A. ordinarium* varies with local and landscape scale environmental characteristics; ii) to evaluate the response of the probability of detection and occupancy of the species that integrate the amphibian assemblage from northeastern Michoacan to landscape characteristics; iii) to compare amphibian richness and number of species at risk between localities where *A. ordinarium* has been detected and those where it has not, and; iv) to estimate the response of different facets of amphibian diversity to land-use change and to compare diversity values in relation to the incidence of *A. ordinarium*.

With the particular objectives defined, in *Chapter 1*, I began to describe the negative effects of land-use change on biodiversity and in its different facets. Also, I mentioned the advantages and limitations of using focal species in conservation strategies.

To achieve the objective of getting an accurate estimation of *A. ordinarium* distribution, in *Chapter 2*, it was evaluated its probabilities of detection and occupancy and its response to environmental variables at different spatial scales. For this, detection-non-detection data for *A. ordinarium* were recorded from 60 stream sections (sampling units) during two 2018 seasons (dry and rainy) with three sampling events per season. For every sampling unit it was recorded the altitude, the proportion of each type of coverage was estimated in a 500 m radius around (crops, induced pasture, primary and secondary forest), also water physicochemical variables at each sampling event (temperature, pH, dissolved oxygen, electrical conductivity). The obtained results show that the probabilities of detection and occupancy of *A. ordinarium* were defined by different variables according to the sampling season. The occupancy was affected by the proportion of crops in the landscape and altitude in the dry season, and both dissolved oxygen and electrical conductivity were important in the rainy season. As for the detection of *A. ordinarium*, it was affected by temperature and stream depth only in the dry season. Also, the estimated *A. ordinarium* distribution was lower compared to the most recent projections, which do not include the probability of detection.

Once the localities inhabited by *A. ordinarium* were identified, *Chapter 3* focused on two aspects. The first was to define the distribution of the rest of the amphibians that inhabit riparian environments in Northeastern Michoacan and their response to land-use change. The second aspect was to compare the richness of amphibians and species at risk in relation to the incidence of *A. ordinarium*. To achieve this, detection-non-detection data from 12 sampling events conducted between 2018 and 2019 in the 60 previously selected stream sections were used. The effect of four land-use cover types and altitude on amphibian occupancy probability was evaluated, as well as the effect of temperature, environmental humidity, and the date of each sampling event on detection probability. The results showed that the most important variable to explain the distribution of amphibians in the region was the proportion of crops, within a 500 m radius. Likewise, a greater number of threatened species was estimated in the assemblages that included *A. ordinarium*, which supports the proposal of *A. ordinarium* as a flagship species to protect amphibian species in modified landscapes.

With amphibian occurrence defined in each of the 60 stream sections, *Chapter 4* evaluated the response of beta, functional and phylogenetic diversity of amphibian assemblages to the proportion of crops and compared their values in relation to the incidence of *A. ordinarium*. For this, incidence estimates for each amphibian species from *Chapter 3* were used, as they consider the detection probability of the species. The functional traits used to estimate the functional diversity of the assemblages were associated with habitat use, reproductive strategy and biomass. A regional phylogeny including only detected species was used to estimate phylogenetic diversity. The results indicated a second-order linear response to crop proportion for the different biodiversity facets. The proposal of *A. ordinarium* as a flagship species was supported by the fact that this species is part of assemblages with higher functional and phylogenetic diversity.

Finally, in *Chapter 5* I synthesized and discussed the most relevant results of the previous chapters. It is recognized that land-use change did not generally decrease the occurrence of amphibians in the region. Likewise, neither the functional properties nor the phylogenetic relationships of the assemblages were reduced in the most modified landscapes. The flagship species proposal of *A. ordinarium* is supported by the number of threatened species with which it coincides, as well as the functional and phylogenetic diversity values of the assemblages it integrates. To promote the conservation of amphibians along with riparian environments, it is necessary to carry out actions such as: environmental education programs, payment for environmental services, and the adoption of less impactful land uses. It is also necessary to evaluate the benefits for amphibians of protecting the riparian area designated as a federal zone in Mexico, up to 10 meters adjacent to the riverbed, a space that could be insufficient to conserve their populations.

Capítulo 1
Introducción general

Marco Tulio Oropeza-Sánchez

Cambio de uso de suelo y su amenaza para la biodiversidad

El cambio de uso de suelo, asociado con la demanda de recursos de zonas urbanas, representa la principal amenaza para la persistencia de la biodiversidad, aún dentro de áreas naturales protegidas (Seto et al. 2012; Huang et al. 2018). Tan solo entre 1990 y 2020, el cambio de uso de suelo ha resultado en la pérdida de 420 millones de hectáreas de vegetación nativa a nivel mundial (FAO 2020). En México se estima que durante los últimos 30 años la pérdida de cobertura boscosa fue de más de 7 millones de hectáreas, y las zonas más afectadas fueron los bosques tropicales (Bonilla-Moheno & Aide 2020; FRA 2020).

El cambio de uso de suelo, al reducir el área de la cobertura boscosa, disminuye el espacio y la disponibilidad de otros recursos para las especies, lo que genera pérdida de individuos y hasta la desaparición de poblaciones (eventos de extinción local; Fahrig, 2003; Hanski, 2011). El conjunto de especies que coinciden espacialmente, o ensamble de especies, en la vegetación nativa conservada cuenta con una estructura y composición que son el resultado de procesos ecológicos y evolutivos particulares (Cadotte & Tucker, 2017). Al tener lugar el cambio de uso de suelo los ensambles frecuentemente terminan dominados por especies tolerantes a ambientes modificados, las cuales presentan un uso poco especializado de recursos, alta capacidad de dispersión y son poco sensibles a la variación de condiciones ambientales (e.g., Frishkoff et al. 2014; Mumme et al. 2015). Por lo anterior, el cambio de uso de suelo origina eventos donde especies sensibles a la modificación ambiental son remplazadas por otras más tolerantes (Ceballos et al. 2017).

Las características de las especies que suelen definir su sensibilidad al cambio de uso de suelo están asociadas con la capacidad de colonizar nuevos hábitats y el uso de recursos.

Por lo que especies más vulnerables al cambio de uso de suelo poseen rasgos como: un mayor tamaño corporal (Purvis et al. 2000), una baja capacidad de dispersión (Bommarco et al. 2010), el uso especialización del tipo de hábitat (Davies et al. 2004), así como un área de distribución geográfica restringida (Purvis et al. 2000; Nowakowski et al. 2017). A nivel mundial todos los grupos de vertebrados terrestres cuentan con especies amenazadas: 41% de anfibios, 30% de mamíferos, 18% de reptiles y 14% de aves (IUCN 2021). Asimismo, la proporción de especies con disminución en sus poblaciones también es alarmante, al acercarse a 30% en todos los vertebrados terrestres, por lo que de seguir estas tendencias el número de especie bajo amenaza continuará incrementando (Ceballos et al. 2017).

Efectos del cambio de uso de suelo en diferentes facetas de la biodiversidad

Generalmente la información del número de especies y su abundancia en los ensambles es empleada para la determinar la diversidad de especies (Hamilton 2005). Acorde a la escala espacial la diversidad de especies puede diferenciarse en diversidad alfa (α), beta (β) y gamma (γ), cada uno de estos aspectos es resultado de factores locales y regionales en diferente proporción (Arellano & Halffter 2003). La diversidad alfa, reconocida como la estructura y composición de los ensambles locales en un paisaje, es resultado de condiciones locales (e.g. diversidad local de recursos alimentarios y microhábitats; Gavish et al. 2019). En cuanto a la diversidad beta, respectiva a la diferencia de especies entre ensambles, pueden involucrarse tanto factores locales (e. g., características de microhábitat; Perez-Rocha et al. 2018) como regionales (e. g., conectividad entre ensambles; Gavish et al. 2019). Finalmente, la diversidad gamma, que es la diversidad de especies en el paisaje, es resultado en mayor proporción de procesos como la colonización, extinción y especiación, frecuentemente influenciados por los tipos de vegetación en el paisaje y como se distribuyen en él (Arellano & Halffter 2003; Hendrickx et al. 2007). El cambio de uso de suelo es un proceso que modifica los tipos de vegetación y su arreglo, por lo que es asociado con los cambios en la diversidad de especies a escala paisaje (Ernoult & Alard 2011; Ruiz-Cobo et al. 2010). Sin embargo, para evitar la pérdida de especies y definir estrategias efectivas de conservación es importante entender los patrones que definen la diversidad de especies a través del paisaje y sus componentes (Bergamin et al. 2017; Socolar et al. 2016; Tukiainen et al. 2019).

El cambio de uso de suelo puede modificar las diferentes facetas de la biodiversidad que no logran apreciarse con estimaciones basadas en la identidad taxonómica de las especies (Bryant et al. 2008; Weinstein et al. 2014). Por ejemplo, la diversidad funcional, relativa a la variedad de formas y funciones de ensambles específicos, es accesible a partir de emplear rasgos morfológicos, fisiológicos y etológicos de las especies en métricas de distancia (Mason et al. 2005; Laliberté & Legendre 2010). Las coberturas de vegetación conservada se caracterizan por contar con una mayor diversidad de funciones, debido a una alta disponibilidad y diversidad de recursos (e. g., Mumme et al. 2015; Hernández-Ordóñez et al. 2019). Por ejemplo, en Chiapas, México, el bosque tropical maduro al contar con una estructura vegetal más compleja (árboles, arbustos, lianas, etc.) comparada con el bosque en regeneración, permite una mayor diversidad de anfibios (Hernández-Ordóñez et al. 2019). Debido a que algunos rasgos particulares de las especies son más susceptibles a desaparecer como resultado del cambio de uso de suelo, en paisajes modificados los cambios en la composición de especies derivan en una menor diversidad funcional (e. g., Hernández-Ordóñez et al. 2019; Moreira et al. 2021).

En el caso de la diversidad filogenética, que representa las relaciones evolutivas de las especies en los ensambles, puede considerarse un equivalente de la diversidad funcional (Winter et al. 2013). Los rasgos funcionales compartidos entre especies frecuentemente representan rasgos filogenéticamente conservados (e. g., Kozak & Wiens 2010; Losos 2008; Sato et al. 2020). Sin embargo, existen casos donde los ensambles de especies comparten rasgos funcionales como resultado de convergencia evolutiva (e. g., Muscarella et al. 2016). Las estimaciones de diversidad filogenética resultan ventajosas cuando no se cuenta con información detallada de los rasgos funcionales de las especies (Tucker et al. 2017). Asimismo, la diversidad filogenética ha sido de utilidad para enfatizar la importancia de ambientes conservados, y mostrar efectos negativos del cambio de uso de suelo, y otras formas de disturbio, que no son perceptibles al evaluar solo la riqueza de especies (D'agata et al. 2014; Grab et al. 2019).

En ambientes conservados la composición de ensambles es definida principalmente por la competencia interespecífica, donde el patrón frecuentemente observado de estructura filogenética es sobredispersión (que sugiere coincidencia de especies lejanamente emparentadas; Menezes et al. 2020). En cambio, el patrón asociado a disturbios ambientales como el cambio de uso de suelo es el de agrupamiento filogenético, debido a que especies tolerantes al disturbio y cercanamente emparentadas terminan agrupadas en dichos ambientes (Frishkoff et al. 2014). No obstante, un número reducido de funciones y relaciones filogenéticas cercanas en los ensambles puede incrementar su vulnerabilidad a disturbios posteriores (Forest et al. 2007; Laliberté et al. 2010). Por ende, los efectos negativos del cambio de uso de suelo en poblaciones y ensambles representan una amenaza constante para conservar la biodiversidad y sus diferentes facetas (Cadotte & Tucker 2017; Forest et al. 2007).

Estrategias de conservación enfocadas a especies particulares

Dada la constante disminución poblacional de las especies a nivel mundial, se requieren estrategias de conservación que representen una inversión efectiva con los recursos disponibles (Arponen 2012; McCarthy et al. 2008). Las estrategias de conservación pueden establecerse con el propósito de proteger las áreas con una mayor riqueza de especies (hotspots) o áreas que incluyan la distribución de especies prioritarias para la conservación (Arponen 2012; Myers et al. 2000). Las especies de alta prioridad para la conservación, denominadas también especies focales, frecuentemente son definidas por su alto riesgo de extinción o por sus funciones en los ecosistemas (Lambeck 1997; Zacharias & Roff 2001). Sin embargo, cuando las áreas de mayor riqueza no coinciden con el área de distribución de especies prioritarias pueden generarse conflictos en el planteamiento y en la asignación de recursos para las estrategias de conservación (e.g., Andelman & Fagan 2000; Kershaw et al. 1995; Lombard 1995; Orme et al. 2005).

Entre las propuestas de especies focales existen algunas que tienen como segundo objetivo la protección de especies con las que coinciden espacialmente, tal como las especies bandera y especies paraguas (Andelman & Fagan 2000; Zacharias & Roff 2001). Estas categorías de especies focales buscan mediante la protección del área de distribución de especies carismáticas, amenazadas o con funciones importantes para los ecosistemas, conferir protección a otras especies, denominadas especies beneficiarias (Roberge & Angelstam 2004).

Las especies bandera son seleccionadas principalmente por su atractivo ante la sociedad y, dependiendo de su reconocimiento, incluso pueden emplearse para promover la conservación de ecosistemas completos (Barua et al. 2011; Bowen-Jones & Entwistle 2002; Bride et al. 2008). Por ejemplo, la propuesta de proteger el lago de Xochimilco a partir de conservar el hábitat del ajolote *Ambystoma mexicanum* (Bride et al. 2008). En cuanto a las especies paraguas, su área de distribución debe contar con recursos suficientes para mantener poblaciones de las especies beneficiarias, y compartir su respuesta a los disturbios que amenazan su persistencia (Lambeck 1997). Por ejemplo, el caso del ostrero americano (*Haematopus palliatus*) que mostró preferencia por áreas de vegetación conservada para su anidamiento y al resguardar dichas áreas se pueden proteger a otras especies de aves en el centro y sureste de New Jersey, USA, con el mismo patrón de anidamiento (Maslo et al. 2016).

La respuesta a los disturbios ambientales, por lo general, es especie-específica. Por ejemplo, la respuesta a la fragmentación del hábitat es definida por los rasgos de historia de vida de cada especie y por su escala de percepción del paisaje (McGarigal & Cushman 2002; Lu et al. 2012). Por lo anterior, en comunidades compuestas por especies con una gran diversidad de rasgos de historias de vida puede ser complicado seleccionar una especie que represente la totalidad de respuestas a un disturbio particular (Caro et al. 2004; Lambeck 1997; Nekaris et al. 2015). En este sentido, para lograr la conservación efectiva de un grupo de especies la propuesta de especie bandera puede ser más práctico que especie paraguas (Nekaris et al. 2015).

El uso de especies paraguas ha tenido éxito cuando las especies beneficiarias son del mismo nivel trófico, lo que ha sido asociado con la similitud de requerimientos como el espacio para satisfacer las necesidades fisiológicas. Ejemplos de este patrón existen en mamíferos terrestres grandes, aves y algunas especies de insectos (Branton & Richardson 2011; Roberge & Angelstam 2004; Suter et al. 2002). Las especies más amenazadas por el cambio de uso de suelo frecuentemente están asociadas a un tipo particular de hábitat, cuentan con una distribución restringida y una baja capacidad de dispersión. Por ejemplo, a nivel mundial se reporta que anfibios (vertebrados reconocidos por su baja capacidad de dispersión) que cuentan con una distribución geográficas más restringida tienden a mostrar decremento en sus poblaciones frente al cambio de uso de suelo (Nowakowski et al. 2017). En este sentido, el empleo de especies de amplia distribución como especies paraguas, puede verse limitado debido a que los requerimientos de especies beneficiarias no coinciden del todo con los de estas especies (e.g., Branton & Richardson 2011; Caro et al. 2004). Para asegurar la efectividad de las especies paraguas en la protección de especies beneficiarias, es necesario contar con información confiable de su distribución y su respuesta a los disturbios ambientales (Lambeck 1997).

Limitaciones en los métodos de evaluación de poblaciones

Los datos de distribución de las especies son resultado del proceso de estado (donde y como se distribuyen las especies) y el proceso de observación (como son detectadas las especies cuando están presentes; Guillera-Arroita et al. 2014). Las estimaciones poblacionales o de ensambles que no distinguen los procesos de estado y detección interpretan la no detección de especies como una ausencia real, lo que genera reportes poco confiables e inventarios incompletos (Gu & Swihart 2004; Guillera-Arroita 2017). En consecuencia, los inventarios incompletos comprometen el éxito de los planes de conservación, por un lado, al omitir áreas ocupadas por especies aun no detectadas, y al subestimar el número de especies beneficiarias en áreas protegidas (Roberge & Angelstam 2004).

Distintos métodos son utilizados en las estimaciones de parámetros poblacionales, sin omitir la probabilidad de detección de las especies como el muestreo por distancia, el muestreo de doble observador, o técnicas de marcaje y recaptura como el modelo Jolly-Seber (Sutherland 2006). Llevar a cabo estos métodos no siempre es posible por limitantes temporales (periodos de actividad asociados a la estacionalidad ambiental), de acceso (terreno irregular o accidentado), de financiamiento (elevado costo de marcaje), esfuerzo de muestreo o limitaciones logísticas. Una alternativa para llevar a cabo estimaciones poblacionales sin omitir la probabilidad de detección y de bajo costo (en cuanto a tiempo y financiamiento) son los modelos de ocupación (MacKenzie et al. 2002). Los modelos de ocupación cuentan con variantes para estimar parámetros como la proporción de área ocupada, el tamaño de poblaciones, interacciones entre especies, metapoblaciones, y hasta metacomunidades (Ocock et al. 2016; Tournier et al. 2017; Steen et al. 2014). Como resultado de emplear modelos de ocupación se ha logrado evaluar tanto la respuesta de las especies a diferentes variables predictivas como la precisión de estas aseveraciones (Guillera-Arroita 2017).

Los modelos de ocupación requieren múltiples eventos de muestreo e incluyen supuestos como (i) unidades de muestreo cerradas a eventos de colonización o abandono durante el periodo de muestreo; (ii) detección de especies independiente entre localidades; (iii) la probabilidad de ocupación constante a través de las unidades o debe ser asociada con variables de las unidades; y (iv) la probabilidad de detección es constante a través de los muestreos y unidades o debe ser asociada a variables de las unidades o muestreos

(MacKenzie et al. 2002). En consecuencia, el empleo de los modelos de ocupación exige un diseño de muestreo restringido temporalmente, para reducir los errores de detección, y en el cual se asegure la independencia espacial de los datos. Asimismo, por la limitante temporal de los modelos de ocupación requieren de balance entre el número de localidades a evaluar y el número de muestreos, para evitar comprometer la precisión de las estimaciones (Bailey et al. 2007; MacKenzie & Royle 2005).

Entre las ventajas derivadas del uso de modelos de ocupación están reconocer el grado de precisión de las estimaciones y la obtención de datos confiables para análisis o aseveraciones posteriores (Guillera-Arroita et al. 2010 y 2014). Las estimaciones derivadas de modelos de ocupación, o aquellos que consideran la probabilidad de detección de las especies, han sido empleadas para definir modelos de distribución de especies y diferentes facetas de la biodiversidad (e.g., Ibarra & Martin 2015; Kéry et al. 2010; Petracca et al. 2014). Por lo que el uso de modelos de ocupación habilita el desarrollo y evaluación de estrategias de conservación basadas en estimaciones precisas del tamaño de poblaciones y composición de ensambles, urgentes para las especies o grupos de especies más vulnerables.

El riesgo de extinción de los anfibios y la importancia de la vegetación ribereña

La mayoría de las especies de anfibios necesitan de los hábitats acuáticos y terrestres para completar su ciclo de vida, por lo que tienen un papel importante en los ecosistemas al involucrase en la transferencia de nutrientes entre hábitats (Cortés-Gomez et al. 2015). No obstante, son el grupo de vertebrados con más especies amenazadas (41%; IUCN 2021) por fenómenos como el cambio de uso de suelo, el cambio climático, la contaminación, enfermedades emergentes y la introducción de especies exóticas (Hof et al. 2011; Wake & Vredenburg 2008). En México la proporción de anfibios amenazados (60% de las especies) rebasa la cifra a nivel mundial y el cambio de uso de suelo es la principal amenaza (Frías-Alvarez et al. 2010). Debido a la crisis que amenaza a los anfibios es prioritario determinar el estado actual de las especies, sus poblaciones y los factores que amenazan la persistencia de estas.

Los anfibios poseen una variedad de rasgos de historias de vida que les permiten explotar una gran diversidad de microhábitats durante su ciclo de vida como: hábitats acuáticos, diferentes estratos de vegetación, y hasta galerías subterráneas (Haddad & Prado 2005). Estos vertebrados cuentan con periodos de actividad que pueden estar asociados con su dinámica de reproducción. Se reconocen especies de anfibios activas en periodos particulares del año (con más de un evento de reproducción al año) y especies activas en periodos muy breves (con eventos de reproducción “explosivos”; Wells 2007). Por esta gama de atributos su detección es limitada, lo que dificulta los estudios demográficos a largo plazo, la obtención de información poblacional confiable, su respuesta a cambios ambientales y el desarrollo de estrategias de conservación (Barata et al. 2017; Halstead et al. 2018; Schmidt 2005).

Debido a su ciclo de vida complejo, muchas especies de anfibios además de cuerpos de agua requieren de la vegetación que los rodea, o vegetación ribereña, en la que encuentran una fuente de recursos alimentarios, un refugio para evadir la desecación y sitios de reproducción (Boissinot et al., 2015; Gray & Smith, 2005; Peterman & Semlitsch, 2014). Los ambientes ribereños brindan numerosos servicios ecosistémicos como prevenir la erosión del suelo, purificación del agua e incluso evitar enfermedades en el ser humano (Land et al. 2016; Mokondoko et al. 2016). No obstante, la vegetación ribereña es uno de los ecosistemas más amenazados por el cambio de uso de suelo. Entre 1970 y 2015 se estima que su área original ha disminuido 35% alrededor del mundo y para Latinoamérica la disminución estimada es de 59% (Darrah et al. 2019).

El caso del noreste de Michoacán y el potencial de la salamandra *Ambystoma ordinarium* como una especie focal para la conservación de anfibios

En el estado de Michoacán, México, colindan el Eje Neovolcánico y la Depresión del Balsas, reconocidos centros de diversificación y endemismo de anfibios (Flores-Villela & Goyenechea, 2003; Urbina-Cardona & Flores-Villela, 2010). En esta región de Michoacán se conoce que residen 51 especies de anfibios, de las cuales 26 son consideradas en riesgo de extinción (Alvarado-Díaz et al., 2013). Debido a actividades agrícolas y ganaderas el estado de Michoacán conserva ca. 60% de su cobertura vegetal original (INEGI 2017). En consecuencia, es importante reconocer los factores que definen los patrones de distribución de los anfibios del noreste de Michoacán, para desarrollar estrategias efectivas de conservación.

Entre las especies residentes del noreste de Michoacán se distingue la salamandra *Ambystoma ordinarium* por ser una especie protegida (Pr) por la NOM-059 (SEMARNAT, 2019) y en categoría de En Peligro por la IUCN (2021). Debido a que *A. ordinarium* es endémico a los arroyos del noreste de Michoacán priorizar su área de distribución podría favorecer la conservación de otros anfibios habitantes de ambientes ribereños (Escalera-Vázquez et al., 2018). No obstante, las estimaciones más recientes de su área de distribución no toman en cuenta su detectabilidad. Para evitar subestimaciones debemos llevar a cabo evaluaciones que incluyan la probabilidad de detección de *A. ordinarium*. Asimismo, debemos considerar la probabilidad de detección del resto de anfibios para definir apropiadamente que especies pueden llegar a incluirse en el área de distribución de *A. ordinarium*. Por consiguiente, lograr estimaciones precisas de los patrones de distribución de los anfibios del noreste de Michoacán puede sentar las bases de estrategias efectivas de conservación para estos vertebrados y, en consecuencia, para los ambientes ribereños que habitan.

Objetivos de la tesis

El objetivo principal de esta tesis es evaluar la posibilidad de emplear a *Ambystoma ordinarium* como una especie focal para los anfibios de ambientes ribereños del noreste de Michoacán como especies beneficiarias. Con este propósito se plantearon los siguientes objetivos específicos:

1. Evaluar en ambientes ribereños del noreste de Michoacán cómo responde la probabilidad de detección y de ocupación de *A. ordinarium* a características ambientales de escala local y escala de paisaje (*Capítulo 2*).
2. Evaluar la respuesta de la probabilidad de ocupación y detección de las especies que integran el ensamble de anfibios en ambientes ribereños del noreste de Michoacán a las características del paisaje (*Capítulo 3*).
3. Comparar la riqueza de anfibios y número de especies en riesgo entre localidades del noreste de Michoacán en las que se ha detectado y en las que no la incidencia de *A. ordinarium* (*Capítulo 3*).
4. Estimar la respuesta de diferentes facetas de la diversidad de anfibios del noreste de Michoacán al cambio de uso de suelo y comparar los valores de diversidad entre localidades con relación a la incidencia de *A. ordinarium* (*Capítulo 4*).

Descripción de la región de estudio (*Capítulos 2*, *3* y *4*)

El área de estudio se localiza en el noreste de Michoacán, región donde colindan las provincias fisiográficas Eje Neovolcánico y Depresión del Balsas, reconocidos centros de endemismo y diversificación de anfibios (Figura 1; Flores-Villela & Goyenechea, 2003; Urbina-Cardona & Flores-Villela, 2010). En esta región se han registrado un total de 51 especies de anfibios, de las cuales 26 son consideradas en riesgo de extinción (Alvarado-Díaz et al., 2013). La altitud del área de estudio varía entre 700 y 3000 m s.n.m.; el promedio anual de precipitación varía entre 600 y 1500 mm y la temperatura promedio anual oscila entre 10 y 26°C. Como consecuencia de las actividades de ganadería y agricultura, el estado de Michoacán mantiene alrededor de 60% de su cobertura vegetal original, compuesta por bosque de coníferas, bosque de encino, bosque mesófilo de montaña y bosque tropical seco (INEGI, 2017). Actualmente la zona de estudio abarca los municipios de Acuitzio, Charo, Hidalgo, Indaparapeo, Jungapeo, Morelia, Queréndaro, Salvador Escalante, Tacámbaro, Tancítaro, Tiquicheo, Tuxpan, Tzitzio, Villa Madero, Zinapécuaro y Zitácuaro.

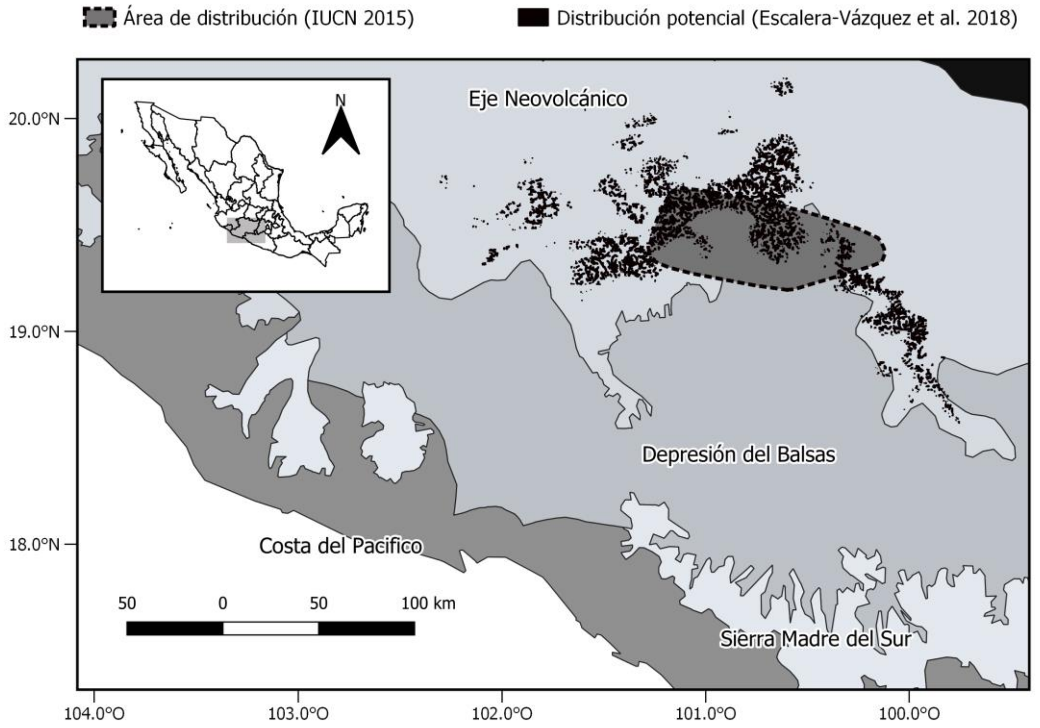

Figura 1. Localización del área de estudio en México. Los sitios de colecta de datos para los *Capítulos 2*, *3* y *4* de esta tesis se distribuyeron en: el espacio combinado que incluye el área de ocupación (del polígono en línea interrumpida; IUCN 2015) y el área de distribución potencial de *Ambystoma ordinarium* (Escalera-Vázquez et al. 2018; el área en negro). Las áreas en distinto tono de gris hacen referencia a las provincias fisiográficas en la región.

Capítulo 2

Occupancy models including local and landscape variables are useful to assess the distribution of a salamander species at risk

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Occupancy models including local and landscape variables are useful to assess the distribution of a salamander species at risk

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Abstract

Numerous amphibian species are at risk of extinction worldwide. Therefore, reliable estimations of the distribution and abundance of these species are necessary for their conservation. Generally, amphibians are difficult to detect in the wild, which compromises the accuracy of long-term population monitoring and management. Occupancy models are useful tools to assess how environmental variables, at a local and at a landscape scale, affect the distribution and abundance of organisms taking into account species imperfect detectability. In this study, we evaluated with an environmental multiscale approach the seasonal variation of the occupation area of the threatened salamander, *Ambystoma ordinarium* along its distribution range. We obtained readings in 60 streams of physicochemical variables associated with habitat quality and landscape features. We found that detection and occupation probability of *A. ordinarium* are seasonally associated with different environmental variables. During the dry season, detectability was positively associated with temperature and stream depth, whereas occupancy was positively associated with the proportion of crops in the landscape and stream elevation. In the rainy season, the detection probability was not explained by any variable considered, and occupancy was negatively associated with stream's electrical conductivity and dissolved oxygen. Based on the estimation of occupied sites, we showed that *A. ordinarium* presents a more restricted distribution range than previously projected. Therefore, our results reveal the importance of evaluating the accuracy of distribution estimates for the conservation of threatened species as *A. ordinarium*.

KEYWORDS

amphibians, detectability, occupancy, seasonal environment, species distribution models

1 | INTRODUCTION

Because amphibians are markedly sensitive to changes in temperature and humidity, their distribution and activity can be affected by environmental seasonality. These environmental changes can lead to physiological stress (Saenz, Fitzgerald, Baum, & Conner, 2006; Smith, Barichivich, Staiger, Smith, & Dodd, 2006). In ecosystems with strong seasonal variation, the highest risk of stress by environmental conditions occurs during the dry season when activity and distribution of amphibians is regulated by local factors, such as the availability of refuges with optimal conditions (Kenison, Litt, Pilliod, & Mcmahon, 2016; López, Scarabotti, & Ghirardi, 2011). Contrastingly, during the rainy season, in which physiological stress is less plausible, the activity and distribution of amphibians are frequently affected by factors at the landscape level, such as distance among habitat patches and the type of land use surrounding these patches. These factors influence the distribution of amphibian species, especially when amphibians leave their habitat patch to carry out activities associated with reproduction and dispersal (Moreira, Moura, & Maltchik, 2016; Ribeiro Jr, Siqueira, Brejão, & Zipkin, 2018; Trenham, Koenig, & Shaffer, 2001).

Considering that 41% of amphibian species are listed as threatened by the International Union for Conservation of Nature red list (IUCN, 2019), it is necessary to develop accurate estimations of the distribution and abundance patterns of species at risk, especially those inhabiting markedly seasonal environments. A limiting factor to achieve these goals is that amphibians present several traits (e.g., secretive habits, cryptic coloration, seasonal activity) that make their detection difficult in the field, hindering, therefore, the implementation of reliable long-term population monitoring (Barata, Griffiths, & Ridout, 2017). Additionally, population estimations that do not consider species' detectability levels (frequently found in amphibian studies; Guimarães, Doherty, & Munguía-Steyer, 2014) result in unreliable estimates of population size and of the biological processes affecting its dynamics (Royle & Dorazio, 2008). A useful approach to overcome this limitation is the use of hierarchical models that estimate detectability, jointly with population parameters, such as occupancy (i.e., the probability to detect at least an individual of a given species) within a given area or series of areas (MacKenzie et al., 2002; Royle & Dorazio, 2006).

Taking into account that population dynamics of amphibians is not related to a particular scale of environmental conditions, the use of variables in a multiscale approach is an option to obtaining robust and reliable estimations of the relation between amphibian species and their habitats, as has been shown for other animal groups (Jaskula & Brodman, 2000; McGarigal, Wan, Zeller, Timm, & Cushman, 2016; Moreira et al., 2016; Ribeiro Jr et al., 2018; Shirk, Raphael, & Cushman, 2014; Zeller et al., 2014). Nevertheless, if these estimations do not consider species detectability and the variation associated with environmental seasonality, it is more likely to obtain biased estimations that compromise the success of conservation efforts (Guillera-Arroita, 2017). Hierarchical models can incorporate the effects of environmental variables at multiple scales without omitting variations in species detectability. In addition, these models represent a reliable option to accurately explain the response of amphibians to habitat conditions.

The Michoacan stream salamander (*Ambystoma ordinarium*) is an endangered stream salamander of the Ambystomatidae family. This family includes fully aquatic neotenic species, and 16 of the 32 species of this family are at risk, presenting population declines strongly associated with landscape modification as consequence of human activities (e.g., urbanization, land-use changes and pollution; AmphibiaWeb, 2020). Several physicochemical variables, such as temperature (°C), pH, electrical conductivity (μS/cm) and dissolved oxygen (mg/L) have been reported to be associated with habitat quality and abundance of this species (Soto-Rojas, Suazo-Ortuño, Montoya Laos, & Alvarado-Díaz, 2017). Although it is known that some types of land-use changes can negatively affect the distribution of some amphibians (Moreira et al., 2016; Ribeiro Jr et al., 2018), information about this response is noticeably limited for *A. ordinarium*.

The objectives of the present study were to (a) evaluate the effect of the seasonal variations of local environmental conditions as well as the effect of land use on the occupancy of the endangered Michoacán stream salamander *A. ordinarium* and (b) evaluate the accuracy of models of the potential distribution of *A. ordinarium* that did not account for detection probability by using estimates of the occupied area calculated by occupancy models (Guillera-Arroita, Lahoz-Monfort, MacKenzie, Wintle, & McCarthy, 2014). The use of this approach can generate information about how human disturbances affect the occurrence of an endangered species with cryptic traits inhabiting a seasonal forest ecosystem. Considering that seasonal environmental dynamics implies a marked importance of local factors during the dry season, such as refuge availability, and of landscape factors during the rainy season, such as type of land use, we expect that the occupancy of *A. ordinarium* will be associated with local variables in the dry season and with landscape variables in the rainy season. Also, due to this environmental seasonality, we expect that the proportion of area occupied by this species will be less in the dry season than in the rainy season.

2 | METHODS

2.1 | Study species and area description

The Michoacán mountain stream salamander (*A. ordinarium*) is a facultative paedomorphic species that breeds year around (Duellman & Trueb, 1994). The species is protected (especial protection, Pr) by the Mexican government (SEMARNAT, 2015) and is listed as endangered (EN) by the IUCN (2019). The species distribution is restricted to the Northeast of Michoacán state (Mexico) (Anderson & Worthington, 1971; Soto-Rojas et al., 2017), and its total occupation range is less than 500 km^2 (IUCN, 2019). The study region presents two marked seasons: the dry season (from November to May) with a monthly average rainfall of 15 mm and the rainy season (from June to October) with a monthly average rainfall of 150 mm. This region consists of vegetation mosaics composed of conifer, oak, deciduous and mountain cloud forests. To define the study area for the search of *A. ordinarium*, we used the area of occupancy estimated by the IUCN SSC Amphibian Specialist Group (2015) and the potential distribution area estimated by Escalera-Vázquez, Hernández-Guzmán, Soto-Rojas, & Suazo-Ortuño et al. (2018; Figure 1).

2.2 | Data collecting

We systematically selected 60 stream sections as sampling units, including all streams that presented an independent streamflow, that were at least 3 km apart from each other and that presented different proportions of native vegetation cover within a buffer of 500 m. With this systematic stream selection, we also tried to cover most of the study areas of the combined estimated areas of IUCN SSC Amphibian Specialist Group (2015) and Escalera-Vázquez et al. (2018; Figure 1). Considering the low vagility of *A. ordinarium* (Ruíz-Martínez, Alvarado-Díaz, Suazo-Ortuño, & Pérez-Munguía, 2014), this distance of separation among units satisfied the condition of sampling spatial independence. Along a 50 m transect on each stream, we searched for neotenic adults, juveniles, larvae and eggs, trying to cover the entire riverbed. The specimen search was designed to meet the assumptions of the single-season occupancy models (MacKenzie et al., 2002). For the closure assumption (Bailey, MacKenzie, & Nichols, 2014), we carried out three sampling events during the dry and three during the rainy season in each of the 60 units. We assumed that the occupancy state of the units did not change within each season. Nevertheless, because of logistic constraints, of a total of 60 sampling units, 50 were sampled six times, whereas 10 units were sampled only five times. Each sampling event lasted 13 days on average. During each day of a sampling event, searching in each of the sampling units was carried out for 20 min by the same person between 09:00 to 18:00 hr. Within this period, the time of day in which searching was carried out was different for the same sampling unit among sampling events. Searching was carried out following the Visual Encounter Surveys (Crump & Scott Jr, 1994). To integrate the heterogeneity of environmental conditions of each season in the probability detection of *A. ordinarium*, a period of 25 days among sampling events was considered.

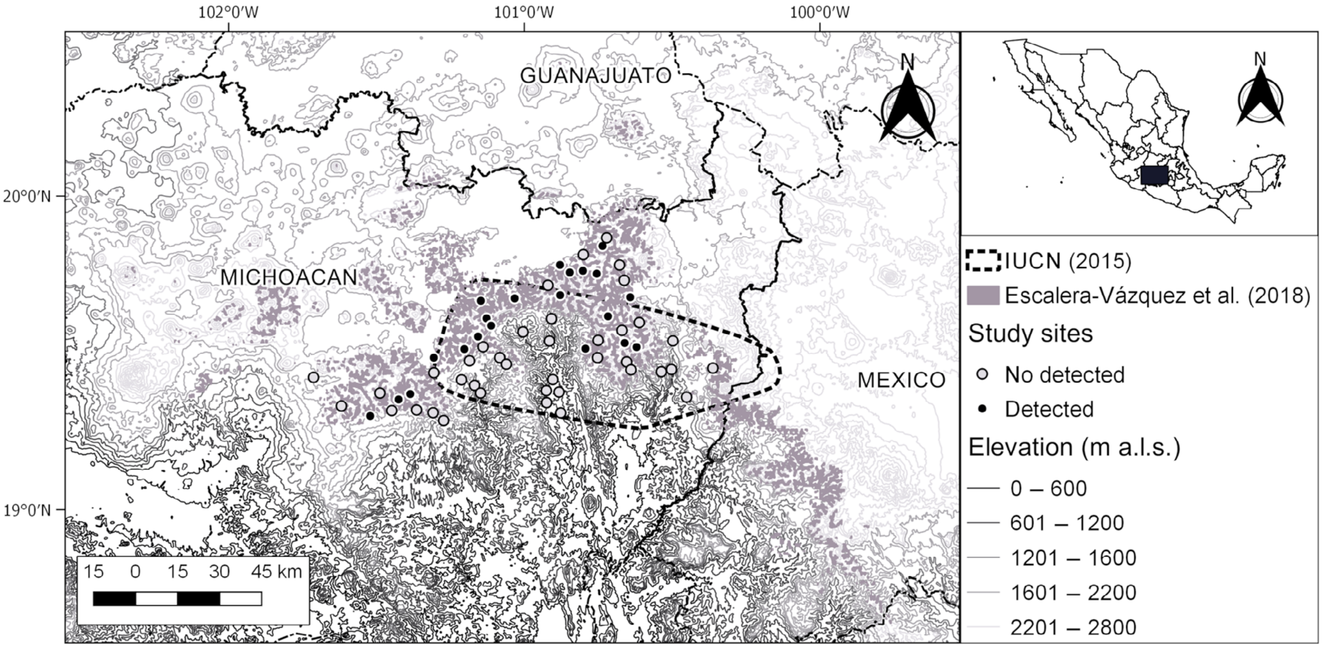

FIGURE 1 Location of the study sites, detection condition for *Ambystoma ordinarium*, area of occupancy of *A. ordinarium* suggested by the IUCN SSC Amphibian Specialist Group (2015) and the potential distribution proposed by Escalera-Vázquez et al. (2018)

Additionally, between the last sampling event of the dry season and the first sampling event of the rainy season a period of 45 days was considered. Adult specimens were captured using 30 cm diameter handle nets, whereas larvae and eggs were only registered. This study was carried out in strict accordance with the guidelines for the use of live amphibians and reptiles in field research compiled by the American Society of Ichthyologists and Herpetologists (ASIH). Specimen handling was carried out with the scientific collecting permit number SGPA/DGVS/001450/18 granted by SEMARNAT.

2.3 | Habitat characteristics

At a transect scale, for each sampling unit, during each sampling event, we registered physicochemical variables associated with the habitat quality of *A. ordinarium*, including the following (Soto-Rojas et al., 2017): temperature (°C), pH, electrical conductivity (μS/cm) and dissolved oxygen (mg/L). These variables were measured with a Hanna HI98194 multiparameter device. Additionally, we measured canopy cover (%) from digital photographs analyzed with the ImageJ software, version 1.43 (Korhonen, Korhonen, Rautiainen, & Stenberg, 2006). Finally, stream depth was measured with a 2 m (±0.1 cm) ruler. All the variables and photographs were recorded at three points (0, 25 and 50 m) along a 50 m transect.

At a landscape scale, the variables were taken within a 500 m radius from the center point of each sampling unit. We estimated the proportion of different land uses that have proven to be reliable predictors of occupation probability for some amphibian species (Moreira et al., 2016; Ribeiro Jr et al., 2018), including the following: native vegetation (nat), crops (crops) and livestock (lives). We employed Sentinel-2 satellite photographs from February 2018, downloaded in May 2018 through the United States Geological Survey (USGS) website with 0101805166330 confirmation order. The photographs were processed with the QGIS software, version 2.8.2 (Quantum GIS Development Team, 2014), and its complement Semiautomatic Classification Plugin (Gémes, Tobak, & Van Leeuwen, 2016). Finally, we defined the proportion area for each land use at every sampling unit.

2.4 | Data analysis

To evaluate seasonal changes in the variables associated with water quality (temperature, pH, electrical conductivity and dissolved oxygen), canopy cover and streams depth, we fitted linear mixed models, considering season as a fixed factor and sampling unit as a random factor (Crawley, 2007). To analyze occupancy probability, for each unit and season we generated a species detection history matrix (including all development stages), where detection events were represented as 1, no detection with a 0 and missing data as NA. Occupancy probability was evaluated for each season employing a single-season approach (MacKenzie et al., 2002). All predictive variables were standardized to facilitate maximum likelihood estimations (Chandler, 2017).

Since environmental variables can be correlated, frequently causing collinearity problems in the models, those variables with a Pearson's correlation $r \geq \pm 0.7$ (Dormann et al., 2013), in both occupancy and detection estimations, were included in different models. Elevation presented a high r value with temperature ($r = -0.77$ in dry and −0.81 in rainy season) and pH (−0.72 in dry and −0.84 in rainy season). Temperature was positively correlated, in both dry and rainy season, with electrical conductivity (0.72 and 0.79, respectively). The native vegetation proportion was negatively correlated with livestock (−0.73) and crops (−0.84) proportion (Supporting Information Figure S1). To model occupancy (Ψ) and detection probabilities (p), we included different combinations of predictor variables. We fitted a null model that considers occupancy (Ψ) and detection probabilities (p) constant among sites. From the null model, we constructed models that sequentially included predictors to explain the probability of detection: canopy cover (canop), water temperature (temp), stream depth (depth) and their second order interactions. Due to the small sample size and to facilitate the interpretation and representation of results, we considered a maximum of two variables. Additionally, to avoid over-parametrization commonly present in complex models (Burnham & Anderson 2002).

Each developed model represented an alternative hypothesis for explaining data under the selection model paradigm, which was evaluated for Akaike information criterion for small samples (AICc; Burnham, Anderson, & Huyvaert, 2011), difference values of AICc (ΔAICc) between zero and two were handled like substantial evidence of model support, and to evaluating the proportional support among models we considered AICc weight (*w*; Mazerolle, 2006). Once the model with better support was defined (the model with the lowest AICc value and ΔAICc >2 compared to the rest of the models), we included all predictive variables that explained the occupancy probability (Ψ). In the case that two or more models presented a value ΔAICc <2, we conducted model averaging for each variable included in these models. The estimate and the 95% CI of each variable was weighted by the *w* value of all models that included it. If the 95% CI of the estimates included the zero value, these were not considered reliable predictors (Mazerolle, 2006). At a landscape scale, we used the proportion area of native vegetation (nat), crops (crops) and livestock (lives); whereas for the local variables such as water temperature (M_temp), pH (M_pH), log-transformed electrical conductivity (lcond), dissolved oxygen (M_DO), canopy proportion (M_canop) and stream depth (M_depth), we considered seasonal average values as well as the elevation (elev) of the sampling units.

To avoid model over-parameterization, we included only one variable at the landscape scale in the models and used two predictive variables as maximum in these for explaining the occupancy probability (Ψ). As recommend by MacKenzie & Bailey (2004), we evaluated whether AICc values were affected by model over-dispersion ($\hat{c} > 1$), estimating the X^2 test for evaluated goodness-of-fitness, also obtaining the variance inflation factor ($\hat{c}$), after 1,000 Bootstrap iterations selecting the model with the best support (ΔAICc <2). Considering $\hat{c}$ estimated values $1 \leq \hat{c} \leq 4$ as evidence that the models do not present structural lack of fit (Burnham & Anderson 2002). In the case of counts with a $\hat{c} > 1$ (over-dispersion), we employed the AIC for small samples that considered model overdispersion (QAICc) and subsequent values of difference and weight of AICc (ΔQAICc and *w* correspondently; Mazerolle, 2006). Finally, the occupancy model with the best support for each season was employed to estimate the proportion of sites occupied (PAO; Fiske & Chandler, 2017), with a confidence interval of 95%. All analyses were performed with the software R version 3.5.1 (R Core Team, 2018), and the packages lme4 (Bates, Maechler, Bolker, & Walker, 2015), unmarked (Fiske & Chandler, 2011), AICcmodavg (Mazerolle, 2019) and usdm (Naimi, Hamm, Groen, Skidmore, & Toxopeus, 2014).

3 | RESULTS

The environmental variables at local scale were significantly different between seasons; during the rainy season temperature was significantly higher (X^2 = 13.82, $p < 0.001$), as well as canopy cover (X^2 = 96.43, $p < 0.001$) and stream depth (X^2 = 186.03, $p <$ 0 .001), whereas pH (X^2 = 269.6, $p < 0.001$), electrical conductivity (X^2 = 146, $p < 0.001$) and dissolved oxygen (X^2 = 5.05, p = 0 .024) were significantly higher during the dry season (Figure S2). During the dry season, we detected *A. ordinarium* at different developmental stages in 20 units, whereas only at 13 units during the rainy season (Figure S3). Nevertheless, due to the high overlap of confidence intervals between seasons, mean detection probability did not differ between dry (p = 0.7 [95% CI = 0.52–0.83]) and rainy season (0.56 [0.36–0.75]).

The occupancy model that best explained the detection probability for *A. ordinarium* during the dry season included the interaction between temperature and stream depth (temp:depth; ΔAICc <2, *w* = 0.50; Table S1). In this season, we evaluated mean temperature (M_temp) and stream depth (M_depth) as covariables to explain occupancy probability, but the effect of these variables to explain detection probability was substituted by the detection probability mean value in the occupancy models. The model with the best support for the occupancy probability included the additive effect of the proportion of crops in the landscape (crops) and stream elevation (elev; ΔAICc <2, *w* = 0.68; Table S2). For this model, there was sparse evidence of lack-of-fit (X^2 = 10.67, p = 0.21, $\hat{c} = 1.33$); hence, QAICc was used for the model selection and standard errors inflated by a factor of $\hat{c} = 1.33$. This model continued with the best support for occupancy probability (ΔQAIC <2, *w* = 0.49; Table S3). The interaction between temperature and stream depth (temp:depth) had a positive effect in the detection probability ($\hat{p} = 1.36$ [95% CI = 0.32–2.4]), the highest value was estimated at 10.3°C and 5.5 cm depth and at 33.6°C and 93.3 cm depth (Figure 2a). For occupancy, there was a positive effect of crop proportion ($\hat{\Psi} = 1.05$ [95% CI = 0.28–1.82]; Figure 2b) and elevation (2.2 [0.62–3.84]; Figure 2c). The highest value of occupancy probability was estimated for sites with crop proportion close to 44% and at 2800 m of elevation (Figure 2d).

During the rainy season, the occupancy models that best explained the detection probability for *A. ordinarium* (ΔAICc <2) included temperature and stream depth (Table S4). After model averaging of variables that were similarly supported, we decided to include temperature as predictive variable, because it presented a reliable negative effect for detection probability ($\hat{\bar{p}}$ = −1.11, CI 95% = −2.2 to −0.01). In the rainy season, we evaluated mean temperature (M_temp) as covariable for explaining occupancy probability but its effect for explaining detection probability was substituted by the detection probability mean value in these models. The model with the best support included a negative response for the occupancy probability to an increase of electrical conductivity (lcond) and dissolved oxygen (M_OD; ΔAICc <2, *w* = 0.74; Table S5). For this model, there was sparse evidence of lack-of-fit (X^2 = 10.56, p = 0.4, $\hat{c} = 1.02$); hence, QAICc was used for the model selection and standard errors inflated by a factor of $\hat{c} = 1.02$. This model continued with the best support for occupancy probability (ΔQAIC <2, *w* = 0.72; Table S6).

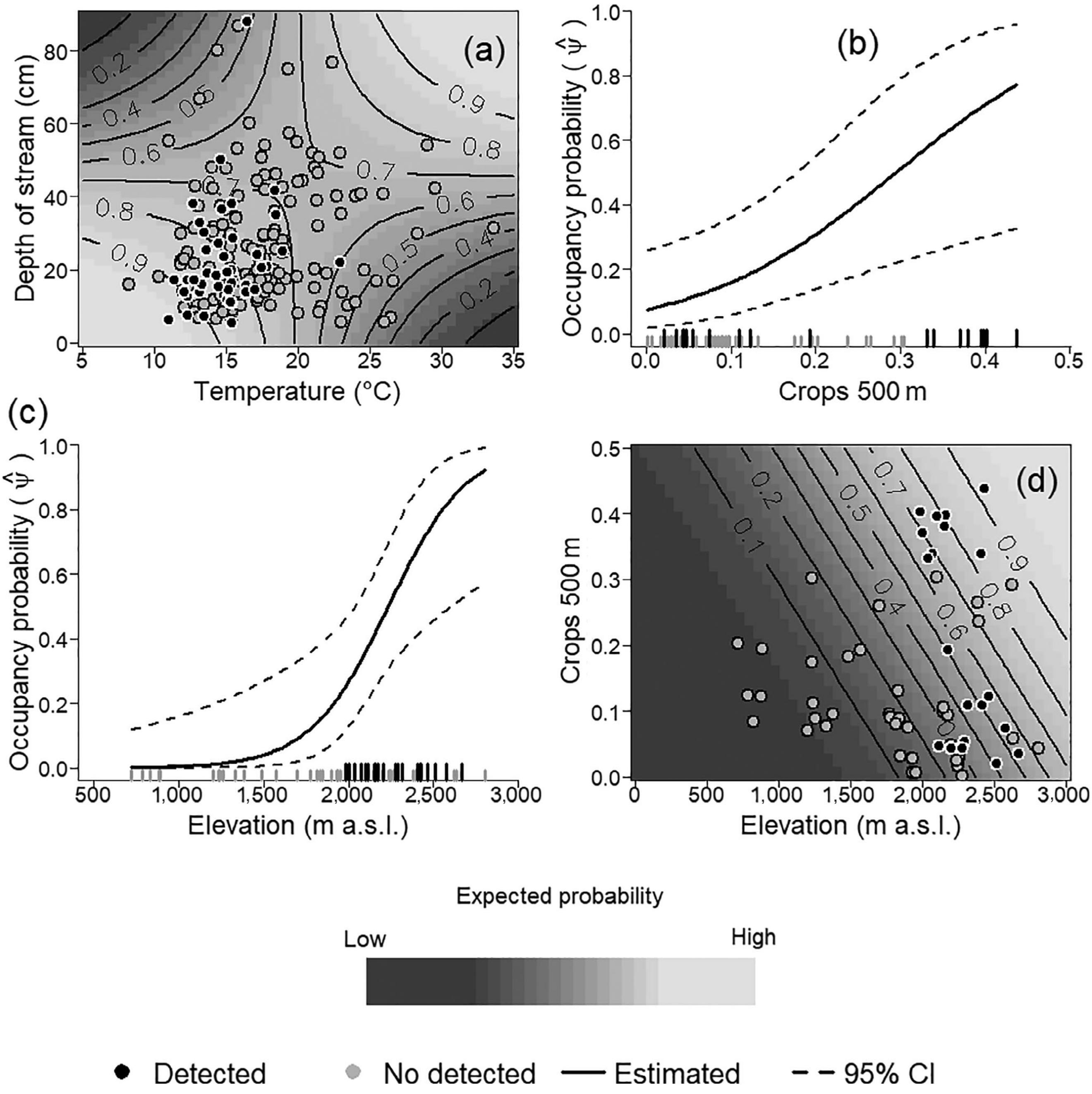

FIGURE 2 Detection and occupancy probabilities for *Ambystoma ordinarium* to different predictive variables during dry season: (a) detection probability related to temperature and stream depth interaction; (b) occupancy probability related to the proportion crops on a 500 m radius; (c) occupancy probability related to elevation and (d) occupancy probability related to the additive effect of crop proportion and elevation

The temperature showed a positive effect in detection probability ($\hat{p} = 0.44$); however, as confidence intervals range included the zero value (95% CI = −0.84 to 1.72), this variable did not represent a reliable predictor. There was a negative response of occupancy probability to an increase of conductivity ($\hat{\Psi} = -2.57$ [95% CI = −4.67 to −0.44]; Figure 3a) and of dissolved oxygen (−2.51 [−4.7 to −0.32]; Figure 3b). The higher occupancy probability was estimated at 19.6 μS/cm of conductivity ($\hat{\Psi} = 0.83$) and at 5.0 mg/L of dissolved oxygen ($\hat{\Psi} = 0.96$; Figure 3c).

Finally, the estimated values of proportion of occupied sites (PAO) for dry and rainy season were higher than the proportion of sites where *A. ordinarium* was currently detected (Figure 4). Furthermore, the overlapping of confidence intervals did not show differences of PAO between estimates for dry (PAO = 0.35 [95% CI = 0.33–0.41]) and rainy season (0.23 [0.21–0.38]). From the total

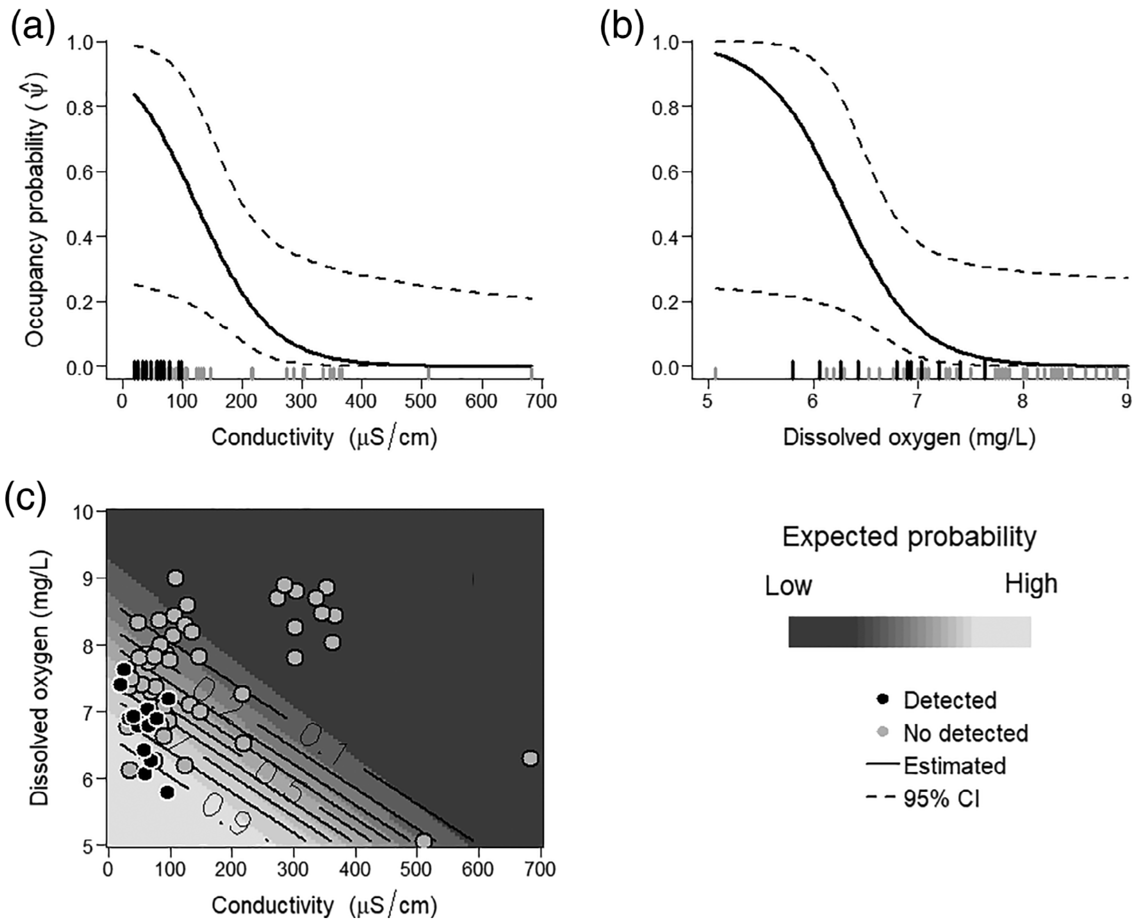

FIGURE 3 Occupancy probability for *Ambystoma ordinarium* related to different predictive variables (average values) during rainy season: (a) occupancy probability and water conductivity; (b) occupancy probability and dissolved oxygen and (c) occupancy probability and the additive effect of conductivity and dissolved oxygen

of our 37 sampling units located within the IUCN SSC Amphibian Specialist Group (2015) proposed area, *A. ordinarium* was detected only in 9 (24%); whereas the species was detected only in 20 of our 40 sampling units (50%; Figure 1) included in the potential distribution area proposed by Escalera-Vázquez et al. (2018).

4 | DISCUSSION

Overall, the results indicated that *A. ordinarium* detection and occupancy probabilities were seasonally affected by different environmental variables at the local and landscape scales. Contrary to our predictions, the occupancy probability of *A. ordinarium* during the dry season was explained by the proportion of crops in the landscape and by stream elevation. Also, opposite to predictions, local environmental variables such as electrical conductivity and dissolved oxygen in the streams explained the occupancy probability of *A. ordinarium* during the rainy season. Our results also showed a narrower spatial distribution of *A. ordinarium* than the projections proposed by IUCN SSC Amphibian Specialist Group (2015) and Escalera-Vázquez et al. (2018) in the study region.

4.1 | Environmental variables and seasonal detectability

Although there were no differences between mean detection probabilities of *A. ordinarium* between seasons, the detection probability was explained by different predictive variables between seasons. The relationship of detection probability with the interaction between temperature and stream depth during the dry season could be due to the thermal tolerance of mountain salamanders, which has been reported to be close to 20°C in species such as the Dusky Salamander (*Desmognathus fuscus*), the Northern Two-lined Salamander (*Eurycea bislineata*) and the Red Salamander (*Pseudotriton ruber*; Grant, Wiewel, & Rice, 2014). Furthermore, *A. ordinarium* probability of detection related to stream depth could be due to a greater availability of refuges

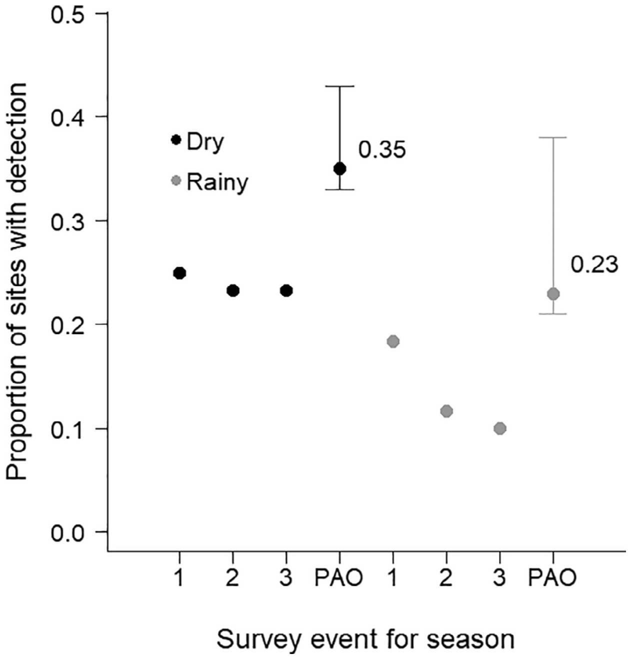

FIGURE 4 Proportion of sites with detections in each sampling event and proportion of sites occupied estimated (PAO) for each season (dry and rainy)

to avoid predators, as reported in larvae of the Blue-spotted Salamander (*Ambystoma laterale*; Jaskula & Brodman, 2000) and the Long-toed Salamander (*Ambystoma macrodactylum*; Kenison et al., 2016). The fact that the detection probability of *A. ordinarium* could not be explained by any of the local environmental variables considered during the rainy season might be a consequence of increased turbidity of streams, as shown for the Northwestern Salamander (*Ambystoma gracile*) and *A. macrodactylum* (Hoffman, Larson, & Brokes, 2003). Further research should include stream level of turbidity as a variable to assess the occupancy of *A. ordinarium*. Our results showed that population estimates of *A. ordinarium* must take into account the detectability of the species considering the effect of local environmental conditions and their variation associated with seasonality.

4.2 | Efficiency of models with an environmental multiscale approach

Including variables at different spatial and temporal scales might be an efficient approach to achieve reliable estimates of species distribution (Shirk et al., 2014; Zeller et al., 2014), as well as to avoid overestimation (Mazerolle & Villard, 1999), especially for amphibian species that have a two-phase life cycle (Becker et al., 2007). Studies to estimates occupancy probability of species with terrestrial and aquatic life cycles, such as the Montevideo Treefrog (*Hypsiboas pulchellus*) and the Striped Snouted Tree-frog (*Scinax squalirostris*) have recognized the importance of the surrounding vegetation type and the conditions of water bodies (Moreira et al., 2016). Additionally, considering land use and topographic characteristics around the selected study sites have been shown to be important when studying species assemblages (Ribeiro Jr et al., 2018). In this study, we observed that the population dynamics of *A. ordinarium*, a species not requiring the terrestrial environment to complete its life cycle, could also be influenced by the surrounding land use and habitat quality, depending on the season. Therefore, to obtain a more accurate approximation of species responses to environmental alteration for conservation purposes, we should consider response variables at multiple spatiotemporal scales.

4.3 | Land-use change

Land-use change is considered the main threat to amphibians. Our results, however, suggested that occupancy probability by *A. ordinarium* during the dry season was positively related to the proportion of croplands, although in our sampling units the associated landscapes presented a maximum cover of crops of 44%. A possible explanation for this finding is that this species is able to remain at the larval stage to avoid adverse terrestrial environments (facultative paedomorphosis), which has been observed in the Mole Salamander (*Ambystoma talpoidum*; Semlitsch, Harris, & Wilbur, 1990). In this sense, *A. ordinarium* populations might be avoiding unfavorable conditions in terrestrial habitats, by remaining in its aquatic form. Additionally, stream-associated salamanders, due to their complex life cycles, have the possibility to disperse within a stream network or overland (Grant, Nichols, Lowe, & Fagan 2010). In the case of *A. ordinarium*, its facultative paedomorphosis might facilitate dispersion within streams, rather than overland, avoiding adverse conditions on modified landscapes, such as the risk of desiccation or predation. This aquatic dispersion might also be important to maintain optimum size of the populations in streams associated with croplands.

For species at risk of extinction, the maintenance of genetic diversity in their populations is critical for their persistence (Frankham, 2010). It has been reported that within landscapes dominated by agriculture, the genetic diversity of populations can be reduced, such as in the Marbled Salamander (*Ambystoma opacum*), the Spotted Salamander (*Ambystoma maculatum*) and the Jefferson Salamander (*Ambystoma jeffersonianum*) (Crawford, Peterman, Kuhns, & Eggert, 2016; Greenwald, Purrenhage, & Savage, 2009), because a reduction of the effective population size and the gene flow (Mills, 2012). Even species with high dispersal capacity, such as the Stripped Toad (*Rhinella ornata*), are at risk due to their small populations within these landscapes (Dixo, Metzger, Morgante, & Zamudio, 2009). The negative effect of land-use change on population genetics could be mitigated if patches of natural vegetation are maintained in the landscapes, which facilitates dispersion as has been shown for populations of the California Tiger Salamander (*Ambystoma californiense*; Wang, Savage, & Shaffer, 2009). Thus, conservation strategies for *A. ordinarium* populations should consider the maintenance of natural vegetation patches across human modified landscapes, while maintaining optimal levels of water conductivity and dissolved oxygen of streams within the geographic range where the species can thrive.

4.4 | Importance of local environmental variables

The distribution of *A. ordinarium* has been documented at elevations of 2,000 to 3,000 m above sea level (Anderson & Worthington, 1971; Escalera-Vázquez et al., 2018). For other amphibian species, elevation has been considered an important factor influencing their distribution, such as in the case of the Mountain Yellow-legged Frog (*Rana muscosa*; Knapp, Matthews, Preisler, & Jellison, 2003) and the European Common Frog (*Rana temporaria*; Băncilă, Cogălniceanu, Ozgul, & Schmidt, 2017). Our study showed that there was a correlation between elevation and four variables associated with habitat quality for *A. ordinarium* (dissolved oxygen, electrical conductivity, pH and temperature; Soto-Rojas et al., 2017). Therefore, the occupation of this species at higher elevation during the dry season may be due to the fact that these sites present optimal conditions for the species.

High electrical conductivity has been associated with a decrease in habitat quality for *A. ordinarium* (Soto-Rojas et al., 2017), which is consistent with our results since during the rainy season we did not detect individuals in sampling units with conductivity levels greater than 100 μS/cm. Other amphibian species have shown high levels of corticosterone (hormone associated with stress) in water bodies with high conductivity levels (Chambers, 2011). Likewise, a negative effect on survival of embryos and larvae of *A. maculatum* has been reported at high conductivity levels (Karraker, Gibbs, & Vonesh, 2008), so the increase in conductivity levels might have a negative impact on *A. ordinarium* populations.

Because the ambystomatids have pulmonary, branchial and cutaneous breathing (Burggren & Pinder, 1991), they are able to survive at low oxygen conditions (Zambrano, Contreras, Mazari-Hiriart, & Zarco-Arista, 2009). Therefore, the fact that *A. ordinarium* probability of occupation showed a negative association with an increase of oxygen could be explained by the fact that predatory species such as fish, benefit from high oxygen conditions. There is evidence that the Carp (*Cyprinus carpio*) and the Nile Tilapia (*Oreochromis niloticus*) consume the eggs of the Axolotl (*Ambystoma mexicanum*; Zambrano, Valiente, & Vander Zanden, 2010). The Rainbow Trout (*Oncorhynchus mykiss*) has been reported in several of the study sites where *A. ordinarium* is present (Soto-Rojas et al., 2017), and therefore, it will be important to study the impact of these invasive fish species on populations of this salamander.

4.5 | Proportion of occupied sites (PAO)

Our results showed that *A. ordinarium* does not currently inhabit all streams within the distribution areas proposed by the IUCN SSC Amphibian Specialist Group (2015) and by Escalera-Vázquez et al. (2018). Because the area of occupancy used by IUCN represents a polygon that includes the geographical points where the species has been detected, it does not reflect the association of *A. ordinarium* with any environmental variable. Therefore, the IUCN projection for the occurrence of *A. ordinarium* is inaccurate. The fact that the species was not detected in more than half of the sampling units located within the area of occupancy used by IUCN might be in part a consequence of the importance of local environmental variables in the occupancy probability at the local and landscape scales (Escalera-Vázquez et al., 2018; Guillera-Arroita, Lahoz-Monfort, & Elith, 2014; Merow, Smith, & Silander, 2013). Therefore, it is important to integrate variables at more than one spatiotemporal scale and consider detectability to explain the distribution of a given species (Peterman, Crawford, & Kuhns, 2013).

4.6 | Final considerations

Our results showed that the use of habitat characteristics at several spatiotemporal scales to estimate the occupation probability of *A. ordinarium* allowed the acquisition of detailed information of the species response to environmental conditions. Although a positive effect of agriculture (percentage of crop cover) on the probability of occupation was found, it is unknown how this land use is affecting the survival, reproductive success, migration and terrestrial dispersal of *A. ordinarium*. In this study, we showed that the occupation area of this species is 50% lower than that reported in studies not considering detectability projections. Although in our study we did not obtain information that indicated that the distribution area of *A. ordinarium* is 100 km^2 or lower (as required by IUCN Standards and Petitions Committee 2019) to change the status of *A. ordinarium* from endangered (EN) to critically endangered (CR), hierarchical occupancy model provides better estimates of the ecological component ("true" occurrence state) while accounting for imperfect detection, providing more reliable data to evaluate the extinction risk of *A. ordinarium*.

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CONFLICT OF INTEREST

The authors declared no potential conflicts of interest.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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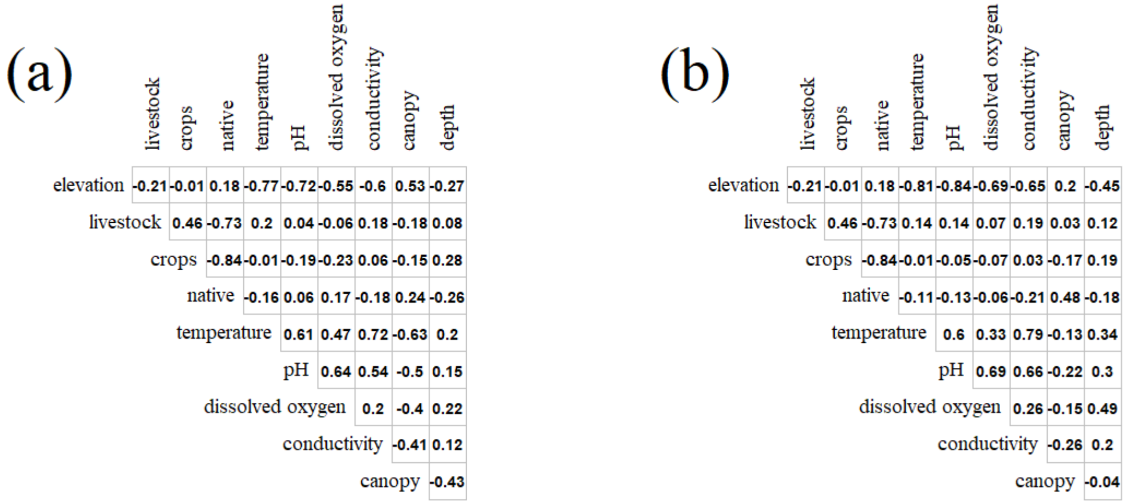
Capítulo 2 | Supporting Information for **“Occupancy models including local and landscape variables are useful to assess the distribution of a salamander species at risk”**

Marco Tulio Oropeza-Sánchez, Ireri Suazo-Ortuño, Julieta Benítez-Malvido & Roberto Muguía-Steyer

Submitted to *Population Ecology*



(a)

	livestock	crops	native	temperature	pH	dissolved oxygen	conductivity	canopy	depth
elevation	-0.21	-0.01	0.18	-0.77	-0.72	-0.55	-0.6	0.53	-0.27
livestock		0.46	-0.73	0.2	0.04	-0.06	0.18	-0.18	0.08
crops			-0.84	-0.01	-0.19	-0.23	0.06	-0.15	0.28
native				-0.16	0.06	0.17	-0.18	0.24	-0.26
temperature					0.61	0.47	0.72	-0.63	0.2
pH						0.64	0.54	-0.5	0.15
dissolved oxygen							0.2	-0.4	0.22
conductivity								-0.41	0.12
canopy									-0.43

(b)

	livestock	crops	native	temperature	pH	dissolved oxygen	conductivity	canopy	depth
elevation	-0.21	-0.01	0.18	-0.81	-0.84	-0.69	-0.65	0.2	-0.45
livestock		0.46	-0.73	0.14	0.14	0.07	0.19	0.03	0.12
crops			-0.84	-0.01	-0.05	-0.07	0.03	-0.17	0.19
native				-0.11	-0.13	-0.06	-0.21	0.48	-0.18
temperature					0.6	0.33	0.79	-0.13	0.34
pH						0.69	0.66	-0.22	0.3
dissolved oxygen							0.26	-0.15	0.49
conductivity								-0.26	0.2
canopy									-0.04

Figure S1**. Pearson’s correlation coefficients (*r*) among predictive variables for explain *Ambystoma ordinarium* occupancy probability**. a) correlation coefficients among predictive variables in dry season and b) correlation coefficients in rainy season.

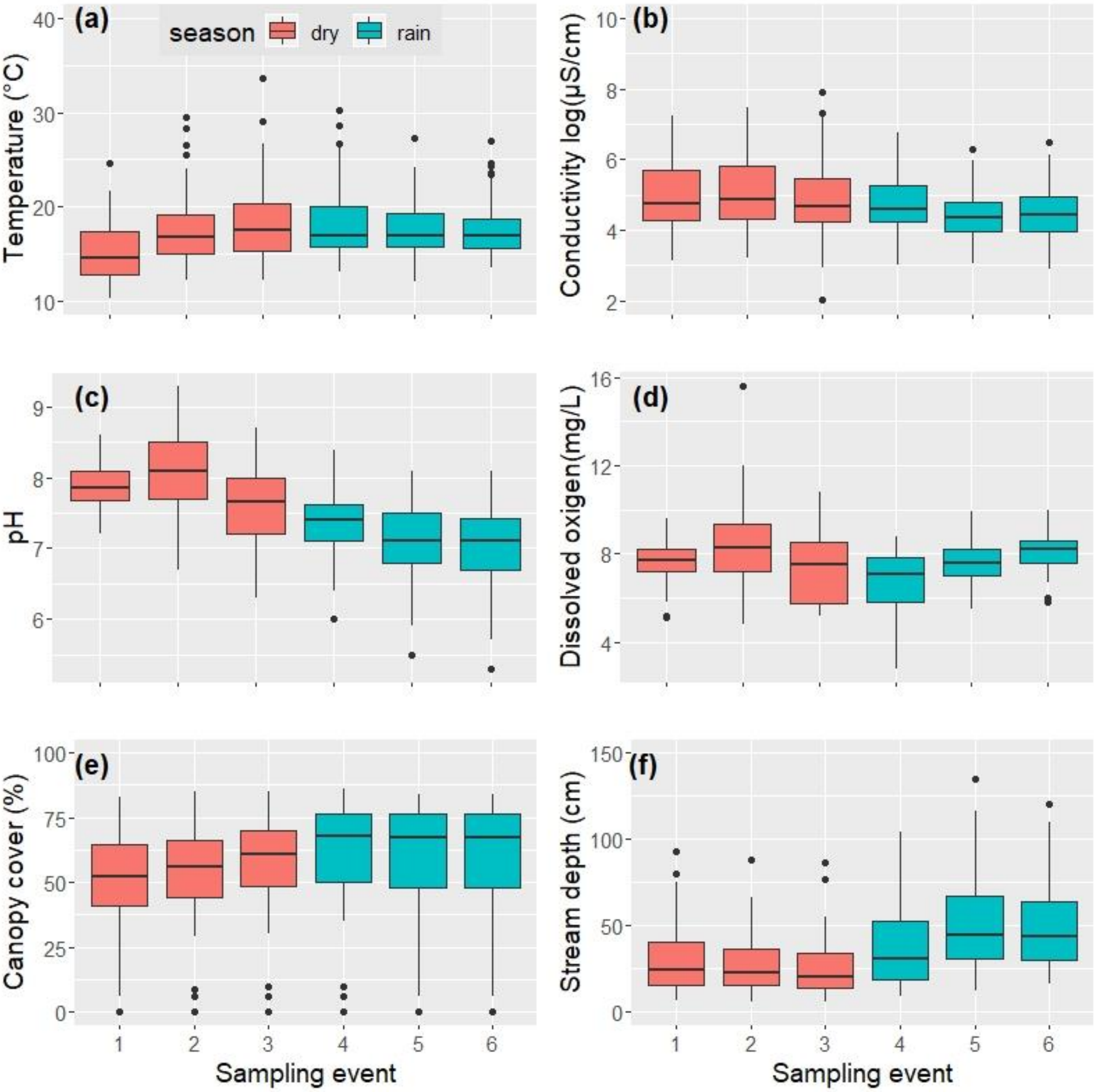


Figure S2**. Values for variable associated with water quality between seasons**. Boxplots represents the median, second and third quartile, as well minimum y maximum values belong to Temperature (a); pH (b); Electrical conductivity (c); Dissolved oxygen (d); Canopy cover (e) and; Stream depth (f) for each sampling event.

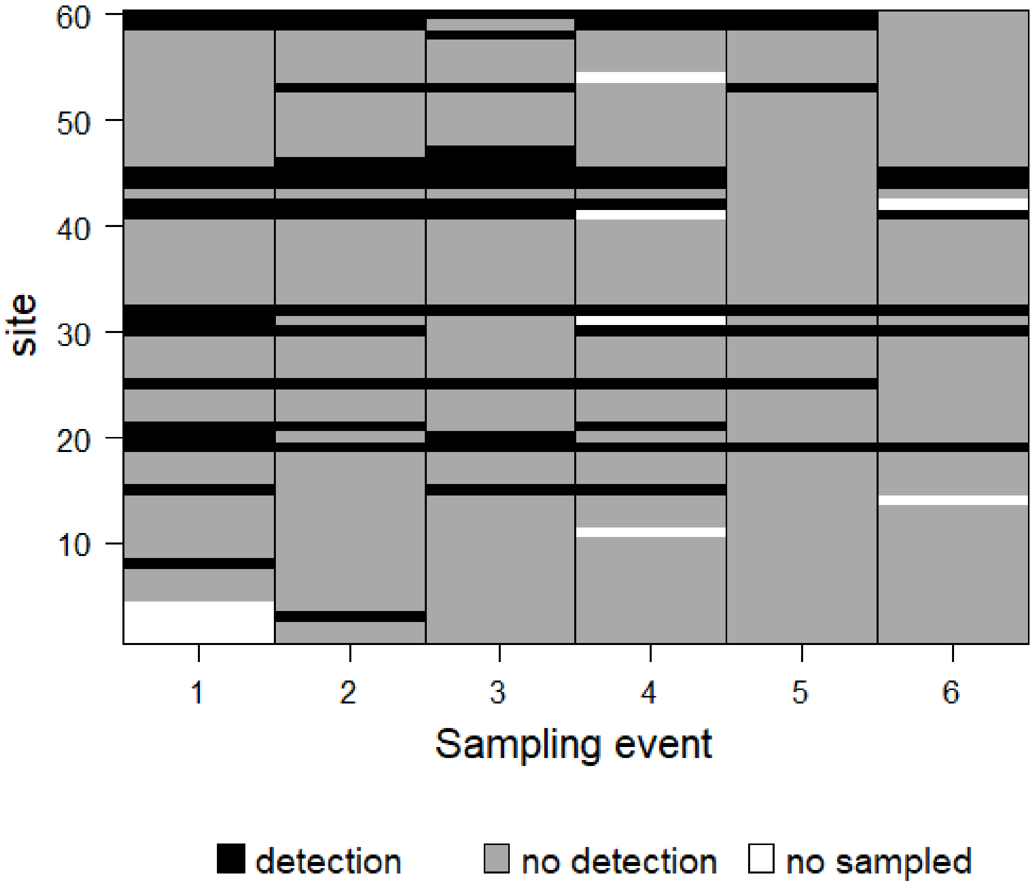


Figure S3**. Detection histories for *Ambystoma ordinarium* on 60 sampling units**. Dry season sampling events were from one until three and four to six corresponded to rainy season.

Table S1**. Model selection based on Akaike Information Criterion for small samples (AICc) to explain species detectability in dry season.** Occupancy models for explain *Ambystoma ordinarium* detection probability (p) with its number of parameters (K), values of AICc, delta AICc (ΔAICc), AICc weight (*w*), and Deviance (-2LL).

Model		K	-2LL	AICc	ΔAICc	*w*
ψ	p					
(constant)	(depth) : (temp)	3	136.86	143.28	0.00	0.50
(constant)	(depth) + (temp)	4	137.34	146.07	2.78	0.12
(constant)	(temp)	3	139.93	146.36	3.07	0.11
(constant)	(canopy) : (temp)	3	140.50	146.92	3.64	0.08
(constant)	(depth)	3	141.08	147.51	4.23	0.06
(constant)	(canopy) + (temp)	4	139.72	148.45	5.17	0.04
(constant)	(constant)	2	144.28	148.49	5.20	0.04
(constant)	(canopy) + (depth)	4	141.03	149.76	6.48	0.02
(constant)	(canopy) : (depth)	4	141.43	150.16	6.88	0.02
(constant)	(canopy)	3	144.27	150.70	7.42	0.01

Table S2**. Model selection based on Akaike Information Criterion for small samples (AICc) to explain species occupancy in dry season.** Occupancy models for explain the *Ambystoma ordinarium* occupancy probability (ψ) in dry season with its number of parameters (K), values of AICc, delta AICc (ΔAICc), AICc weight (*w*), and Deviance (-2LL).

Model		K	-2LL	AICc	ΔAICc	*w*
ψ	p					
(crops) + (elev)	(temp) : (depth)	5	110.57	121.68	0.00	0.68
(crops) + (lcond)	(temp) : (depth)	5	113.93	125.04	3.36	0.13
(elev) + $(\text{elev})^2$	(temp) : (depth)	5	115.23	126.34	4.67	0.07
(nat) + (elev)	(temp) : (depth)	5	116.11	127.22	5.55	0.04
(elev)	(temp) : (depth)	4	120.50	129.23	7.55	0.02
(crops) + (M_ph)	(temp) : (depth)	5	118.79	129.91	8.23	0.01
(elev) + (lcond)	(temp) : (depth)	5	119.09	130.20	8.52	0.01
(lives) + (elev)	(temp) : (depth)	5	119.29	130.40	8.72	0.01
(elev) + (M_DO)	(temp) : (depth)	5	119.30	130.41	8.74	0.01
(crops) + (M_temp)	(constant)	4	122.56	131.29	9.61	0.01
(lcond) + (M_DO)	(temp) : (depth)	5	120.67	131.79	10.11	0.00
(M_pH) + (lcond)	(temp) : (depth)	5	121.23	132.34	10.67	0.00
(nat) + (lcond)	(temp) : (depth)	5	121.29	132.40	10.73	0.00
(M_pH)	(temp) : (depth)	4	124.41	133.13	11.46	0.00
(lcond)	(temp) : (depth)	4	125.31	134.03	12.36	0.00
(nat) + (M_pH)	(temp) : (depth)	5	123.26	134.37	12.70	0.00
(M_pH) + (M_DO)	(temp) : (depth)	5	123.74	134.85	13.17	0.00
(lives) + (lcond)	(temp) : (depth)	5	124.01	135.13	13.45	0.00
(lives) + (M_pH)	(temp) : (depth)	5	124.05	135.16	13.48	0.00
(crops) + (M_DO)	(temp) : (depth)	5	124.07	135.18	13.50	0.00
(nat) + (M_temp)	(constant)	4	127.08	135.81	14.13	0.00
(crops) + (M_canop)	(temp) : (depth)	5	124.78	135.89	14.21	0.00
(lcond) + (M_canop)	(temp) : (depth)	5	125.30	136.41	14.73	0.00
(crops)	(temp) : (depth)	4	128.58	137.31	15.63	0.00
(M_temp)	(constant)	3	131.49	137.92	16.25	0.00
(lives) + (M_temp)	(constant)	4	129.47	138.20	16.52	0.00
(M_DO)	(temp) : (depth)	4	129.73	138.46	16.78	0.00
(nat) + (M_DO)	(temp) : (depth)	5	128.96	140.07	18.39	0.00
(M_depth) + (lcond)	(constant)	4	131.48	140.20	18.53	0.00
(lives) + (M_DO)	(temp) : (depth)	5	129.57	140.68	19.00	0.00
(nat) + (M_canop)	(temp) : (depth)	5	131.46	142.58	20.90	0.00
(M_canop)	(temp) : (depth)	4	134.44	143.17	21.49	0.00
(crops) + (M_depth)	(constant)	4	134.84	143.57	21.89	0.00
(nat)	(temp) : (depth)	4	135.07	143.80	22.12	0.00
(lives) + (M_canop)	(temp) : (depth)	5	133.50	144.61	22.93	0.00
(lives)	(temp) : (depth)	4	136.48	145.20	23.53	0.00
(constant)	(constant)	2	144.28	148.49	26.81	0.00
(M_depth)	(constant)	3	144.22	150.65	28.97	0.00
(nat) + (M_depth)	(constant)	4	142.33	151.06	29.38	0.00
(lives) + (M_depth)	(constant)	4	143.95	152.68	31.00	0.00

Table S3**. Model selection based on Akaike Information Criterion for small samples considering model overdispersion (QAICc) to explain species occupancy in dry season.** Occupancy models for explain the *Ambystoma ordinarium* occupancy probability (ψ) in dry season with its number of parameters (K), values of QAICc, delta QAICc (ΔQAICc), QAICc weight (*w*), and quasi-Deviance (-2LL/$\hat{c}$).

Model		K	-2LL/$\hat{c}$	QAICc	ΔQAICc	*w*
ψ	p					
(crops) + (elev)	(temp) : (depth)	6	83.13	96.72	0.00	0.49
(crops) + (lcond)	(temp) : (depth)	6	85.66	99.25	2.53	0.14
(elev) + (elev)2	(temp) : (depth)	6	86.64	100.22	3.51	0.09
(nat) + (elev)	(temp) : (depth)	6	87.30	100.89	4.17	0.06
(elev)	(temp) : (depth)	5	90.60	101.71	5.00	0.04
(crops) + (M_ph)	(temp) : (depth)	6	89.32	102.90	6.19	0.02
(elev) + (lcond)	(temp) : (depth)	6	89.54	103.13	6.41	0.02
(crops) + (M_temp)	(constant)	5	92.15	103.26	6.55	0.02
(lives) + (elev)	(temp) : (depth)	6	89.69	103.27	6.56	0.02
(elev) + (M_DO)	(temp) : (depth)	6	89.70	103.29	6.57	0.02
(lcond) + (M_DO)	(temp) : (depth)	6	90.73	104.32	7.60	0.01
(M_pH)	(temp) : (depth)	5	93.54	104.65	7.93	0.01
(M_pH) + (lcond)	(temp) : (depth)	6	91.15	104.74	8.02	0.01
(nat) + (lcond)	(temp) : (depth)	6	91.20	104.78	8.07	0.01
(lcond)	(temp) : (depth)	5	94.22	105.33	8.61	0.01
(nat) + (M_pH)	(temp) : (depth)	6	92.68	106.26	9.55	0.00
(M_pH) + (M_DO)	(temp) : (depth)	6	93.03	106.62	9.90	0.00
(nat) + (M_temp)	(constant)	5	95.55	106.66	9.94	0.00
(lives) + (lcond)	(temp) : (depth)	6	93.24	106.83	10.11	0.00
(lives) + (M_pH)	(temp) : (depth)	6	93.27	106.86	10.14	0.00
(crops) + (M_DO)	(temp) : (depth)	6	93.29	106.87	10.15	0.00
(crops) + (M_canop)	(temp) : (depth)	6	93.82	107.40	10.69	0.00
(M_temp)	(constant)	4	98.87	107.59	10.88	0.00
(crops)	(temp) : (depth)	5	96.68	107.79	11.07	0.00
(lcond) + (M_canop)	(temp) : (depth)	6	94.21	107.79	11.08	0.00
(lives) + (M_temp)	(constant)	5	97.35	108.46	11.74	0.00
(M_DO)	(temp) : (depth)	5	97.54	108.65	11.94	0.00
(M_depth) + (lcond)	(constant)	5	98.85	109.97	13.25	0.00
(nat) + (M_DO)	(temp) : (depth)	6	96.96	110.55	13.83	0.00
(lives) + (M_DO)	(temp) : (depth)	6	97.42	111.00	14.29	0.00
(M_canop)	(temp) : (depth)	5	101.08	112.19	15.48	0.00
(nat) + (M_canop)	(temp) : (depth)	6	98.85	112.43	15.71	0.00
(crops) + (M_depth)	(constant)	5	101.38	112.49	15.78	0.00
(nat)	(temp) : (depth)	5	101.56	112.67	15.95	0.00
(lives)	(temp) : (depth)	5	102.61	113.73	17.01	0.00
(lives) + (M_canop)	(temp) : (depth)	6	100.38	113.96	17.24	0.00
(constant)	(constant)	3	108.48	114.91	18.19	0.00
(M_depth)	(constant)	4	108.44	117.16	20.45	0.00
(nat) + (M_depth)	(constant)	5	107.01	118.12	21.41	0.00
(lives) + (M_depth)	(constant)	5	108.23	119.34	22.63	0.00

Table S4**. Model selection based on Akaike Information Criterion for small samples (AICc) to explain species detectability in rainy season.** Occupancy models for explain *Ambystoma ordinarium* detection probability (p) with its number of parameters (K), values of AICc, delta AICc (ΔAICc), AICc weight (*w*), and Deviance (-2LL).

Model		K	-2LL	AICc	ΔAICc	*w*
ψ	p					
(constant)	(temp)	3	106.24	112.67	0.00	0.23
(constant)	(constant)	2	109.12	113.33	0.66	0.16
(constant)	(depth)	3	107.30	113.73	1.06	0.13
(constant)	(depth) + (temp)	4	105.02	113.75	1.08	0.13
(constant)	(canopy) : (depth)	3	108.46	114.89	2.22	0.07
(constant)	(depth) : (temp)	4	106.19	114.92	2.25	0.07
(constant)	(canopy) + (temp)	3	108.84	115.27	2.60	0.06
(constant)	(canopy) : (temp)	3	109.11	115.54	2.87	0.05
(constant)	(canopy)	4	107.24	115.97	3.30	0.04
(constant)	(canopy) + (depth)	4	107.50	116.23	3.56	0.04

Table S5**. Model selection based on Akaike Information Criterion for small samples (AICc) to explain species occupancy in rainy season.** Occupancy models for explain the *Ambystoma ordinarium* occupancy probability (ψ) in rainy season with its number of parameters (K), values of AICc, delta AICc (ΔAICc), AICc weight (*w*), and Deviance (-2LL).

Model		K	-2LL	AICc	ΔAICc	*w*
ψ	p					
(lcond) +(M_OD)	(temp)	5	84.27	95.38	0.00	0.74
(M_pH)	(temp)	4	92.37	101.10	5.72	0.04
(M_temp) + (M_OD)	(constant)	4	92.47	101.20	5.82	0.04
(crops) + (M_pH)	(temp)	5	90.22	101.34	5.95	0.04
(lives) + (M_pH)	(temp)	5	91.26	102.37	6.99	0.02
(crops) + (elev)	(temp)	5	91.52	102.63	7.25	0.02
(crops) + (lcond)	(temp)	5	91.92	103.03	7.65	0.02
(nat) + (M_pH)	(temp)	5	92.37	103.48	8.10	0.01
(M_OD)	(temp)	4	95.24	103.97	8.59	0.01
(crops) + (M_OD)	(temp)	5	93.07	104.18	8.80	0.01
(elev) + $(\text{elev})^2$	(temp)	5	93.23	104.34	8.95	0.01
(elev)	(temp)	4	95.78	104.51	9.13	0.01
(lcond)	(temp)	4	96.29	105.01	9.63	0.01
(lives) + (M_OD)	(temp)	5	94.93	106.04	10.66	0.00
(nat) + (M_OD)	(temp)	5	95.24	106.35	10.97	0.00
(lives) + (elev)	(temp)	5	95.43	106.55	11.16	0.00
(nat) + (elev)	(temp)	5	95.49	106.60	11.22	0.00
(nat) + (lcond)	(temp)	5	95.89	107.00	11.62	0.00
(crops) +_(M_temp)	(constant)	4	98.39	107.12	11.74	0.00
(lives) + (lcond)	(temp)	5	96.09	107.20	11.82	0.00
(lcond) + (M_depth)	(temp)	5	96.12	107.23	11.85	0.00
(lcond) + (M_canop)	(temp)	5	96.22	107.34	11.95	0.00
(M_temp)	(constant)	3	102.13	108.56	13.18	0.00
(lives) +_(M_temp)	(constant)	4	101.67	110.40	15.01	0.00
(nat) +_(M_temp)	(constant)	4	102.08	110.81	15.43	0.00
(crops)	(temp)	4	102.91	111.63	16.25	0.00
(crops) + (M_canop)	(temp)	5	100.64	111.75	16.37	0.00
(crops) + (M_depth)	(temp)	5	101.28	112.39	17.00	0.00
(constant)	(temp)	3	106.24	112.67	17.28	0.00
(constant)	(constant)	2	109.12	113.33	17.94	0.00
(lives)	(temp)	4	105.93	114.66	19.28	0.00
(nat)	(temp)	4	106.20	114.93	19.54	0.00
(nat) + (M_canop)	(temp)	5	104.60	115.71	20.32	0.00
(lives) + (M_canop)	(temp)	5	104.71	115.82	20.43	0.00
(lives) + (M_depth)	(temp)	5	105.38	116.49	21.10	0.00
(nat) + (M_depth)	(temp)	5	105.41	116.53	21.14	0.00

Table S6**. Model selection based on Akaike Information Criterion for small samples considering model overdispersion (QAICc) to explain species occupancy in rainy season.** Occupancy models for explain the *Ambystoma ordinarium* occupancy probability (ψ) in rainy season with its number of parameters (K), values of QAICc, delta QAICc (ΔQAICc), QAICc weight (*w*), and quasi-Deviance (-2LL/$\hat{c}$).

Model		K	-2LL/$\hat{c}$	QAICc	ΔQAICc	*w*
ψ	p					
(lcond) +(M_OD)	(temp)	6	81.00	96.20	0.00	0.72
(M_pH)	(temp)	5	88.79	101.67	5.47	0.05
(M_temp) + (M_OD)	(constant)	5	88.88	101.77	5.56	0.04
(crops) + (M_pH)	(temp)	6	86.72	102.04	5.83	0.04
(lives) + (M_pH)	(temp)	6	87.72	103.06	6.85	0.02
(crops) + (elev)	(temp)	6	87.97	103.31	7.11	0.02
(crops) + (lcond)	(temp)	6	88.35	103.71	7.50	0.02
(nat) + (M_pH)	(temp)	6	88.79	104.15	7.94	0.01
(M_OD)	(temp)	5	91.55	104.49	8.28	0.01
(crops) + (M_OD)	(temp)	6	89.46	104.83	8.63	0.01
(elev) + (elev)^{2}	(temp)	6	89.61	104.98	8.78	0.01
(elev)	(temp)	5	92.07	105.02	8.81	0.01
(lcond)	(temp)	5	92.55	105.51	9.30	0.01
(lives) + (M_OD)	(temp)	6	91.24	106.65	10.45	0.00
(nat) + (M_OD)	(temp)	6	91.54	106.96	10.75	0.00
(lives) + (elev)	(temp)	6	91.73	107.15	10.94	0.00
(nat) + (elev)	(temp)	6	91.79	107.21	11.00	0.00
(crops) +_(M_temp)	(constant)	5	94.57	107.58	11.37	0.00
(nat) + (lcond)	(temp)	6	92.17	107.59	11.39	0.00
(lives) + (lcond)	(temp)	6	92.36	107.79	11.59	0.00
(lcond) + (M_depth)	(temp)	6	92.39	107.82	11.62	0.00
(lcond) + (M_canop)	(constant)	6	92.49	107.92	11.72	0.00
(M_temp)	(constant)	4	98.17	108.86	12.65	0.00
(lives) +_(M_temp)	(constant)	5	97.72	110.79	14.58	0.00
(nat) +_(M_temp)	(constant)	5	98.12	111.19	14.99	0.00
(crops)	(temp)	5	98.91	112.00	15.80	0.00
(crops) + (M_canop)	(temp)	6	96.73	112.25	16.05	0.00
(crops) + (M_depth)	(temp)	6	97.34	112.88	16.67	0.00
(constant)	(constant)	4	102.11	112.88	16.68	0.00
(constant)	(temp)	3	104.88	113.40	17.20	0.00
(lives)	(temp)	5	101.82	114.97	18.76	0.00
(nat)	(temp)	5	102.08	115.23	19.02	0.00
(nat) + (M_canop)	(temp)	6	100.53	116.13	19.92	0.00
(lives) + (M_canop)	(temp)	6	100.64	116.24	20.03	0.00
(lives) + (M_depth)	(temp)	6	101.29	116.90	20.69	0.00
(nat) + (M_depth)	(constant)	6	101.32	116.93	20.73	0.00

Capítulo 3

Habitat modification and amphibian richness along riparian areas of Central Mexico: conservation priorities

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Original Article

Habitat modification and amphibian richness along riparian areas of Central Mexico: conservation priorities

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Abstract

Land-use change frequently affects faunistic populations and communities. Many amphibian species depend on riparian vegetation to complete their life cycles. Since about 41% of amphibian species are globally threatened, accurate estimations of population size, species richness and identification of critical habitats are urgently needed. To evaluate the magnitude of changes in species richness and demography, estimations that include detection probability are necessary. In the present study we employed Multi-Species Occupancy Models to estimate detection probability and the effect of land coverage type (i.e., cropland, induced pasture, secondary and primary vegetation) in a 500 m radius on the occupancy probability and richness of diurnal amphibians in 60 riparian zones on Michoacán state, Central Mexico. Also, we evaluated the potential of the endemic salamander *Ambystoma ordinarium* as a focal species for the conservation of local amphibian species. We found that croplands were the most important land coverage type explaining amphibian distribution in riparian zones, with negative effects on most amphibian species. In riparian zones occupied by *A. ordinarium* we found higher number of species at risk. These findings indicate the importance of riparian zones for local diurnal amphibian communities and the potential of *A. ordinarium* as a flagship species for their conservation.

Keywords: Flagship species, Habitat quality, Occupancy models, Salamanders, Threatened species.

INTRODUCTION

Human population growth in urban centers and the consequent demand for resources are the main drivers of environmental degradation and land-use change (Grimm et al. 2008; Seto et al. 2012). Changes in land-use frequently cause a decrease in population size of native species, loss of local populations, and substitution of sensitive to disturbs species by an others more tolerant species (Fahrig 2003; Socolar et al. 2016). To mitigate the negative effects of land-use change, conservation strategies have prioritized the protection of areas with greater species richness (multi-species strategies), or areas where focal species (i.e., keystone or threatened species) are present (Zacharias and Roff 2001; Arponen 2012; Donaldson et al. 2017).

Among various connotations, focal species can be considered as umbrella and flagship species providing protection to other local species. For a species to be considered an umbrella or flagship species, it must have populations under threat by an environmental degradation process, presenting restricted distribution and low dispersal capacity (Lambeck 1997). Umbrella species are those selected because they share similar environmental requirements and threats with other species in need of protection; while flagship species must be charismatic and share their spatial distribution with other first concern species (Lambeck 1997; Lindenmayer et al. 2002; Donaldson et al. 2017). Nevertheless, to achieve successful conservation strategies, we need suitable information regarding species distribution and causes of endangerment (Lambeck 1997).

Reliable estimations about species responses to environmental changes require the evaluation of ecological (e.g., abundance and distribution) and sampling (detection probability) aspects (Kéry and Royle 2008; Guillera-Arroita 2017). By using occupancy models the assessment of both aspects provide accurate estimations of species distribution (Kéry et al. 2010), abundance (Ocock et al. 2016), metapopulation dynamics (Heard et al. 2013) and specific richness patterns (Grant et al. 2013). In addition, occupancy patterns of species associated with landscape attributes, including the following: proportion of conserved primary vegetation, proportion of modified coverages and altitude, have been described through these models (Zipkin et al. 2009; McGrann and Furnas 2016; Valentine et al. 2020). Therefore, the use of occupancy models is an important tool to assessing the response of species to land-use change, a critical aspect when considering the conservation of species at risk.

Amphibians are very sensitive to environmental degradation as 41% of all known species are globally threatened, mainly by land-use change (IUCN, 2021). These vertebrates are vulnerable to land-use change as many species need the connection between aquatic and terrestrial habitats to complete their life cycles (Becker et al. 2007, 2010). Therefore, the vegetation adjacent to water bodies (i.e., riparian vegetation) is important to many amphibian species as this habitat provides suitable conditions (e.g., high environmental humidity) for reproduction and maintenance of their populations (Rodríguez-Mendoza and Pineda 2010; Suazo-Ortuño et al. 2011). Thus, considering the high levels of extinction risk of many amphibian species, conservation strategies require reliable estimations of species distributions as well as the identification of critical areas for their conservation.

In Michoacán state, Mexico, the physiographic provinces Neovolcanic axis and Balsas Depression converge, and both are recognized as diversification and endemism centers for amphibians (Flores-Villela and Goyenechea 2003; Urbina-Cardona and Flores-Villela 2010). In this region, 51 amphibian species have been described, 25 of which are at risk of extinction (Alvarado-Díaz et al. 2013). As a consequence of agriculture and livestock activities only 60% of Michoacan original vegetation coverage remains relatively well preserved (INEGI 2017). Therefore, for conservation of Michoacan amphibians it is fundamental to recognize the factors that define the patterns of amphibian richness and prioritize areas for their conservation.

In this study, we consider the salamander *Ambystoma ordinarium* as a potential focal species (flagship or umbrella species) because it is threatened by land-use change, resides in riparian habitats and it is endemic to the Northeast Michoacan state (Escalera-Vázquez et al., 2018; IUCN, 2021). The objective of this study was to describe the environmental factors influencing amphibian richness in order to prioritize conservation riparian areas and to assess the value of *A. ordinarium* as a focal species in Northeast Michoacan. In this context (i) we evaluated various environmental variables in the landscape potentially associated to amphibian distribution; (ii) we estimated the number of amphibian species, as well as species considered as at risk of extinction; and (iii) we evaluated the number of species and species at risk in relation to the incidence of *A. ordinarium*.

METHODS

Study area

To define the study area, we simultaneously used *A. ordinarium* area of occupancy estimated by the IUCN SSC Amphibian Specialist Group (2015) and its potential distribution area estimated by Escalera-Vázquez et al. (2018), in Northeast Michoacán, Mexico. In this region, the original vegetation was composed of coniferous forest, mixed conifer and oak forest, cloud mountain forest and deciduous forest. However, most original vegetation has been replaced by croplands, cattle pastures, and tree orchards. Also, there is secondary vegetation that is recovering after agricultural activities. The altitude in this region varies between 700 and 3000 m a.s.l., the annual rainfall ranges from 600 to 1500 mm, and the annual average temperature ranges from 10 to 26 °C (Cuervo-Robayo et al. 2014a; 2014b).

A total of 47 amphibian species have been associated to riparian vegetation from Northeast Michoacan (Alvarado-Díaz et al. 2013). In the study area, amphibian assemblages in riparian vegetation, including *A. ordinarium*, are composed by i) species dependent of high environmental humidity for reproduction (i.e., *Craugastor* spp., *Eleutheodactylus* spp., *Pseudoeurycea* spp., and *Isthmura bellii*); ii) species associated to riparian vegetation throughout the year (i.e., *Lithobates* spp., and species of the Hylidae family); and iii) species with an explosive reproductive mode that inhabit riparian vegetation at particular periods of the year (i.e., *Incillius* spp and *Rhinella horribilis*).

Sampling design

To define the species that make up the riparian zone assemblages in study area, we carried out visual encounter surveys in 60 sampling units along study area (Crump and Scott 1994). The sampling units consisted of 50 m long stream sections and a 50 × 25 m sampling plot located along each stream sections, at left or right bank (chosen randomly) towards uplands. To ensure the spatial independence among riparian zones we only selected stream sections that were at least 3 km apart, considering the average dispersal capacity of amphibians (Figure 1; Rittenhouse and Semlitsch 2007). Additionally, to represent the environmental variation of the region, we selected stream sections with different proportion of primary forest along an altitudinal gradient (700 and 3000 m a.s.l.).

From February 2018 to October 2019, we conducted 12 sampling events in each sampling unit. Each event lasted on average 12 days, to record the variation in the environmental conditions we used periods from 21 to 45 days between sampling events. Because of unsafety conditions, search for amphibians was only diurnal, between 09:00 and 18:00 hours. So, the amphibian assemblages we studied only include diurnal species. The order and time of the day in which we sampled the units differed at each sampling event. The search for amphibians was carried out by i) checking microhabitats accessible from the ground, including the following: tree hollows, below logs and rocks, leaf litter and riverbanks; and ii) microhabitats inside the stream, including: the bottom of the channel and among roots and rocks, using a 30 cm in diameter hand collecting net. The sampling effort per sampling unit was of 40 minutes/person per sampling event. We only recorded juveniles and adults and identified to species level all specimens collected in the field. Except for those species at risk, one individual of each species was deposited in the herpetological collection of the Universidad Michoacana de San Nicolás de Hidalgo. Scientific collecting permit number SGPA/DGVS/001450/18 granted by SEMARNAT. The capture and handling of individuals were carried out in strict accordance with the guidelines for the use of live amphibians and reptiles in field research compiled by American Society of Ichthyologists and Herpetologists (ASIH).

Environmental variables

To define the diurnal amphibian assemblage response to environmental traits, we recorded sampling event and sampling unit variables. Sampling event variables known to be associated with amphibian activity, including the following: air temperature (°C), air relative humidity (%) and date (Julian calendar). Temperature and humidity were recorded with a Bacharach Psicometer mod 0012-7012. As sampling unit variables, we registered landscape variables associated to amphibian presence. Within a 500 m radius from the center of each sampling unit we estimated the proportion of eight coverage types, including the following: water bodies, bare ground, urban settlements, orchards, croplands, induced pasture, secondary and primary vegetation, as well as altitude (m a.s.l.). The 500 m radius was selected by considering the standard estimate of amphibian core habitat average (Rittenhouse and Semlitsch 2007). Land-use coverages were estimated using satellite photographs Sentinel- 2, in February 2018 (United States Geological Survey, USGS). The photographs were processed with the software QGIS, version 2.8.2 (Quantum GIS Development Team 2014) and its complement Semiautomatic Classification Plugin (Gémes et al. 2016).

Statistical analysis

To estimate amphibian species richness and response to different environmental variables as well as to assess the potential of *A. ordinarium* as an umbrella species, taking into account the differences in inter-species detection, we implemented Multi-Species Occupancy Models (MSOM) with data augmentation, using Bayesian inference (Kéry and Royle 2009). We defined the posterior distribution of simulate metacommunity size as $N = n + \Sigma_{i=k}^{nz} w_{n+k}$, where n is the detected species, nz is the number of species that we never detected added to the data set (as zero histories) and w is the occurrence of each species in the metacommunity. We specified the w value for each k species in the metacommunity as $w_k \sim$ Bernoulli (Ω), where Ω is the probability that k species belongs to the N size metacommunity. We specified the occurrence of each k species, imperfectly observed, at the unit i, as $z_{ik} \sim$ Bernoulli ($\psi_{ik} w_k$), where ψ_{ik} is the probability that k species will occupy the unit i. Finally, we defined the detection process for each species in each sampling unit as $y_{ijk} \sim$ Bernoulli ($p_{ijk} z_{ik}$), where y_{ijk} is the detection/no detection history at the j-th sampling event, with the detection probability p_{ijk}.

We established the upper limit of the metacommunity size ($M = 47$) considering the species reported for the region. We modeled species-specific occupancy and detection probability based on explanatory variables (cov) specified as $\text{logit}(\psi_{ik}) = \alpha_{\psi,\,k} + \beta_{\psi,\,\text{cov},\,k} * \text{cov}_k$ and $\text{logit}(p_{ijk}) = \alpha_{p,\,k} + \beta_{p,\,cov,\,k} * \text{cov}_{jk}$. We estimated the metacommunity response to each explanatory variables by considering species-specific parameters as independent random effects, defined as $\alpha_{\theta,i} \sim \text{Normal}\ (\mu_{\alpha_\theta},\sigma^2_{\alpha_\theta})$ and $\beta_{\theta,\text{cov},i} \sim \text{Normal}(\ \mu_{\beta_{\theta,cov}},\sigma^2_{\beta_{\theta,cov}})$, with $\theta = (\psi,p)$ (Kéry and Royle 2009).

Model construction

We standardized explanatory variables with mean zero and standard deviation equal to one. The standardization allows consistence among established prior distributions with all parameters, enable the assessment between effects of explanatory variables, and a faster convergence of the posterior distribution probabilities of each parameter (Broms et al. 2016). We developed the models resulting from the combination of the following explanatory variables. To estimate detection probability, we considered sampling variables. To model the detection probability, we used linear responses as the logistic regression is expressed as a sigmoidal form and can help to identify the optimal value from some section of the environmental gradient (Bio et al. 1998). We avoided the use of temp and humd in the same model since they were highly correlated (r = 0.64) but included both variables separately in the same number of models. To estimate the probability of occupancy we considered four types of coverage with higher extension along study area: primary (native forest) and secondary vegetation (successional vegetation), crops (cropland) and livestock (induced pasture; Supporting Information Figure S1), and the altitude (alt) of each sampling unit. To estimate the primary vegetation effect on species occupancy probability we only considered a linear response. Also, to estimate the species occupancy probability and their response to modified coverages and altitude, in the models made we used both linear and quadratic effect. The reason for this is that frequently there is a species-specific optimal altitude and peaks of species richness in intermediate values of modified land coverages can be observed (Kéry and Royle 2009; Holoubek and Jensen 2015; Gao and Carmel 2020). The variables employed, the structure and hypothesis for each model are presented in Table 1.

We developed the models using weakly informative priors, for Ω it was a uniform distribution (0, 1), for μ_{α_θ} and $\mu_{\beta_{\theta,cov}}$ we used a normal distribution with mean zero and standard deviation of 0.01, and uniform distribution (0, 10) for its accuracy $\sigma^2_{\alpha_\theta}$ and $\sigma^2_{\beta_{\theta,cov}}$. We developed MSOM in Nimble 0.10.1 (de Valpine et al., 2020), specialized package in

Bayesian analysis using Markov chain Monte Carlo (MCMC) of R software. We estimated the posterior probability distributions of model parameters from three MCMC with 300 000 iterations. In order to reduce the autocorrelation of the chains, we considered the first and 150 000 iterations as burn-in and a thinning rate of 30. At the end we employed 15, 000 samples for the estimation of posterior probability distributions of each parameter. We assessed the convergence of values among the three chains using the Gelman-Rubin statistic (R; Gelman and Rubin 1992) and by visually inspecting and comparing each MCMC chain's sample traceplots and posterior sampling distributions. We considered a R value near to one as evidence of chains' convergence ($R \leq 1.1$ as acceptable value; Gelman and Rubin 1992; Doherty et al. 2020). To compare the model support and perform model selection, we used the Watanabe-Akaike Information Criterion (WAIC; Watanabe 2010; Hooten and Hobbs 2015). In addition, to assess the sensibility of the estimate of the potential number of species (N) and their credibility intervals to 95% (95% CI) to the data augmentation, we verified the variation in the values estimates of N in models where $M =$ 150 (Royle and Dorazio 2012).

Considering the z_{ik} values of the model with greater support, the species richness in each sampling unit was calculated by adding up the number of estimated species for each unit (the z values). Also, to calculate the number of threatened species in each unit, z_{ik} values were calculate using species results with an Environmental Vulnerability Score (EVS) ≥ 12 (Alvarado-Díaz et al. 2013; Wilson et al. 2013). The EVS is employed to evaluate species vulnerability to extinct using distribution data and traits associated with life history, in the study area the EVS of amphibian species oscillates since three to 17, high values represent higher risk (Wilson and McCranie 2004; Wilson et al. 2013). Finally, to evaluate the potential of *A. ordinarium* as a flagship species we compared the number of species and species at risk between units where *A. ordinarium* has been detected with those where *A. ordinarium* was undetected. We compared the differences with Generalized Linear Models with Poisson distribution. All analyses were made with the R software version 4.0 (R Core Team, 2020). Details of the implemented code are shown in Supplementary material.

RESULTS

We registered a total of 20 amphibian species in the diurnal assemblage. Ten species are considered as at risk of extinction. The number of detected species by sampling unit varied from 0 to 5, while in four sampling units we did not detect any species (Supporting Information Figure S2). The salamander *Ambystoma ordinarium* and the frog *Lithobates neovolcanicus* were the species with the highest number of units with detections.

We selected *Ambystoma* and *Crops* as the top two models to describe the diurnal amphibian data based on the lowest WAIC values (Table 2). However, *Ambystoma* model was more sensible that *Crops* model to data augmentation because it contains more uncertainty in metacommunity size predicted values (*N*; Table 2). This indicates the *Ambystoma* model is a poorer fit that *Crops* model to the data. Thus, to estimate the diurnal amphibian response to environmental variables and species richness we used the *Crops* model.

The *Crops* model included the variables humd ($\mu_{\beta_{p,humd}}$) to explain the metacommunity probability detection, and the linear ($\mu_{\beta_{\psi,crops}}$) and quadratic effect of crops ($\mu_{\beta_{\psi,crops^2}}$) to explain the metacommunity occupancy probability. The median value of metacommunity size from *Crops* model was 25 species (95% CI = 20 42), which means that, in addition to the 20 species detected, five never detected species are part of the metacommunity. The estimate of *N* proved to be unaffected by data augmentation compared to other mo dels, as it did not vary considerably by increasing the upper limit of potential species to 150 (*N* (95% CI) = 26 (20 49)). Additionally, *Crops* model estimated a detection probability ($\grave{p}$) < 0.06 for three of ten amphibian threatened species (Figure 2a), but no one of these species had 95% CI with an amplitude greater that 0.5 in their occupancy probability $\grave{\psi}$ (Figure 2b).

Air humidity did not represent a reliable predictor for the detection probability of any species by integrating the zero value into 95% CI (Supporting Information Figure S3a). The metacommunity detection probability response to humidity was -0.1 (95% CI = -0.27 0.05). The linear effect of crop coverage did not represent a reliable predictor for any amphibian occupancy probability. The linear effect of crops on the metacommunity ($\mu_{\beta_{\psi,crops}}$

) had a coefficient of -0.26 (95%CI = -0.84 0.22; Figure S3b). The quadratic effect of crops had a strong response in six species, a negative coefficient in *Lithobates zweffeli*, *Tlalocohyla smithii,* and *Rhinella horribilis*, a positive coefficient in *L. neovolcanicus*, *Dryophites eximius* and *A. ordinarium*, also the coefficient for the metacommunity ($\mu_{\beta_{\psi,crops^2}}$) was -0.82 (-2.2 0.14; Figure S3c).

With the *Crops* model we explored the response to crop proportion in the landscape on each species occupancy probability (ψ) (Figure 3). We predicted the highest value of ψ in units with a higher proportion of crops (near to 0.4) for *L. neovolcanicus*, *D. eximius*, *Dryophites arenicolor*, *Incilius occidentalis* and *A. ordinarium*. In units with crop proportion lower to 0.2, we predicted the highest value of ψ for *Lithobates spectabilis, Craugastor hobartsmithi* and *Ithsmura belli*. Most species (*L. zweifelli*, *Lithobates berlandieri*, *Sarcohyla bistincta*, *T. smithii*, *Agalychnis dacnicolor*, *Craugastor occidentalis*, *Eleutherodactylus nitidus*, *Incillius marmoreus, R. horribilis* and *Pseudoeurycea leprosa*) had high value of ψ in sampling units with crop proportion between 0.1 and 0.2, and a decrease as they approached to 0.45 proportion. In units with an intermediate crop proportion (between 0.2 and 0.3) *Lithobates montezumae* presented its highest ψ value. In this interval *C. pygmaeus* presented its lowest ψ value.

Species richness per sampling unit ranged from three to seven species. We found that high species richness values were not restricted to a particular level of the altitudinal gradient (Figure 4a). In units where *A. ordinarium* was detected we did not find more species (between four and seven species), than in units where it was not detected (between three and seven; $X^2 = 3.02$, df = 58, p = 0.08). Finally, the number of species at risk ranged from one to five. There was a significant difference in the number of species at risk between sampling units where *A. ordinarium* was detected (between two and five) with those unit in which it was undetected (between one and three; $X^2 = 7.8$, df = 58, p = 0.005; Figure 4b).

DISCUSSION

In Northeast Michoacan, cropland proportion in the landscape was the most important variable explaining the distribution of diurnal amphibian assemblages in riparian zones, with distinct species responses. High values of amphibian richness were not restricted to riparian zones in a particular altitudinal level. In sampling units occupied by *A. ordinarium* we estimated greater number of species at risk. These findings support the consideration of *A. ordinarium* as a focal species, a flagship species specifically, for amphibian conservation.

Potential community size

Most amphibians are highly sensitive to high temperature and low environmental humidity, so they frequently present higher activity at night or during the rainy season (Wells 2010). Despite the accuracy of our estimations on the number of potential species belonging to the metacommunity, they can only be suited for diurnal assemblages. Except for leopard frogs (11 *Lithobates* spp.) and *A. ordinarium,* the rest of riparian amphibians in the region are mainly active at night (35 species), so our model could have omitted most nocturnal species. Due unsafety and logistic constrains (e. g., traveling time among sampling units and terrain), in study area night visual encounter surveys represent an unplausible alternative to denote the importance of riparian zones for amphibians. Although, carrying out samplings for acoustic records (employing tape recorder) or set traps can be alternatives to assess the population and assemblage dynamics of amphibians in riparian vegetation (e. g. Smith et al. 2006; Weir et al. 2009).

Proportion of crops as a predictive variable for species distribution

Assessing the response of species to land-use change is a fundamental step in the development of conservation strategies (Manton et al. 2019; Wagner et al. 2021). Our results showed that amphibian species do not share similar responses to the proportion of crop in the landscape. This pattern could be associated to species-specific environmental tolerance to temperature and humidity. Salamanders of the Plethodontidae family and leaf litter frogs in the *Craugastor* and *Eleutherodactylus* genera, frequently manifest low tolerance to high environmental temperatures and modified habitats (Nowakowski et al. 2018; Meza-Parral et al. 2020); which corresponds with the negative response of *Ishtmura belli, Pseudoeurycea leprosa*, and leaf litter frogs to an increase in the proportion of crop. Although, the negative response of most leaf litter frog species to the increase in the proportion of crop in the landscape could also be a consequence of their cryptic coloration in forested areas, becoming more conspicuous in modified landscapes, compromising their survival (Delhey and Peters 2017).

In this study the leopard frog *Lithobathes neovolcanicus* and some tree frogs showed a positive response to occupancy probability with the increase of cropland proportion. Similarly, in other studies some leopard and tree frogs have been recognized by their ability of inhabiting modified environments, even their detection is higher than in preserved environments (i.e., Suazo-Ortuño et al. 2011; Díaz-García et al. 2017; Aguilar-López et al. 2020). For these frog species, the ability of inhabiting modified landscapes has been considered as consequence of its high temperature tolerance (Tracy et al. 2008; Meza-Parral et al. 2020). Plethodontidae salamanders and leaf litter frogs need terrestrial environments where temperature and humidity are stables for their reproduction, specifically to spawn their eggs (Haddad and Prado 2005; Siqueira et al. 2021). However, leopard and tree frog reproduction depend on the availability of water bodies, then their reproductive mode could represent an advantage in modified riparian areas.

Land-use change is recognized as the main threat to amphibian populations, decreasing the survival of larvae and of individuals soon after their metamorphosis, and therefore, lowering reproductive success (Muenz et al. 2006; Boissinot et al. 2015; Boualit et al. 2019). In our study, the distribution of some amphibian species was positively associated to land-use change. Further studies in the region could be focused in assessing population parameters and dynamics of the recorded species. This information would show whether land-use change implies a threat to the maintenance of amphibian populations.

Importance of riparian zones for amphibian conservation

Riparian vegetation presents characteristics such as stable temperatures and humidity, as well as access to relatively well-preserved water bodies, compared with non-riparian habitats. Therefore, riparian vegetation provides food and shelter for amphibians, mitigating negative conditions associated to land-use change (Muenz et al. 2006; Slaght et al. 2013; Boissinot et al. 2015). For many amphibian species during the larvae and pre-reproductive stages the riparian zone represents an appropriate microhabitat for the completion of their metamorphosis with minimal desiccation risk (Gray and Smith 2005; Peterman and Semlitsch 2014); whereas at the adult stage, the riparian zone offers adequate reproduction sites (Boissinot et al. 2015). Because the advantages of riparian zones for amphibian populations, strategies aimed to amphibian conservation must consider the persistence of streamside vegetation (Rodríguez-Mendoza and Pineda 2010; Suazo-Ortuño et al. 2011).

In human modified landscapes the maintenance of the genetic diversity within populations is a key element for species conservation (Frankham 2010). Riparian zones have been recognized as optional routes for migration and dispersal where genetic variability in amphibian populations is maintained (Grant et al. 2010). In addition, riparian vegetation offers several ecosystem services and prevents soil erosion (Brouwer et al. 2011; Land et al. 2016; Mokondoko et al. 2016). The protection of riparian vegetation, therefore, is fundamental for amphibian conservation and for the adequate management of water bodies and soil, especially in regions with high proportion of land-use change such as Northeastern Michoacán.

Potential of *Ambystoma ordinarium* as a focal species

Assigning the category of umbrella species is a difficult task due to the variety of responses that a group of species may have to environmental conditions (e.g., Andelman and Fagan 2000). In this context, flagship species have the advantage that their only requirement is their spatial overlap with the species aimed to protect (Zacharias and Roff 2001; Caro et al. 2004). Since we did not observe a similar response of the amphibian species recorded to any of the environmental factors considered, prioritizing the distribution area of *A.*

ordinarium and assigning it the flagship species category could help amphibian conservation in this highly modified region.

Because we observed the highest number of species at risk in the sampling units occupied by *A. ordinarium* we consider important to protect them jointly with some lower altitude units where high amphibian richness was also estimated. As consequence, conservation efforts would be applied to protect at least the diurnal amphibians in the study region. Since land-use change is the main extinction threat to amphibians in Mexico, for the study region we suggest minimizing the transition of native vegetation to crops (Frías-Alvarez et al. 2010). To achieve this goal government programs such as the pay for environmental services or micro watershed restoration may be an option, at least while long-term actions are carried out including environmental education programs that ensure the conservation of amphibians and riparian vegetation in the region (CONAFOR 2020; Mokondoko et al. 2016).

Final considerations

Our results showed the how proportion of croplands in the landscape affects the patters of diurnal amphibian richness in Northeastern Michoacan. We also found evidence that protecting the distribution area of *A. ordinarium* can be advantageous to conserve species at risk, in less modificated landscapes. Furthermore, the protection of zones with the greater species richness and with high vegetation coverage that promoted the connection of amphibian populations should be considered in conservation plans. The usefulness of considering *A. ordinarium* as a potential focal species for conservation, should be further evaluated by studies that consider other biodiversity facets such as beta, phylogenetic and functional diversity in sampling units inhabited by *A. ordinarium*.

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Tables

Table 1. Multi-Species Occupancy Models developed for explaining richness patterns of amphibians in Northwest Michoacán riparian zones. We show the environmental variables for explaining each parameter (detection or occupancy), their structure and the hypothesis represented. Altitude = alt, primary vegetation = prim, secondary vegetation = sec, crops = crops, livestock = liv, temperature = temp, relative humidity = humd, date = date.

Model	Occupancy variables	Detection variables	Hypothesis and predictions
Ambystoma	(crops) + (alt)	(temp)	The amphibian species in the study region are mostly tolerant to agricultural coverages and have preferences for high-altitude zones. Thus, every amphibian species in the study region shows similar responses to modified coverages as *Ambystoma ordinarium*.
Altitude	(alt) + $(\text{alt})^2$	(humd) + (date)	The study region is inhabited by species from two physiographic provinces with distinct altitude features; therefore, most amphibian species co-occur at intermediate altitudes with the highest richness.
Primary	(prim)	(temp) + (date)	The amphibian community, in the study region, is represented by species mostly adapted to the original natural environments. Therefore, greatest species richness would be found in landscapes with greater proportion of primary vegetation.
Secondary	(sec) + $(\text{sec})^2$	(temp)	The amphibian community is composed by resilient species capable of inhabiting secondary vegetation regrowth. Therefore, greater species richness would be recorded in zones with high proportion of secondary vegetation.
Crops	(crop) + $(\text{crop})^2$	(humd)	The amphibian community is composed by species with high or moderate tolerance to agricultural landscapes. Therefore, highest species richness would be recorded in zones with high to intermediate proportion of crops.
Livestock	(lives) + $(\text{lives})^2$	(humd)	The amphibian community is composed by species with high or moderate tolerance to induced pasture in the landscape. Therefore, highest species richness would be recorded in zones with high or intermediate proportion of

pasture.

Table 2. Multi-Species Occupancy Models, considering different environmental variables, developed for explaining the amphibian richness patterns in riparian zones of Northwest Michoacán, Mexico. We show the Watanabe-Akaike Information Criteria value (WAIC) and the potential number of species (*N*); when the upper limit (*M*) is 47 and 150, and their 95% credibility intervals. Bold letters correspond to the model with greater support and more accurate estimation.

Model	WAIC	*N* (2.5% — 97.5% CI)	
		M = 47	*M* = 150
Crops	**1869.1**	**25 (20 — 42)**	**26 (20 — 49)**
Ambystoma	1870.46	32 (21 — 46)	53 (23 —141)
Livestock	1875.49	25 (20 — 44)	25 (20 — 53)
Secondary	1878.72	29 (21 — 46)	33 (21 — 121)
Primary	1889.8	27 (21 — 44)	26 (20 — 65)
Altitude	1900.98	38 (24 — 47)	76 (28 — 145)

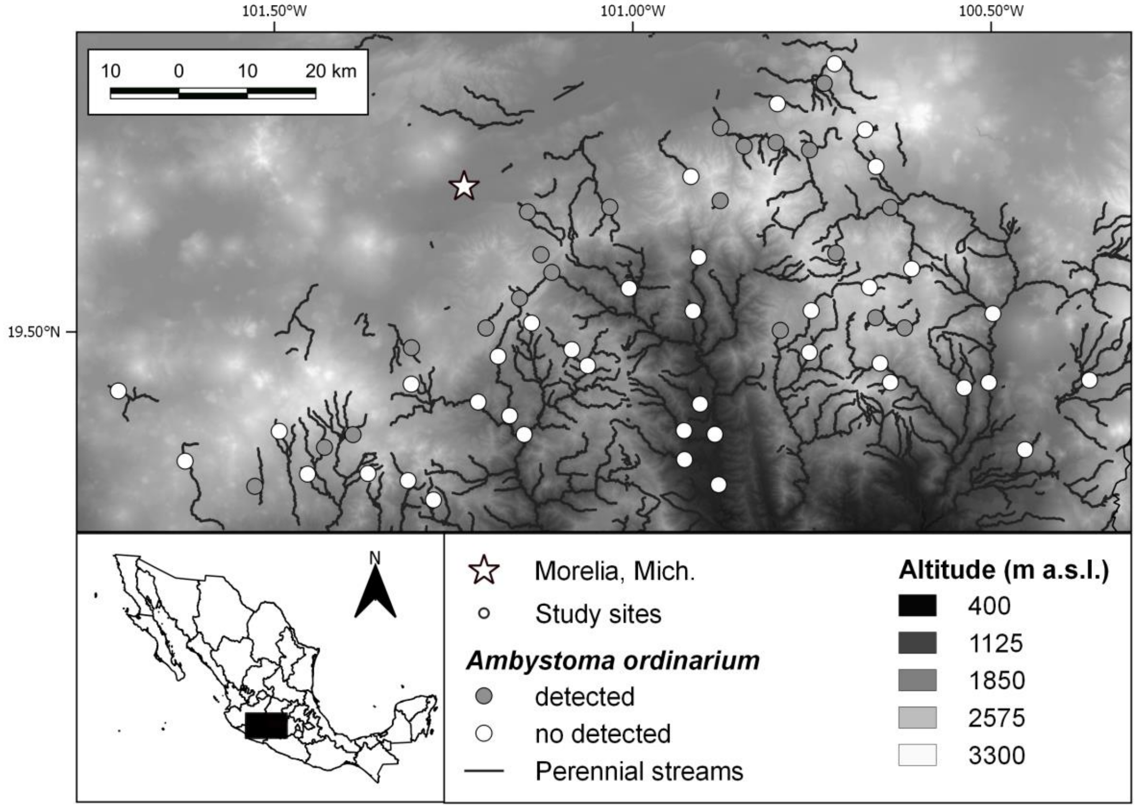

Figure 1. Study region in Northwest Michoacán, Mexico. Each sampling unit, its altitude, and the detection of *A. ordinarium* are shown.

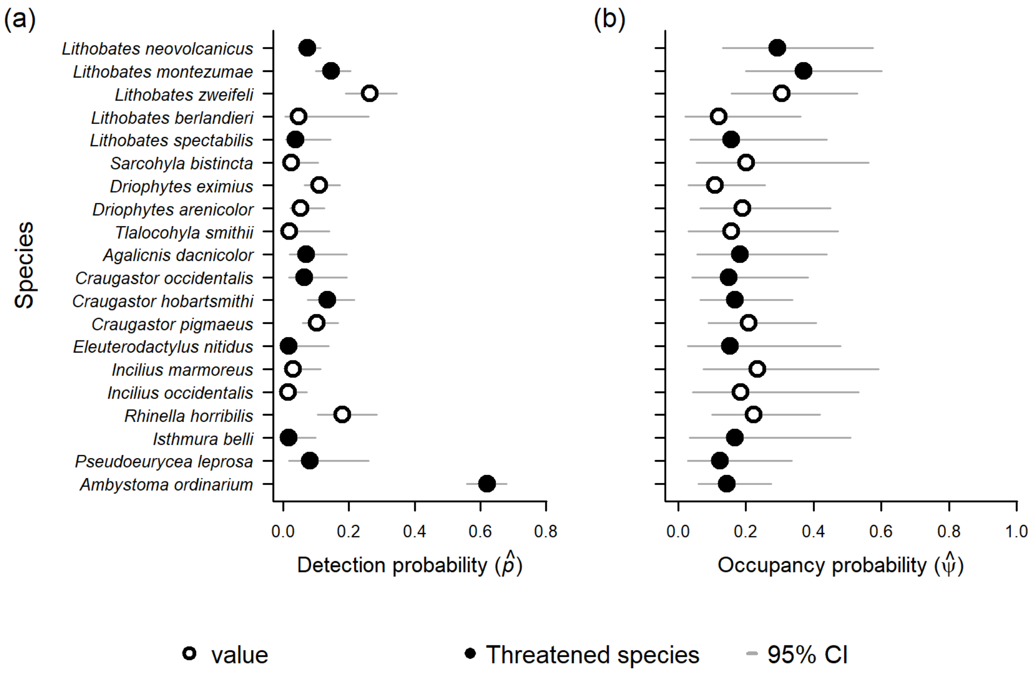

Figure 2. Mean probability estimated of (a) detection and (b) occupancy for each amphibian species in all sampling units.

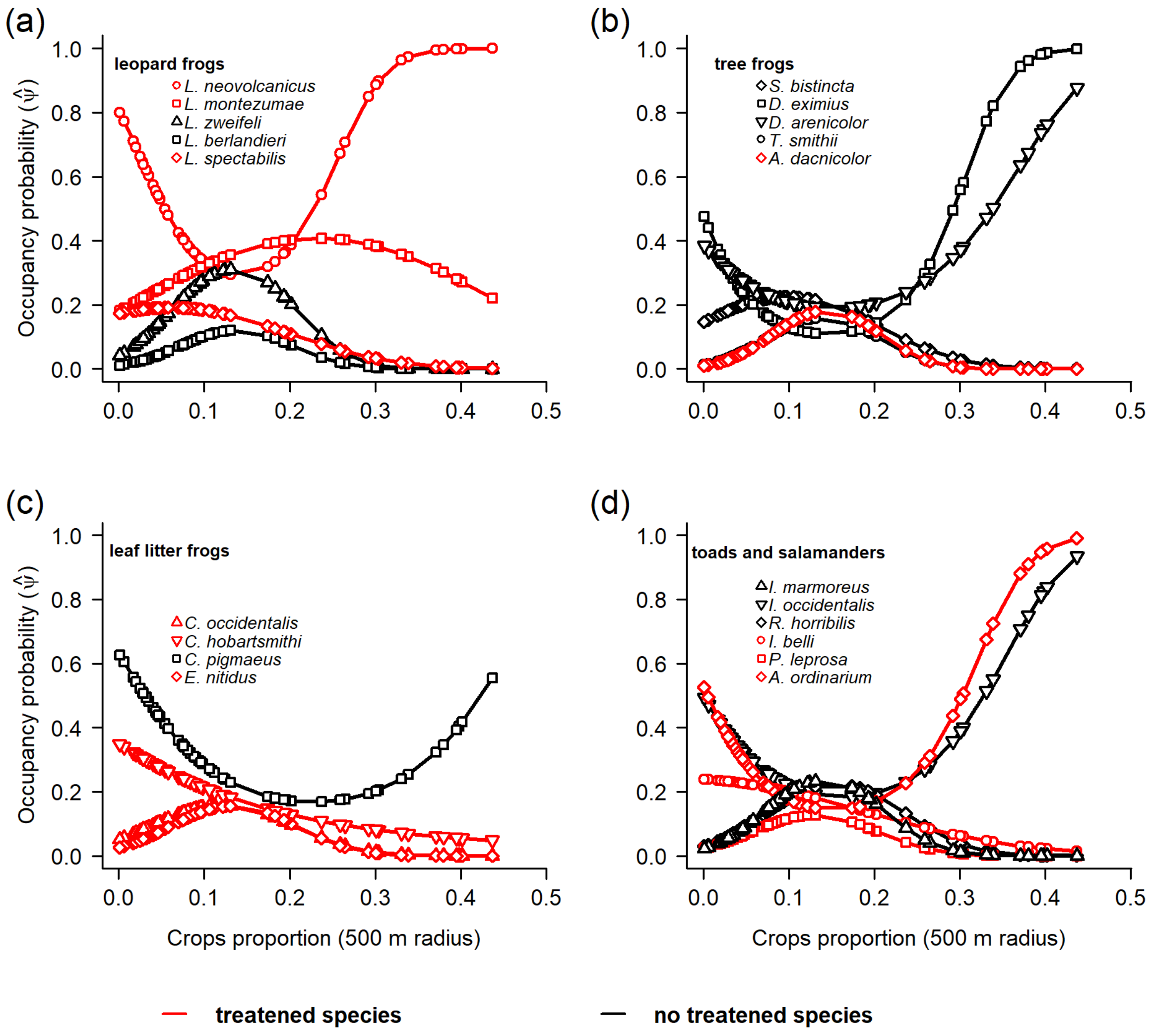

Figure 3. Linear and quadratic effect of crop proportion on occupancy of 20 amphibian species detected. The figure shows the response of each species in the following categories (a) leopard frogs, (b) tree frogs, (c) leaf litter frogs and (d) toads and salamanders.

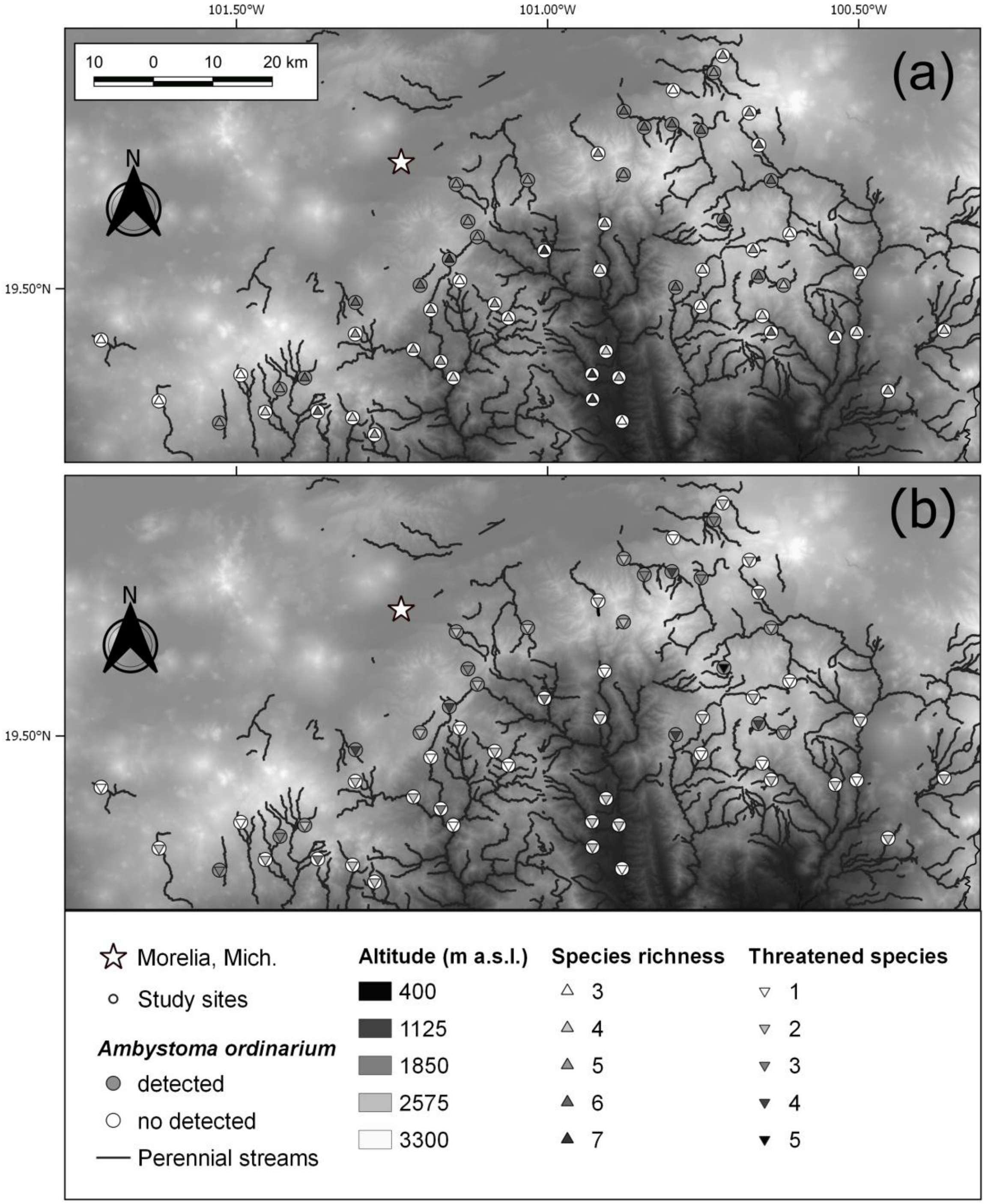

Figure 4. Estimated values for (a) species richness and (b) number of species at risk for each sampling unit.

Capítulo 3 | Supporting Information for **“Habitat modification and amphibian richness along riparian areas of Central Mexico: conservation priorities”**

Marco Tulio Oropeza-Sánchez, Ireri Suazo-Ortuño, Julieta Benítez-Malvido, Roberto Muguía-Steyer & Erandi Monroy-Hernández

Submitted to *Ecological Research*

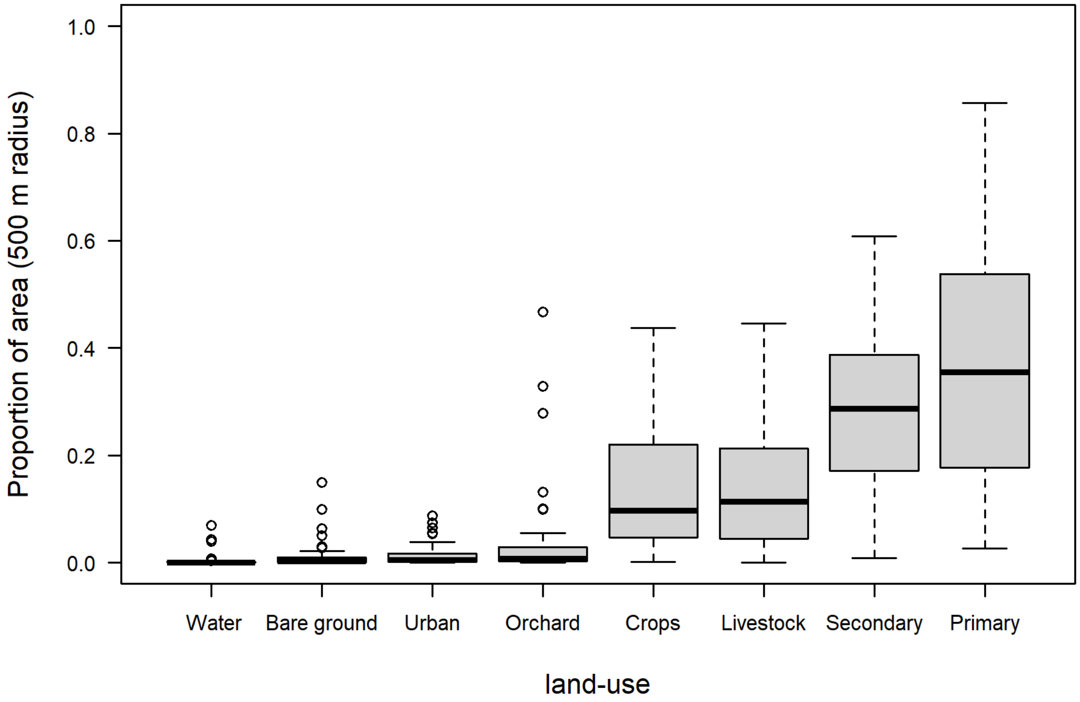

Figure s1. Proportion of each land-use type on a 500 m radius for the 60 sampling units.

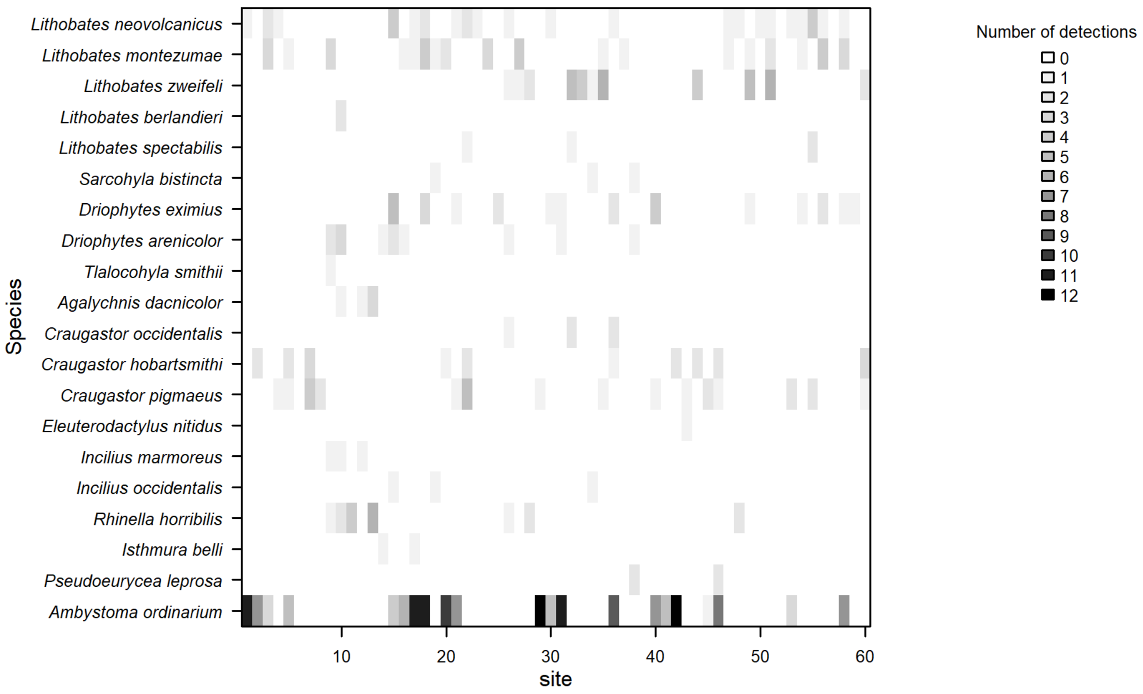

Figure 2S. Detection/no detection records for 20 amphibian species detected on riparian zones from Northwest Michoacán state.

```
##############################################
### Multi-Species Occupancy Models for amphibians ###
### from Northwest of Michoacan, Mexico 2020 #######
####  for "Habitat modification and amphibian #######
###### richness along riparian areas of ############
#### Central Mexico: conservation priorities"#######
#############################################


library("coda")
library("boa")
library("plot.matrix")
library("psycho")
library("MCMCpack")
library("ggmcmc")
library("grid")
library("devtools")
library("R2jags")
library('nimble')
library('MCMCvis')


data <- read.table("anf_div.csv", header = T, sep = ",") #data set

str(data) # data structure


#List of species


(species.list <- levels(as.factor(data$latname))) # alphabetic list of scientific names


(spec.name.list <- tapply(data$specid, data$latname, mean)) # species ID


(spec.id.list <- unique(data$specid))    # ID list


(ordered.spec.name.list <- spec.name.list[order(spec.name.list)]) # ID-order list


DET <- as.matrix(data[,7:18])  # detection events from 2018-2019


# array 3D: site x rep x species


nsite <- 60                    # number of sites
```

```
nrep <- 12                        # number of replicate surveys


nspec <- length(species.list)   # 20 species occur in the data


Y <- array(NA, dim = c(nsite, nrep, nspec)) # data array


for(i in 1:nspec){          # data organization
  Y[,,i] <- DET[((i-1)*nsite+1):(i*nsite),]
}
dimnames(Y) <- list(NULL, NULL, names(ordered.spec.name.list))


# frecuency of samples for every site
table(nsurveys <- apply(Y[,,1], 1, function(x) sum(!is.na(x))))


# number of sites observed for each speies
histor <- apply(Y, c(1,3), max, na.rm = TRUE)## detectión history by species

histor[histor == -Inf] <- NA  ##eliminated non logical values

sort(obs.occ <- apply(histor, 2, sum, na.rm = TRUE))#total detection by species


####species detection in every site

det <- apply(Y, c(3,1), sum, na.rm = TRUE)

####detection graphs####

mpalet <- colorRampPalette(c("white","blue", "red")) #color combination


m <- matrix(c(1,2),nrow = 1,ncol = 2,byrow = TRUE) ##panel structure


layout(mat = m, widths = c(0.9,0.2))##dimensions by row
```

```
par(mar = c(4,13,2,4), cex= 0.8, ann = T, xaxt = "n", tcl=-0.5,mgp=c(1.5,1,0))

plot(det, key = NULL, col = mpalet(13), main = "", border = F,
    ylab = "", xlab = "", las =2, font = 3, axes = F)

x <- seq(10,60,10)

box()

axis(1, xaxt = "s",at=x,labels=x, col.axis="black", las=1,# x axis values
    lty = 1, tcl=-0.5,mgp=c(1.5,1,0))

title(xlab="site", line=2.2, cex.lab=1.3)

title(ylab="Species", line= 11, cex.lab=1.3)

#Add legend
par(mar=c(2,1,2,1), cex= 1)

plot(NULL)

legend(x="top", title = "Number of detections",
      legend=c(0:12), xjust = 0.5,
      fill= mpalet(13), box.lty=0,
      bg = NULL, horiz = F, inset = 0,
      x.intersp = 0.4, cex = 0.8)

# Occurrence frecuence plot
par(mfrow = c(1,1),mar=c(5,5,2,2), cex= 0.8, mgp=c(2.5,1,0), xaxt = "s")

plot(sort(obs.occ), xlab = "Species number", ylab = "Number of quads with detections")
```

```
# Redefining nspec as species observed
( nspec <- dim(Y)[3] )

#Detection histories detail
str(Y)

# number of species by site
(histor <- apply(Y, c(1,3), max, na.rm = TRUE))

histor[histor == "-Inf"] <- NA

sort(C <- apply(histor, 1, sum))     # Compute and print sorted species counts

##Observed richness plot###
plot(table(C), xlim = c(0, 5), ylim = c(0,25), bty = "l",
    xlab = "Observed number of species", ylab = "Number of quadrats", frame = F)

abline(v = mean(C, na.rm = TRUE), col = "blue", lwd = 3)##observed richness mean

#####################Occupancy model for community #############

ysum <- apply(Y, c(1,3), sum, na.rm = T) # Collapse to detection frequency

nz <- 27  # Number of potential species in community, later we change this value to 130
        #to evaluate the effect of potrntial community size in N estimate

M <- nspec + nz # Size of augmented data set ('supercommunity')

# environmental variables
orig.ele <- data$elev[1:nsite]
```

```
ele <- data.frame(scale(orig.ele))[,,2]

orig.forest <- data$prim_500[1:nsite]

forest <- data.frame(scale(orig.forest))[,,2]

orig.cult <- data$cult_500[1:nsite]

cult <- data.frame(scale(orig.cult))[,,2]

orig.sec <- data$second_500[1:nsite]

sec <- data.frame(scale(orig.sec))[,,2]

orig.liv <- data$livest_500[1:nsite]

liv <- data.frame(scale(orig.liv))[,,2]

#event variables
temp <- scale(cbind(data$temp_1, data$temp_2, data$temp_3,
            data$temp_4, data$temp_5, data$temp_6,
            data$temp_7, data$temp_8, data$temp_9,
            data$temp_10, data$temp_11, data$temp_12))[1:nsite,]

humd <- scale(cbind(data$humd_1, data$humd_2, data$humd_3,
            data$humd_4, data$humd_5, data$humd_6,
            data$humd_7, data$humd_8, data$humd_9,
            data$humd_10, data$humd_11, data$humd_12))[1:nsite,]


date <- scale(cbind(data$date_1, data$date_2, data$date_3,
            data$date_4, data$date_5, data$date_6,
            data$date_7, data$date_8, data$date_9,
            data$date_10, data$date_11, data$date_12))[1:nsite,] /366*360#transform to radians


#correlation test
```

```
library(corrplot)

cor(c(temp),c(humd))

cor(c(date),c(humd))

cor(c(temp), c(date))

yaug <- array(0, dim=c(nsite, nrep, nspec+nz)) # array with only zeroes

yaug[,,1:nspec] <- Y ##include data of detected species

missings <- is.na(yaug[,,1]) #

for(k in (nspec+1):(nspec+nz)){#data of unobserved species
  yaug[,,k][missings] <- NA
}

##data for analysis
str( win.data1 <- list(y = yaug, nsite = nrow(ysum), nrep = 12,nspec = nspec,
                       nz = nz,  M = nspec + nz, forest = forest,
                       sec = sec, cult = cult, liv = liv, ele = ele,
                       temp = temp, humd = humd,date = date))

wst <- rep(1, nspec+nz)       # Simply set everybody at occurring

zst <- array(1, dim = c(nsite, nspec+nz)) # ditto

############### code for test crops: linear and quadratic effect ###############

code.crops <-  nimbleCode({
  # Priors
  omega ~ dunif(0,1)
```

```
# Priors for species-specific effects in occupancy and detection

for(k in 1:M){
  lpsi[k] ~ dnorm(mu.lpsi, tau.lpsi) # Hyperparams describe community
  betalpsi1[k] ~ dnorm(mu.betalpsi1, tau.betalpsi1)
  betalpsi2[k] ~ dnorm(mu.betalpsi2, tau.betalpsi2)
  lp[k] ~ dnorm(mu.lp, tau.lp)
  betalp1[k] ~ dnorm(mu.betalp1, tau.betalp1)
}

# Hyperpriors
# For the model of occupancy
mu.lpsi ~ dnorm(0,0.01)
tau.lpsi <- pow(sd.lpsi, -2)
sd.lpsi ~ dunif(0,100)
mu.betalpsi1 ~ dnorm(0,0.1)
tau.betalpsi1 <- pow(sd.betalpsi1, -2)
sd.betalpsi1 ~ dunif(0, 100)
mu.betalpsi2 ~ dnorm(0,0.1)
tau.betalpsi2 <- pow(sd.betalpsi2, -2)
sd.betalpsi2 ~ dunif(0,100)


# For the model of detection
mu.lp ~ dnorm(0,0.1)
tau.lp <- pow(sd.lp, -2)
sd.lp ~ dunif(0, 100)
mu.betalp1 ~ dnorm(0,0.1)
tau.betalp1 <- pow(sd.betalp1, -2)
sd.betalp1 ~ dunif(0,100)
```

```
# Superpopulation process: Ntotal species sampled out of M available
for(k in 1:M){
  w[k] ~ dbern(omega)
}

# Ecological model for true occurrence (process model)
for(k in 1:M){
  for (i in 1:nsite) {
    logit(psi[i,k]) <- lpsi[k] + betalpsi1[k] * cult[i] + betalpsi2[k] * pow(cult[i],2)
    mu.psi[i,k] <- w[k] * psi[i,k]
    z[i,k] ~ dbern(mu.psi[i,k])
  }
}
# Observation model for replicated detection/nondetection observations
for(k in 1:M){
  for (i in 1:nsite){
    for(j in 1:nrep){
      logit(p[i,j,k]) <- lp[k] + betalp1[k] * humd[i,j]
      mu.p[i,j,k] <- z[i,k] * p[i,j,k]
      y[i,j,k] ~ dbern(mu.p[i,j,k])
    }
  }
}

n0 <- sum(w[(nspec+1):(nspec+nz)]) # Number of unseen species
Ntotal <- sum(w[1:M]) # Total metacommunity size

# we do this for nz [ 250 (i.e., M [ 395)
lpsiS[1:(nspec+1)] <- lpsi[1:(nspec+1)]
betalpsi1S[1:(nspec+1)] <- betalpsi1[1:(nspec+1)]
betalpsi2S[1:(nspec+1)] <- betalpsi2[1:(nspec+1)]
```

```
  lpS[1:(nspec+1)] <- lp[1:(nspec+1)]
  betalp1S[1:(nspec+1)] <- betalp1[1:(nspec+1)]
})
inits <- function() list(z = zst, w = wst, lpsi = rnorm(n = nspec+nz),
                         betalpsi1 = rnorm(n = nspec+nz),
                         betalpsi2 = rnorm(n = nspec+nz),
                         lp = rnorm(n =nspec+nz),
                         betalp1 = rnorm(n = nspec+nz))

initsValues <- inits()

Rmodel <- nimbleModel(code.crops, constants = win.data1, inits = initsValues,
                      calculate = F)

## Configure and construct the MCMC configuration
#object for construct an MCMC object
mcmcConf <- configureMCMC(Rmodel,
                          enableWAIC = TRUE)

#define and add monitors to estimate WAIC
monitors <- c('omega', 'Ntotal','mu.lpsi', 'sd.lpsi',
              'mu.betalpsi1', 'sd.betalpsi1',
              'mu.betalpsi2', 'sd.betalpsi2',
              'mu.lp', 'sd.lp', 'mu.betalp1',
              'sd.betalp1', 'lpsi', 'z', 'lp',
              'betalp1', 'betalpsi1', 'betalpsi2')

mcmcConf$addMonitors(monitors)

#set thin value
mcmcConf$setThin(30)
```

```
#define an uncopilated MCMC object
Rmcmc <- buildMCMC(mcmcConf, enableWAIC = TRUE)

##compile the MCMC funtion
C.mcmc <- compileNimble(Rmodel)

#provide the project to the compiled
div.MCMC <- compileNimble(Rmcmc, project=C.mcmc)

#function for reduce the memory usage
nimbleOptions(clearNimbleFunctionsAfterCompiling = TRUE)

## run model
system.time(crops.nimble <- runMCMC(div.MCMC, niter=300000,
                                    nchains=3,
                                    nburnin=150000,
                                    samples = T,
                                    samplesAsCodaMCMC = T,
                                    summary = T,
                                    WAIC=TRUE))

crops.nimble$WAIC
#[1] 1869.106

###r-hat values
gelman.diag(crops.nimble$samples[,c(1,237:247)], multivariate=FALSE)

#traceplots
MCMCtrace(crops.nimble$samples[,c(1,237:247)], pdf = T, type = 'both',
          filename = 'crop.N47-msom-2021', Rhat = T, n.eff = T)
```

```
#posterior values estimate
summary(crops.nimble$samples[,c(1,237:247)])

#### posterior p and psi ####

#posterior values of community p and CI
det.amb <- summary(crops.nimble$samples[,c(143:163)],
                   quantiles = c(0.025, 0.25, 0.5, 0.75, 0.975))

det.anf <- as.data.frame(plogis(cbind('det' = det.amb$statistics[c(1:20),1],
                                      'LCI' = det.amb$quantiles[c(1:20),1],
                                      'UCI' = det.amb$quantiles[c(1:20),5])))

(spec.name <- tapply(data$specid, data$latname, mean)) # species ID

(ordered.spec <- spec.name[order(spec.name)]) # ID-order list

det.anf$name <- names(ordered.spec)

m <- matrix(c(1,2,3,3),nrow = 2,ncol = 2,byrow = T) ## panel sructure

layout(mat = m, widths = c(0.5,0.5), heights = c(0.8,0.2))##row dimensions

sp <- c(1:20)

par( mar = c(4,14,2,2), yaxt = "n", cex = 0.8,ann = T,
     tcl=-0.5,mgp=c(3,1,0) )

plot(det.anf[,1], sp, col = "black", cex= 2, lwd=2, ylim = c(20,1),
     bty = "l", xlim = c(0,0.77), las = 1, cex.lab=1.3, ylab = "",
```

```
     xlab = expression(paste("Detection probability (", italic(hat(p)),")", sep="")))

segments(det.anf[,2],sp,  det.anf[,3], sp,  col = "darkgrey")#set CI

points(det.anf[,1], sp, pch = 21, col = "black",cex= 2, bg = "white" ,lwd =2)

axis(2, at = sp, labels = det.anf[,4], yaxt = "s", las  = 1, font = 3, cex = 1)

sig1 <- det.anf[,1] < 0.06

points(det.anf[,1][sig1 == T], sp[sig1 == T], pch = 21, col = "black",cex= 2, bg = "black" ,lwd =2)

title(ylab="Species", line= 12, cex.lab=1.5)

mtext("(A)", side = 3, line = -2, outer = T, at = 0.02, cex = 1.3)



#posterior values of community psi and CI

psi.anf <- summary(crops.nimble$samples[,c(190:209)],
                              quantiles = c(0.025, 0.25, 0.5, 0.75, 0.975))

psi.anf <- as.data.frame(plogis(cbind('det' = psi.anf$statistics[c(1:20),1],
                                      'LCI' = psi.anf$quantiles[c(1:20),1],
                                      'UCI' = psi.anf$quantiles[c(1:20),5])))

psi.anf$name <-names(ordered.spec)

par( mar = c(4,4,2,8), yaxt = "n",cex = 0.8,ann = T,
     tcl=-0.5,mgp=c(3,1,0)  )
plot(psi.anf[,1], sp, col = "black", cex= 2, lwd=2, ylim = c(20,1),
```

```
     bty = "l", xlim = c(0,0.963), las = 1, cex.lab=1.3, ylab = "",
     xlab = expression(paste("Occupancy probability (", italic(hat(psi)),")", sep="")))

axis(2, at = sp, labels = rep(",20), yaxt = "s", las  = 1, font = 3, cex = 1)

segments(psi.anf[,2],sp,  psi.anf[,3], sp,  col = "darkgrey")

sig2 <- (psi.anf[,3] - psi.anf[,2]) > 0.5 ##selection of species estimates with long CI

points(psi.anf[,1], sp, pch = 21, col = "black",cex= 2, bg = "white" ,lwd =2)

points(psi.anf[,1][sig1 == T], sp[sig1 == T], pch = 21, col = "black",cex= 2, bg = "black" ,lwd =2)

mtext("(B)", side = 3, line = -2, outer = T, at = 0.52, cex = 1.3)

####add legend

par(mar = c(1,3,1,1), cex.axis = 1.3, cex.lab = 1.5)

plot(NULL)

legend(x = "center",
       col =  c("black","black","darkgrey"), lty = c(NA,NA,1),
       pch = c(21,16,NA), cex = 1.5, lwd = 2,
       legend = c(" value",
                  expression(paste("", italic(hat(p))," < 0.06", sep="")),
                  "95% CI"),
       seg.len = 0.4, xjust = 0.5,
       box.lty=0, text.width = 0.2,
       bg = NULL, horiz = T, inset = 0,
       x.intersp = 0.5)
```

```
##### response from community ####

###Linear effect of humidity

sp.p.humd <- as.data.frame(crops.nimble$summary$all.chains[c(2:21), c(1,4,5)])

sp.p.humd <- summary(crops.nimble$samples[,c(2:21)],
                   quantiles = c(0.025,  0.5,  0.975))

sp.p.humd <- as.data.frame(cbind('det' = sp.p.humd$quantiles[c(1:20),2],
                                     '95LCI' = sp.p.humd$quantiles[c(1:20),1],
                                     '95UCI' = sp.p.humd$quantiles[c(1:20),3]))

m <- matrix(c(1,2,3,4),nrow = 4,byrow = T) ##panel structure

layout(mat = m, heights = c(0.35,0.35,0.5,0.2))

par(mar = c(2,5,2,2),  ann = T,
    tcl=-0.5,mgp=c(2.5,0.8,0), xaxt = "n", yaxt ='s')

plot(1:20,sp.p.humd[,1],  ylim = c(-1, 1),
     ylab = "Linear effect of \nHumidity on detection", xlab =
       "", pch = 16, las = 1, cex.lab = 1.3, cex.axis = 1.1)

axis(1, at = c(1:20), labels = rep('',20), xaxt = "s",
     las  = 1, font = 3, cex = 1, line = 0)

segments(1:20,sp.p.humd[,2],  1:20,sp.p.humd[,3], col = "grey", lwd = 2)

points(1:20,sp.p.humd[,1],  pch = 19)
```

```
sig.hum <- (sp.p.humd[,2] * sp.p.humd[,3]) > 0

segments((1:20)[sig.hum == 1], sp.p.humd[,2][sig.hum == 1],
        (1:20)[sig.hum == 1],sp.p.humd[,3][sig.hum == 1],
        col = "blue", lwd = 2)

mu.p.humd <- crops.nimble$summary$all.chains[237,c(1,4,5)]

abline(h = 0, lwd = 1.5, col = "black", lty =2)

abline(h = mu.p.humd[1], lwd = 1.5, col = "darkred")

abline(h = mu.p.humd[c(2,3)], lwd = 1.5, col = "darkred", lty = 2)

mtext("(A)", side = 3, line = -2, outer = T, at = 0.02, cex = 1.3)

###Linear effect of crops

sp.psi.crops <- as.data.frame(crops.nimble$summary$all.chains[c(48:67), c(1,4,5)])

sp.psi.crops <- summary(crops.nimble$samples[,c(48:67)],
                  quantiles = c(0.025, 0.5,  0.975))

sp.psi.crops <- as.data.frame(cbind('det' = sp.psi.crops$quantiles[c(1:20),2],
                            '95LCI' = sp.psi.crops$quantiles[c(1:20),1],
                            '95UCI' = sp.psi.crops$quantiles[c(1:20),3]))

plot(1:20,sp.psi.crops[,1],  ylim = c(-2.5, 2.5),
    ylab = "Linear effect of \nCrops on occupancy", xlab =
      "", pch = 16, cex.lab = 1.3, cex.axis = 1.1, las = 1)
```

```
axis(1, at = c(1:20), labels = rep(",20), xaxt = "s",
    las  = 1, font = 3, cex = 1, line = 0)

segments(1:20,sp.psi.crops[,2],   1:20,sp.psi.crops[,3], col = "grey", lwd = 2)

points(1:20,sp.psi.crops[,1],  pch = 19)

sig.crops <- (sp.psi.crops[,2] * sp.psi.crops[,3]) > 0

segments((1:20)[sig.crops == 1],sp.psi.crops[,2][sig.crops == 1],
        (1:20)[sig.crops == 1],sp.psi.crops[,3][sig.crops== 1],
        col = "black", lwd = 2)

mu.psi.crops <- crops.nimble$summary$all.chains[238,c(1,4,5)]

abline(h = 0, lwd = 1.5, col = "black", lty =2)

abline(h = mu.psi.crops[1], lwd = 1.5, col = "darkred")

abline(h = mu.psi.crops[c(2,3)], lwd = 1.5, col = "darkred", lty = 2)

mtext("(B)", side = 3, line = -20, outer = T, at = 0.02, cex = 1.3)



####Quadratic effect of crops

sp.psi.crops2 <- as.data.frame(crops.nimble$summary$all.chains[c(96:115), c(1,4,5)])

sp.psi.crops2 <- summary(crops.nimble$samples[,c(96:116)],
```

```
                        quantiles = c(0.025, 0.5, 0.975))

sp.psi.crops2 <- as.data.frame(cbind('psi' = sp.psi.crops2$quantiles[c(1:20),2],
                                   '95LCI' = sp.psi.crops2$quantiles[c(1:20),1],
                                   '95UCI' = sp.psi.crops2$quantiles[c(1:20),3]))

par(mar = c(7,5,2,2),  ann = T,
    tcl=-0.5,mgp=c(2.5,0.8,0), xaxt = "n")

plot(1:20, sp.psi.crops2[,1], ylim = c(-6, 6),
     ylab = "Quadratic effect of \nCrops on occupancy", xlab =
       "", pch = 16, cex.lab = 1.3, cex.axis = 1.1, las =1)

axis(1, at = c(1:20), labels = rep('',20), xaxt = "s",
     las  = 1, font = 3, cex = 1, line = 0)

segments(1:20, sp.psi.crops2[,2], 1:20,sp.psi.crops2[,3],  col = "grey", lwd = 2)

points(1:20, sp.psi.crops2[,1], pch = 19)

sig.crops2 <- (sp.psi.crops2[,2] * sp.psi.crops2[,3]) > 0

segments((1:20)[sig.crops2 == 1],sp.psi.crops2[,2][sig.crops2 == 1],
          (1:20)[sig.crops2 == 1],sp.psi.crops2[,3][sig.crops2 == 1],
          col = "black", lwd = 2)
mu.psi.crops2 <- crops.nimble$summary$all.chains[239,c(1,4,5)]

abline(h = 0, lwd = 1.5, col = "black", lty =2)

abline(h = mu.psi.crops2[1], lwd = 1.5, col = "darkred", lty = 1)
```

```r
abline(h = mu.psi.crops2[c(2,3)], lwd = 1.5, col = "darkred", lty = 2)

par(mar = c(1,3,3,1), cex.axis = 1.3, cex.lab = 1.5)

mtext("(C)", side = 3, line = -39, outer = T, at = 0.02, cex = 1.3)

(spec.name.abr <- tapply(data$specid, data$abr, mean)) # species ID

(ordered.spec.abr.list <- spec.name.abr[order(spec.name.abr)]) # ID-order list

text(x = 1:20,
    y = par("usr")[3] - 0.45,
    labels = names(ordered.spec.abr.list),
    xpd = NA, adj = 1.1, font = 3,
    ## Rotate the labels by 35 degrees.
    srt = 45,
    cex = 1)

title(xlab="Species", line= 6, cex.lab=1.3)

#add legend

plot(c(0,10),c(0,1),type = 'n', axes = F,xlab = ", ylab = ",
    main = 'Estimate coefficients', cex = 3)
legend(x = "center",
      legend=c("species coefficient","95% CI",
             "community coefficient", "95% CI community coefficient",
             "95% CI zero value no incluided",
             "85% CI zero value no incluided"),
      col=c("black", "darkgrey","darkred", "darkred","black","blue"),
      pch = c(19,NA,NA,NA,NA,NA), lty=c(NA,1,1,2, 1,1),
```

```
        cex=1.3, box.lty=0, text.font = 1, lwd = 1.5,xjust=0, yjust=0,text.width = 2.2,
        bg = NULL, horiz = F, x.intersp=0.3, seg.len = 1.5, ncol = 2)

##### Predicted values for species occupancy #####

predS <- array(NA, dim = c(60,nspec))

coef.psi <- crops.nimble$summary$all.chains[c(190:209),1]# lpsi values

coef.crops <- crops.nimble$summary$all.chains[c(49:68), 1]# beta1 values

coef.crops2 <- crops.nimble$summary$all.chains[c(96:115), 1]# beta2 values

psi.coef <- cbind('int.psi' = coef.psi,
                            'beta1' = coef.crops,  ## bind data
                    'beta2' = coef.crops2)

for(i in 1:nspec){    # estimate values for each species
predS[,i] <- plogis(psi.coef[i,1] + psi.coef[i,2] * cult +
                        psi.coef[i,3] * cult^2)
}

predS <- (as.data.frame(predS))

colnames(predS)<- row.names(det)

m <- matrix(c(1,2),nrow = 2,byrow = TRUE) #el

layout(mat = m,heights = c(0.8,0.2))##

par(mar = c(5,5,2,2), cex.lab = 1.3, cex.axis = 1.3)
```

```
linePallet <- colorRampPalette(c("orange","red","green", "blue","black"))

cl <- linePallet(20)

sect <- rep(21:25, 4)

plot(orig.cult, predS[,1], bty = 'l',
    las = 1,type = 'n', xlim = c(0,0.481),
     ylim = c(0,1), xlab = "Crops",
     ylab = expression(paste("Occupancy probability ( ", italic(hat(psi)),")", sep="")))

for (i in 1:20) {#responde estimate for every species
  lines(smooth.spline( predS[,i] ~ orig.cult),
        col = cl[i],
        #lty = sect[i],
        lwd = 2)#;
  points(predS[,i] ~ orig.cult, col = cl[i],
        lwd = 2, pch = sect[i], bg = "white")

}

par(mar = c(1,1,1,1), cex.axis = 1.3, cex.lab = 1.5)

plot(c(0,10),c(0,1),type = 'n', axes = F,xlab = '', ylab = '',
     main = 'Species', cex = 1.8)

(spec.name.abr <- tapply(data$specid, data$abr, mean)) # species ID

(ordered.spec.abr.list <- spec.name.abr[order(spec.name.abr)]) # ID-order list
```

```
legend(x = "center",
       legend=names(ordered.spec.abr.list),
       pch = sect,
       #lwd = 2,
       col = cl,
       cex=0.8, box.lty=0, text.font = 3, xjust=0,
       yjust=0,text.width = 2, y.intersp=.9,
       bg = NULL, horiz = F, x.intersp=.5,
       seg.len = 1.2, ncol = 4)

##############posterior Nsites###################

posterior_N <- as.matrix(crops.nimble$samples)##posterior z data

nsampb <- dim(posterior_N)[1]

zSite <- array(NA, dim = c(nsite, M, nsampb))

posterior_N[1,]

for(j in 1:nsampb){ # Fill z matrix by column (default)
  cat(paste("\nMCMC sample", j, "\n"))
  zSite[,,j] <- posterior_N[j, 248:3067]
}

Nsit <- array(NA, dim = c(nsite, nsampb))

for(k in 1:nsampb){#species richness for every site
  for(i in 1:nsite){
    Nsit[i,k] <- sum(zSite[i,,k])
  }
```

```
}

Rich <- apply(Nsit, 1, median, na.rm = TRUE) # Post. mean of richness at every site

RichSD <- apply(Nsit, 1, sd, na.rm = TRUE) # Post. sd of of richness at every site

criRich <- apply(Nsit, 1, function(x) quantile(x, prob = c(0.025, 0.975), na.rm =
                                              TRUE)) # CRI

posterior_Nsite <- cbind('post. mean' = Rich, 'post. sd' = RichSD,
                         '2.5%' = criRich[1,], '97.5%' = criRich[2,],
                         'East' = data$Este[c(1:60)],
                         'North' = data$Norte[c(1:60)])

par(mfrow = c(1,1), mar = c(5,5,2,2), yaxt = 's')

plot(orig.cult, posterior_Nsite[,1] , las = 1,
     ylim = c(0,15), pch = 16, xlab = "Proportion of crops",
     ylab = "Species richness")

segments(orig.cult,posterior_Nsite[,3],
         orig.cult, posterior_Nsite[,4],  col = "darkgrey")

lines(smooth.spline( posterior_Nsite[,1] ~ orig.cult,
                     w = 2 / posterior_Nsite[,2]),
      lwd = 2, col = "blue")

##for threatened species

ztreat <- zSite[,c(1,2,5,10,11,12,14,18,19,20),] ##species at treat
```

```
Ntreat <- array(NA, dim = c(nsite, nsampb))


for(k in 1:nsampb){
  for(i in 1:nsite){ # Threatened species for every site
    Ntreat[i,k] <- sum(ztreat[i,,k], na.rm = TRUE)
  }
}


SiteTreat <- apply(Ntreat, 1, median, na.rm = TRUE) # Post. mean of threatened species for every
site


treatSD <- apply(Ntreat, 1, sd, na.rm = TRUE) # Post. sd of threatened species for every site


TreatCI <- apply(Ntreat, 1, function(x) quantile(x, prob = c(0.025, 0.975), na.rm =
                                                  TRUE)) # CRI
posterior_Ntreat <- cbind('post. mean' = SiteTreat,
                          'post. sd' = treatSD,
                          '2.5%' = TreatCI[1,], '97.5%' = TreatCI[2,],
                          'East' = data$Este[c(1:60)],
                          'North' = data$Norte[c(1:60)])
par(mfrow = c(1,1), mar = c(5,5,2,2))


plot(orig.cult, posterior_Ntreat[,1] , las = 1,
     ylim = c(0,10), pch = 16, xlab = "Proportion of crops",
     ylab = "Species at risk")


segments(orig.cult,posterior_Ntreat[,3],
         orig.cult, posterior_Ntreat[,4],  col = "darkgrey")


####richness for every site and detection of Ambystoma ordinarium ####


amby.hist <- data[c(1141:1200), c(7:18)]#Ambystoma ordinarium data
```

```
#Ambystoma ordinarium detection history

amb.det <- cbind('site' = c(data[c(1:60), 1]) ,
                 'det' = apply(amby.hist, 1, max, na.rm = T))

dataAmb <- as.data.frame(cbind(amb.det,Rich,##bind data
                               SiteTreat))

dataAmb$Rich <- as.numeric(as.character(dataAmb$Rich))

dataAmb$SiteTreat <- as.numeric(as.character(dataAmb$SiteTreat))

dataAmb$det[dataAmb$det == "0"] <- c('no detected')#do it category

dataAmb$det[dataAmb$det == "1"] <- c('detected')

summary(dataAmb)
boxplot(dataAmb$Rich ~ dataAmb$det, ylab = 'Species richness',
        xlab = ",yaxt = "s")

boxplot(dataAmb$SiteTreat ~ dataAmb$det,ylab = 'Threatened species',
        xlab= ",yaxt = "s")

ambymod <- glm(Rich ~ det, family = quasipoisson, data = dataAmb)

anova(ambymod, test = "Chi")

threatmod <- glm(SiteTreat ~ det, family = quasipoisson, data = dataAmb)

anova(threatmod, test = "Chi")
```

Capítulo 4

Land-use change and amphibian diversity in modified riparian vegetation

Marco Tulio Oropeza-Sánchez, Ireri Suazo-Ortuño, Julieta Benítez-Malvido

Abstract

Land-use changes alter the species composition, the functions, and the phylogenetic structure of amphibian assemblages, being these changes especially harmful along riparian habitats. In Northeast Michoacán, Mexico, the proportion of crop land-cover in the landscape affects the distribution of amphibian species. Using the endemic salamander *Ambystoma ordinarium* as a flagship species and protecting the riparian vegetation where it inhabits, could favor the persistence of other amphibian species. Nevertheless, the implementation of effective conservation strategies requires the estimation of different metrics of biological diversity including beta, functional and phylogenetic diversity. In this study we estimated amphibian diversity metrics along riparian vegetation surrounded by different proportion of croplands. Furthermore, we estimated if amphibian diversity metrics were associated to the incidence of *A. ordinarium*. The results showed that amphibian assemblages were associated to crop coverage following a humped-shaped pattern for all diversity metrics, with high beta diversity and low functional and phylogenetic diversity values. In the presence of *A. ordinarium* amphibian assemblages showed higher values of functional and phylogenetic diversity than those in the absence of the salamander. These results highlight the relevance of *A. ordinarium* as a flagship species for the protection of associated amphibian species.

KEYWORDS: assemblages, conservation priorities, diversity metrics, modified landscapes, salamander, species at risk.

INTRODUCTION

Land-use change is the main threat to the maintenance of biodiversity. This process alters the structure and composition of species assemblage (IPBES 2019). These alterations include changes in species abundance, composition, and local extinction. Furthermore, some habitat specialist species are replaced by more generalist, disturbance tolerant species (Ceballos et al. 2017; Frishkoff et al. 2014; Hanski 2011). The function of species assemblages is defined from species morphological, physiological, and ethological traits, because land-use change modifies species composition, species functions are compromise too (Laliberté & Legendre 2010; Mumme et al. 2015). Shared traits among species frequently result from phylogenetic conservative traits (e. g., Kozak & Wiens 2010; Losos 2008; Sato et al. 2020). As consequence assemblages integrated by tolerant disturbance species and phylogenetically closely related species could possess lower resilience to further habitat disturbance (Forest et al. 2007; Winter et al. 2013). Since land-use change modifies numerous assemblages attributes the analysis of different diversity metrics is a valuable tool to develop effective conservation strategies.

Beta diversity is used for understanding changes in the patterns of compositional species assemblages and can help explaining how these changes are associated to land-use change (Socolar et al. 2016). Also, beta diversity components including species turnover and nestedness, are used to define the processes that shape assemblages and therefore, to select suitable conservation strategies (Bergamin et al. 2017). When the assemblages show a nestedness pattern (species loss or gain), the protection of areas with higher species richness could be the ideal option. In addition, when species turnover pattern is dominant (species substitution) the selection of multiple areas with complementary species could be the best option for conservation plans. In contrast, by employing metrics of functional diversity information about productivity and stability of a given ecosystem is provided (Mason et al. 2005; Tilman 2001). Lastly the metrics of phylogenetic diversity can be useful for understanding the evolutionary history of species assemblages, as well as the processes that originated them (Winter et al. 2013).

From 1970 to 2015 riparian habitats have diminished 35% worldwide, and Latin America is one of the most affected regions of the world with a loss of 59% (Darrah et al., 2019). The persistence of riparian habitats is critical for the survival of aquatic, semiaquatic and riparian-specialist species (Poff et al., 2011). Riparian habitats provide several ecosystem services, as well as resources for numerous faunal species (Brouwer et al., 2011; Land et al., 2016; McClure et al., 2015; Mokondoko et al., 2016; Suazo-Ortuño et al., 2011). For amphibians, the most threatened vertebrate group, riparian habitats are important, as they frequently represent a key habitat for the completion of their life cycles (Becker et al., 2007; Becker et al., 2010). Riparian habitats provide critical food and reproductive resources for amphibians, and in modified landscapes remnant riparian vegetation offers protection from desiccation (Boissinot et al., 2015; Gray & Smith, 2005; Peterman & Semlitsch, 2014; Suazo-Ortuño et al., 2011).

To face the threats to the maintenance of biodiversity, such as land use change, the first conservation challenge is identifying priority areas and/or hotspots. The high species diversity criterion is commonly employed to select priority areas for conservation, which is associated with a greater functional diversity (Myers et al. 2000; Tilman 2001). In turn, there is the rare species incidence criterion too. Rare species (i. e., with a small geographical range or local low abundance) are targets for conservation by the assumption of greater extinction risk (Mace et al. 2008). Although, rare species can be distinguished by significant functions performed in the ecosystems (e. g., top predators or keystone species; Jain et al. 2014; Lyons et al. 2005). In some cases, rare species that are charismatic have been classified within the flagship category to protect other species or even whole ecosystems within their distribution area (Bride et al. 2008).

In Michoacán State, Mexico, around 40% of original vegetation cover has been transformed to croplands and cattle pasture (INEGI, 2017). For the amphibians in Northeast Michoacan the proportion of crops in the landscape represents an important driver for their distribution (Oropeza-Sánchez unpub. data). Thus, analyzing different metrics of amphibian diversity is an opportunity to test the effect of land-use change in functional and phylogenetic diversity, and defining which areas are key to conserve. Among the Northeast Michoacan amphibians, the endemic salamander *Ambystoma ordinarium* is considered as a species at risk (IUCN, 2021). Because *Ambystoma* species are charismatic, categorizing *A. ordinarium* with the flagship category may be useful to protect riparian vegetation that could benefit other amphibian species (Oropeza-Sánchez unpub. data). Nevertheless, different metrics of biodiversity assessments are needed to propose *A. ordinarum* as a flagship species for amphibian conservation. To support this proposal the objectives of the present study were the following: i) to evaluate beta (and its components), functional and phylogenetic diversity of amphibian assemblages in riparian habitats surrounded by different proportion of cropland cover in landscapes of Northeast Michoacán, and ii) to determine if the incidence of *A. ordinarium* is associated to high amphibian diversity in riparian habitats.

METHODS

Study area

The study area was delimited by combining the projected area of occupancy of *Ambystoma ordinarium* (IUCN SSC Amphibian Specialist Group, 2015) and its potential distribution area in Northeast Michoacán (Escalera-Vázquez et al. 2018). The original vegetation of the study area consisted of pine forest, pine-oak forest, cloud mountain forest and deciduous forest. Elevation ranges from 700 to 3000 m a.s.l., the mean annual temperature varies from 10 to 26ºC and annual rainfall ranges from 600 to 1500 mm (Cuervo-Robayo et al., 2014a; 2014b).

Data collection

The sampling of amphibian species in the study area consisted in the selection of 60 sampling units along riparian zones. Considering the average dispersal capacity in amphibians, the selected stream sections were at least 3 km apart to ensure the spatial independence among riparian zones (Figure 1; Rittenhouse & Semlitsch, 2007). In each stream section a fixed 50 x 25 m plot was established alongside the stream. The combined area of these plots and the adjacent stream were considered as the sampling unit. To consider the heterogeneity of the landscape, we selected sites with different proportion of primary forest surrounding the sampling units.

From February 2018 to October 2019, we carried out 12 sampling events in each sampling unit. Search for amphibians was diurnal between 0900 and 1800 h, because of logistical problems (e.g., insecurity conditions). Therefore, the amphibian assemblages studied only included diurnal species. The amphibian searching was carried out by the inspection of terrestrial microhabitats including tree hollows, under logs and rocks, leaf litter and riverbanks; and inspection of aquatic microhabitats by using a 30 cm in diameter hand net, including the bottom of the stream and by removing roots and rocks. In each sampling unit an effort of 40 minutes/person per sampling event was used. We only recorded juveniles and adults; all specimens collected in the field were identified to the species level. Except for those species at risk, one individual of each species was deposited in the herpetological collection of the Universidad Michoacana de San Nicolás de Hidalgo. Scientific collecting permit number SGPA/DGVS/001450/18 granted by SEMARNAT. The guidelines for handling live amphibians in the field and laboratory followed the American Society of Ichthyologists and Herpetologists (2004).

Data analysis

Previously, we defined the incidence of each amphibian species in sampling units throughout six Multi-Species Occupation Models (Oropeza-Sánchez, unpublished data). In the selected models, we considered the lineal and quadratic effect of the proportion of cropland to explain occupancy probability; and air humidity to estimate the probability of detection for twenty amphibian species. The average sum of estimated occupation states values in each sample unit represents the species richness (Figure 2a). To define species incidence, and to carry out the statistical analyses, we considered the occupation state value ≥ 0.194 as an equivalent to the incidence of each species in each sampling unit (Figure 2b; obtained data are presented at detail in supplementary material).

Diversity metrics

Firstly, we used the Jaccard Index to estimate beta diversity as the mean dissimilarity of a given sampling unit contrasted with the rest of the sampling units (Baselga, 2012). Additionally, we estimated the contribution of species turnover and nestedness to the dissimilarity of each sampling unit.

To estimate functional diversity, we considered species morphological traits that may be associated to microhabitat use, reproductive strategy, and their biomass (Díaz-García et al. 2017; Suazo-Ortuño et al. 2018; Alvarez-Grzybowska et al. 2020). For each species sampled we recorded the following traits: microhabitat, respiration type, microhabitat used for spawning, the presence of free aquatic larvae, presence of interdigital membranes, presence of toe pads, and snout-vent length (SVL; mm) (Table 1). For the estimation of functional diversity at each sampling unit we used four complementary metrics: functional richness (FRich), functional evenness (FEve), functional divergence (FDiv) and functional dispersion (FDis) (Villéger et al., 2008; Laliberté & Legendre, 2010). FRich measures the functional space occupied by species in an assemblage; FEve is an indicator of how uniform is the species distribution in the functional space; FDiv estimates the variance in species traits values in an assemblage; and FDis is the average distance of species with respect to the centroid in the functional space (Pla et al., 2011).

Finally, we evaluated phylogenetic diversity, by building a regional phylogeny that included the 20 species recorded in our study (Hernández-Ordóñez et al., 2019), by pruning the global calibrated phylogeny of 2800 amphibian species of Pyron & Wiens (2011). For each sampling unit we estimated the following metrics: average pair-wise distance (MPD), and the average distance to the nearest taxon (MNTD; Tucker et al. 2017). The MPD is the observed average phylogenetic distance in a community and is defined by the length of the phylogeny branches among all possible taxa in the sample. The MNTD is the average phylogenetic distance to the nearest taxon within a community and is defined by only the distance of the nearest taxon of each species within the phylogeny. In both cases, low MPD and MNTD values represented a clustered pattern in the assemblages, as integrated by nearest phylogenetic species. High MPD and MNTD values suggest over dispersed pattern in assemblages when species are phylogenetically distant.

Statistical analysis

Since we used data of species incidence, we implemented estimators of functional and phylogenetic diversity designed to presence-absence data (Swenson, 2014). To evaluate the contribution of the specific richness to estimations of functional and phylogenetic diversity, from standardized values, we formulated null models following the method of Swenson (2014). However, the generated residual values from null models did not provide a normal distribution and therefore, we did not use standardized values of functional and phylogenetic diversity (Botta-Dukát, 2018).

To evaluate the relation of diversity metrics (beta, functional and phylogenetic) with the proportion of croplands in the landscape we used generalized linear models. For this we employed the estimations of crop proportion within a 500 m radius from the center of each sampling unit (after Oropeza-Sánchez unpublished; supplementary material). In these linear models, the effect of first and second order of cropland proportion were included. We decided to include these effects after graphically evaluating the distribution of estimated values, of the different diversity metrics, in the gradient of cropland proportion. To evaluate the potential of *A. ordinarium* as a flagship species, we estimated beta, functional and phylogenetic diversity by comparing their values between sampling units with and without the presence of *A. ordinarium*. We used Student's t-test and Wilcoxon signed-rank test for comparisons. All analyses were carried out using R (version 4.0; R Core Team, 2020), the statistical packages ape (Paradis & Schliep, 2019), betapart (Baselga et al., 2020) and picante (Kembel et al., 2010).

RESULTS

Overall, we found a significant effect of the proportion of crop land cover in the landscape on the different diversity metrics. The beta diversity and their components were associated with the proportion of crops in the landscape. We observed a negative second order response of dissimilarity (coef.crops = 2.16, coef.crops^2 = -5.08, F = 15.19, df = 57, $p <$ 0.001; Figure 3a) and turnover (coef.crops = 2.27, coef.crops^2 = -5.22, F = 15.99, df = 57, p < 0.001; Figure 3b), but not of species nestedness (F = 0.6, df = 57, p = 0.54; Figure 3c). We estimated the highest values of dissimilarity and species turnover in those sampling units with a proportion of croplands from 20 to 23 %. We did not find differences in species dissimilarity (W = 303, p = 0.1), turnover (t = -1.29, df = 50.28, p = 0.2) or nestedness values (W = 376, p = 0.61) between sampling units where of *A. ordinarium* was detected and where it was not.

In the case of functional diversity, we estimated a positive second order response to the proportion of croplands in two functional diversity metrics: FRich (coef.crops = -150.84, coef.crops^2 = 359.48, F = 24.91, df = 56, p < 0.001; Figure 4a) and FDis (coef.crops = -14.86, coef.crops^2 = 34.70, F = 17.91, df = 57, p < 0.001; Figure 4d). We did not find a significant effect of proportion of crops in the landscape on FEve (F = 1.40, df = 56, p = 0.25; Figure 4b) or FDiv, (F = 2.05, df = 56, p = 0.13; Figure 4c). In sampling units with a crop proportion of about 23 % we estimated the lowest values of FRich and FDis. In sampling units with *A. ordinarium* we estimated higher values of FRich (W = 671, p < 0.001) and FDis (W = 772, p < 0.001). However, we did not find significant differences for FDiv (W = 333, p = 0.29) and FEve (t = -0.52, df = 46.35, p = 0.60).

Finally, for the phylogenetic diversity, we estimated a positive second order effect of cropland proportion in both metrics of phylogenetic diversity, MPD (coef.crops = -1256.8, coef.crops^2 = 2901.9, F = 10.9, df = 57, $p < 0.001$; Figure 5a) and MNTD (coef.crops = -510.7, coef.crops^2 = 1112.1, F = 3.06, df = 57, p = 0.054; Figure 5b). In sampling units with a cropland proportion of ca. 23 % we observed the lowest values of MPD and MNTD. In sampling units with the presence of *A. ordinarium* we estimated higher values of MPD (W = 705, $p < 0.001$) and MNTD (t = 2.0, df = 57.90, p = 0.049).

DISCUSSION

Our results show that amphibian diversity in riparian habitats is associated with the proportion of croplands in their surrounding matrices presenting a hump-shape pattern (Figure 2-5). In sampling units with a cropland proportion of ca. 23 % we estimated high beta diversity, lower FRich, lower FDis and lower phylogenetic diversity. In sampling units in which *A. ordinarium* was present, we recorded high functional and phylogenetic diversity when compared with those units in which this species was absent. These results support the suggestion of using *A. ordinarium* as a flagship species to protect amphibian species with overlapping distribution ranges with this salamander.

Cropland proportion and species dissimilitude

In transformed landscapes dissimilitude patterns suggest that low disturbance tolerant species are substituted by resilient species that can survive on modified environments (MacLean et al. 2018; Socolar et al. 2016). According to this, species turnover should increase with the disturbance level (e.g., Sharma et al. 2020). For amphibian assemblages within landscapes with cropland covers around 20%, we estimated a higher turnover, a signal of environmental filtering at least for this gradient. However, we estimated low dissimilitude values for units with minimal and maximum values of crop proportion in the landscape. Which suggests that assemblage composition could be determined by other factors not directly associated to land-use change.

Land-use change can indirectly affect species diversity throughout bottom-up and top-down driven mechanism (Barnes et al. 2017; Wang et al. 2020). In bottom-up, biodiversity is determined by resource limitation for each trophic level, that is, resource availability drives consumer diversity. While in top-down mechanisms predator abundance defines the diversity patterns of lower trophic levels, by modulating their interactions (e.g., Wang et al. 2020). Northeastern Michoacan includes the distribution area of numerous garter snakes from the genera *Thamnophis*, that are specialize in consume aquatic fauna. It has been reported that garter snakes can be distributed in modified landscapes at least when crop proportion is less than 30% at 1km around (González-Fernández et al. 2018). In this sense, land-use change could cause a cascade effect by limiting predator presence and indirectly allowing the incidence of disturbance tolerant amphibians.

Species dispersal capacity represents a crucial factor for assemblage composition (Soininen et al. 2018). Because land-use change is associated with increase variation in environmental temperature and humidity, the dispersal capacity of amphibians usually decreases in modified landscapes (Arroyo-Rodríguez et al. 2017; Semlitsch et al. 2009). In consequence, landscapes with high crop proportion (ca. 45%) could represent inaccessible areas for some amphibian species. In turn, the presence of species tolerant to modified habitats could be explained by adaptative traits that allow these species to colonize modified landscapes. The amphibian species *Driophytes eximius*, *D. arenicolor*, *Lithobates neovolcanicus* and *A. ordinarium*, were recorded within sampling units in landscapes with high proportion of crop cover. The former species are tolerant to high temperatures and could disperse throughout streams (Lemos-Espinal et al., 2018, Oropeza-Sánchez et al., 2021).

Diversity of traits and the proportion of cropland cover

In highly modified landscapes the common pattern is the incidence of species with similar functional traits as result of ecological filtering events (Menezes et al., 2020; Mori et al., 2013). Although, high values of FRich and FDiv in landscapes with a crop proportion around 45% suggests that factors different to environmental filtering could be driving amphibian ecological functions, for instance a bottom-up cascade effect. It has been reported that low and intermediate intensity landscape modification can maintain high arthropod diversity, an important food resource for several amphibian species (Rader et al. 2014; Tscharntke et al. 2008). Because most amphibians present little specialized diets, resource availability could represent an extra advantage for the incidence of species with different traits and a high functional diversity in landscapes with crop proportion around 45%.

In highly disturbed sampling units, we recorded the presence of leopard frogs (*Lithobates montezumae* and *L. neovolcanicus*), tree frogs (*Dryophites arenicolor* and *D. eximius*), and of the pine toad (*Incilius occidentalis*). Among amphibian species the functional traits such as microhabitat (trees, terrestrial, semiaquatic, and aquatic), and body size were different. However, the presence of these species could be explained because they share adaptive traits that provide tolerance to disturbances, such as thermic tolerance and a reproductive mode no dependent on vegetation structure. In this sense, the recorded high levels of FRich and FDis in modified landscapes could have resulted from a dissociative response to environmental disturbances in amphibians with similar ecological functions. Because functionally similar species present different responses to environmental disturbances, the disassociated response is considered an important assemblage property which increases resilience (Sol et al. 2020). Although, we do not know if local amphibian assemblages can tolerate crop proportion covers above 50%, the preservation of their ecological functions require the greater proportion of forested riparian area available.

In the case of phylogenetic diversity, when there are similar ecological traits between phylogenetically close species in the assemblages (or niche conservatism), it is common to observe phylogenetically close species grouping in modified environments (Gainsbury & Colli, 2019; Hausberger & Korb, 2016; Hernández-Ordóñez et al., 2019). Nevertheless, land-use change can facilitate an overdispersion pattern when species with similar ecological traits, but not phylogenetically related are present (Menezes et al., 2020). In the study region we estimated high amphibian phylogenetic diversity in landscapes with higher proportion of croplands which could have resulted from adaptative traits that have evolved independently (i.e., thermic tolerance, reproductive mode and facultative pedomorphosis). In this sense, the high phylogenetic diversity in modified landscapes is evidence of the diversity of amphibian strategies to cope with environmental disturbances, allowing the prevalence of their functions.

Phylogenetic diversity is considered to be related to functional diversity because of species conserved phylogenetic traits (Kozak & Wiens, 2010; Losos, 2008; Sato et al., 2020). Supporting this concept, our findings showed spatial similarities among species richness, phylogenetic diversity, and functional richness in the gradient of cropland cover in the landscape. In consequence, conserving riparian areas with higher amphibian richness can be useful for the protection of their functions, evolutive history, and therefore to overcome further environmental disturbances (Forest et al., 2007; Winter et al., 2013).

Final considerations and *Ambystoma ordinarium* as a flagship species

Considering that sampling units in which *A. ordinarium* was recorded showed a greater number of species at risk at higher altitude we recommend the use of this salamander as a flagship species (Oropeza-Sánchez, unpub. data). The high values of FRich, FDis and phylogenetic diversity recorded support this recommendation, as protecting the areas where *A. ordinarium* was recorded could help amphibian conservation in the region. Nevertheless, conservation efforts should also focus at low-elevation areas with species other than those co-occurring with *A. ordinarium*. Finally, because the dispersal limitation of amphibians, conservation strategies must take into consideration the establishment of riparian vegetation corridors. In this context, connecting riparian habitats in modified landscapes and those with a higher proportion of native forest would preserve the ideal environmental conditions for increasing amphibian richness and their functional diversity (Santos-Barrera & Urbina Cardona, 2011; Todd & Winne, 2006). Therefore, we must assess other population traits, such as biotic interactions, survival rates, reproductive success, and colonization capability for different amphibian species.

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Tables

Table 1. Amphibian species detected in riparian habitats from Northeastern Michoacán and traits. We show the type of microhabitat most frequently used (Semi aquatic = SemiAqua; Terrestrial = Terr; Arboreal = Tree; and Aquatic = Aqua); breathing type (Pulmonary = Pulm; Cutaneous = Cut; and Gill = Gill); microhabitat used for spawning (Lotic, Lentic, Tree, Rock or Land); the presence of free aquatic larvae, presence of interdigital membranes, presence of toe pads, and snout-vent length (SVL).

species	*habitat*	*breathing*	*egg place*	*larve*	*interdigital membrane*	*terminal disks*	*SVL (mm)*
Lithobates neovolcanicus	SemiAqua	Pulm	Lotic/Lentic	free	present	not	40
Lithobates montezumae	SemiAqua	Pulm	Lotic	free	present	not	44.8
Lithobates zweifelli	SemiAqua	Pulm	Lotic/Lentic	free	present	not	73
Lithobates berlandieri	SemiAqua	Pulm	Lotic/Lentic	free	present	not	65.4
Lithobates spectabilis	SemiAqua	Pulm	Lotic	free	present	not	60
Sarcohyla bistincta	Tree	Pulm	Lotic	free	present	present	33.2
Dryophites eximius	Tree	Pulm	Lotic/Lentic	free	not	present	20.9
Dryophites arenicolor	Tree	Pulm	Lotic/Lentic	free	present	present	32
Tlalocohyla smithii	Tree	Pulm	Lotic/Lentic	free	present	present	21.3
Agalicnis dacnicolor	Tree	Pulm	Tree/Rock	free	present	present	65.1
Craugastor occidentalis	Terr	Pulm	Land	not	not	not	16.25
Craugastor hobartsmithi	Terr	Pulm	Land	not	not	not	15
Craugastor pygmaeus	Terr	Pulm	Land	not	not	not	16.3
Eleutherodactylus nitidus	Terr	Pulm	Land	not	not	not	25.5
Incilius marmoreus	Terr	Pulm	Lentic	free	present	not	43.8
Incilius occidentalis	Terr	Pulm	Lotic/Lentic	free	present	not	50.5
Rhinella horribilis	Terr	Pulm	Lotic/Lentic	free	present	not	95.4
Pseudoeurycea bellii	Terr	Cut	Land	not	not	not	146
Pseudoeurycea leprosa	Terr	Cut	Land	not	not	not	38.3
Ambystoma ordinarium	Terr/Aqua	Pulm/Cut/Braq	Lotic	free	not	not	74.7

Figures

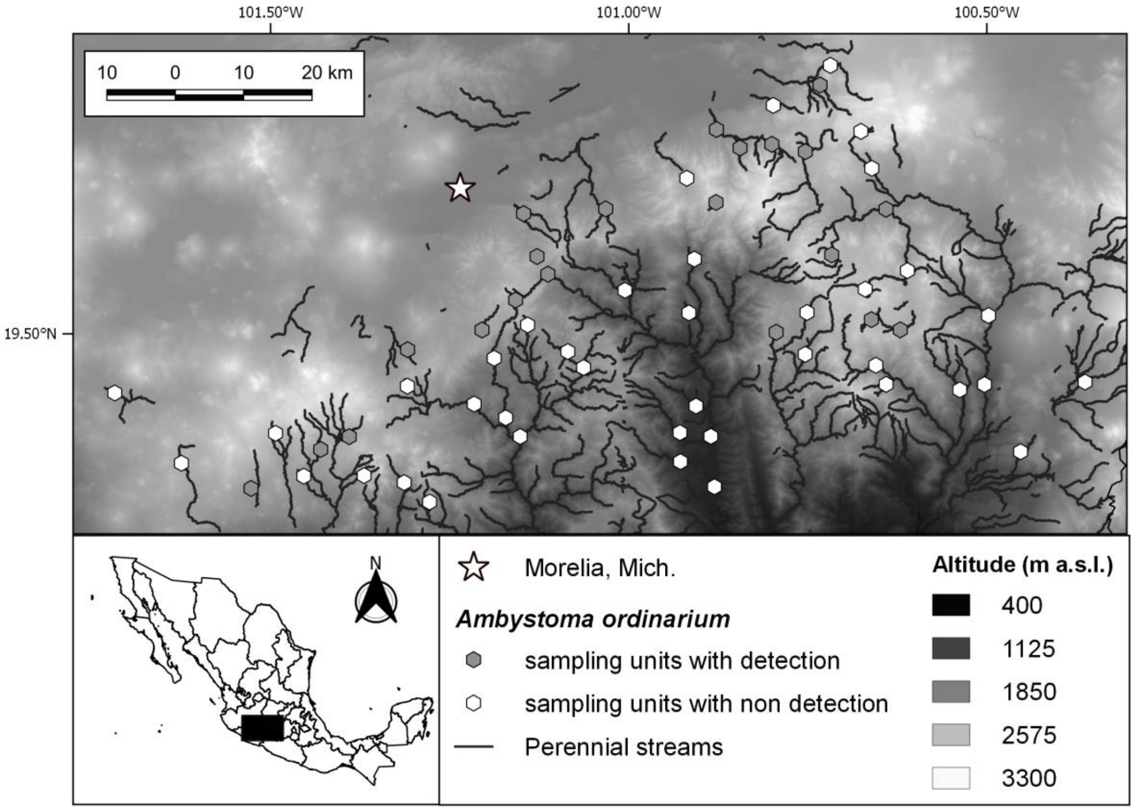

Figure 1. Detection state of *Ambystoma ordinarium* for each sampling unit, in Northeast of Michoacán, Mexico.

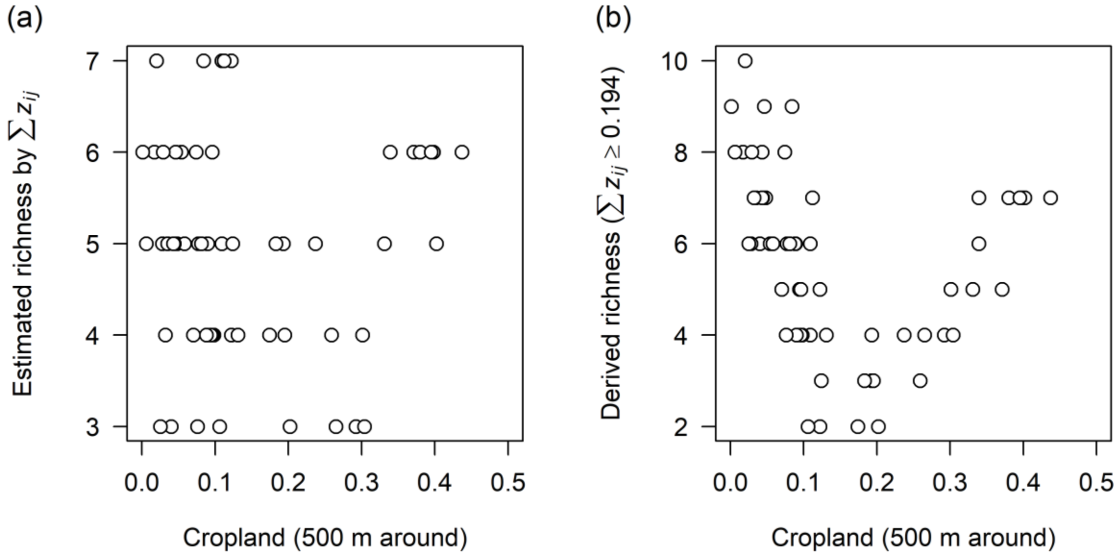

Figure 2. Amphibian species richness for each sampling unit in riparian habitat, Northeastern Michoacán, Mexico. Each sampling unit was surrounded by a different proportion of cropland cover. The sum of estimated values of occupation states (*z*) of each species (*j*) in each sample unit (*i*) by MSOM (a); and species richness values derived when values of $z_{ij} \geq 0.194$ as an equivalent to the incidence of each species *j* in the sampling unit *i* (b).

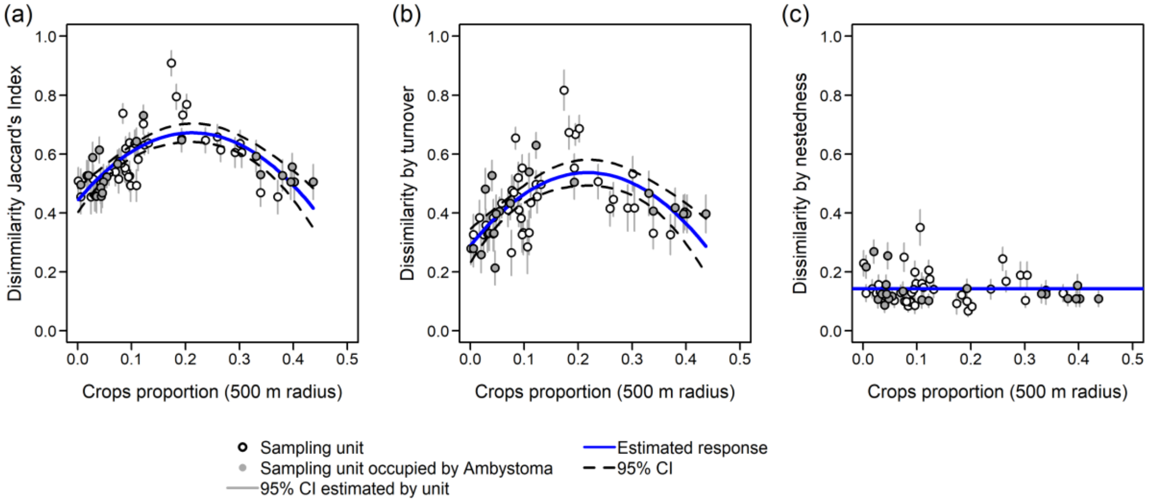

Figure 3. Estimated amphibian beta diversity values for each sampling unit in riparian habitat, Northeastern, Michoacán, Mexico. The plots show the estimated response of amphibians to the proportion of croplands in the landscape and the incidence of *Ambystoma ordinarium*. Plots show the following: (a) estimated values of dissimilarity from Jaccard index; (b) species turnover; and (c) species nestedness.

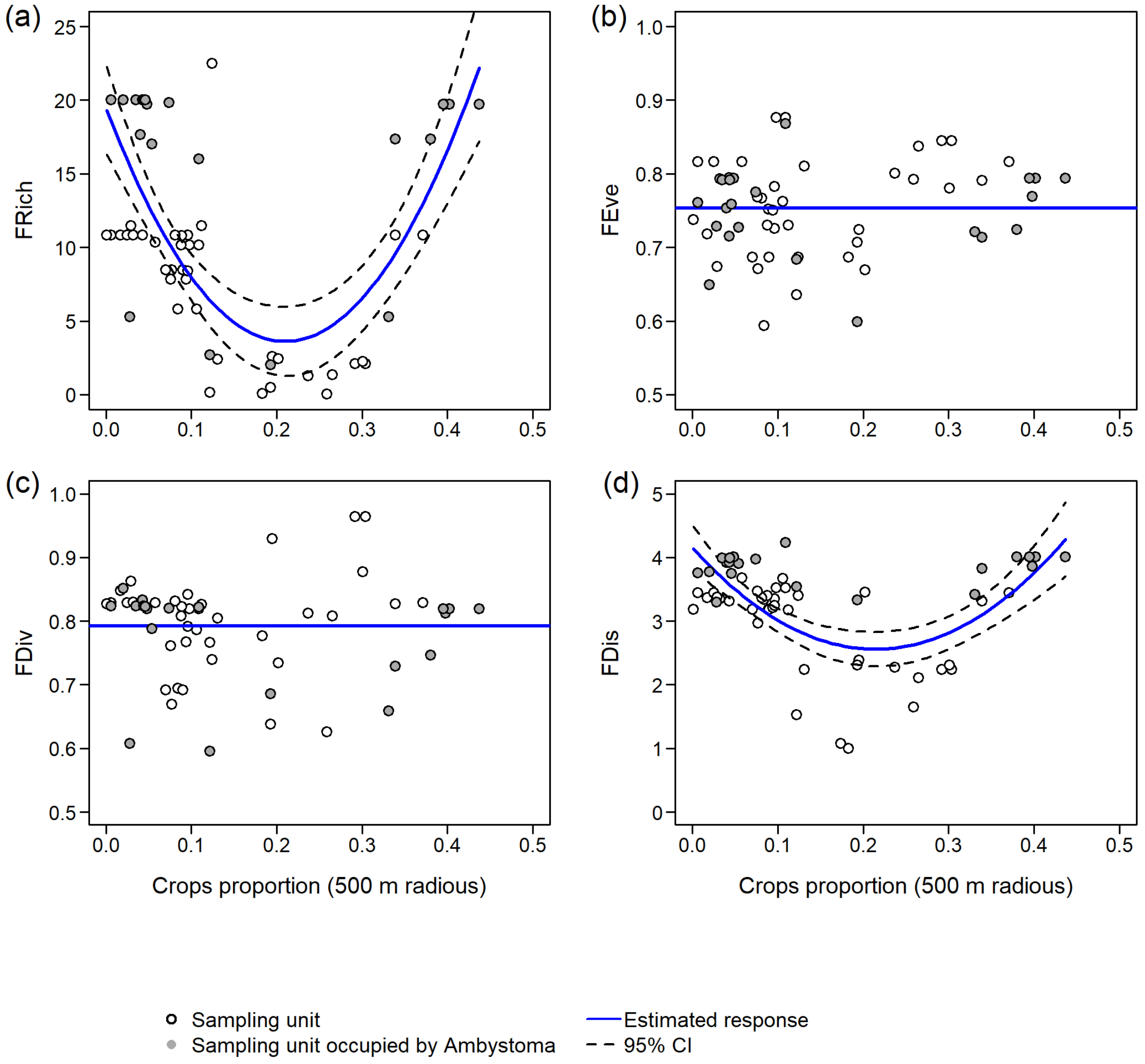

Figure 4. Estimated amphibian functional diversity values for each sampling unit in riparian habitat, Northeastern, Michoacán, Mexico. The plots show the estimated response of amphibians to the proportion of croplands in the landscape and the incidence of *Ambystoma ordinarium*. Plots show the following: a) estimated values of functional richness (FRich; b) functional evenness (FEve); c) functional divergence (FDiv); and d) functional dispersion (FDis).

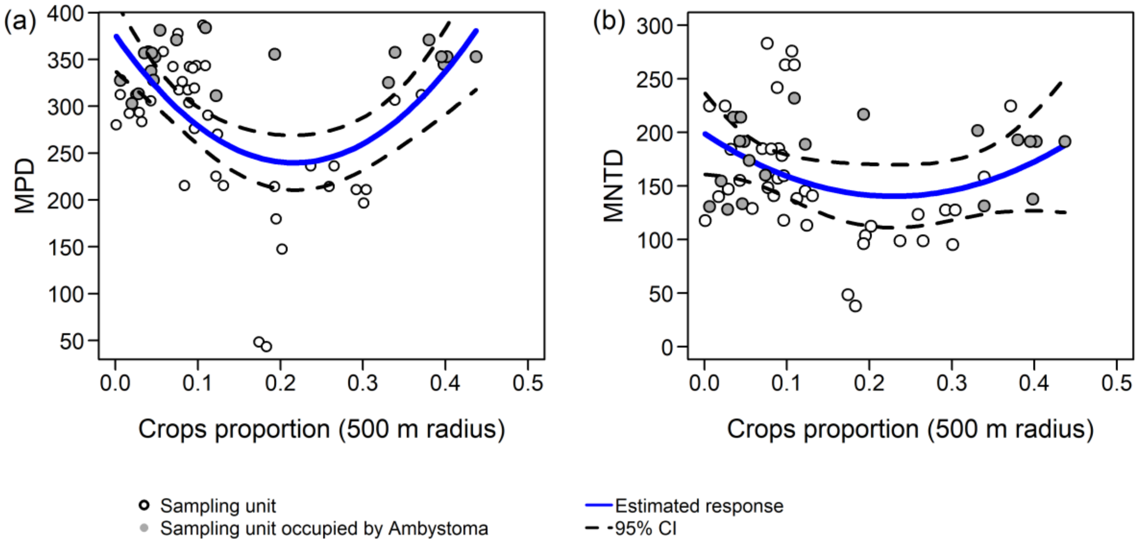

Figure 5. Estimated amphibian phylogenetic diversity values for each sampling unit in riparian habitat, Northeastern, Michoacán, Mexico. The plots show the estimated response of amphibians to the proportion of croplands in the landscape and the incidence of *Ambystoma ordinarium*. Plots show the following: a) the estimated values of average pair-wise distance (MPD); and b) the average distance to the nearest taxon (MNTD).

Capítulo 4 | Supporting Information for **“Land-use change and amphibian diversity in modified riparian vegetation”**

Table S1. Species incidence for all 60 sampling units with their condition of altitude (elev) and proportion of cropland 500 meters around (crops_500).

site	L_neovolcanicus	L_montezuma	L_zweifeli	L_berlandieri	L_spectabilis	S_bistincta	D_eximius	D_arenicolor
1	1	0	0	0	0	0	1	1
2	0	0	0	0	0	0	0	0
3	1	1	0	0	0	0	0	0
4	1	0	0	0	0	0	0	0
5	0	1	0	0	0	0	0	0
6	1	0	0	0	0	0	0	1
7	1	0	0	0	1	0	1	1
8	1	0	0	0	0	0	0	0
9	0	1	0	0	0	0	0	1
10	1	0	0	1	0	0	0	1
11	1	0	0	0	0	0	0	0
12	1	0	0	0	0	0	0	0
13	0	0	0	0	0	0	0	0
14	1	0	0	0	0	0	0	1
15	1	0	0	0	0	0	1	1
16	1	1	0	0	0	0	1	1
17	1	1	0	0	0	0	0	0
18	1	1	0	0	0	0	1	1
19	1	1	0	0	0	1	0	1
20	1	1	0	0	0	0	1	1
21	1	0	0	0	0	0	1	1
22	1	0	0	0	1	0	0	1
23	1	0	0	0	0	0	1	1
24	1	1	0	0	0	0	0	1
25	1	0	0	0	0	0	1	1
26	1	0	1	0	0	0	0	1
27	0	1	1	0	0	0	0	0
28	1	0	1	0	0	0	0	0
29	1	0	0	0	0	0	0	1
30	1	0	0	0	0	0	1	1
31	1	0	0	0	0	0	1	1
32	1	0	1	0	1	0	0	0
33	1	0	1	0	0	0	0	0
34	1	0	1	0	0	1	0	0
35	1	1	1	0	0	0	0	0
36	1	0	0	0	0	0	1	1
37	1	1	0	0	0	0	0	0
38	1	0	0	0	0	1	0	1
39	1	0	0	0	0	0	0	1
40	1	0	0	0	0	0	1	1

site	L_neovolcanicus	L_montezuma	L_zweifeli	L_berlandieri	L_spectabilis	S_bistincta	D_eximius	D_arenicolor
41	0	0	0	0	0	0	0	0
42	1	0	0	0	0	0	0	1
43	1	0	0	0	0	0	0	0
44	1	0	1	0	0	0	0	0
45	1	0	0	0	1	0	1	1
46	1	0	0	0	0	0	0	0
47	1	1	0	0	0	0	0	0
48	1	0	0	0	0	0	1	1
49	0	1	1	0	0	0	1	0
50	1	0	0	0	0	0	0	0
51	1	1	1	0	0	0	0	0
52	0	0	0	0	0	0	0	0
53	1	0	0	0	0	0	0	1
54	1	1	0	0	0	0	1	0
55	1	0	0	0	1	0	0	1
56	1	1	0	0	1	0	1	1
57	1	0	0	0	0	0	0	0
58	1	1	0	0	0	0	1	1
59	1	0	0	0	0	0	1	1
60	1	0	1	0	0	0	0	1

site	T_smithii	A_dacnicolor	C_occidentalis	C_hobartsmithi	C_pygmaeus	E_nitidus	I_marmoreus	I_occidentalis
1	0	0	0	0	1	0	0	0
2	0	0	0	1	0	0	0	0
3	0	0	0	0	0	0	0	0
4	0	0	0	0	1	0	0	0
5	0	0	0	1	1	0	0	0
6	0	0	0	0	1	0	0	0
7	0	0	0	1	1	0	0	0
8	0	0	0	0	1	0	0	0
9	1	0	0	0	0	0	1	0
10	0	1	0	0	0	0	1	0
11	0	0	0	0	0	0	0	0
12	0	1	0	0	0	0	1	0
13	0	1	0	0	0	0	0	0
14	0	0	0	0	1	0	0	1
15	0	0	0	0	0	0	0	0
16	0	0	0	0	0	0	0	0
17	0	0	0	0	0	0	0	0
18	0	0	0	0	0	0	0	0
19	0	0	0	0	1	0	0	0
20	0	0	0	1	0	0	0	0
21	0	0	0	0	1	0	0	1
22	0	0	0	1	1	0	0	0
23	0	0	0	0	0	0	0	0
24	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0
26	0	0	1	0	0	0	0	0
27	0	0	0	0	0	0	0	0
28	0	0	0	0	0	0	0	0
29	0	0	0	0	1	0	0	0
30	0	0	0	0	1	0	0	0
31	0	0	0	0	0	0	0	0
32	0	0	1	0	0	0	0	0
33	0	0	0	0	0	0	0	0
34	0	0	0	0	0	0	0	1
35	0	0	0	0	1	0	0	0
36	0	0	1	1	1	0	0	0
37	0	0	0	0	0	0	0	0
38	0	0	0	0	0	0	0	0
39	0	0	0	0	1	0	0	0

site	T_smithii	A_dacnicolor	C_occidentalis	C_hobartsmithi	C_pygmaeus	E_nitidus	I_marmoreus	I_occidentalis
40	0	0	0	0	1	0	0	0
41	0	0	0	0	0	0	1	0
42	0	0	0	1	1	0	0	0
43	0	0	0	0	1	1	0	0
44	0	0	0	1	0	0	0	0
45	0	0	0	0	1	0	0	0
46	0	0	0	1	1	0	0	0
47	0	0	0	0	0	0	0	0
48	0	0	0	0	0	0	0	0
49	0	0	0	0	0	0	0	0
50	0	0	0	0	0	0	1	0
51	0	0	0	0	0	0	0	0
52	0	0	0	0	0	0	0	0
53	0	0	0	0	1	0	0	0
54	0	0	0	0	0	0	0	0
55	0	0	0	0	1	0	0	0
56	0	0	0	0	1	0	0	0
57	0	0	0	0	0	0	0	0
58	0	0	0	0	1	0	0	0
59	0	0	0	0	1	0	0	0
60	0	0	0	1	1	0	0	0

site	R_horribilis	I_bellii	P_leprosa	A_ordinarium	elev	crops_500
1	0	0	0	1	2429	0.437
2	0	0	0	1	2313	0.109
3	0	0	0	1	2174	0.193
4	0	0	0	0	2144	0.098
5	0	0	0	1	2261	0.04
6	0	0	0	0	1933	0.006
7	0	0	0	0	1772	0.096
8	0	0	0	0	2418	0.109
9	1	0	0	0	887	0.195
10	1	0	0	0	786	0.124
11	1	0	0	0	882	0.122
12	0	0	0	0	828	0.084
13	1	0	0	0	718	0.202
14	0	1	0	0	2004	0.371
15	0	0	0	1	2152	0.38
16	0	0	0	1	2404	0.339
17	0	1	0	1	2291	0.054
18	0	0	0	1	2250	0.028
19	0	0	0	0	2072	0.339
20	0	0	0	1	2159	0.398
21	0	0	0	1	2200	0.048
22	0	0	0	0	2246	0.017
23	0	0	0	0	2623	0.292
24	0	0	0	0	2383	0.265
25	0	0	0	0	2104	0.304
26	1	0	0	0	1240	0.112
27	0	0	0	0	1234	0.174
28	1	0	0	0	1330	0.077
29	0	0	0	1	2669	0.035
30	0	0	0	1	1986	0.402
31	0	0	0	1	2036	0.331
32	0	0	0	0	1258	0.089
33	0	0	0	0	1205	0.07
34	0	0	0	0	1778	0.09
35	0	0	0	0	1573	0.193
36	0	0	0	1	2512	0.02
37	0	0	0	0	2175	0.094
38	0	0	1	0	2633	0.058
39	0	0	0	0	2239	0.025

site	R_horribilis	I_bellii	P_leprosa	A_ordinarium	elev	crops_500
40	0	0	0	1	2100	0.395
41	0	0	0	1	2463	0.122
42	0	0	0	1	2203	0.043
43	0	0	0	0	1836	0.088
44	0	0	0	0	1816	0.081
45	0	0	0	1	1952	0.006
46	0	0	1	1	2577	0.074
47	0	0	0	0	1699	0.259
48	1	0	0	0	1234	0.301
49	0	0	0	0	1382	0.096
50	0	0	0	0	1833	0.131
51	0	0	0	0	1487	0.183
52	0	0	0	0	2147	0.106
53	0	0	0	1	2279	0.044
54	0	0	0	0	2391	0.237
55	0	0	0	0	2807	0.043
56	0	0	0	0	2275	0.001
57	0	0	0	0	1897	0.076
58	0	0	0	1	2116	0.046
59	0	0	0	0	1850	0.032
60	0	0	0	0	1935	0.029

Capítulo 5

Discusión general y conclusión

Marco Tulio Oropeza-Sánchez

Consecuencias de incluir la probabilidad de detección en las estimaciones de distribución y riqueza de anfibios

La mayoría de los anfibios son reconocidos por una capacidad de dispersión muy restringida, y debido a este rasgo limitante su distribución puede verse influida tanto por características del paisaje como por la calidad de los microhábitats disponibles (Pittman et al., 2014). Las estimaciones de distribución de especies que omiten la probabilidad de detección, como los modelos de distribución de especies (SDM por sus siglas en inglés), pueden generar aseveraciones con precisión limitada (Lahoz-Monfort et al., 2014). Asimismo, los SDM frecuentemente implementan en sus estimaciones variables de paisaje más que factores locales, por lo que las estimaciones de distribución de los anfibios, y su respuesta a gradientes ambientales, pueden encontrarse subestimadas. En este sentido, como se muestra en el *Capítulo 2,* además de considerar la probabilidad de detección incluir variables locales puede generar estimaciones precisas y útiles para poner a prueba las aseveraciones de los SDM (McGarigal et al. 2016; Petermar et al. 2013).

El número total de especies que habitan en un área específica, así como el número total de individuos, y su variación a través de gradientes ambientales son temas de particular interés para la ecología (Begon et al. 2006). Las estimaciones de la cobertura de muestra son el método más frecuente de valorar el número de especies potenciales en un área particular, sin embargo, no están exentas a las repercusiones de omitir la probabilidad de detección de las especies (Dorazio et al. 2006). En el *Capítulo 3,* al considerar la probabilidad de detección en evaluaciones de riqueza específica, estimé la incidencia de dos especies no detectadas en cada unidad de muestreo y cinco especies que jamás se lograron detectar en la zona de estudio. A partir de estos resultados, fue posible la evaluación de diferentes métricas de diversidad en el *Capítulo 4*, e incluso se obtuvo evidencia del potencial de *Ambystoma ordinarium* como especie focal y la importancia de los ambientes ribereños para la conservación de los anfibios en el noreste de Michoacán, México.

Impacto de cambio de uso de suelo en la distribución y diversidad de anfibios de ambientes ribereños

Debido a la interrupción entre los hábitat acuático y terrestre, y a la poca tolerancia que tienen la mayoría de los anfibios a la variación de humedad y temperatura ambiental, el cambio de uso de suelo es reconocido como su principal amenaza de extinción (Becker et al., 2007; Becker et al., 2010; IUCN 2021). Sin embargo, como se describe en el *Capítulo 2* y *Capítulo 3* los ambientes ribereños en paisajes modificados pueden mantener valores altos de probabilidad de ocupación para algunas especies y, en consecuencia, una alta riqueza específica. Estos resultados son alentadores debido a que se plantea la posibilidad de conservar a especies de anfibios amenazadas en paisajes ocupados por cultivos, siempre y cuando se logre el manejo adecuado del suelo.

El cambio de uso de suelo generalmente reduce la diversidad de recursos disponibles y, en consecuencia, modifica la estructura y composición de los ensambles (Ceballos et al. 2017; Frishkoff et al. 2014). Esta tendencia se pudo reconocer en paisajes con una proporción de cultivos cercana a 20 % en los *Capítulos 3* y *4*. El patrón observado fue la disminución en riqueza de especies y el incremento en las diferencias de composición de los ensambles, por el recambio de especies. No obstante, conforme incrementó la proporción de cultivos, hasta 45 %, no observamos un declive continuo en la diversidad de formas y funciones de los anfibios (*Capítulo 4*). La respuesta al cambio de uso de suelo ha sido asociada a la señal filogenética, presente en distintos linajes de anfibios (Nowakowski et al. 2018). Como se muestra en el *Capítulo 3* y el *Capítulo 4*, la tolerancia a ambientes modificados se logró apreciar en cinco especies de anfibios en el noreste de Michoacán pertenecientes a distintos linajes. En consecuencia, la diversidad de funcional y filogenética no se han visto afectadas de manera negativa, al igual que la capacidad de resiliencia de los ensambles.

Los resultados del *Capítulo 4* aportan evidencia de que los ensambles de anfibios tolerantes a paisajes modificados poseen diversidad funcional equiparable a la de ensambles en hábitats menos alterados. Entre las características que han permitido a las especies establecer poblaciones en paisajes modificados pueden mencionarse a la paedomorfosis facultativa de *A. ordinarium,* y la tolerancia térmica de las ranas arborícolas (pertenecientes a la familia Hylidae) y de las ranas leopardo (de la familia Ranidae; Semlitsch et al. 1990; Díaz-García et al., 2017; Suazo-Ortuño et al., 2011). En consecuencia, los valores estimados de diversidad (beta, funcional y filogenética) en paisajes con una proporción de cultivo cercana 45% no son resultado de un proceso de filtrado ecológico.

Potencial de *Ambystoma ordinarium* como especie bandera

Las especies bandera frecuentemente son especies carismáticas para la sociedad, pertenecientes a niveles tróficos superiores como mamíferos de gran talla, aves rapaces o insectos migratorios (Bowen-Jones & Entwistle 2002; Branton & Richardson 2011; Roberge & Angelstam 2004; Suter et al. 2002). Los anfibios son afectados por amenazas dentro de un área que puede no ser representativa para el ámbito hogareño de los grandes mamíferos o muchas especies de aves. Debido a que mamíferos y aves no enfrentan las mismas amenazas que la mayoría de las especies de anfibios (e. g., contaminación o enfermedades emergentes), su empleo como especies bandera puede ser poco efectiva para la conservación de los anfibios. Sin embargo, con los resultados que obtuvimos en los *Capítulos 3 y 4*, se estimó que *Ambystoma ordinarium*, una especie de anfibio común en los hábitats ribereños de la región coincide espacialmente con otras especies amenazadas (e. g. la salamandra *Isthmura belli* y las ranas *Craugastor hobartsmithi* y *Lithobates neovolcanicus*). Además, *A. ordinarium* forma parte de ensambles con alta diversidad funcional y filogenética. Por lo anterior creemos que es justificado el reconocimiento de *A. ordinarium* como una especie bandera para los anfibios del noreste de Michoacán, e incluso su conservación puede ser directamente útil para la protección de los ambientes ribereños. Un al papel similar al que desempeña *Ambystoma mexicanum* para la protección del lago de Xochimilco en ciudad de México (Bride et al. 2008).

Importancia de los ambientes ribereños

Los ambientes ribereños tienen el potencial para mantener poblaciones de distintas especies de anfibios, pero como observamos en el *Capítulo 2* la estacionalidad ambiental puede definir la importancia que tienen las características del hábitat. Muchas especies de anfibios, a pesar de contar con un ámbito hogareño restringido a unos cuantos cientos de metros cuadrados pueden llegar a tener eventos de migración (y dispersión) asociados con la reproducción o en búsqueda de recursos (Pittman et al., 2014). El cambio de uso de suelo suele estar asociado con un incremento en la variación de temperatura y humedad ambiental razón por la que la movilidad de los anfibios se ve reducida en paisajes modificados (Arroyo-Rodríguez et al. 2017; Semlitsch et al. 2009). Como resultado en paisajes transformados, él éxito de los procesos de migración y dispersión de los anfibios depende de factores como la disponibilidad de parches de vegetación y el tipo de matriz dominante en el paisaje (Todd et al. 2009; Semlitsch 2008; Scherer et al. 2012). Por lo que, en ambientes con marcada estacionalidad, evaluaciones restringidas a una sola temporada podrían llevar a estimaciones incompletas de la distribución, el tamaño de las poblaciones de los anfibios y su respuesta a los disturbios ambientales (Smith et al. 2014). En este sentido valdría la pena considerar para trabajos a futuro en la región, y estrategias de conservación, la dinámica estacional de los cuerpos de agua, y la importancia de la vegetación circundante para su movilidad.

A pesar de la importancia que tienen los hábitats ribereños para distintas especies, sean residentes o no, tan solo 11.3% de las áreas naturales protegidas en todo el mundo coinciden con este tipo de vegetación (Reis et al. 2017). Debido a la amenaza que representa el cambio de uso de suelo para estos ambientes, se necesitan plantear estrategias de conservación que sean compatibles con las actividades productivas y económicas de la región. Para los anfibios del noreste de Michoacán, se estimó en los *Capítulos 3 y 4* cierto grado de tolerancia al cambio de uso de suelo, al menos hasta una proporción evaluada de 45 %. Para futuros trabajos recomiendo ampliar el gradiente de uso de suelo evaluados, incluyendo áreas ocupadas en su totalidad por cultivos para evaluar si los anfibios evitan establecer poblaciones en dichas condiciones. Mientras tanto, definir áreas de amortiguamiento y áreas núcleo, para mantener la vegetación ribereña puede ser la estrategia más adecuada para beneficio de los anfibios y otras especies, asimismo, considerar actividades para restaurar la vegetación original en las áreas más modificadas (Reis et al. 2017; Saunders et al. 2002).

Conclusión

La presente tesis tuvo como objetivo proporcionar información confiable de la distribución de anfibios en ambientes ribereños y su respuesta al cambio de uso de suelo, conocimiento base para el planteamiento de estrategias de conservación y toma de decisiones (Manton et al., 2019; Wagner et al., 2021). El área ocupada por cultivos de temporada no representa una amenaza para todas las especies de anfibios, sin embargo, para la conservación y mantenimiento de los servicios ecosistémicos de los ambientes ribereños deben considerarse algunas medidas preventivas a mediano y largo plazo. Primero, es necesario llevar a cabo programas de educación ambiental para difundir y lograr el reconocimiento de los anfibios y ambientes ribereños en las comunidades directa e indirectamente beneficiadas. De manera coordinada, incentivar la adopción de medidas que apoyen la protección de la vegetación ribereña, como la participación de propietarios clave en programas de pago por servicios ambientales y la adopción de usos de suelo de menor impacto (Sánchez-Azofeifa et al. 2007; Grass et al. 2019). Finalmente, en México el área designada como zona federal es de hasta diez metros contiguos al cauce, donde el estado tiene la capacidad de limitar el cambio de uso de suelo y otras fuentes de disturbio (CONAGUA 2014). No obstante, es necesario evaluar la capacidad que tiene esta área para asegurar los servicios ecosistémicos y las poblaciones de anfibios en alto riesgo de extinción, y en caso de ser insuficiente reconsiderar las dimensiones de la zona federal.

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