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POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE GEOLOGÍA

ANÁLISIS DE LA DISTRIBUCIÓN ESPACIAL Y TEMPORAL DEL AGUA COMO RECURSO LIMITANTE PARA LOS VERTEBRADOS SILVESTRES EN LA REGIÓN DE CALAKMUL, CAMPECHE, MÉXICO

TESIS

QUE PARA OPTAR POR EL GRADO DE:

DOCTOR EN CIENCIAS

PRESENTA:

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CIUDAD UNIVERSITARIA, CD. MX., FEBRERO, 2026

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Me permito informar a usted que en la reunión ordinaria (Virtual) del Comité Académico del Posgrado en Ciencias Biológicas, celebrada el día **13 de octubre de 2025** se aprobó el siguiente jurado para el examen de grado de **DOCTOR EN CIENCIAS** del estudiante **DELGADO MARTÍNEZ CARLOS MAURICIO** con número de cuenta **413015525** con la tesis titulada **"Análisis de la distribución espacial y temporal del agua como recurso limitante para los vertebrados silvestres en la región de Calakmul, Campeche, México",** realizada bajo la dirección de la **DR. EDUARDO MENDOZA RAMÍREZ,** quedando integrado de la siguiente manera:

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

A T E N T A M E N T E
"POR MI RAZA HABLARÁ EL ESPÍRITU"
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Índice

Resumen

En los ecosistemas tropicales estacionalmente secos, como el que protege la Reserva de la Biosfera de Calakmul en el estado de Campeche, en México, la disponibilidad de agua superficial es una limitante ecológica que influye de manera directa sobre los patrones de comportamiento, distribución y coexistencia de la fauna terrestre. Debido a la geología kárstica de la región, la mayor parte del agua de lluvia se infiltra rápidamente en el suelo, por lo que el agua superficial se encuentra principalmente en cuerpos de agua lénticos, muchos de ellos temporales, tales como las aguadas (depresiones kársticas con arcillas que retienen el agua pluvial), las sartenejas (pequeñas oquedades naturales en la roca madre donde se acumula el agua de lluvia) y los dendrotelmata (cavidades en los árboles que colectan agua pluvial). En este contexto, con limitado acceso al agua superficial, las especies desarrollan estrategias para reducir la competencia por el recurso. La presente tesis tuvo como objetivo general analizar cómo la variación en la disponibilidad de estos cuerpos de agua incide en los patrones de actividad espaciotemporal de aves y mamíferos, así como evaluar su viabilidad futura ante distintos escenarios de cambio climático. Para ello, se abordaron cuatro objetivos particulares: (1) sintetizar el conocimiento existente en la literatura científica sobre el uso de cuerpos de agua por aves y mamíferos (mapeo sistemático); (2) analizar, mediante el uso de cámaras trampa, el uso diferencial de aguadas, sartenejas y dendrotelmata por parte de aves y mamíferos; (3) evaluar la partición temporal del uso de los cuerpos de agua a través de tres métricas complementarias calculadas a nivel de cuerpo de agua; y (4) desarrollar modelos predictivos a partir de datos climáticos y características físicas de los cuerpos de agua para proyectar la duración de los hidroperiodos bajo distintos escenarios de cambio climático (SSP2-4.5, SSP5-3.4-OS y SSP5-8.5) en tres horizontes temporales: 2031-2040,

2061-2070 y 2091-2100. El mapeo sistemático permitió identificar un sesgo importante hacia estudios realizados en ecosistemas áridos y semiáridos, así como una notable escasez de investigaciones sobre cuerpos de agua arbóreos. El análisis del uso diferencial mostró patrones de partición espacial asociados principalmente con el tamaño corporal y el tipo de locomoción de las especies, lo que sugiere la existencia de una segregación funcional que puede favorecer la coexistencia de la fauna. La evaluación de la partición temporal evidenció una tendencia generalizada hacia la segregación, principalmente en cuerpos de agua con mayor riqueza de especies y entre los pares de especies con mayores diferencias de tamaño; no se encontró evidencia de que variables como la frecuencia de depredadores, la temporada climática o la proximidad a otros cuerpos de agua tuvieran un efecto significativo sobre los patrones de actividad de la fauna. Los modelos predictivos indicaron que las aguadas presentan una mayor estabilidad hidrológica debido a su tamaño, mientras que las sartenejas, y especialmente los dendrotelmata, pueden tener una alta vulnerabilidad ante los escenarios de cambio climático, lo que provocaría su reducción significativa a lo largo del siglo XXI, particularmente bajo trayectorias de altas emisiones. En conjunto, los resultados obtenidos indican que los mecanismos de partición espacial y temporal son fundamentales para la organización ecológica de la fauna en bosques tropicales estacionales como el de Calakmul, y que dichos mecanismos podrían verse comprometidos ante un escenario de creciente variabilidad climática. Los capítulos que constituyen esta tesis aportan evidencia empírica y predictiva relevante para el diseño de estrategias de conservación adaptativa en paisajes tropicales, subrayando la importancia de mantener la diversidad de cuerpos de agua temporales, implementar medidas específicas frente a sequías extremas e integrar el conocimiento científico en la toma de decisiones, especialmente en un contexto regional sometido a crecientes presiones antrópicas.

Abstract

In seasonally dry tropical ecosystems, such as the Calakmul Biosphere Reserve in Campeche, Mexico, the availability of surface water constitutes a major ecological constraint that directly influences the behavior, distribution, and coexistence of terrestrial wildlife. Due to the karstic geology of the region, most rainfall rapidly infiltrates into the ground, and surface water is thus restricted to lentic water bodies, many of them temporary. These include waterholes (karstic depressions where clay deposits retain rainwater), rock pools (small natural cavities in the bedrock that collect rainfall), and tree holes (tree cavities that accumulate rainwater). In this context of limited water supply, animal species must develop strategies to reduce interspecific competition for water. This dissertation examines how variation in the availability of these water bodies shapes the spatiotemporal activity patterns of birds and mammals and evaluates their future viability under climate change. We addressed four objectives: (1) conduct a systematic mapping review of the scientific literature on the use of water bodies by birds and mammals; (2) analyze, using camera traps, the differential use of waterholes, rock pools, and tree holes by birds and mammals; (3) assess temporal partitioning of water body use with three complementary metrics at the water body scale; and (4) develop predictive models of hydroperiod duration from climatic variables and physical attributes of water bodies to project outcomes under SSP2-4.5, SSP5-3.4-OS, and SSP5-8.5 for 2031-2040, 2061-2070, and 2091-2100. The systematic mapping review revealed a strong bias toward arid and semi-arid systems and a marked paucity of studies on arboreal water bodies; camera-trap analyses showed spatial partitioning largely associated with body size and locomotion mode, consistent with functional segregation that may facilitate coexistence; the temporal assessment indicated a generalized tendency toward segregation, stronger in water bodies with higher local species richness and among species pairs with greater differences in body size, while predator frequency, season, and proximity to other water bodies showed no detectable effects; and the predictive models indicated greater hydrological stability in waterholes, whereas rock pools, and especially tree holes, are highly vulnerable, with substantial hydroperiod declines projected through the 21st century, particularly under high-emissions trajectories. Together, these findings highlight the key role of spatial and temporal partitioning in structuring vertebrate communities under water limitation, while also demonstrating the potential fragility of these mechanisms under intensifying climatic variability. The results provide both empirical and predictive insights that can guide adaptive conservation planning in tropical landscapes. They emphasize the ecological importance of maintaining diverse temporary water bodies, implementing targeted measures to buffer the impacts of extreme droughts, and integrating scientific evidence into decision-making processes in regions increasingly subjected to anthropogenic pressures.

Key words. Calakmul Biosphere Reserve, hydrology, resource partitioning, species coexistence, water availability.

Referencia bibliográfica completa a los artículos

Capítulo I. Global patterns and gaps in the study of terrestrial birds and mammals' use of freshwater sources: a mapping review

Artículo generado a partir de la investigación

Cita completa:

Delgado-Martínez, C. M., Kolb, M., Pascual-Ramírez, F., and Mendoza, E. (2025). Global patterns and gaps in the study of terrestrial birds and mammals' use of freshwater sources: A mapping review. *Wildlife Biology,* e01379. https://doi.org/10.1002/wlb3.01379

Capítulo II. Differential utilization of surface and arboreal water bodies by birds and mammals in a seasonally dry Neotropical forest in southern Mexico

Artículo de requisito para obtener el grado

Cita completa:

Delgado-Martínez, C. M., Kolb, M., Pascual-Ramírez, F., and Mendoza, E. (2023). Differential utilization of surface and arboreal water bodies by birds and mammals in a seasonally dry Neotropical forest in southern Mexico. *Ecology and Evolution, 13*(11), e10781. https://doi.org/10.1002/ece3.10781

Capítulo III. Sharing the oasis: A site-level approach to analyzing water use partitioning by neotropical forest birds and mammals

Artículo generado a partir de la investigación

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Delgado-Martínez, C. M., Kolb, M., Pascual-Ramírez, F., and Mendoza, E. (Enviado). Sharing the oasis: A site-level approach to analyzing water use partitioning by neotropical forest birds and mammals (Artículo sometido a *Biotropica* el 02/05/2025). Ver manuscrito en el Anexo 1.

Introducción

El acelerado crecimiento de la población humana y sus patrones de consumo han propiciado que nuestra especie disponga de una proporción cada vez mayor de los recursos naturales disponibles. Se estima que, debido a la alta demanda de alimentos, cerca del 70 % del agua dulce se destina a la producción agrícola y ganadera (IPBES, 2019). El uso intensivo del agua se combina con una reducción considerable que se anticipa habrá en su disponibilidad y calidad debido al cambio climático (IPCC, 2023). Este escenario representa una seria amenaza para la humanidad, pero también tiene profundas implicaciones para los ecosistemas y las distintas especies que los habitan (Duncan et al., 2012; IPBES, 2019).

La disponibilidad del agua juega un papel crucial en múltiples aspectos de la ecología de los vertebrados terrestres, incidiendo directa e indirectamente en su dinámica poblacional, patrones de movimiento, distribución espacial y temporal, así como la conectividad del hábitat. Estos efectos han sido ampliamente documentados en ecosistemas áridos y semiáridos como los matorrales y desiertos en Estados Unidos de América y las sabanas del sureste de África, donde el agua es evidentemente un recurso limitante (Chamaillé-Jammes et al., 2016; Gandiwa et al., 2016). En estos ecosistemas se ha visto que, en especial durante la temporada seca, las fuentes de agua concentran a las distintas especies de vertebrados y modulan su comportamiento. Por ejemplo, los elefantes africanos (*Loxodonta africana*) ajustan sus desplazamientos en torno a los pocos cuerpos de agua que permanecen disponibles al final de la sequía (Chamaillé-Jammes et al., 2013), mientras que la presencia de depredadores puede llevar a que algunas especies modifiquen sus horarios de visita a los cuerpos de agua (Amoroso et al., 2020). Sin embargo, incluso en regiones tropicales con vegetación exuberante, el agua superficial puede ser escasa debido a condiciones geológicas particulares. Tal es el caso de los bosques tropicales de la región de Calakmul, Campeche, en el sureste de México, un ecosistema fuertemente moldeado por la presencia de cuerpos de agua temporales, debido a que los suelos kársticos restringen la formación de cuerpos de agua perennes, lo que representa un desafío constante para la fauna que habita la región (Galindo-Leal, 1999; García-Gil et al., 2002; Torrescano-Valle and Folan, 2015).

La fauna silvestre de Calakmul depende principalmente de cuerpos de agua temporales formados por la acumulación de agua pluvial, entre los que se incluyen las aguadas, las sartenejas y los dendrotelmata. Las aguadas son geoformas kársticas originadas por la disolución de la roca calcárea, proceso que genera depresiones naturales donde se acumulan arcillas que disminuyen la permeabilidad del suelo y permiten la retención de agua pluvial y de arroyos intermitentes (Kranjc, 2013); constituyen los cuerpos de agua de mayor tamaño dentro de la Reserva de la Biosfera de Calakmul, con una superficie que por lo general no supera los 5000 m^2, y son esenciales para una amplia diversidad de especies de aves y mamíferos (Reyna-Hurtado et al., 2010, 2015; Figura 1). Las sartenejas son geoformas epikársticas formadas por la disolución de la roca madre expuesta, lo que da lugar a oquedades donde se acumula agua de lluvia; estos cuerpos de cuerpos de agua por lo general cubren menos de un metro cuadrado y almacenan menos de 100 litros de agua (Flores, 1983; Lundberg, 2013; Figura 2). Por otro lado, los dendrotelmata (un tipo particular de fitotelmata) se forman con la acumulación de agua de lluvia en cavidades de los árboles; son cuerpos de agua que, por lo general, tienen un volumen inferior a 20 litros (pers. obs.; Figura 3). A pesar de su menor tamaño, tanto las sartenejas como los dendrotelmata son ampliamente utilizados por la fauna de la región (Delgado-Martínez et al., 2022 a, b).

Durante las últimas décadas, la región de Calakmul ha experimentado modificaciones de sus condiciones ambientales asociadas con el cambio climático, en particular un incremento en la frecuencia de sequías y alteraciones en los patrones estacionales de precipitación y temperatura (Fernández-Eguiarte et al., 2015; Mardero et al., 2012, 2020). Estos cambios modifican a su vez la distribución espaciotemporal del agua y, con ello, impactan a las especies que dependen de los cuerpos de agua.

Dada la importancia de estos cuerpos de agua, y debido al cambio climático y la creciente presión antropogénica que experimenta la región, es de particular relevancia entender cómo éstos son usados por la fauna silvestre. Así mismo, el conocer la variación en la disponibilidad, de estos cuerpos de agua nos permite identificar los factores que rigen la ecología de la fauna silvestre en esta región. Por otra parte, el contar con información precisa sobre estos aspectos puede contribuir a generar estrategias de manejo que permitan mitigar los efectos sinérgicos del cambio climático y las actividades humanas sobre la biodiversidad de la región (O'Farrill et al., 2014; Paredes et al., 2017).

Esta tesis de doctorado tiene como objetivo general analizar el papel que la variación espaciotemporal en la disponibilidad de agua en las aguadas, sartenejas y dendrotelmata tienen sobre los patrones de uso por parte de aves y mamíferos, así como la viabilidad futura de los cuerpos de agua dentro de la Reserva de la Biosfera Calakmul. El documento está estructurado de la siguiente manera:

- Una introducción general.
- Un mapeo sistemático de los estudios existentes a nivel global sobre el uso de cuerpos de agua como sitios de hidratación para aves y mamíferos, publicado en la revista *Wildlife Biology* (https://doi.org/10.1002/wlb3.01379).

- Un artículo de investigación que aborda el uso diferencial que hacen las aves y los mamíferos medianos y grandes de los distintos tipos de cuerpos de agua en Calakmul, publicado en la revista *Ecology and Evolution* (https://doi.org/10.1002/ece3.10781).
- Un tercer capítulo (Anexo 1), que analiza la partición temporal del uso de los cuerpos de agua por diferentes especies de aves y mamíferos, utilizando tres escalas temporales distintas y un enfoque espacial a nivel de sitio, actualmente en revisión en la revista *Biotropica*.
- Un cuarto capítulo (Anexo 2) en el que se implementan modelos de distintos escenarios futuros de cambio climático para evaluar su efecto potencial sobre el hidroperiodo de las aguadas, sartenejas y dendrotelmata, a ser enviado a la revista *Hydrology Research* para su publicación.
- Finalmente, esta tesis concluye con una discusión general que integra los hallazgos principales de los distintos capítulos y reflexiona sobre sus implicaciones para la conservación y el manejo de los recursos hídricos en la región.

Figura 1. Ejemplos representativos de las aguadas de la región de Calakmul.

Figura 2. Las sartenejas son cuerpos de agua que se forman en oquedades en la roca madre expuesta de la región de Calakmul.

Figura 3. Los dentrotelmata son acumulaciones de agua pluvial en oquedades naturales en los árboles. Ejemplos representativos de la región de Calakmul.

Conclusiones generales

La presente tesis se planteó con el objetivo de entender cómo la actividad de aves y mamíferos se vincula con la disponibilidad espaciotemporal de agua en distintos tipos de cuerpos de agua (i.e., aguadas, sartenejas y dendrotelmata) y cómo esta disponibilidad podría modificarse bajo escenarios futuros de cambio climático utilizando como sistema de estudio la Reserva de la Biosfera Calakmul (RBC). A partir de cuatro capítulos complementarios, se integró una síntesis bibliográfica, evidencia empírica y modelación predictiva para responder a una pregunta central: ¿Cómo influye la variación espaciotemporal del agua sobre la ecología de aves y mamíferos en un ecosistema tropical kárstico?

El primer capítulo ofreció una revisión sistemática del conocimiento global sobre el uso de cuerpos de agua por aves y mamíferos. Este ejercicio permitió contextualizar la presente investigación en Calakmul y evidenciar importantes vacíos de información. En particular, se observó una fuerte concentración de investigaciones en ecosistemas áridos y semiáridos, donde el papel del agua como recurso limitante ha sido ampliamente documentado. Sin embargo, ecosistemas tropicales con una extensa vegetación que pueden presentar limitaciones hídricas igualmente severas durante largos periodos del año, han sido poco explorados bajo esta perspectiva. Aun menos frecuente es la consideración de cuerpos de agua arbóreos como los dendrotelmata, cuyo pequeño tamaño y difícil acceso han contribuido a su subrepresentación en la literatura científica.

Posteriormente, en el segundo capítulo, se evaluó empíricamente el uso que diferentes grupos de aves y mamíferos hacen de los cuerpos de agua en Calakmul, lo que permitió documentar el uso diferencial de aguadas, sartenejas y dendrotelmata. Se encontró una clara segregación en el uso de estos cuerpos de agua, determinada principalmente por características funcionales como la locomoción y el tamaño corporal. Las especies terrestres y de mayor tamaño utilizaron preferentemente las aguadas, mientras que las especies pequeñas, arbóreas o escansoriales accedieron de forma recurrente a los dendrotelmata. Este patrón de uso sugiere que, en un contexto de recursos limitados, la fauna desarrolla mecanismos que permiten una partición espacial del uso del agua, lo cual reduce la competencia directa y favorece la coexistencia. Además, la diferenciación en el uso de los cuerpos de agua podría tener implicaciones en las interacciones trófica, dado que algunos sitios pueden actuar como puntos de encuentro entre presas y depredadores, o como nodos clave en las redes de interacciones.

El tercer capítulo de esta tesis exploró en detalle la partición temporal en el uso de cuerpos de agua mediante tres variables complementarias. Los resultados mostraron que la mayoría de las especies estudiadas evitan usar un mismo cuerpo de agua de manera simultánea con otra especie. La partición temporal observada no fue aleatoria, estuvo influida por variables bióticas como la riqueza de especies y las diferencias de tamaño corporal entre pares. Dicho capítulo permitió también realizar una crítica al método más ampliamente usado en los estudios que evalúan la partición temporal y propone que la partición temporal debe ser abordada desde una escala a nivel de sitio y usando escalas temporales que tengan relevancia biológica.

Los resultados del segundo y tercer capítulo indican que la coexistencia en ecosistemas con recursos limitados puede estar facilitada por una combinación de mecanismos espaciales y temporales de partición, y que estos mecanismos operan de forma simultánea. La evidencia presentada refuerza la idea de que los cuerpos de agua no son solo sitios de hidratación, sino elementos que influyen en la estructuración de comunidades de aves y mamíferos terrestres.

El cuarto capítulo abordó la viabilidad futura de los cuerpos de agua estudiados bajo distintos escenarios climáticos, mediante la modelación de los hidroperiodos en función de variables climáticas. Los modelos desarrollados indicaron que variables como la presencia previa de agua, el tamaño del cuerpo de agua, la precipitación acumulada y la temperatura máxima son los principales predictores de la permanencia hídrica. A partir de ello, se proyectaron los hidroperiodos esperados bajo tres trayectorias climáticas distintas (SSP2-4.5, SSP5-3.4-OS y SSP5-8.5). Los resultados mostraron una tendencia clara hacia la reducción de los hidroperiodos en todos los tipos de cuerpos de agua, siendo los dendrotelmata los más afectados. Las sartenejas también se mostraron sensibles, mientras que las aguadas, aunque más estables por su mayor tamaño, no estarían exentas de secarse en condiciones extremas. Esto representa una amenaza concreta para la fauna que depende de estos sitios, especialmente en épocas de sequías prolongadas.

Cabe destacar que los efectos ecológicos de la reducción en la disponibilidad de agua no serían lineales ni homogéneos. Por ejemplo, la reducción de los hidroperiodos de los dendrotelmata podría afectar de manera desproporcionada a especies arborícolas, alterando la dinámica espacial de estas especies. Asimismo, el colapso de aguadas durante sequías prolongadas podría generar concentraciones atípicas de fauna, aumentando la competencia intra e interespecífica, así como la incidencia de depredación o transmisión de enfermedades. En conjunto, estas modificaciones en los hidroperiodos podrían tener efectos negativos sobre la estructura y el funcionamiento del ecosistema en general.

La evidencia generada por esta tesis tiene implicaciones concretas para la conservación de la biodiversidad en Calakmul. En primer lugar, resalta la necesidad de proteger los distintos tipos de cuerpos de agua, valorando su función complementaria dentro del ecosistema. Las aguadas, por su tamaño y persistencia, deben ser consideradas elementos críticos para la conservación y deberían ser prioritarias en planes de conservación tanto dentro como fuera de las áreas naturales protegidas de la Selva Maya. Una estrategia de manejo integral y adaptativo podría incluir el mantenimiento de árboles con cavidades naturales, y la implementación temporal de bebederos artificiales en el dosel durante eventos extremos de sequía. Estas medidas deberían ser diseñadas (i.e., ubicación espacial, cantidad y frecuencia) con base en la distribución, frecuencia y accesibilidad de los cuerpos de agua naturales, y complementadas con monitoreo biológico continuo para evaluar su eficacia.

Como toda investigación, este trabajo presenta ciertas limitaciones que deben ser reconocidas para interpretar adecuadamente sus alcances. En primer lugar, el monitoreo de los cuerpos de agua fue necesariamente limitado en tiempo y espacio, lo cual restringe la posibilidad de capturar eventos hidrológicos atípicos o variaciones interanuales. Asimismo, debido a las restricciones técnicas de las cámaras trampa, no fue posible registrar de manera eficiente a especies con una masa corporal menor a 220 gramos, lo que deja fuera de los análisis a un conjunto importante de la fauna local. A esto se suma la falta de datos climáticos de largo plazo colectados directamente en el sitio de estudio, lo cual obligó a utilizar estaciones meteorológicas regionales como referencia. No obstante, estas limitaciones también abren oportunidades claras para futuras investigaciones. Se recomienda incorporar sensores automáticos de nivel de agua que permitan reconstruir los hidroperiodos con mayor resolución temporal, así como desarrollar modelos que integren simultáneamente escenarios de cambio climático y uso del suelo. Además, sería valioso extender el análisis a otros grupos taxonómicos como reptiles, anfibios e insectos. Estas perspectivas permitirían una comprensión más profunda y completa de la relación entre fauna y agua en ecosistemas tropicales.

Finalmente, aunque la fauna de la región ha desarrollado estrategias complejas para acceder al agua en un entorno donde su disponibilidad es altamente estacional, la creciente variabilidad climática y la presión humana representan amenazas potenciales que requieren respuestas de conservación basadas en evidencia científica. A pesar de la relevancia de la Reserva de la Biosfera de Calakmul para la conservación de la biodiversidad tropical en México, los proyectos que actualmente se desarrollan en la región plantean nuevos retos y configuran una nueva realidad para esta reserva. En particular, la construcción del Tren Maya y de un hotel en el corazón del área protegida, ambos iniciados después del periodo de muestreo de este estudio exigen traducir el conocimiento científico en propuestas prácticas y pertinentes (Reyna-Hurtado, 2024). Este trabajo proporciona una línea base para evaluar el impacto de dichos proyectos en la dinámica del uso del agua por aves y mamíferos, y para proponer estrategias creativas que promuevan tanto la conservación de la biodiversidad como el bienestar de las comunidades aledañas a la reserva.

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Anexo 1

Capítulo III. Sharing the oasis: A site-level approach to analyzing water use partitioning by neotropical forest birds and mammals

Abstract

Understanding how species share limited resources is a fundamental question in ecology. In water-limited ecosystems, temporal partitioning can be key in facilitating vertebrate species coexistence. The partitioning of water use among vertebrates has been studied in water-limited, open-canopy ecosystems such as African savannas. In contrast, little information is available for tropical ecosystems with dense vegetation, especially when data are analyzed at the site level, where local factors can strongly influence species interactions. We applied a site-level approach to analyze water use partitioning by birds and mammals in the seasonally dry forest of Calakmul, Mexico, across different time frames. We deployed camera traps at 23 waterholes and 22 rock pools to record bird and mammal occurrences and analyze diel activity overlap, temporal co-occurrence, and time-to-encounter of species pairs. Then, we assessed the influence of biotic (species richness, body mass differences, and predator frequency) and abiotic (water availability) factors on these variables. Our results indicate that most species pairs (161/242) exhibit high temporal partitioning by using water sources on different days and at different times. Temporal partitioning was more evident in waterholes than in rock pools and increased with species richness and body mass differences. Predator frequency and water availability had no significant effect on temporal partitioning. Our findings highlight the relevance of analyzing temporal partitioning across different time frames and incorporating the effect of different covariables to gain a more exhaustive understanding of mechanisms favoring species coexistence.

Keywords: Calakmul, camera trapping, Mexico, resource partitioning, temporal overlap

Introduction

The shared use of critical resources in limited supply strongly compels animals to develop coexistence strategies (Mori and Menchetti, 2019; Schmied née Stommel et al., 2024). Resource partitioning is a strategy in which species specialize in different variants of the same resource or use the same resource at different places or times, favoring coexistence (Schoener, 1974; Walter, 1991). Examples include frugivorous mammals that consume palm fruits but differ in the specific plant species they prefer (Akkawi et al., 2020), the use of flowers at different positions on plants by hummingbird species (Lara et al., 2009), and the occupation of burrows by different mammal species at different times (Mori and Menchetti, 2019). Several studies have shown that the temporal axis plays a particularly important role in resource partitioning among vertebrate species (Beilke et al., 2021; Olea et al., 2022; Smith et al., 2023). However, significant knowledge gaps remain, particularly regarding the specific factors that influence temporal partitioning at fine spatio-temporal scales and the relative importance of these factors (Frey et al., 2017; Sévêque et al., 2022).

Various biotic factors have been proposed to affect temporal partitioning in terrestrial vertebrate communities. For example, it has been observed that animal species in more diverse communities tend to exhibit a greater degree of segregation in their activity than those in less diverse communities, likely as a strategy for coexistence (Castro-Arellano and Lacher, 2009; Monterroso et al., 2014). In addition, species that are more similar in functional traits, such as body mass and trophic guild, are more likely to show more accentuated temporal partitioning to avoid negative interactions such as competition (Di Bitetti et al., 2010; Edwards et al., 2015). Predator presence is another factor impacting temporal activity patterns of animals accessing resources, with subordinate predators and prey species modifying their activity patterns to reduce direct interactions (Amoroso et al., 2020; Valeix et al., 2009). On the other hand, abiotic factors also affect animals' temporal segregation. For example, higher temperatures may reduce temporal segregation as species shift to nocturnal activity to avoid excessive heat during the day (Rafiq et al., 2023). Similarly, precipitation has been shown to influence temporal partitioning, with increased rainfall potentially reducing partitioning due to changes in resource availability (Herfindal et al., 2017; Valeix et al., 2007). Complex relationships among biotic and abiotic factors may drive temporal partitioning in animal communities; however, few studies have simultaneously analyzed the effects of these factors on temporal patterns and partitioning (Frey et al., 2017).

In addition, some aspects of the methodological approaches most commonly used to analyze animals' temporal activity patterns may limit our understanding of the factors that influence them (Frey et al., 2017). For example, many studies use primarily descriptive approaches, limiting the exploration of mechanisms driving temporal patterns. Furthermore, it is common practice to pool data from multiple sampling units (e.g., camera traps) or aggregate data across different treatment levels (e.g., hunted vs. unhunted areas) to generate a single estimate of temporal activity for pairwise species comparisons (Iannarilli et al., 2024). Failure to account for potential differences in temporal activity among sampling units can result in a loss of information and limit the ability to analyze variables that influence temporal activity at fine spatial scales (Sévêque et al., 2022). Another issue is the heavy emphasis on analyzing diel activity patterns, typically estimated using kernel density estimators (Iannarilli et al., 2024). While diel activity is undoubtedly important, it is only one of several facets of temporal activity. For example, two species may substantially overlap in their diel activity patterns but rarely coincide on the same days and locations (Watabe et al., 2022). Our understanding of temporal partitioning could be significantly enhanced by undertaking a broader analytical approach integrating different temporal frames, fine-scale spatial variability, and biotic and abiotic covariates.

Seasonally dry tropical forests, defined as forests located in the intertropical region with a mean annual temperature above 17 °C, a mean annual precipitation greater than 200 mm, and a rainy season during which at least 80% of the total annual precipitation falls within fewer than 180 days (Allen et al., 2017; Maass and Burgos, 2011; Murphy and Lugo, 1986), provide an ideal setting for studying the temporal partitioning of animal activity. These forests typically support diverse communities of terrestrial birds and mammals (Portillo-Quintero et al., 2015). However, during dry seasons, which can last up to eight months, rainfall decreases to less than 40 mm per month, significantly reducing the availability of free-standing water (Maass and Burgos, 2011; Murphy and Lugo, 1986). This situation is further exacerbated in forests growing over karst landscapes (Hartmann et al., 2013). Consequently, water bodies in seasonally dry tropical forests become hotspots of animal activity, providing an excellent opportunity to study temporal partitioning. Although several studies have evaluated temporal partitioning at water sources, most have focused on arid and semi-arid regions with open canopies, such as African savannas (Delgado-Martínez et al., 2025). In addition, only a small proportion of these studies used a site-level approach (e.g., Atwood *et al.* 2011, Edwards *et al.* 2015), limiting the possibility of reaching a full understanding of the mechanisms underlying the partitioning of water use by wildlife.

In this study, we investigated the patterns of temporal activity partitioning, focusing on birds and mammals visiting surface water bodies in the seasonally dry forest of Calakmul, in southern Mexico. We analyzed three complementary response variables measured at the site level: diel activity overlap (i.e. similarity of daily activity patterns of species pairs, Figure S1a), temporal co-occurrence (i.e. degree of co-occurrence of species pairs at the same site and day, Figure S1b), and time-to-encounter (i.e. time interval between consecutive detections of species pairs within 24 h intervals, Figure S1c). Our site-level approach allows us to incorporate the analysis of how biotic and abiotic covariates influence temporal partitioning. We hypothesize that temporal partitioning will increase with greater species richness and predator frequency but decrease with higher body mass ratios of species pairs. Additionally, we hypothesize that temporal partitioning will increase with higher water availability (i.e., larger size of water bodies, higher seasonal precipitation, and proximity to large water sources). We expect that, given the high diversity of birds and mammals in our study area and the naturally low availability of water, temporal partitioning at water sources will be common. A better knowledge of how wildlife shares a key resource such as water would greatly help to further our understanding of the mechanisms favoring coexistence of species in highly biodiverse regions but also would inform better resource management and conservation efforts, as well as policy development.

Methods

Study site

Fieldwork was conducted in the southern core zone of the Calakmul Biosphere Reserve (CBR, 18°16'01" – 18°08'49" N, 89°43'26" – 89°49'23" W) in the state of Campeche, southern Mexico (Figure S2). The CBR was decreed in 1989 and covers 728,908-ha, making it the largest natural protected area of tropical forest in Mexico (Galindo-Leal, 1999; Gómez-

Pompa and Dirzo, 1995). Together with the Maya Biosphere Reserve in Guatemala, the CBR constitutes Mesoamerica's largest tract of tropical forest (Potapov et al., 2017). The CBR is one of the last strongholds in Mexico for iconic species such as the jaguar (*Panthera onca*) and the Baird's tapir (*Tapirus bairdii*), making it critical for biodiversity conservation in Mexico and Mesoamerica (Hidalgo-Mihart et al., 2025; Naranjo, 2018). The study area is part of a 63,000-ha section of the CBR that was initially classified as part of the buffer zone but was reclassified to be part of the core zone in August 2023 (DOF, 2023). During this study, only ecotourism and research activities were allowed in our study area; the only human modification to the original vegetation was a narrow road (about 4 meters wide) leading to the Calakmul archaeological site (INE 1999).

The CBR has a tropical wet and dry climate with a dry winter (Köppen-Geiger classification: Aw; Beck *et al.* 2018). The region has a rainy season from May to October, a dry season from November to April (Mardero et al., 2020; Vidal-Zepeda, 2005) and a mean annual precipitation of 1,076 mm (CONAGUA, 2023; Martínez and Galindo-Leal, 2002). The region has a significant water deficit due to its karstic soils, which result in rapid water infiltration and a lack of perennial streams (Ensley et al., 2021; Torrescano-Valle and Folan, 2015). Thus, surface water deposits in this area depend mainly on rainfall and consist of seasonal waterholes (known locally as *aguadas*) and small rock pools in the epikarst where rainwater accumulates (known locally as *sartenejas*). Seasonal waterholes are dolines formed by the dissolution of limestone, where clay accumulation reduces water percolation and promotes water accumulation; they typically cover less than 5000 m^2 (García-Gil et al., 2002; Kranjc, 2013). Rock pools are natural depressions in exposed bedrock, typically less than one square meter in area, where rainfall collects. A more detailed description of these water bodies can be found in Delgado-Martínez *et al.* (2023).

Sampling of water bodies

We sampled 23 waterholes and 22 rock pools by setting one camera trap in each. To avoid spatial autocorrelation, we did not simultaneously monitor water bodies of the same type less than 500 m apart. We sampled each water body for at least 45 days during the wet and dry seasons (from July 2021 to September 2022). We programmed camera traps to take 20-second-long videos each time they were activated and to have a 5-second delay before reactivation. We deployed three camera-trap models: Browning Spec Ops Elite HP4 (BTC-8E-HP4, Birmingham, Alabama, USA), Browning Strike Force Elite HD (BTC-5HDE, Birmingham, Alabama, USA), and Bushnell Trophy Cam HD Aggressor (119876C, Overland Park, Kansas, USA). Further details about sampling can be found in Delgado-Martínez et al. (2023).

Data processing

We discarded the records of species smaller than 220 g because the camera traps do not efficiently record them due to their small size (Ortmann and Johnson, 2021). We grouped consecutive videos of the same species recorded by the same camera, following Camargo-Sanabria and Mendoza (2016), to determine species- and site-specific independence times.

Depending on the case, these values ranged from 1 to 180 minutes (see Camargo-Sanabria and Mendoza for more details). These grouped videos were classified as single visits.

Data analysis

We generated camera station-season combinations, where each camera station represents a different water body and season corresponds to the rainy or dry seasons, for species with at least 20 records in each combination. We used these combinations to evaluate the activity partitioning of water sources by conducting diel activity overlap, temporal co-occurrence, and time-to-encounter analyses (Figure S1). We discarded those species-pair combinations that included an exclusively nocturnal species and an exclusively diurnal species, as in the case of *Cuniculus paca* and *Dasyprocta punctata*, because such combinations could generate an overestimation of temporal partitioning due to their naturally non-overlapping activity windows.

Temporal partitioning analyses

We described the diel activity patterns of the target species by using kernel density estimators (Figure S1a). Based on the approach described by Meredith and Ridout (2018), we estimated the diel overlap between species occurring in the same site-season combination by calculating the overlapping coefficient estimator Δ_1 for small samples (fewer than 75 observations) and Δ_4 for large samples (more than 75 observations). This coefficient ranges from 0 to 1, where a coefficient of 0 indicates that the species have entirely different diel activity patterns, and a coefficient of 1 indicates that the species have identical diel activity patterns. We conducted this analysis using the *overlap* R package (Ridout and Linkie, 2009).

To determine whether the daily visitation of the species pairs aggregates, segregates, or occurs randomly, we performed a temporal co-occurrence analysis using a matrix of daily presence/absence for each species pair within each site-season combination (Figure S1b). This method assesses the probability that the observed frequency of co-occurrence between two species is less than, greater than, or not different from the expected frequency if the two species were occurring independently. The probability of co-occurrence can range from 0, indicating that the two species never occur on the same day, to 1, indicating that the two species always occur together on the same days. We conducted this analysis using the *cooccur* R package (Griffith et al., 2016).

Using multi-response permutation procedures, we calculated the time-to-encounter for both species in each species pair and site-season combination (Karanth et al., 2017). For each species pair, we selected a focal species and determined the minimum time until the subsequent detection of the second species. (Figure S1c). We repeated the same procedure, but changing the focal species in the pair. This process generated a set of observed times-to-encounter for each species. To compare these times with a null model, we conducted 10,000 simulations to create a random distribution of times-to-encounter for each site-season combination's initial and final day of camera trap operation. For both observed and simulated sets, we included detections up to 24 hours after each initial detection. We retained only those pairs with at least three encounters within 24 hours. To compare the median observed time-to-encounter with the simulated null distribution, we calculated the p-value as the proportion of instances where the observed median was greater than the medians of the null distribution.

A large value indicates temporal aggregation, while a small value suggests temporal segregation on a temporal scale of 24 hours (Watabe et al., 2022).

Summarizing temporal partitioning

We summarized the diel activity overlap and probability of co-occurrence of species pairs using a two-dimensional kernel density estimation conducted with the *MASS* R package (Venables and Ripley, 2002). We split this distribution into four equivalent quadrants: (1) species pairs with probabilities of co-occurrence and diel activity overlap from 0 to 0.5, representing the highest level of temporal partitioning, as species are not co-occurring and visit water bodies at different times of the day, (2) species pairs with probabilities of co-occurrence from 0 to 0.5 and diel activity overlap from 0.5 to 1, representing species that use the water bodies at similar times of the day but on different days; (3) species pairs with probabilities of co-occurrence from 0.5 to 1 and diel activity overlap from 0 to 0.5, representing species pairs that co-occur daily but at different times of the day; and (4) species pairs with probabilities of co-occurrence from 0.5 to 1 and diel activity overlap from 0.5 to 1, representing the highest level of temporal overlap. We counted the number of species pairs in each quadrant and conducted a contingency table analysis to compare the observed distribution with a homogeneous one (Franke et al., 2012).

Modeling factors influencing temporal partitioning

To identify the factors that impact temporal partitioning, we used diel activity overlap, the probability of co-occurrence, and time-to-encounter as response variables. We scaled the observed medians of times-to-encounter from 0 to 1 by dividing the median by 24. Using the *glmmTMB* R package, we independently modeled the three response variables by fitting generalized linear mixed models with a logit link function and beta distribution that is recommended to be used for continuous variables ranging from 0 to 1 (Brooks et al., 2017). We included a categorical variable with levels representing the different water bodies we sampled as a random effect in each model. We included the following covariates in the models: (a) species richness, which is the total number of bird and mammal species recorded at a site in a specific season, (b) body mass difference, which is the absolute difference between the mass of the focal species in each pair; (c) predator frequency, calculated using the equation: (number of events/sampling effort) × 100 camera trap days (O'Brien et al., 2003), where the number of events refers to the total count of visits of predator species (i.e., *Panthera onca*, *Puma concolor*, *Leopardus pardalis*, *L. wiedii*, and *Spizaetus ornatus*), and the sampling effort is the total number of days a camera trap was active; (d) distance to the nearest waterhole, obtained using a layer containing the location of waterholes within the reserve (García-Gil et al., 2002) to measure the distance between sampled water bodies and the nearest waterhole; (e) type of water body (waterhole or rock pool); and (f) season, defined as dry if sampling was carried out between November and April, or rainy if it was between May and October. Before fitting the models, we conducted pairwise comparisons among response numerical variables to check for correlations. We found no significant correlations between the covariates; therefore, we included all of them in the models. After data exploration, no variable transformations were needed (Zuur et al., 2010).

Due to the number of covariates we conducted an automated model selection for each response variable using the *glmulti* R package (Calcagno, 2020). The best models were identified through exhaustive screening of the candidate models based on the Akaike Information Criterion (AIC). This procedure was conducted in two steps. First, we ran the model selection without allowing interactions among the covariates; during this step, our candidate set contained 64 models. This output was used as a variable selection procedure, and for this step, we retained variables with model-averaged importance greater than 0.6. If only one variable met this criterion, we did not proceed to the next step and used this single variable to model the response variable. Second, we ran the model selection, allowing pairwise interactions between the variables. When there were multiple models within 2 AIC units, preventing the choice of a single best model, we included variables with model-averaged importance higher than 0.6 in the final model.

Results

We accumulated a sampling effort of 2,203 days in the waterholes and 2,828 days in the rock pools. We recorded 15 bird and 20 mammal species in the waterholes and 16 bird and 20 mammal species in the rock pools. We had 242 site-season species pairs: 115 in the waterholes and 127 in the rock pools. We found that most species pairs (240/242) showed some degree of segregation (Figure 1), either by using the water bodies on different days (probability of co-occurrence lower than 0.5) or at different times of the day (diel activity overlap lower than 0.5). Moreover, a high proportion of species pairs (161/242) partitioned their visits simultaneously along both axes (Figure 2). Only two species pairs showed temporal aggregation, using the water bodies on the same days and at similar hours: *Crax rubra*-*Meleagris ocellata* and *C. rubra*-*Penelope purpurascens*, both in waterholes. We found that more species pairs segregated along the days and hours than expected by chance, and fewer species pairs aggregated along these axes ($X^2 = 282.13$, $p < 0.001$).

Covariate effects on diel activity overlap

We found that the type of water body, species richness, and body mass difference had a model-averaged importance higher than 0.6 (Figure S3). The best model included these three covariates without interactions (Table S1, AIC = -188.8). We found a higher diel activity overlap among species pairs in the rock pools than in the waterholes (mean ± SE in waterholes = 0.33 ± 0.02, rock pools = 0.44 ± 0.04, $p < 0.01$). Furthermore, diel activity overlap was lower ($p < 0.001$) as the species richness and body mass differences increased (Figure 3).

Covariate effects on probability of co-occurrence

We found that only species richness had a model-averaged importance higher than 0.6 (Figure S4). Therefore, our best model included only the intercept and species richness (Table S2, AIC = -361.1). This model showed that the higher the species richness, the lower the probability of co-occurrence (Figure 4); however, this effect was only marginally significant ($p = 0.051$).

Covariate effects on times-to-encounter

We examined the times-to-encounter in 228 species pairs. Of these, 17 pairs (7.5%) showed statistical evidence of temporal segregation ($p < 0.05$), while 19 pairs (8.3%) showed evidence of temporal aggregation ($p > 0.95$). We found that none of the covariates had model-averaged importance higher than 0.6, with the best model including only the intercept (Figure S5, AIC = -59.2). Among the species pairs that exhibited temporal aggregation, the most frequent were *C. rubra – Odocoileus virginianus*, appearing in six different site-season combinations; *C. rubra – D. punctata*, recorded in three combinations; and *C. rubra – P. purpurascens*, observed in two combinations.

Discussion

Our site-level approach, combined with three different temporal frames, allowed us to analyze site-specific covariates and examine fine-scale temporal partitioning. Interestingly, most species pairs showed temporal segregation, while significant temporal aggregation was rare. Our findings partially support our initial predictions. Temporal partitioning varied with water body type, species richness, and body mass differences, with higher diel activity overlap occurring in rock pools and lower overlap at sites with greater species richness and among species pairs with larger body mass differences. However, contrary to our expectations, predator frequency, season, and proximity to large water bodies had no discernible effect. Among other things, our results highlight that the widely used metric of diel activity overlap did not detect the fine-scale temporal partitioning we observed.

Previous studies have shown that birds and mammals can partition the temporal axis when sharing water sources to reduce direct competition (Edwards et al., 2015, 2017;

Valeix et al., 2007). Our study provides additional evidence of temporal partitioning in the use of water sources, showing that this phenomenon occurs at a fine spatial scale and across different temporal frames. Even in rock pools during the dry season, when water availability is at its lowest, we found that the general pattern is that birds and mammals partition their use of water sources, with more than one species rarely exploiting the resource simultaneously or within short intervals (Figure S6). However, such temporal segregation may not only result from low water availability, as it can also reflect species-specific activity pattern (Helm et al., 2017). This pattern of temporal partitioning is similar to that observed in arid environments in other regions, where species adjust activity timing to balance resource access, competition, and predation risk, facilitating the coexistence of several species at water sources (Atwood et al., 2011; Valeix et al., 2008). Along with temporal partitioning, spatial partitioning can also play an essential role in water use, as species may utilize different types of water bodies or locations (Delgado-Martínez et al., 2023), adding another dimension to resource partitioning.

We found no evidence that predator abundance influences temporal partitioning, despite the well-documented role of predators in shaping prey behavior through the creation of a landscape of fear (Gaynor et al., 2019); a pattern also reported in mammal communities in Africa where predator presence does not necessarily generate strong temporal segregation (Ndachena et al., 2025; Smith et al., 2023). To better understand the potential influence of predators, future studies could adopt a functional trait approach that avoids discarding rare species with few records by incorporating all observations into broader functional categories (Schmitz, 2017). Similarly, we found no evidence that water availability, in terms of seasonality (dry vs. wet) or proximity to waterholes, influenced temporal partitioning. This suggests that animals may avoid interspecific interactions at water bodies regardless of standing water availability in the ecosystem to minimize adverse outcomes such as aggressive encounters or predation. However, there may be a threshold of extremely low water availability beyond which temporal segregation is no longer feasible, forcing species to overlap in time despite potential risks (Ferry et al., 2016; Perera-Romero et al., 2021).

Only a small proportion of species pairs exhibited significant temporal aggregation. For example, the pairs *C. rubra–D. punctata* and *C. rubra–O. virginianus* showed significant temporal aggregation based on time-to-encounter analyses. These temporal associations might reflect mutualistic interactions, as the presence of one species can lower predation risk and reduce vigilance requirements for both species involved (Davis and Ebersole, 2016; Sharpe et al., 2010). If a water body contains sufficient water to meet the requirements of co-occurring species, no adverse effects would be expected to emerge from these interactions; however, if the water body is small and water availability is reduced (e.g., late in the dry season), exploitative competition could arise, potentially reducing the fitness of subordinate species (Jensen, 1987). We acknowledge that our analysis did not include small bird species, mainly passerines, since these observations were discarded due to the low efficiency of camera traps in recording small-bodied animals (Ortmann and Johnson, 2021). However, multiple instances were noted where more than one passerine species simultaneously used water bodies. Thus, temporal aggregation may be common among small birds that tend to form mixed-species flocks, possibly reducing predation risk (Sridhar et al., 2009).

If we had relied solely on the most common approach for comparing temporal activity (i.e., kernel density estimators), our results would differ substantially, showing more cases of temporal aggregation, even when analyzing data at the site level. Therefore, our results are in agreement with other studies pinpointing the limitations of relying only on kernel density estimators to assess temporal segregation. We recommend using various temporal frames, as we did in this study, or adopting more recent approaches, such as hierarchical models with trigonometric terms and cyclic cubic splines, to enhance the analysis of temporal patterns and partitioning (Iannarilli et al., 2024; Watabe et al., 2022).

Niche partitioning has been a cornerstone of ecology since the last century, with time playing a central role as an axis for differentiation (Hutchinson, 1957; Schoener, 1974). Early theoretical and empirical studies suggested that species could reduce competition by segregating their activity in time, yet temporal partitioning was historically less documented than spatial or dietary differentiation (Kronfeld-Schor and Dayan, 2003). However, technological and methodological advances, such as camera traps and statistical modeling, are currently enabling fine-scale analyses that are helping to generate stronger empirical evidence of how species partition time to coexist. In this context, our findings provide further empirical evidence of the ecological importance of fine-scale temporal partitioning as a mechanism facilitating species coexistence in water-limited ecosystems.

As human activities expand globally and climate change intensifies, affecting water access, availability, and quality for humans and wildlife, the observed pattern of temporal partitioning may shift. In the Calakmul region, where this study was conducted, recent research has shown rainfall patterns are increasingly becoming uneven throughout the year with more intense rainfall events, and an increased frequency of droughts (Mardero et al., 2020). If these trends continue, temporal aggregation at water bodies will likely become more common, with negative consequences for subordinate and highly-water-dependent species (Gorta et al., 2021; Votto et al., 2020). Therefore, understanding the mechanisms that enable diverse animal communities to coexist while sharing water resources is essential, not only for scientific purposes but also to inform strategies aimed at improving human-wildlife coexistence.

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Figure legends

Figure 1. Examples of different strategies animals use to partition water bodies in space and time. Although recorded at the same time and in the same type of water body, a puma (a) and a jaguar (b) visited different waterholes on different days. Similarly, although recorded at the same site and at the same time, a jaguar (c) and a great curassow (d) visited the rock pool on different days. Finally, great curassows (e) and white-lipped peccaries (f) visited two different waterholes at the same time on the same day.

Figure 2. Distribution of species pairs in a two-dimensional temporal partitioning scenario. Contours represent the 50th, 75th, and 95th percentiles of the kernel density estimation. Pairs in the lower-left quadrant indicate species that visited the water body on different days and at different times of the day, while pairs in the upper-left quadrant represent species that visited the water body on the same days and at similar times.

Figure 3. Effect of body mass differences between species on diel activity overlap in (a) ponds and (b) rock pools, considering scenarios of low and high species richness.

Figure 4. Effect of site species richness on the probability of co-occurrence at water bodies in the Calakmul Biosphere Reserve.

Figure 1

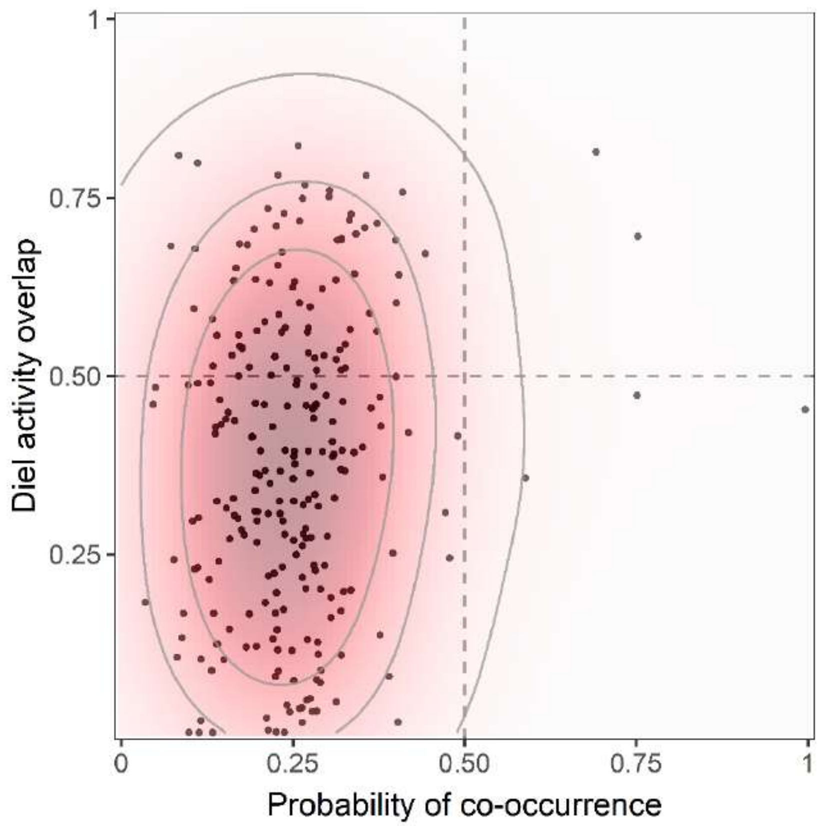


Figure 2

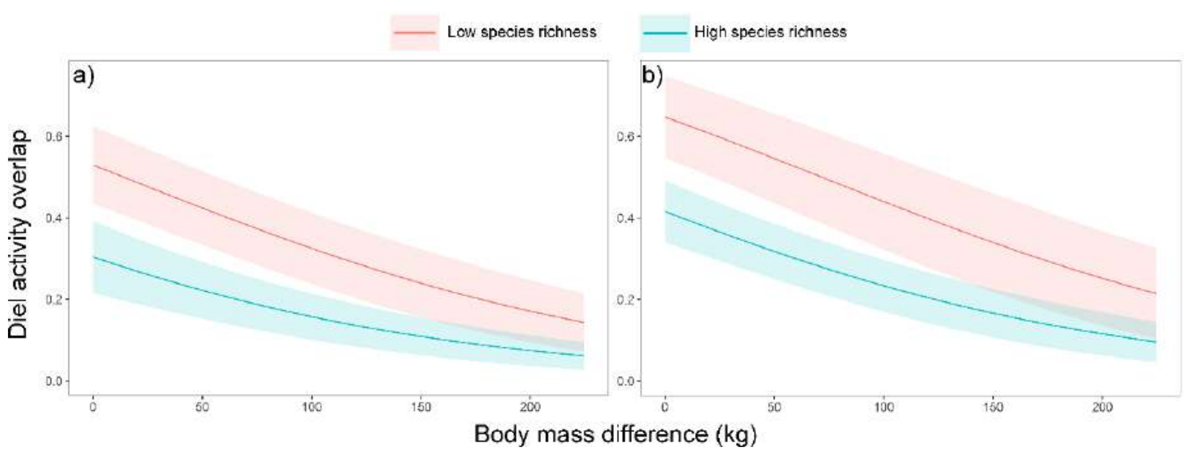


Figure 3

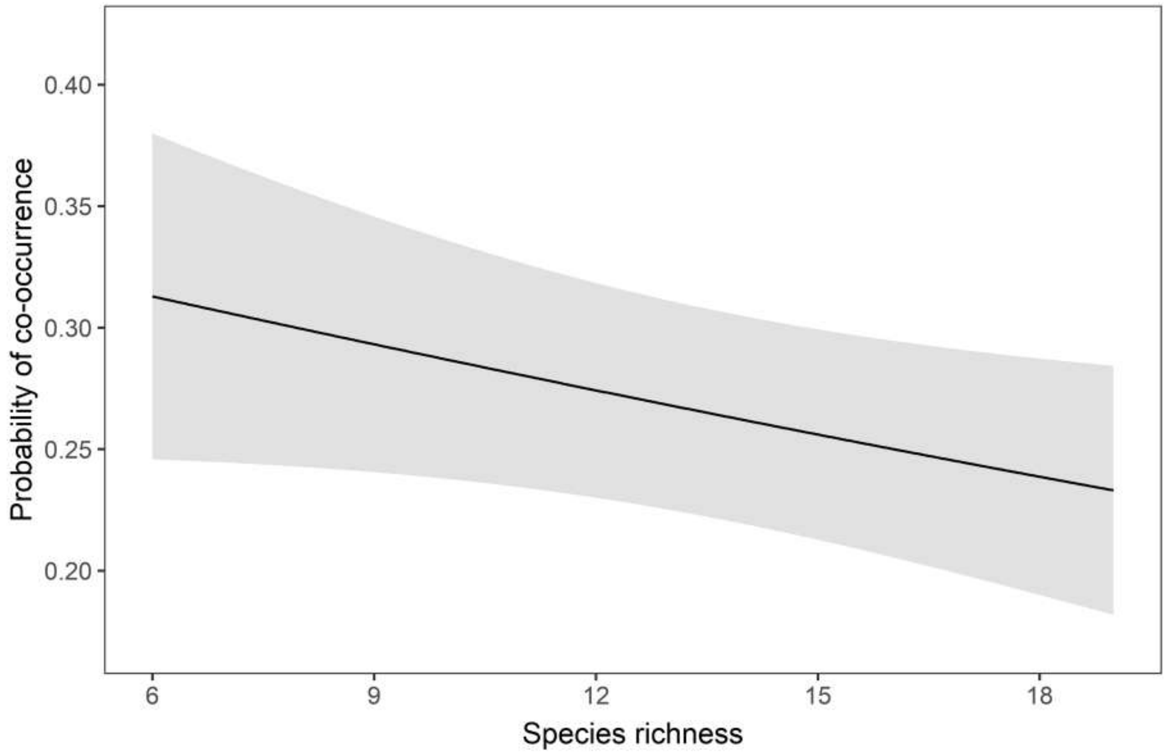

0.40
0.35
0.30
0.25
0.20
Probability of co-occurrence
6
9
12
15
18
Species richness

Figure 4

Supporting information for

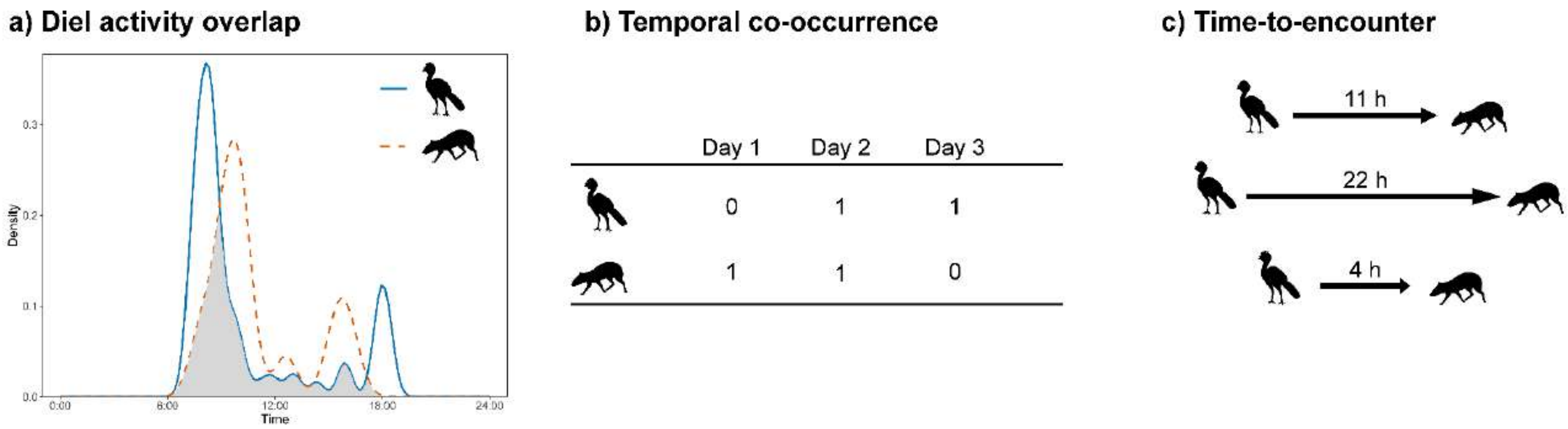
Sharing the oasis: A site-level approach to analyzing water use partitioning by forest birds and mammals across different frames

Table S1. Results of the generalized linear mixed model assessing the effects of biotic and abiotic factors on diel activity overlap. The model included the site as a random intercept (variance = 0.119).

	Estimate	Std. Error	z value	*p*-value
Intercept	1.045	0.343	3.043	**< 0.01**
Species richness	-0.073	0.022	-3.278	**< 0.001**
Body mass difference	-0.008	0.001	-6.905	**< 0.001**
Type of water body (waterholes)	-0.490	0.188	-2.599	**< 0.01**

Table S2. Results of the generalized linear mixed model assessing the effect of species richness on temporal co-occurrence. The model included the site as a random intercept (variance = 0.346).

	Estimate	Std. Error	z value	*p*-value
Intercept	-0.600	0.237	-2.532	< 0.05
Species richness	-0.031	0.016	-1.950	0.051



• It calculates the degree to which two or more species share the same time periods for their daily activity patterns

• Data: time (00:00-23:59)

• Interpretation: low values indicate different time periods of activity, while high values indicate similar periods of activity

• It calculates the probability that two species occur on the same day

• Data: detection-nondetection (0/1) at the daily basis

• Interpretation: low values indicate occurrence on different days, while high values indicate occurrence on the same days

• It indicates whether two species aggregate or segregate over a 24-hour period

• Data: time elapsed from the detection of sp1 to the detection of sp2 within 24-hour periods

• Interpretation: low median values indicate temporal aggregation, while high values indicate temporal segregation

Figure S1. Three analytical approaches used in this study to assess temporal partitioning at the site level, modified from Watabe et al. (2022).

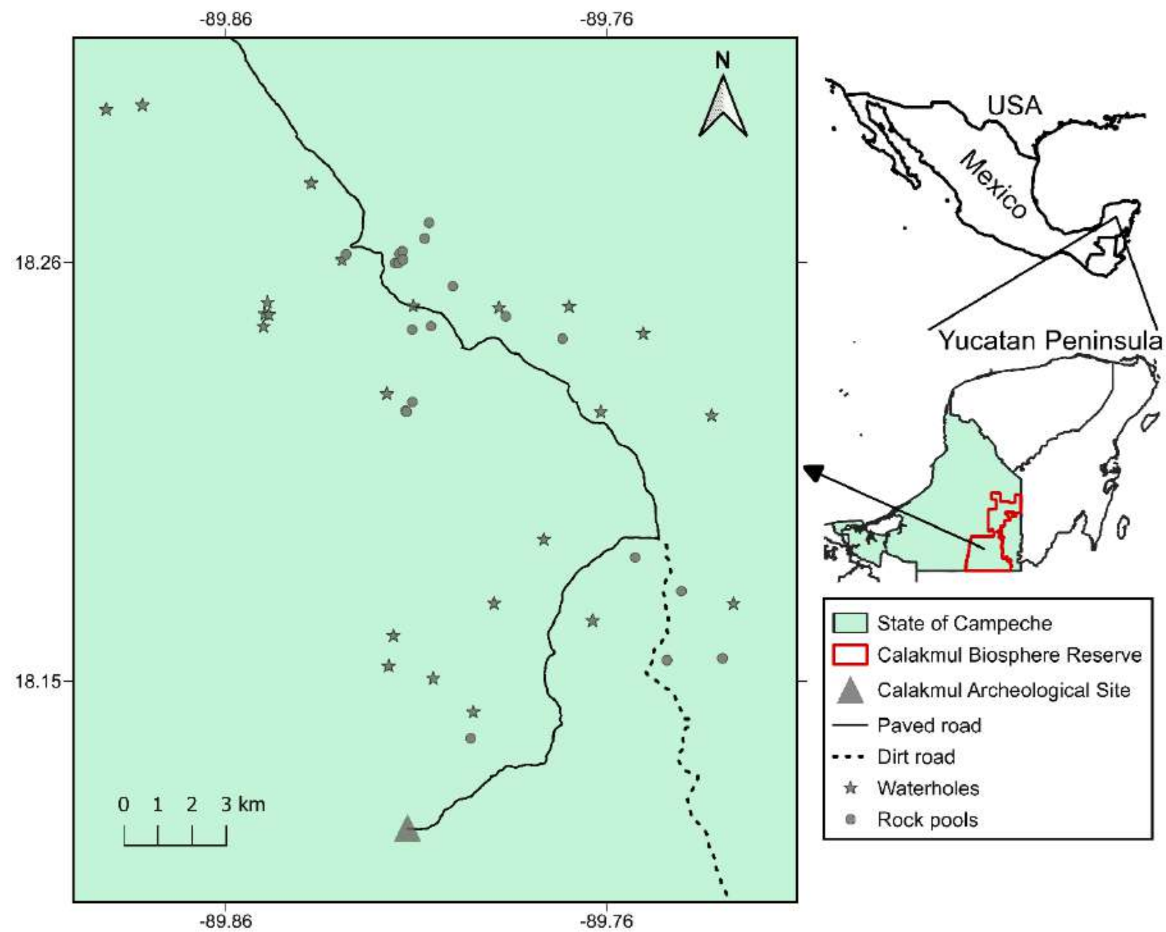


Figure S2. Study area and locations of water bodies monitored with camera traps in the Calakmul Biosphere Reserve, Campeche, Mexico.

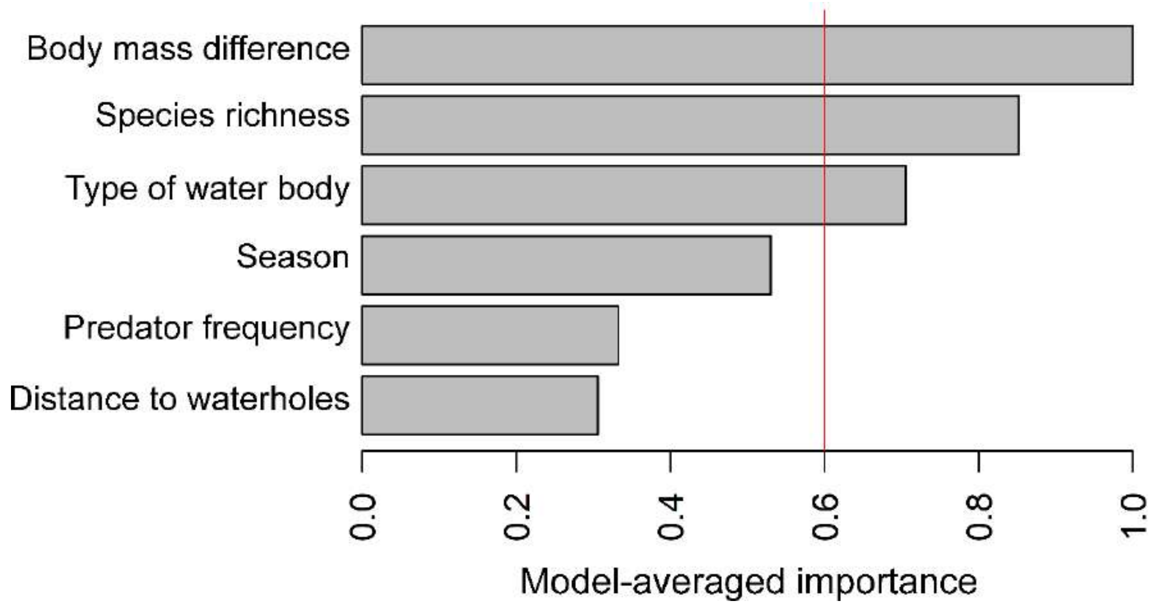


Figure S3. Model-averaged importance of covariates from the model selection of the best-fitting models (without interactions) predicting diel activity overlap.

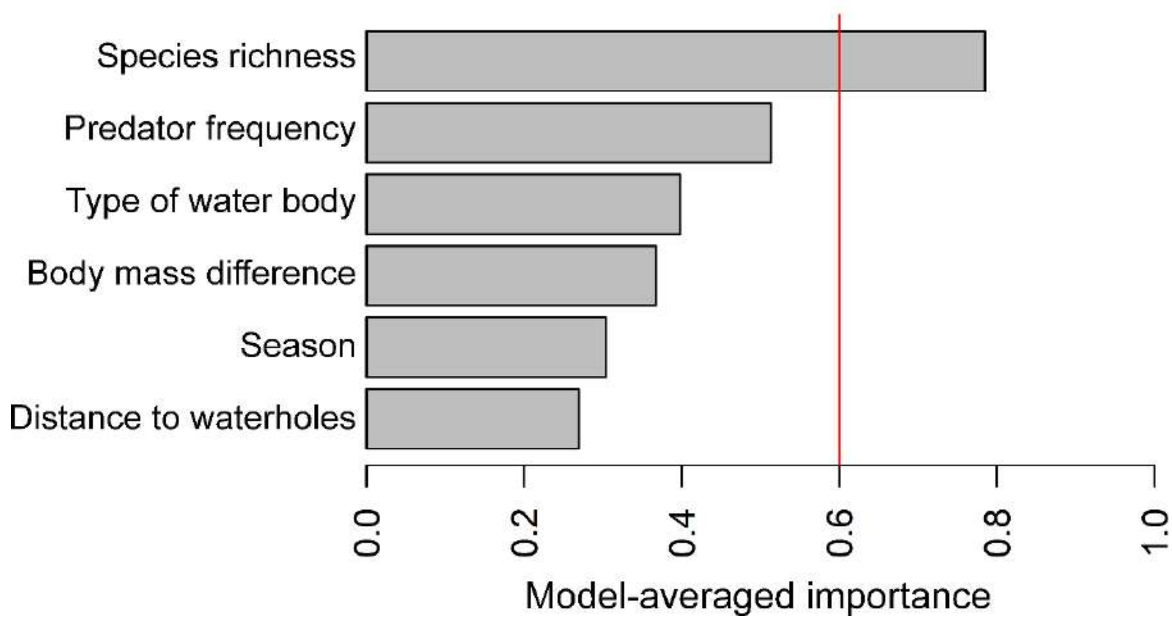


Figure S4. Model-averaged importance of covariates from the model selection of the best-fitting models (without interactions) predicting temporal co-occurrence.

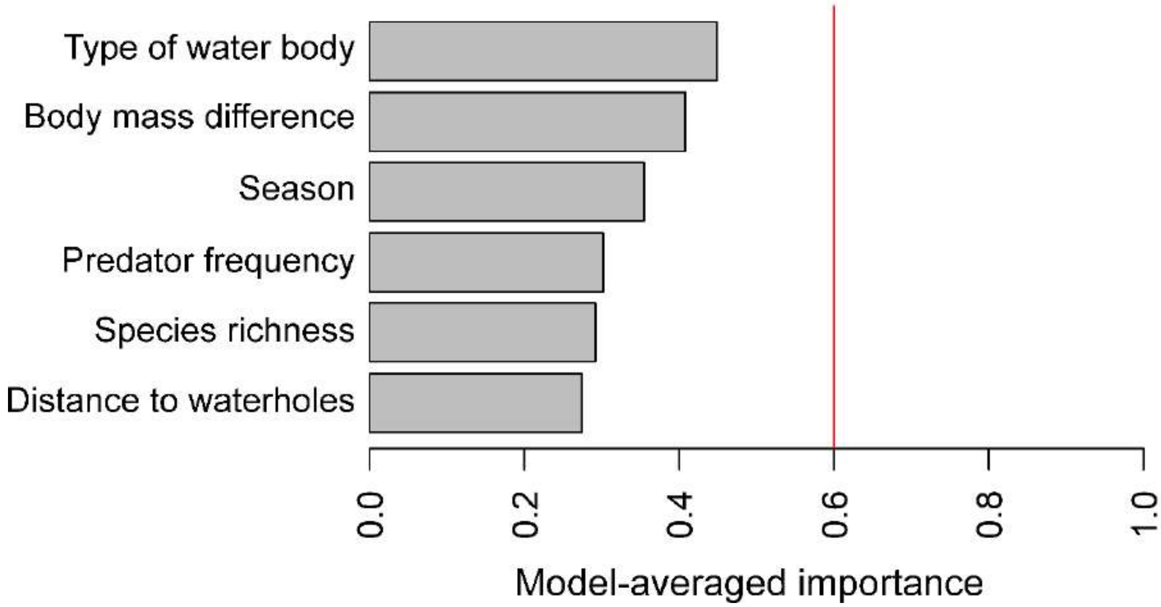


Figure S5. Model-averaged importance of covariates from the model selection of the best-fitting models (without interactions) predicting time-to-encounter.

Figure S6. Although rare, there were instances where more than one species was recorded using the water bodies simultaneously: a white-nosed coati (*Nasua narica*) and ocellated turkeys (*Meleagris ocellata*) are co-occurring in this waterhole.

Anexo 2

Capítulo IV. Factors that determine water availability in surface and arboreal water bodies of a tropical karst ecosystem: a climate change perspective

Abstract

Climate change significantly impacts global water availability, particularly affecting temporary freshwater habitats through altered rainfall and temperature patterns. In the tropical karst ecosystem of Calakmul, Mexico, characterized by porous limestone geology, water availability is predominantly rainfall-dependent, manifesting primarily in temporary surface and arboreal habitats such as waterholes, rock pools, and tree holes. This study employed comprehensive field observations, camera trap monitoring, and local climate data to model water presence across these habitats using generalized linear models. Future hydroperiods were predicted under various climate scenarios defined by Shared Socioeconomic Pathways (SSPs), specifically SSP2-4.5, SSP5-3.4-OS, and SSP5-8.5. Results identified previous water presence, water body size, accumulated rainfall patterns, and maximum temperatures as key predictors of water availability. Waterholes exhibited greater hydrological stability due to their larger sizes and deeper storage capacities, while rock pools and especially tree holes demonstrated heightened sensitivity to climatic variability due to smaller volumes and increased evaporation in canopy environments. Climate projections indicate significant hydroperiod reductions, with severity intensifying under higher emission scenarios, particularly the SSP5-8.5 pathway. Tree holes are predicted to experience the most substantial hydroperiod reductions, with potential cascading effects on canopy-dependent biodiversity. These findings underscore the urgent need for targeted conservation management strategies, including canopy water provisioning interventions, to

mitigate climate-driven impacts on biodiversity and preserve ecological functionality within vulnerable tropical karst ecosystems.

Keywords: Calakmul, dendrotelma, hydroperiod, temporary waters

Introduction

Climate change is one of humankind's most critical and pervasive challenges in the 21st century. Its impact is now evident across all regions and from the local to the global scale, including the water cycle (IPCC, 2023). Over recent decades, more frequent and intense weather extremes have disrupted environmental and socio-economic systems, further compounding the impacts on the water cycle (Nhamo et al., 2025; Yang et al., 2021). One of the most immediate and widespread consequences is the alteration of water availability, as phenomena such as shifting precipitation patterns, prolonged droughts, floods, and intensified evapotranspiration reduce the quantity and quality of freshwater resources (Grover, 2015; IPCC, 2023). These hydrological changes profoundly impact biodiversity, threatening freshwater-dependent species, altering natural dynamics, and exacerbating anthropogenic pressures (Bellard et al., 2012; Wiens and Zelinka, 2024). As freshwater ecosystems become increasingly degraded, wildlife and human populations face heightened vulnerability, particularly in regions already experiencing water stress (Bell et al., 2018; van den Bosch et al., 2025).

Temporary water bodies are among the freshwater systems most affected by climate change (Parra et al., 2021). These habitats, defined by recurring dry periods of variable duration and cyclical fluctuations between wet and dry phases, are widely distributed across all biomes and represent the most common type of water bodies in numeric terms (Williams, 1987). They include intermittent streams, seasonal ponds, rain puddles, rock pools, and water-retaining structures in plants such as bromeliads and tree holes (Colburn, 2008). Although often overlooked due to their temporal nature, temporary waters play a crucial role in maintaining biodiversity, supporting organisms across all biological kingdoms (IGB, 2023). For example, many animals rely on them for different life stages such as breeding, feeding, and refuge (Calhoun et al., 2014; Petermann and Gossner, 2022). At the same time, non-aquatic organisms may depend on these habitats for hydration, thermoregulation, or hunting (Gossner et al., 2020; Lee et al., 2017; Marteau et al., 2023). As a result, the spatial and temporal dynamics of temporary waters can profoundly influence ecological patterns, from individual fitness to community and ecosystem-level processes. Considering ongoing climatic and anthropogenic pressures, understanding the role, dynamics and vulnerability of these systems is a research priority.

The hydrological regime of temporary waters can be described in terms of hydroperiod (i.e., the duration of inundation), flood timing (i.e., when water bodies are filled), and the frequency of hydroperiods throughout the year (Colburn, 2008). Climate change threatens to disrupt the dry-wet cyclical dynamics of temporary waters, leading to shorter, delayed, or premature flooding, and in some cases, the complete absence of wet phases, increasing the unpredictability of water availability in these systems (Brooks, 2009; Grillas et al., 2021; Parra et al., 2021). In landscapes lacking permanent water bodies, such changes can have far-reaching consequences, as temporary waters can shape the structure and functioning of entire ecosystems. Given their ecological importance and vulnerability to climate change, there is a growing need to study how temporary waters respond to climate change (Biggs et al., 2017). Developing predictive models that can accurately forecast hydroperiod changes under different climate scenarios is essential for understanding future impacts and guiding effective conservation and management strategies (Cartwright et al., 2022; Fay et al., 2016).

One example of an ecosystem strongly shaped by temporary waters is the Calakmul tropical forest, located within the seasonally dry tropical forests of the Peten Plateau in southern Mexico. Due to its karstic geology, characterized by porous limestone subjected to chemical weathering and erosion, the region lacks extensive permanent surface water bodies, resulting in freshwater availability that is closely tied to rainfall (Ensley et al., 2021; García-Gil et al., 2002; Torrescano-Valle and Folan, 2015). Consequently, the ecosystem dynamics in Calakmul are predominantly driven by seasonal precipitation and temporary water bodies. Four main types of temporary waters dominate this landscape: intermittent streams, waterholes, epikarst rock pools, and water-filled tree holes. Intermittent streams only flow following heavy rainfall and remain dry for most of the year, yet they contribute significantly to short-term water redistribution across the landscape (pers. obs.). Waterholes are karstic depressions sealed by accumulated clay that retain rainwater seasonally, with many drying out entirely during the dry season and only the largest persisting through extended droughts (Back and Lesser, 1981; García-Gil et al., 2002; O'Farrill et al., 2014). Rock pools, small depressions formed by limestone dissolution on exposed bedrock, are numerous and typically store water for several weeks following precipitation events (Delgado-Martínez et al., 2023; Flores, 1983). Similarly, water-filled tree holes accumulate rainwater in arboreal cavities and exhibit highly variable hydroperiods, with some drying quickly and others retaining water year-round (Kitching, 2000). Recent findings highlight that these temporary waters are essential for sustaining wildlife in Calakmul, acting as complementary water sources for different animal groups (Delgado-Martínez et al., 2023). The hydrological regime of these water bodies depends directly on precipitation patterns, making them particularly sensitive to climatic variability. Indeed, climate change has already begun altering rainfall patterns in the region, increasing drought frequency and intensity, and leading to more irregular and extreme rainfall events (Mardero et al., 2020). These changes threaten the predictability and duration of hydroperiods in temporary waters, potentially disrupting the ecological dynamics and biodiversity they sustain. Given their vulnerability to climatic fluctuations, advancing our understanding of temporary waters is essential for predicting ecosystem responses and implementing effective conservation and water management strategies.

Previous efforts to model the hydrology of temporary waters have predominantly focused on temperate and subtropical systems, leaving significant gaps in our understanding of tropical environments (Jocque et al., 2010; Olmo et al., 2024). Most existing models rely on simplified water-balance approaches, which estimate water level changes based on precipitation as input and evapotranspiration as the main output (e.g., Hulsmans et al., 2008; Vanschoenwinkel et al., 2009). These models typically assume minimal lateral flows or groundwater exchange, making them broadly applicable but limited in capturing localized complexities, especially in heterogeneous landscapes such as karst. While this approach has been applied to some karst systems (e.g., Cartwright and Wolfe, 2021; Greenberg et al., 2015), the unique hydrodynamics of karst systems, characterized by subsurface drainage, perched aquifers, and variable connectivity, often require adapted or more complex modeling frameworks (Hartmann et al., 2013). However, the number of hydroperiod studies specifically focused on karst systems remains limited and mostly restricted to temperate regions. Observational and modeling studies indicate that climate change generally leads to shorter hydroperiods, increased variability, and altered water availability due to intensified evaporation and changes in rainfall distribution (Brooks, 2009; Greenberg et al., 2015; Hulsmans et al., 2008). For instance, modeling of karst ponds under future climate scenarios predicted significantly shallower water depths and reduced hydroperiods (Greenberg et al., 2015). Conversely, a notable exception has been documented in a temperate karst setting where long-term observational reconstructions revealed an increase in hydroperiod over the past century, associated with increased regional precipitation (Cartwright and Wolfe, 2021). Despite these advances, hydrological models remain notably scarce for tropical environments, particularly for small temporary water bodies such as rock pools and water-filled tree holes. While the influence of basin morphometry and rainfall on rock pool hydrology is recognized, global research efforts remain scarce, leaving major knowledge gaps (Jocque et al., 2010; Vanschoenwinkel et al., 2009). Even less is known about tree holes, which lack quantitative analyses entirely. In Calakmul, the only published assessment of climate impacts on surface waters is by O'Farrill et al. (2014), who suggested that extreme droughts could dry out even the largest waterholes. Given this gap, Calakmul presents a critical opportunity to apply empirical models based on field observations to improve our understanding of how climate change may affect surface and arboreal temporary waters in tropical karst landscapes key to support wildlife.

In this study, we take advantage of the unique hydrological and ecological characteristics of the Calakmul region to model the dynamics of temporary water bodies in a tropical karst landscape. The absence of extensive permanent surface water, together with the presence of rainfall-fed habitats such as waterholes, rock pools, and water-filled tree holes, creates a natural setting where water availability is highly sensitive to climatic variability. Building on this context, the research aims to explore future scenarios for the presence or absence of water in these water bodies. To achieve this, we developed a predictive model based on field observations of water presence and existing climatic variables and applied it under climate change scenarios. Specifically, we first identified the factors that best predict water presence across different types of temporary water bodies and then evaluated how climate change may alter their hydroperiods throughout the year. We hypothesize that (1) climatic variables and physical features of water bodies jointly determine water availability in water bodies, with heavy precipitation events and maximum temperatures as primary predictors, modulated by the size of the water body; (2) hydroperiods will be significantly reduced under future climate scenarios compared to historical baselines, primarily due to increased temperatures and more irregular or delayed rainfall; and (3) different types of temporary water bodies will respond differently to climate change, with waterholes exhibiting greater hydrological stability due to their larger water-holding capacities.

Methods

Study site

Fieldwork was conducted in the Calakmul Biosphere Reserve (CBR; 89° 43' 26" – 89° 49' 23" W, 18° 16' 01" – 18° 8' 49" N) in the state of Campeche, southern Mexico (Figure 1). Covering 728,908 hectares, the CBR is the largest protected area of tropical forest in Mexico (Galindo-Leal, 1999; Gómez-Pompa and Dirzo, 1995). Our study was carried out only within a small section of the CBR, specifically in its southern portion. The region has a tropical wet and dry climate with a dry winter (Köppen-Geiger classification: Aw; Beck et al., 2018) and exhibits strong precipitation seasonality, with a rainy season from May to October and a dry season from November to April, during which monthly precipitation drops below 60 mm (Mardero et al., 2020; Vidal-Zepeda, 2005). Mean annual precipitation is 1076 mm

(CONAGUA, 2023; Martínez and Galindo-Leal, 2002). The average annual temperature is 25.7°C, with mean annual minimum and maximum temperatures of 18.7°C and 32.8°C, respectively (CONAGUA, 2023; Figure 2). Due to its karstic geology, the region experiences a significant water deficit, as rapid infiltration through porous limestone prevents the formation of perennial surface water bodies (Ensley et al., 2021; García-Gil et al., 2002; Torrescano-Valle and Folan, 2015). As a result, water availability in the region is almost exclusively rainfall-dependent, with free-standing water confined to temporary water bodies such as waterholes, rock pools, and water-filled tree holes (see Introduction for more detailed descriptions).

Monitoring of hydroperiods

We reconstructed hydroperiods of the different types of water bodies using empirical data collected in the field. For waterholes, water presence was determined through direct site visits and camera traps aimed at collecting wildlife visitation data, which additionally offered observations for the presence of surface water. In total, 19 waterholes were monitored from July 2021 to July 2024. For rock pools and tree holes, we installed camera traps (Bushnell Trophy Cam HD Aggressor 119876C; Overland Park, Kansas, USA) using a camera tree mount to position them for direct observation of the water (Figure 3). After a short testing period of approximately one month, during which the cameras took a picture every hour to identify the times of day when water presence could be reliably detected, the cameras were configured in time-lapse mode to capture images every 15 minutes for two 15-minute periods each day, one period from 12:00 to 12:15 and the second from 00:00 to 00:15, having four pictures per day. In some instances, pictures during night hours were more useful than daylight hours because of the reflection of the infrared flash on the water surface. We chose to use a binary response variable to describe water status (presence/absence) to avoid potential disturbances to wildlife that might result from installing stage gauges in these small water bodies. We monitored seven rock pools and six tree holes from February 2022 to September 2022, covering the dry and rainy seasons. The hydroperiod of waterholes was reconstructed monthly due to the reliance on site visits. In contrast, the hydroperiod of rock pools and tree holes was established daily using the images generated by camera traps. Additionally, in January 2022, a rain gauge and a thermometer were installed within the CBR to record local rainfall and temperature, with temperature measured every 30 minutes.

Covariates that explain water presence

Because no weather data were available for our study site before the installation of the rain gauge and the thermometer, we evaluated five nearby CONAGUA-operated weather stations in the Calakmul region to identify the most suitable proxy for earlier conditions (CONAGUA, 2023). We assessed the correlation between rainfall and temperature records from each station and the data collected by our rain gauge and selected the station with the highest linear correlation to estimate rainfall and temperature conditions before January 2022. We defined different sets of climatic covariates for modeling each type of water body. For waterholes we defined covariates on a monthly scale, whereas for rock pools and tree holes, we included daily-scale covariates (Table 1).

Among the climatic covariates, we excluded the highly correlated covariates ($r \geq 0.80$) to avoid multicollinearity. The resulting set of variables included a categorical variable describing the presence or absence of water the day or month before the observation. Furthermore, we included water body size as a covariate; for waterholes, size was defined as the maximum surface area (measured in square meters) recorded using a GPS. For rock pools and tree holes, size was calculated as volume based on field measurements of length, width, and depth.

Modeling of water presence

To identify the covariates that best explain the presence or absence of water in each type of temporary water body (i.e., waterholes, rock pools, and tree holes), we employed a modeling approach that relates reconstructed hydroperiods to the retained weather variables. First, all predictors were standardized to a zero mean and unit variance, and their distributions were checked for large gaps. We then modeled water presence or absence using generalized linear models with a binomial distribution and a logit link function. After excluding highly correlated variables, more than 10 covariates remained; to account for this number of potential predictors and the uncertainty regarding which should be included, we performed automated model selection with the *glmulti* R package (Calcagno, 2020; R Core Team, 2024). This approach was chosen because it efficiently evaluates large sets of predictor combinations, ranks models using information-theoretic criteria, and enables multi-model inference, offering greater robustness and reproducibility than stepwise approaches (Calcagno and de Mazancourt, 2010; Heinze et al., 2018). The best models were identified through exhaustive screening of the candidate models based on the Akaike Information Criterion (AIC). This procedure was conducted in two steps. First, we ran the model selection without allowing interactions among the covariates. This output was used as a variable selection procedure, and for this step, we retained variables with model-averaged importance higher than 0.6. Second, we ran the model selection, allowing pairwise interactions between the variables. We included variables with model-averaged importance higher than 0.6 in the final model when multiple models within 2 AIC units occurred, preventing the choice of a single best model. To evaluate the performance of the selected model, we predicted the probabilities of water presence using the fitted model. The predicted probabilities were then used to calculate the Area Under the Receiver Operating Characteristic Curve (AUC) using the *pROC* package (Robin et al., 2011). The AUC was employed as a metric to assess the model's ability to discriminate between the presence and absence of water. Additionally, we calculated the Variance Inflation Factor (VIF) for the predictors in the model to assess potential multicollinearity among the explanatory variables, since VIF measures how much the variance of a regression coefficient is inflated due to linear correlations with other predictors (Fox and Monette, 1992).

Climate change impacts on hydroperiods

We used historical weather data (01/01/1988–31/12/2020) from the national climatological stations network as a baseline to model water presence and establish reference conditions for comparison with future scenarios (CONAGUA, 2023). Daily precipitation and maximum temperature were obtained from the selected weather station near our study site (station ID: 4037), with the initial period (01/01/1988–31/12/1990) serving as a stabilization phase to reduce uncertainty in predictions. Using this historical dataset, we predicted water presence on a monthly scale for waterholes and a daily scale for rock pools and tree holes, categorizing observations by water body type and size (small, medium, or large). Predictions were initialized with a starting value of 1 (presence), and probabilities of water presence were calculated from the fitted generalized linear models. An optimal classification threshold for each water body was determined using the *coords* function from the *pROC* R package (Robin et al., 2011). We defined small, medium, and large size categories for each water body type based on the distribution of sizes of the focal sites, using the 25th, 50th, and 75th percentiles as reference points. Specifically, categories were set at (1) 900, 2000, and 3000 m^2 for waterholes; (2) 10, 30, and 50 L for rock pools; and (3) 6, 15, and 24 L for tree holes.

To evaluate future changes under three scenarios of climate change relative to the historical baseline, we applied the same procedure used for historical data to predict water presence continuously from 2015 to 2100, using weather variables derived from the MIROC6 global climate model (CMIP6). We selected the MIROC6 climate model based on previous studies identifying it as one of the best-performing models for our study region (Almazroui et al., 2021; Andrade-Velázquez and Montero-Martínez, 2023; Ortega et al., 2021). We selected three Shared Socioeconomic Pathways (SSPs): SSP2-4.5, a moderate-emissions scenario based on current development trends; SSP5-3.4-OS, a high-growth pathway with delayed but aggressive climate mitigation; and SSP5-8.5, a fossil-fuel-intensive scenario with no significant emissions reductions (Meinshausen et al., 2020). High-resolution (0.25°) daily data on precipitation and maximum temperature were extracted for the grid cell encompassing our study site (Gebrechorkos et al., 2023). To analyze the scenarios, we focused on three decadal periods: 2031–2040, 2061–2070, and 2091–2100, representing the short, mid, and long-term, respectively.

For each combination of water body type, size, SSP scenario, and decadal period, we calculated the annual proportion of months (for waterholes) or days (for rock pools and tree holes) with predicted water presence. This yielded ten annual proportions for each combination. To assess potential impacts of climate change, we compared future proportions with the historical baseline using pairwise permutation tests. The observed difference in mean proportions served as the test statistic. Under the null hypothesis of no difference, a null distribution was generated by permuting model labels 10,000 times, and two-sided p-values were calculated. Additionally, 95% confidence intervals for differences in means were estimated using 10,000 bootstrap resamples.

To describe projected changes in maximum temperature and annual precipitation, we calculated mean annual values for each SSP scenario across the three future periods of analysis. For maximum temperature, we computed the mean of daily maximum temperatures for each year; for precipitation, we used the annual sum of daily rainfall values. These metrics were then averaged across years within each period and compared to the historical baseline (1991–2020). Absolute and relative differences were calculated to quantify the magnitude of change under each scenario.

Results

Our monitoring allowed us to determine water presence/absence in 427, 930, and 464 instances in waterholes, rock pools, and tree holes, respectively. Across the sampling period of waterholes (2021–2024), water absence represented about 11% of all records, but patterns were highly uneven across years and waterhole sizes. In 2021 and 2023, waterhole desiccation was almost absent, affecting only a few small waterholes, less than 3 and 12% of observations respectively. In contrast, 2022 showed a pronounced dry pulse, when nearly

40% of small waterhole observations and 5% of medium ones had dried up, while large waterholes remained stable. The most extreme conditions were recorded in 2024, with more than half of the small waterhole observations (57%) and over a third of large ones (36%) showing water absence. During the monitoring of rock pools, water absence was recorded in 32.8% of the daily observations. Drying was most frequent in small rock pools, with absence in 65% of records, while medium and large pools showed water absence in 27 and 31% of cases, respectively. Temporally, dried-up rock pools concentrated between March and May, with a maximum of 127 dry observations in April, whereas no cases were detected in June or September. In tree holes, water absence was recorded in 81 of 464 observations (17.5%), mostly between March and May 2022. In terms of size categories, small tree holes recorded 28 dry observations out of 97, medium tree holes 53 out of 170, while large cavities showed no dry observations across 197 samples. Drying peaked in April and May.

Generalized linear models for water presence

The best model for predicting water presence in waterholes included the following covariates: water presence in the previous month, waterhole size, accumulated rainfall in the previous month, accumulated rainfall over the preceding 20 months, and mean of daily maximum temperatures over the preceding 14 months (AICC = 116.22, AUC = 0.954, VIF < 2; Table 2). Water presence in the previous month had the strongest positive effect on water presence ($p < 0.001$). Similarly, waterhole size was positively associated with water retention, with larger waterholes having a higher probability of containing water ($p < 0.01$). Accumulated rainfall in the previous month also showed a significant positive effect on water presence ($p < 0.001$), whereas accumulated rainfall over the previous 20 months had a marginally significant positive effect ($p < 0.10$)

For rock pools, the best model included water presence on the previous day, number of days without rain, mean of maximum temperatures on the previous two days, number of days without heavy rain, accumulated rainfall on the previous two days, rock pool size, and three interaction terms: the interaction between mean of maximum temperatures on the previous two days and rock pool size, water presence on the previous day and rock pool size, and mean of maximum temperatures on the previous two days and accumulated rainfall on the previous two days (AUC = 0.982, VIF < 2; Table 3). Water presence on the previous day had the strongest positive effect on the current water presence ($p < 0.001$). In contrast, days without rain, the mean of maximum temperatures on the previous two days, and days without heavy rain had negative effects ($p < 0.001$). Among the interaction terms, the interactions between the mean of maximum temperatures and rock pool size, and between water presence the day before and rock pool size were statistically significant.

For tree holes, the best model included water presence on the previous day, days without heavy rain, mean maximum temperature over the previous 9 days, and tree hole size (AUC = 0.997, VIF < 2; Table 4). Water presence on the previous day and size had a positive effect on water presence. In contrast, both days without heavy rainfall and maximum temperatures over the previous 9 days were negatively associated with water presence.

Climate change impacts on hydroperiod

In the short term, no changes are projected to waterholes in any of the climate change scenarios. However, by the mid-term, small and medium waterholes will show decreased hydroperiods under SSP5-8.5. In the long term, all waterholes are expected to decrease their hydroperiods under SSP5-8.5 (Figure 4a). For rock pools, no changes are projected in the short-term under any scenario. In the mid-term, however, small rock pools are expected to experience reduced hydroperiods under SSP5-8.5. By the long-term, all size classes are projected to show shortened hydroperiods under SSP5-8.5, whereas large rock pools are expected to increase their hydroperiods under SSP5-3.4-OS (Figure 4b). Tree holes show a more consistent negative trend for water presence. In the short term, small tree holes are projected to have reduced hydroperiods under all three SSPs. Medium and large tree holes are expected to experience reductions under SSP5-3.4-OS and SSP5-8.5. In both the mid- and long-term, all size classes are predicted to undergo reductions in hydroperiod across all scenarios, with the most severe reductions occurring under SSP5-8.5 (Figure 4c).

We found that maximum temperatures are projected to increase across all future scenarios, with absolute differences ranging from 2.6 to 6.5 °C. The most severe increase is expected in the long term under the SSP5-8.5 scenario (Table 5). Regarding annual precipitation, all scenarios indicate an increase ranging from 38 to 227 mm per year, except for SSP5-8.5 in the mid-term, which shows a reduction of 32 mm (Table 6).

Discussion

This study advances the understanding of temporary water bodies in tropical ecosystems by identifying the climatic drivers of water presence, accounting for physical features such as type and size, and projecting future hydroperiods under different climate scenarios. Importantly, it presents the first empirical model to include tree holes (dendrotelmata), extending hydroperiod analyses beyond surface water bodies. This inclusion is particularly relevant in the Calakmul region, where wildlife has been documented to rely frequently on both arboreal and surface water sources (Delgado-Martínez et al., 2023). By incorporating these elements, our findings provide a basis for anticipating the impacts of climate change on wildlife water use and for developing adaptive strategies to safeguard biodiversity in water-limited tropical forests.

Our results showed that water presence in temporary water bodies is primarily driven by antecedent hydrological conditions, local climate, and physical attributes of the water body. Previous water presence consistently emerged as the strongest predictor across all water bodies, underscoring the temporal autocorrelation that characterizes the hydroperiod dynamics. Water body size also played a key role, with larger waterholes and tree holes more likely to retain water, and rock pool size modulating climatic effects through interactions. High temperatures consistently reduced water presence, while rainfall effects varied depending on timing and water body type: recent precipitation promoted water retention, whereas prolonged dry spells reduced it. This general pattern was consistent across both temporal scales used to assess hydroperiods (i.e., months for waterholes and days for rock pools and tree holes). These findings highlight the interplay between climatic variability and physical features in shaping water availability in the tropical karst landscape of Calakmul. Climate change is expected to reduce hydroperiods across all temporary water bodies, with severity increasing over time and under higher-emissions scenarios. Waterholes are projected to remain stable in the short-term, but small and medium waterholes will experience reductions by the mid-term under SSP5-8.5, extending to all sizes in the long term. Rock pools show no short-term changes, but small rock pools decline in the mid-term, and all sizes are affected in the long term under SSP5-8.5. Tree holes display the most consistent decline, with small cavities affected in the short term across all scenarios, and all size classes showing significant reductions in the mid- and long-term, particularly under SSP5-8.5.

The predictors identified in our models align closely with patterns reported across various temporary water bodies. The buffering effect of size is well documented, with larger basins more likely to retain water during dry periods due to their lower surface-area-to-volume ratio, particularly in deeper basins (Altermatt et al., 2009; Brooks and Hayashi, 2002; Garmendia and Pedrola-Monfort, 2010). Similarly, the negative influence of high temperatures and dry spells on hydroperiod is a consistent finding across multiple hydrological systems, where elevated temperatures increase evaporative losses and prolonged rain-free periods prevent recharge, accelerating desiccation (Altermatt et al., 2009; Cartwright et al., 2022). Therefore, evaporation emerged as a key driver of hydroperiod reduction across all water body types. Its effects are especially pronounced in small and shallow basins, where high surface-area-to-volume ratios intensify water loss, but they also operate more broadly across the system. Although most of this research originates from temperate and subtropical systems, the consistency of these drivers underscores that the same climatic and physical processes, particularly evaporative losses, govern hydroperiods across biomes, especially in systems with comparable geological substrates and vegetation structures. By demonstrating their relevance in a tropical karst setting, our study extends this understanding and provides a framework that can be used to anticipate water availability in other rainfall-dependent landscapes lacking permanent surface water.

In addition to climatic and physical drivers, the combined effects of land-use change, and geomorphic processes can severely impact the hydroperiods of waterholes. Small, shallow waterholes, especially those near roads or croplands, are particularly vulnerable to sediment infilling from runoff, which can progressively reduce, and in some cases eliminate, their water storage capacity (Gonzalez Rodriguez et al., 2023; Lv et al., 2024). Roads and agriculture amplify erosion and sediment delivery, further accelerating infilling in nearby basins (Ramos-Scharrón, 2018; Stenfert Kroese et al., 2020). Under scenarios of more intense rainfall, these dynamics are likely to accelerate, making small waterholes the most at risk of capacity loss, and potentially enhancing the already observed patterns of shortened hydroperiods in the Calakmul region.

Among the different water body types, tree holes are projected to be the most vulnerable to climate change, with hydroperiod reductions making evident even in the short-term and intensifying over time. This heightened sensitivity can be attributed to the interplay among small volumes, microclimatic exposure, and rainfall dynamics. Tree holes are usually located in the different layers of the forest canopy, where temperatures are higher, humidity is lower, and wind speeds are greater compared to the forest floor (Kumagai et al., 2001; McCay, 2003). Such conditions promote higher evaporation rates, making canopy-held water sources more susceptible to drying (Yanoviak, 1999). In our models, water presence in tree holes was especially dependent on recent heavy rainfall, which suggests that tree holes fill mainly by stemflow that occurs during such rainfall events (Zhang et al., 2021). This reliance becomes more critical considering recent regional trends, as the number of consecutive dry days is increasing while rainfall is becoming concentrated over fewer events (Rodríguez-González and Cerezo-Mota, 2025). These climatic shifts reduce the frequency and reliability of rainfall needed to replenish tree holes, further accelerating their drying. Together, these factors help explain why tree holes exhibited the strongest and most consistent declines in hydroperiod under all future climate scenarios.

Our findings highlight the critical role of emissions pathways in determining the future of temporary water bodies in tropical karst ecosystems. The most extreme reductions in hydroperiods occurred under SSP5-8.5, a high-emissions scenario characterized by continued reliance on fossil fuels and minimal climate policy (Cook et al., 2020). In contrast, more moderate scenarios such as SSP2-4.5 and SSP5-3.4-OS, which assume varying degrees of mitigation and eventual shifts toward sustainability, projected less severe or delayed impacts (O'Neill et al., 2016). These differences underscore the importance of global mitigation efforts to prevent widespread hydrological degradation. Avoiding the most severe scenario is essential, as these changes will not only affect wildlife but also local communities that depend on these ecosystems, potentially triggering cascading ecological and socio-economic effects (IPCC, 2023). By showing that the shortening of hydroperiod is closely tied to future emissions, our study reinforces the urgency of ambitious climate action to safeguard both biodiversity and human well-being in vulnerable tropical regions.

While our study provides valuable insights into the dynamics of temporary water bodies in a tropical karst system, some limitations should be acknowledged. First, the monitoring duration for rock pools and tree holes was limited to a single year, which may not fully capture interannual variability or rare extreme events (Cartwright and Wolfe, 2021). Second, the number of monitored sites per water body type, particularly for tree holes and rock pools, limits the spatial generalizability of our results. Third, although we incorporated volume-based measurements that account for depth in rock pools and tree holes, we were not able to measure water depth in waterholes, and instead we relied on surface area as a proxy for size (Brooks and Hayashi, 2002). This limits our ability to model water retention more precisely in these larger systems (Kroll and Song, 2013). Additionally, our reliance on a single weather station to reconstruct past climate introduces uncertainty, as local microclimatic conditions may vary (De Frenne et al., 2025). To enhance the predictive capacity of future models, some improvements should be considered. For example, incorporating water depth measurements in waterholes would allow a more precise estimation of water retention and hydroperiods, and continuous depth monitoring using automated water level loggers could provide high-resolution temporal data beyond the binary presence/absence currently used. Furthermore, expanding the set of climatic predictors, such as relative humidity, wind speed, and solar radiation, would improve the representation of evaporative dynamics.

In the context of wildlife water use in Calakmul, previous studies have documented a differential reliance on surface and arboreal water sources (Delgado-Martínez et al., 2023). Our findings indicate that water-filled tree holes will be the most affected under climate change, with hydroperiod reductions projected as early as the short-term and severe declines by the long-term under SSP5-8.5. Under such conditions, species that typically rely on arboreal water sources, such as monkeys and canopy birds, may be forced to descend to access surface water, increasing their exposure to predation (Estrada and Marshall, 2024). The most critical scenario is projected for the long term under SSP5-8.5, when all water body types and sizes are expected to experience significant reductions in hydroperiod. In this context, wildlife is likely to concentrate around the few remaining water sources, particularly large waterholes, which are more likely to retain water (Mihailou et al., 2022; Valeix, 2011).

Increased animal aggregation may intensify competition and antagonistic interactions, further stressing vulnerable populations (Ferry et al., 2016; Perera-Romero et al., 2021). Such declines in water availability could severely impact the long-term viability of water-dependent species, many of which are classified as endangered, including Baird's tapir, white-lipped peccaries, and water-associated birds such as herons, by reducing the number of suitable sites and potentially triggering cascading effects throughout the vertebrate community (van den Bosch et al., 2025).

To mitigate antagonistic interactions among vertebrates competing for increasingly scarce water resources, a range of management strategies can be considered. One of the most widely implemented approaches in water-limited environments is water provisioning, which has been traditionally focused on surface sources (Krausman et al., 2006). However, our findings highlight the urgent need to expand these efforts to the canopy, where water availability is projected to decline most severely. Despite its importance, canopy water provisioning remains largely unexplored globally. Installing water stations in the canopy could provide critical support for arboreal species (Mella et al., 2019), helping them cope with future water shortages and reducing their need to descend to the ground, where they are more vulnerable to predation and competition (Estrada and Marshall, 2024). Such interventions could prevent mass mortality events like those observed in howler monkeys during recent extreme heat waves in southern Mexico (Pozo-Montuy et al., 2024). Canopy provisioning efforts could be especially valuable if coupled with surface provisioning in key sites, such as areas used for breeding or where young individuals are present.

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Tables

Table 1. Climatic covariates used for explaining water presence in waterholes, rock pools, and tree holes.

Water body type	Covariates
Waterholes	Accumulated rainfall over the previous 1–24 months
	Months since the last torrential rainfall event (≥ 50 mm in a day)
	Mean of daily maximum temperatures over the previous 1–24 months
Rock pools and tree holes	Days since the last rain (zero rainfall)
	Days since the last light rain (< 2.5 mm)
	Days since the last moderate rain (≥ 2.5 mm but < 10 mm)
	Days since the last heavy rain (≥ 10 mm but < 50 mm)
	Accumulated rainfall over the previous 1–14 days
	Mean daily maximum temperature over the previous 1–14 days

Table 2. Summary of model estimates for predictors of water presence for waterholes.

	Estimate	Std. Error	z-value	*p*-value
(Intercept)	-1.204	0.945	-1.274	0.203
Water presence in the previous month	6.461	1.137	5.683	**< 0.001**
Accumulated rainfall (one month)	3.328	0.816	4.079	**< 0.001**
Waterhole size	1.035	0.405	2.558	**< 0.05**
Accumulated rainfall (20 months)	0.567	0.301	1.882	0.060
Mean maximum temperature (14 months)	-0.112	0.267	-0.420	0.675

Table 3. Summary of model estimates for predictors of water presence for rock pools.

	Estimate	Std. Error	z-value	*p*-value
(Intercept)	-2.426	0.363	-6.680	**< 0.001**
Water presence in the previous day	5.781	0.481	12.029	**< 0.001**
Days since the last heavy rain	-1.138	0.289	-3.939	**< 0.001**
Rock pool size	-1.251	0.377	-3.319	**< 0.01**
Mean maximum temperature (2 days)	-1.533	0.306	-5.017	**< 0.001**
Days since the last rain	-1.768	0.417	-4.237	**< 0.001**
Accumulated rainfall (2 days)	0.418	0.248	1.686	0.092
Rock pool size:Mean maximum temperature (2 days)	0.802	0.348	2.308	**< 0.05**
Rock pool size:Water presence in the previous day	1.813	0.476	3.807	**< 0.001**
Mean maximum temperature (2 days): Accumulated rainfall (2 days)	-0.673	0.424	-1.588	0.112

Table 4. Summary of model estimates for predictors of water presence for tree holes.

	Estimate	Std. Error	z-value	*p*-value
(Intercept)	0.580	1.008	0.576	0.565
Water presence on the previous day	5.700	1.052	5.420	**< 0.001**
Days since the last heavy rain	-1.721	0.524	-3.283	**< 0.01**
Mean maximum temperature (9 days)	-2.651	0.761	-3.483	**< 0.001**
Tree hole size	1.765	0.833	2.120	**< 0.05**

Table 5. Absolute and relative changes in temperature (°C) under different SSP scenarios compared to historical reference values.

Period	SSP	Mean	SD	Absolute difference	Relative difference
1991-2020	Historical	29.570	1.965	NA	NA
2031-2040	2-4.5	32.283	0.607	2.713	9.174
2031-2040	5-3.4-OS	32.264	0.667	2.693	9.109
2031-2040	5-8.5	32.175	0.501	2.605	8.809
2061-2070	2-4.5	32.875	0.447	3.305	11.176
2061-2070	5-3.4-OS	33.470	0.598	3.899	13.186
2061-2070	5-8.5	34.275	0.808	4.705	15.911
2091-2100	2-4.5	33.234	0.351	3.664	12.389
2091-2100	5-3.4-OS	33.103	0.692	3.533	11.948
2091-2100	5-8.5	36.074	0.678	6.504	21.995

Table 6. Absolute and relative changes in annual rainfall (mm) under different SSP scenarios compared to historical reference values.

Period	SSP	Mean	SD	Absolute difference	Relative difference
1991-2020	Historical	909.372	199.687	NA	NA
2031-2040	2-4.5	1102.734	222.528	193.362	21.263
2031-2040	5-3.4-OS	1019.352	167.510	109.980	12.094
2031-2040	5-8.5	1033.532	163.360	124.159	13.653
2061-2070	2-4.5	1065.981	161.377	156.608	17.222
2061-2070	5-3.4-OS	1030.917	217.462	121.544	13.366
2061-2070	5-8.5	876.849	181.278	-32.523	-3.576
2091-2100	2-4.5	1136.695	219.983	227.322	24.998
2091-2100	5-3.4-OS	1119.764	277.902	210.392	23.136
2091-2100	5-8.5	947.755	222.149	38.383	4.221

Figure legends

Figure 1. Study area and location of monitored water bodies in the Calakmul Biosphere Reserve, Campeche, Mexico.

Figure 2. Historical average monthly precipitation and temperature in the Calakmul region (1979-2018).

Figure 3. A camera trap mounted on a tree to directly monitor water presence within a tree hole.

Figure 4. Potential impacts of three Shared Socioeconomic Pathways (SSP2-4.5: moderate emissions, SSP5-3.4-OS: delayed mitigation, and SSP5-8.5: high emissions) on the hydroperiods of (a) waterholes, (b) rock pools, and (c) tree holes across three future decadal periods. The left axis indicates the proportion of days per year that each water body type is expected to retain water. A minus sign (–) denotes a statistically significant decrease in hydroperiod relative to the historical baseline, while a plus sign (+) indicates a statistically significant increase.

Figures

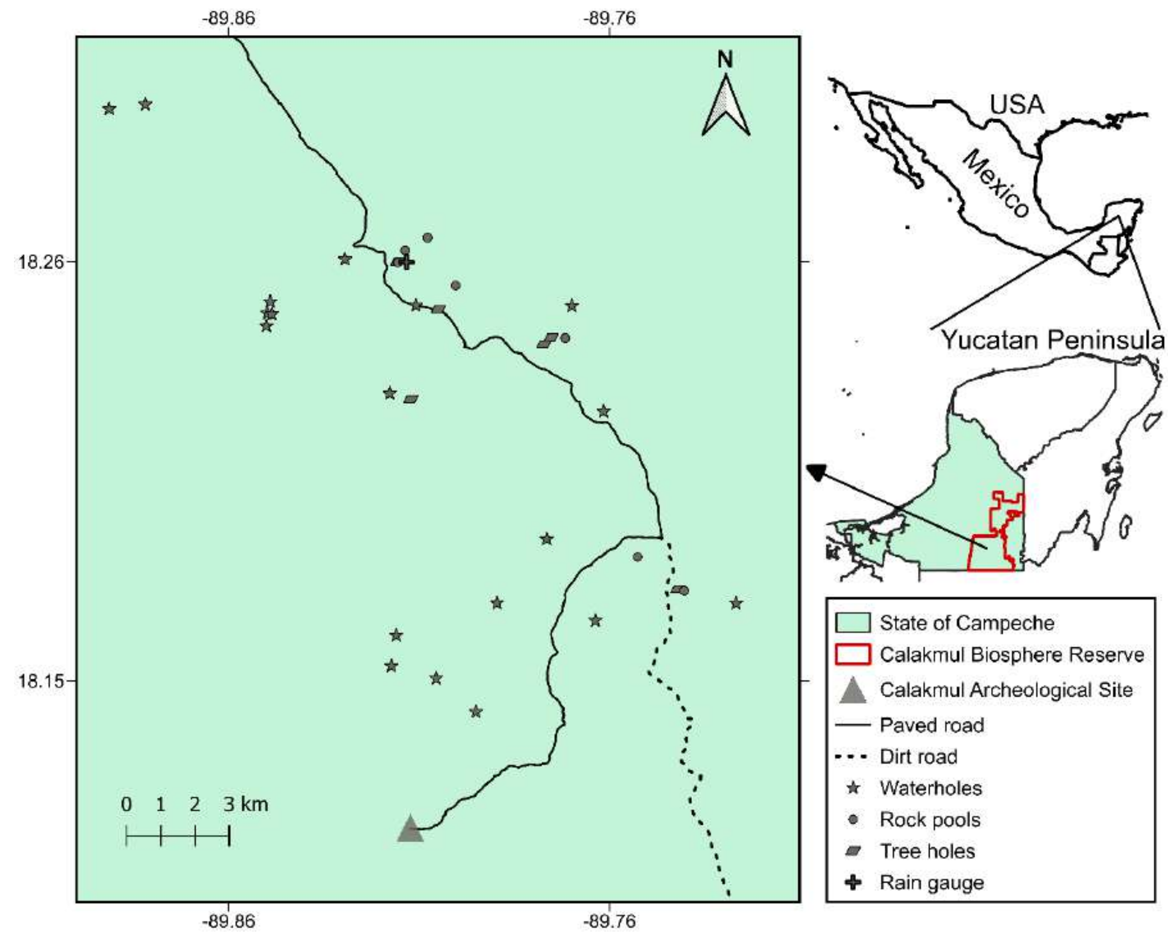

Figure 1

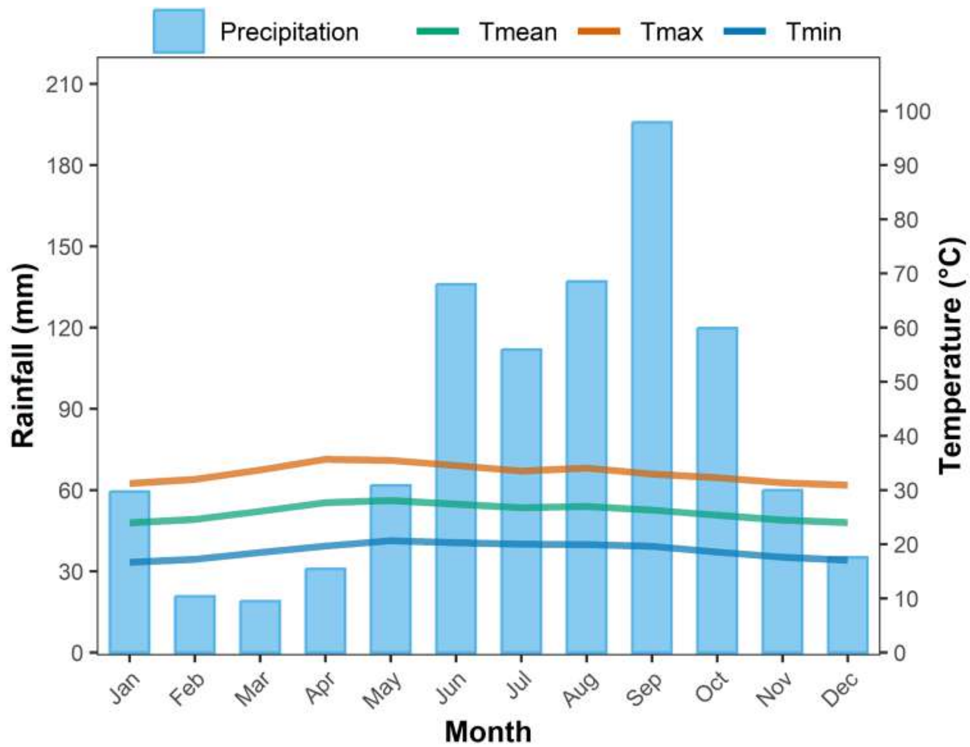
Precipitation
Tmean
Tmax
Tmin
Rainfall (mm)
210
180
150
120
90
60
30
0
Temperature (°C)
100
90
80
70
60
50
40
30
20
10
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Figure 2

Figure 3

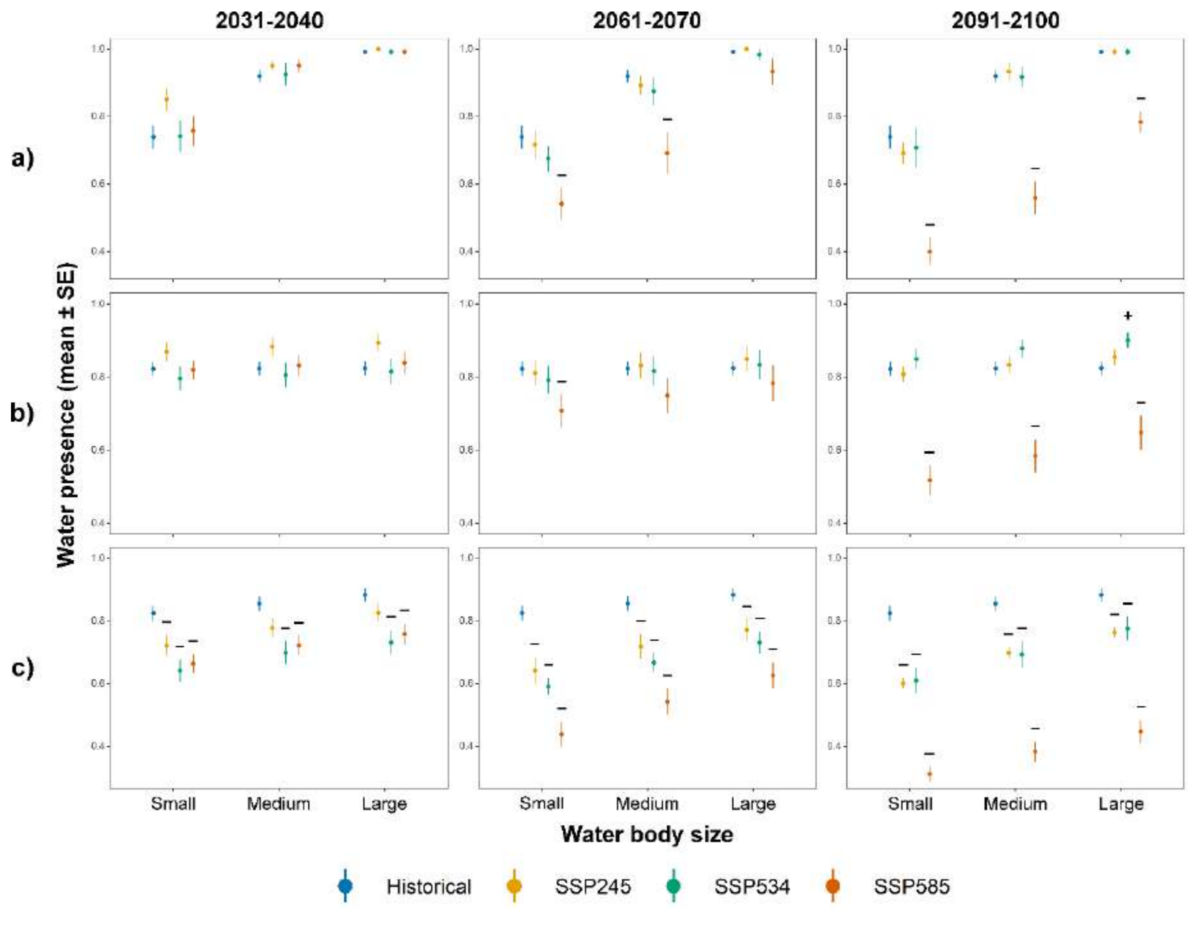
2031-2040
2061-2070
2091-2100
a)
b)
c)
Water presence (mean ± SE)
Small
Medium
Large
Water body size
Historical
SSP245
SSP534
SSP585

Figure 4