



**UNIVERSIDAD NACIONAL AUTÓNOMA DE MÉXICO**  
**POSGRADO EN CIENCIAS BIOLÓGICAS**  
INSTITUTO DE BIOLOGÍA  
ECOLOGÍA

**REQUERIMIENTOS DE HÁBITAT DE RAPACES DIURNAS Y SU RELACIÓN CON  
VARIABLES AMBIENTALES A DISTINTAS ESCALAS EN EL BOSQUE SECO DE  
JALISCO**

**TESIS**

QUE PARA OPTAR POR EL GRADO DE:

**DOCTORA EN CIENCIAS**

PRESENTA:

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**MÉXICO, CD. MX. ENERO 2020**

COORDINACIÓN DEL POSGRADO EN CIENCIAS BIOLÓGICAS

INSTITUTO DE BIOLOGÍA

OFICIO CPCB/030/2020

ASUNTO: Oficio de Jurado

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

Me permito informar a usted que en la reunión del Subcomité por Campo de Conocimiento de Ecología, Manejo Integral de Ecosistemas, Biología Evolutiva y Sistemática del Posgrado en Ciencias Biológicas, celebrada el día 4 de noviembre de 2019, se aprobó el siguiente jurado para el examen de grado de **DOCTORA EN CIENCIAS** de la alumna **MARTÍNEZ RUIZ MARISELA** con número de cuenta **512026563** con la tesis titulada: "**Requerimientos de hábitat de rapaces diurnas y su relación con variables ambientales a distintas escalas en el bosque seco de Jalisco**", realizada bajo la dirección de la **DRA. KATHERINE RENTON**, quedando integrado de la siguiente manera:

Presidente:	DRA. BERTHA PATRICIA ESCALANTE PLIEGO
Vocal:	DR. LUIS ANTONIO SÁNCHEZ GONZÁLEZ
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Suplente	DRA. MARÍA DEL CORO ARIZMENDI ARRIAGA

Sin otro particular, me es grato enviarle un cordial saludo

**ATENTAMENTE**  
"POR MI RAZA HABLARA EL ESPIRITU"  
Cd. Universitaria, Cd. Mx., a 8 de enero de 2020.

**COORDINADOR DEL PROGRAMA**

  
**DR. ADOLFO GERARDO NAVARRO SIGÜENZA**

c.c.p. Expediente del (la) interesado (a)



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## RESUMEN

Los disturbios naturales y antropogénicos modifican el hábitat para los organismos. Para grupos funcionales de aves, como los depredadores tope, poco se conoce acerca de sus requerimientos de hábitat, su relación con el paisaje y de cómo responden ante los disturbios. En este estudio, se evaluó la respuesta de las rapaces diurnas del bosque tropical seco ante disturbios naturales producidos por huracanes, así como a la estacionalidad del hábitat y a la estructura del paisaje. Se establecieron 29 transectos de 1.5 km para determinar la densidad, riqueza y estructura de los ensambles de rapaces diurnas durante la época seca y lluviosa en cuatro hábitats del bosque tropical seco, en áreas afectadas y no afectadas por los vientos máximos de un huracán mayor. Por otra parte, se usó un análisis multi-escalar para determinar la escala del efecto del paisaje en la diversidad de rapaces diurnas y se compararon escalas del efecto entre rapaces con distinto grado de especialización del hábitat y dieta, variables del paisaje y variables de respuesta. Por último, se evaluó la influencia relativa de la estructura del paisaje en la abundancia, riqueza y diversidad temporal de rapaces diurnas del bosque seco.

En el primer capítulo de la tesis, se demuestra que hubo menor densidad de rapaces diurnas en los bosques afectados por un huracán mayor en comparación con bosques no afectados. En cambio, los humedales con vegetación de manglar en áreas afectadas por el huracán mostraron mayor riqueza, equitatividad y similitud en ensambles de rapaces, comparado con los humedales que se encontraron fuera del área impactada por el huracán. Estos resultados sugieren que en áreas afectadas por el huracán las rapaces diurnas expandieron sus áreas de actividad y usaron los humedales como hábitat de refugio.

En el segundo capítulo, se demuestra que la estacionalidad del hábitat influye en la diversidad de rapaces diurnas, con mayor diversidad de rapaces en la región durante la época seca. Los hábitats más estacionales, como el bosque deciduo y las áreas agrícolas mostraron variación temporal significativa en densidad de rapaces, tanto en áreas afectadas como no afectadas por el huracán. Sin embargo, los hábitats con menor variación estacional como humedales y el bosque semideciduo, solo mostraron variación temporal en densidad de rapaces en áreas afectadas por el huracán. De esta forma,

nuestros resultados indicaron que la perturbación de un huracán de alta intensidad puede modificar la dinámica espacio-temporal del ensamble de rapaces diurnas en diferentes hábitat del bosque tropical seco.

Los resultados del Capítulo III demostraron que para las rapaces diurnas la cobertura forestal tuvo un escala del efecto del paisaje mayor que la dureza de la matriz y el densidad de borde. Por otro lado, la escala del efecto no difirió entre rasgos biológicos de las rapaces, o por respuesta biológica evaluada. Estos resultados sugieren que la escala del efecto está determinada por las variables del paisaje, y que las rapaces diurnas están fuertemente asociadas con la cobertura forestal medida en escalas mayores, probablemente debido a que la cobertura forestal está relacionada con el éxito de dispersión en escalas espaciales grandes.

Por último, en el Capítulo IV se determinó que la estructura del paisaje influye sobre la diversidad de rapaces diurnas del bosque tropical seco. La cobertura forestal fue la variable más importante para las rapaces forestales, mientras que tanto la composición como la configuración del paisaje influyeron sobre la diversidad de rapaces del borde y rapaces asociadas a áreas abiertas. La cobertura forestal se relacionó con mayor estabilidad temporal en los ensambles de rapaces forestales, mientras que las rapaces generalistas del bosque mostraron mayor diversidad beta temporal con mayor cantidad del hábitat y densidad de borde, probablemente por la heterogeneidad de los hábitat en el paisaje. La fragmentación del hábitat tuvo efectos positivos en la diversidad de rapaces especialistas y generalistas del bosque, lo cual apoya estudios previos que demostraron efectos positivos de la fragmentación del hábitat en la diversidad de especies.

En conclusión, en la presente tesis se demuestra que las aves rapaces responden a cambios en el hábitat ocasionados por disturbios naturales mayores, además algunos hábitat pueden funcionar como refugio tras dichos eventos, los cuales además influyen en la dinámica espacio-temporal de las rapaces en un ecosistema estacional. La abundancia, riqueza de especies de rapaces diurnas del bosque seco están asociadas con la cobertura forestal medida en escalas espaciales mayores, y la cobertura forestal es un factor importante para la diversidad temporal de rapaces del bosque seco. Especies de rapaces diurnas con menor grado de especialización del hábitat se ven beneficiadas por la fragmentación del hábitat.

## **ABSTRACT**

Natural and anthropogenic disturbances modify habitat for organisms. Little is known about habitat requirements and responses to natural disturbances for some functional groups, such as top predators. In this study, I evaluated the response of tropical dry forest diurnal raptors to natural disturbances generated by hurricanes, as well as to habitat seasonality and landscape structure. I established 29 transects of 1.5 km in length to determine density, richness and the structure of diurnal raptor assemblages during the dry and rainy season. Transects were distributed in four habitats of the tropical dry forest, both in areas affected and not affected by the maximum winds of a major hurricane.

On the other hand, I used a multi-scalar analysis to determine the scale of the landscape effect on the diversity of diurnal raptors. Scales of effect were compared among raptors with different degrees of habitat and diet specialization, landscape variables, and response variables. Finally, I evaluated the relative influence of landscape composition and configuration on the abundance, richness and temporal diversity of diurnal raptors in the dry forest was evaluated.

The first chapter of this thesis shows that there was a lower density of diurnal raptors in forests affected by a major hurricane in comparison to unaffected forests. In contrast, wetlands with mangrove vegetation in areas affected by the hurricane showed greater richness, evenness and similarity of raptor assemblages, in comparison to wetlands that were outside the range of maximum hurricane winds. These results suggest that raptors expanded their areas of activity and used wetlands as a refuge after hurricane disturbance.

Chapter II shows that habitat seasonality influences the diversity of diurnal raptors, with greater diversity of raptors in the region during the dry season. The more seasonal habitats, such as deciduous forest and agricultural areas, showed significant temporal variation in raptor density, both in areas affected and not affected by the hurricane. However, less seasonal habitats such as wetlands and the semi-deciduous forest showed temporal variation in raptor density only in areas affected by the hurricane. Thus, our results indicated that the disturbance of a high intensity hurricane can modify the spatio-

temporal dynamics of the diurnal raptor assemblage in different habitats of the tropical dry forest.

Results of Chapter III showed that forest cover had a significant greater scale of effect than matrix hardness and edge density for diurnal raptors in the dry forest. On the other hand, the scale of the effect did not differ between biological traits of the raptors, or by the biological response evaluated. These results suggest that diurnal raptors are strongly associated to forest cover measured at larger scales, probably because forest cover is related to dispersal success over large spatial scales.

Finally, in Chapter IV we demonstrated that landscape structure influences diversity of tropical dry forest diurnal raptors. Forest cover was the most important variable for forest raptors, while both the composition and landscape configuration influenced the diversity of edge-raptors and raptors associated with open areas. Forest cover was associated to greater temporal stability in forest raptor assemblages, while generalist forest raptors showed greater temporal beta diversity with greater habitat amount and edge density, probably due landscape habitat heterogeneity. Habitat fragmentation had positive effects on the abundance and richness of raptors, both in forest specialists and generalists, supporting previous studies that have shown positive effects of habitat fragmentation on species diversity.

In conclusion, this thesis demonstrates that raptors respond to habitat changes due to major natural disturbances, and that some habitats can function as a refuge after such events. Natural disturbances influence spatio-temporal dynamics of raptors in a seasonal ecosystem. Dry forest diurnal raptors are associated to forest cover measured at larger spatial scales, and forest cover is an important factor for the temporal diversity of raptors. Species of diurnal raptors with a lower degree of habitat specialization benefit from habitat fragmentation.

## **INTRODUCCIÓN GENERAL**

### **Influencia del hábitat a escala del paisaje en aves**

Las aves son organismos móviles que tienen requerimientos espaciales amplios, por lo que variables medidas en escala del paisaje influyen en su abundancia y riqueza (Dolman 2012). Durante las últimas dos décadas, se ha demostrado que la estructura del paisaje tiene efectos importantes en poblaciones y comunidades de diferentes taxa (Laurance et al. 2002; Fahrig 2003). El paisaje se compone de dos atributos principales: (1) la composición, en términos de tipos y proporción de coberturas de vegetación, y (2) la configuración, que describe el arreglo espacial de las coberturas y considera variables como el número, arreglo y distribución de parches, y extensión de bordes (Dunning et al. 1992; Fahrig 2003). La hipótesis de cantidad del hábitat establece que la disminución de hábitat en el paisaje tiene efectos más importantes que la configuración del paisaje (Andrén 1994; Fahrig 2003, 2013). De acuerdo con esto, se ha observado que la presencia y abundancia de aves son más influenciados por la cobertura forestal (composición) que por la configuración (tamaño, forma y número de parches, contraste de borde) del paisaje (McGarigal and McComb 1995; Trzcinski et al. 1999). Se ha determinado que la pérdida del hábitat tiene importantes efectos negativos para las aves en ambientes templados (Best et al. 2001; Schmiegelow and Mönkkönen 2002; Quesnelle et al. 2013) y en los trópicos (Cerezo et al. 2010; Carrara et al. 2015). Sin embargo, la evidencia muestra que la configuración del paisaje tiene efectos negativos significativos en la ocurrencia y persistencia de aves cuando la cantidad del hábitat es baja (Jansson and Anglestam 1999; Betts et al. 2006; Zuckerberg and Porter 2010). Algunos estudios en aves muestran que las variables asociadas a la fragmentación del hábitat (densidad de borde, número de parches de hábitat) pueden tener efectos positivos, negativos o neutros (McGarigal and McComb 1995; Trzcinski et al. 1999; Betts et al. 2006; Smith et al. 2011; Quesnelle et al. 2013). El estudio de la influencia de la estructura del paisaje es necesario para develar las asociaciones de las especies con el hábitat a escala paisajística.

## **Rasgos biológicos de las especies**

Los rasgos biológicos de las especies influyen en el efecto que la composición y configuración del paisaje tienen sobre éstas. En este sentido, se predice que las especies especialistas se beneficien de ambientes homogéneos y sean más afectadas por la pérdida del hábitat, mientras los generalistas pueden beneficiarse en ambientes heterogéneos, siendo menos afectadas por los procesos de fragmentación y cambio de uso de suelo (Futuyma and Moreno 1998; Kassen 2002). En Francia, Devictor et al. (2008) determinaron que las especies de aves con mayor especialización del hábitat mostraron menor abundancia con un incremento en la fragmentación y pérdida del hábitat en paisajes de 4 km<sup>2</sup>. Respecto a su distribución, se encontró que las especies especialistas se localizan en paisajes con menor grado de fragmentación, comparado con las generalistas (Devictor et al. 2008). Asimismo, con un enfoque multi-escala en un bosque lluvioso de México, Carrara et al. (2015) determinaron que la diversidad de aves especialistas del interior del bosque está más fuertemente influenciada por la composición y configuración del paisaje, comparado con la diversidad de aves generalistas. Además, a escala menor (100 ha), la diversidad de aves especialistas incrementó con la cobertura de bosque maduro, mientras que la diversidad de aves generalistas incrementó con la reducción en cobertura de bosque maduro (Carrara et al. 2015). Sin embargo, hay escasa información sobre cuáles son las variables ambientales del paisaje que afectan a las especies de aves especialistas y generalistas en los trópicos, o cual es el efecto sobre grupos de aves con distintos requerimientos espaciales.

## **La escala del efecto del paisaje**

Los efectos de la composición y configuración del paisaje para las aves y la importancia relativa de estos pueden cambiar de acuerdo con el tamaño del paisaje considerado, por lo que estudios sobre la influencia de estructura del paisaje se abordan más frecuentemente usando un enfoque multi-escala. Vergara y Armesto (2009) determinaron que las abundancias de nueve especies de aves en bosques templados de Chile estuvieron influenciadas por interacciones entre variables ambientales en tres escalas: a nivel de paisaje, del área local, y dentro de parches. Asimismo, Smith et al. (2011) demostraron que, para aves forestales de bosques de coníferas en Canadá, la



composición del paisaje tiene un efecto positivo constante, donde el incremento en cantidad del hábitat está asociado con mayor riqueza y ocurrencia de aves en más de tres escalas de paisaje, además de que la intensidad del efecto de la composición de hábitat incrementa con el tamaño del paisaje considerado. En este sentido, resulta importante determinar cuál es la escala a la que la estructura del paisaje predice mejor una respuesta biológica, como la riqueza y abundancia de los organismos (Jackson and Fahrig 2012). La denominada “escala del efecto” es la extensión espacial en la que la estructura predice de mejor forma una respuesta biológica (Jackson and Fahrig 2012). Se han desarrollado algunas hipótesis acerca de los mecanismos detrás de la escala del efecto del paisaje en los organismos. Entre estas, se propone que los rasgos biológicos de las especies se encuentran dentro de los posibles mecanismos que tienen influencia en la escala del efecto, además de las variables del paisaje y las variables de respuesta consideradas (Miguet et al. 2016). En aves, Thornton y Fletcher (2014) encontraron una asociación positiva del tamaño corporal (indicativo de los requerimientos de área) con una mayor escala del efecto. Otras hipótesis plantean que un alto nivel trófico también se relaciona con escalas del efecto mayores (Miguet et al. 2016). Por otra parte, el grado de especialización de las especies podría generar escalas del efecto mayores/menores de acuerdo al taxón de estudio (Miguet et al. 2016). Desafortunadamente, la mayoría de los estudios que evalúan la relación de variables ambientales con respuestas de las especies no consideran suficientes escalas para poder predecir la escala del efecto (Jackson and Fahrig 2012). Por lo tanto, se carece de evidencia empírica para soportar las predicciones y se reconoce que el estudio de los mecanismos de la escala del efecto es muy reciente.

### **Influencia de las perturbaciones y estacionalidad del hábitat**

Además de la influencia de los rasgos biológicos de las especies, las perturbaciones antrópicas y naturales pueden causar cambios en la disponibilidad de recursos y en el ambiente físico que influyen sobre las comunidades de aves. Las perturbaciones antrópicas modifican la estructura del hábitat con efectos cuantificables sobre las aves a diferentes escalas, comprendiendo cambios en la composición del paisaje debido a la pérdida del hábitat original, expansión de paisajes modificados por el hombre y la subdivisión del hábitat en remanentes aislados del mismo (Pimm et al. 1995;

Lindenmayer and Fischer 2006). Por otro lado, las perturbaciones naturales de los huracanes provocan la defoliación, pérdida de flores y frutos, y la destrucción de árboles (Whigham et al. 1991). Las respuestas de las especies de aves ante esta perturbación natural pueden diferir de acuerdo con sus requerimientos específicos o grupos funcionales.

Algunos estudios muestran que en las selvas tropicales, las especies de aves residentes serían más afectadas que las migratorias por el impacto de los huracanes (Waide 1991). En el bosque tropical de tierras bajas en Nicaragua, se registró un menor número de especies de aves residentes en zonas afectadas por el Huracán Joan que en las zonas no afectadas (Will 1991). Asimismo, en el bosque seco de Yucatán, se determinó que las aves migratorias fueron menos afectadas por el Huracán Gilbert en comparación con las residentes (Lynch 1991). Por otro lado, varios estudios han determinado que después del paso de un huracán en las selvas tropicales, la abundancia de aves frugívoras y nectarívoras disminuye, mientras las aves insectívoras y omnívoras pueden aumentar en abundancia (Askins and Ewert 1991; Lynch 1991; Waide 1991). Sin embargo, ningún estudio ha evaluado el impacto de huracanes sobre la comunidad de aves de presa, particularmente de los ordenes Accipitriformes y Falconiformes que son carnívoras y omnívoras, además de que son especies que se mueven en grandes áreas, por lo que la influencia de perturbaciones como huracanes pudiera diferir de los patrones observados para aves paseriformes. El evaluar la respuesta de las aves ante eventos climáticos extremos como huracanes cobra importancia debido a que, durante las últimas décadas, la intensidad y frecuencia de los huracanes ha aumentado (Webster et al. 2005).

Por otra parte, se conoce que la dependencia de las especies hacia un tipo de hábitat podría presentarse únicamente en una temporada del año o durante procesos claves del ciclo de vida, como la reproducción. Algunas rapaces usan hábitats particulares durante periodos específicos del año, lo que hace necesario evaluar el uso del hábitat en más de una temporada (Tapia et al. 2007). Por lo tanto, la estacionalidad es un aspecto relevante que debe ser considerado, pero que no ha sido incorporado en este tipo de estudios. En este sentido, los bosques tropicales secos, con su alta estacionalidad, ofrecen la oportunidad de abordar la temporalidad en el estudio de las asociaciones de aves con el hábitat. Además, los bosques tropicales secos son

ecosistemas sometidos a altas tasas de deforestación y fragmentación (Miles et al. 2006) y deberían considerarse como seriamente amenazados (Janzen 1988).

### **Relevancia de evaluar influencia del hábitat para las aves rapaces**

Las rapaces son aves con alta capacidad de movimiento y que presentan ámbitos hogareños amplios, por lo cual podrían estar más influenciadas por variables del paisaje que por variables de escala local. Cabe destacar que la mayoría de los estudios de uso de hábitat, distribución y densidad de las aves rapaces se han enfocado en una escala, generalmente el micro-hábitat, mientras que pocos estudios han considerado un análisis multi-escala del paisaje para la comunidad de rapaces. Dos estudios, en Europa y África, determinaron que la cobertura forestal y productividad de la vegetación se relacionan positivamente con la densidad de rapaces en más de una escala (Sánchez-Zapata, J.F. & Calvo 1999; Anadón et al. 2010). Estudios especie-específicos de rapaces en Norteamérica mostraron un patrón similar donde la abundancia de la especie de rapaz se relaciona con la cobertura forestal en diferentes escalas (Wright et al. 1997; Finn et al. 2002). Sin embargo, a pesar de que el 90% de todas las rapaces diurnas ocurren en los trópicos y que el Neotrópico alberga la mayoría de géneros endémicos de rapaces tropicales, aún no hay estudios de la comunidad de rapaces y su relación con variables ambientales a diferentes escalas en el Neotrópico (Bildstein et al. 1998; Mindell et al. 2018). Además, las rapaces forestales tropicales se encuentran más amenazadas y en peligro de extinción y presentan poblaciones en declive en comparación con aquellas rapaces fuera de los trópicos (McClure et al. 2018). El conocer los factores que influyen en la diversidad de las aves rapaces es de relevancia ya que las rapaces influyen en la estructura y dinámica de los ecosistemas naturales (Thiollay 2007); debido a su posición en la cadena trófica como depredadores, estas aves determinan los patrones estructurales y de composición de las comunidades de sus presas, y además proveen servicios a los ecosistemas (O'Bryan et al. 2018). Asimismo, se les considera como indicadores de la calidad de los ecosistemas debido a la sensibilidad que presentan ante las perturbaciones antropogénicas (Newton 1979). En este sentido, las rapaces son usadas como especies sustitutas en materia de conservación debido a que ocupan grandes áreas incorporando el hábitat de muchas otras especies (Sergio et al. 2006).

En el presente estudio evalué la influencia de la perturbación natural por un huracán de categoría mayor en la diversidad de rapaces diurnas del bosque seco. Asimismo, evalué si la estacionalidad del bosque tropical seco influye en la diversidad de rapaces diurnas y si la variación espacio-temporal de la comunidad de rapaces difiere entre áreas afectadas y no afectadas por el disturbio del huracán. Por otro lado, evalué el efecto relativo de las variables de la composición y configuración del paisaje en el ensamble de rapaces diurnas del bosque tropical seco. En particular, apliqué un análisis multi-escalar para determinar la escala del efecto del paisaje y la influencia de las variables de estructura del paisaje para el ensamble de rapaces diurnas. De esta forma se pueden determinar con mayor precisión las variables ambientales que explican el ensamble de rapaces. Asimismo, se pueden definir las características del hábitat y la escala adecuada que resulten de importancia para la conservación de este grupo de aves (Wiens 1989, Levin 1992). Además, se puede determinar si existen respuestas especie-específicas, por grado de especialización, o si ocurre un patrón general en este grupo de aves. De esta forma, en la presente tesis se generó información novedosa sobre los requerimientos ecológicos de las rapaces neotropicales que son poco conocidas (Thiollay 2007), y el presente trabajo contribuye al conocimiento de la comunidad de rapaces del bosque seco, donde han sido pobremente estudiadas.

## **HIPÓTESIS Y OBJETIVOS**

### **Capítulo I. Habitat heterogeneity facilitates resilience of diurnal raptor communities to hurricane disturbance.**

**Hipótesis:** Dado que las perturbaciones naturales modifican el hábitat para las aves, se espera que la densidad y riqueza de rapaces diurnas difieran entre las áreas afectadas y no afectadas por el Huracán Patricia. Asimismo, dado que los bosques son más afectados por el paso de huracanes, y ya que se ha reportado una reducción en la abundancia de algunos grupos aves tras el paso de huracanes, se predice una menor densidad y riqueza de rapaces en los bosques ubicados en el paso del huracán, comparado con bosques fuera del rango de los vientos máximos del huracán.

#### **Objetivos**

- Determinar la distribución espacial de las rapaces diurnas en los diferentes hábitats del bosque seco en la costa de Jalisco
- Estimar la densidad y riqueza de rapaces diurnas en hábitats afectados y no afectados por el Huracán Patricia
- Comparar la densidad y riqueza de rapaces entre hábitats afectados y no afectados
- Evaluar la equitatividad y composición de las comunidades de rapaces en los hábitat del bosque seco en su condición de afectado y no afectado por el huracán

## **Capítulo II. Variación espacio-temporal en la diversidad de rapaces diurnas en el bosque tropical seco de Jalisco bajo influencia de un evento climático extremo**

**Hipótesis:** Dado que la asociación de las especies hacia un tipo de hábitat puede ser temporal, se espera que la densidad y riqueza de rapaces diurnas varíe entre los diferentes hábitats y entre las épocas seca y lluviosa del bosque tropical seco. Asimismo, se espera que la variación en densidad y riqueza de rapaces sea mayor en hábitats más estacionales, como el bosque caducifolio, donde hay mayor estacionalidad fenológica de la vegetación, que en el bosque subcaducifolio y humedales que mantienen vegetación perenne.

Dado que los eventos climáticos extremos como huracanes modifican la estructura del hábitat y la disponibilidad de recursos para las aves, se espera que la perturbación por un huracán de alta categoría modifique la variación en densidad y riqueza de rapaces diurnas.

### **Objetivos:**

- Determinar la densidad y riqueza de rapaces diurnas en los distintos hábitats del bosque seco en las épocas seca lluviosa
- Evaluar si hay variación temporal o estacional en densidad y riqueza de rapaces, así como variación espacial entre distintos hábitat del bosque seco
- Evaluar si la variación espacio-temporal de la diversidad de rapaces es diferente en áreas afectadas y no afectadas por el huracán Patricia.

### **Capítulo III. Patterns and drivers of the scale of landscape effect on diurnal raptors in a fragmented tropical dry forest**

**Hipótesis:** La escala del efecto del paisaje corresponde a la escala espacial en la cual se maximiza la relación de variables del paisaje con una respuesta biológica. Los rasgos biológicos de las especies, como el grado de especialización, pueden influir en la escala del efecto del paisaje. En particular, se espera que especies con mayor grado de especialización presenten escalas del efecto mayores/menores que aquellas especies con menor grado de especialización.

La escala del efecto puede ser diferente para las variables de estructura del paisaje consideradas. En particular, se espera que la escala del efecto sea mayor para las métricas del paisaje que influyen en la dispersión, como la cantidad de hábitat y/o calidad de la matriz. En este sentido, se espera que la escala del efecto sea menor para variables del paisaje relacionadas con la eficiencia de forrajeo y disponibilidad de recursos de anidación, como la densidad de borde y el número de parches de hábitat en el paisaje.

La escala del efecto del paisaje puede diferir dependiendo la respuesta biológica considerada. En particular, se espera que la escala del efecto sea menor para respuestas biológicas relacionadas con la fecundidad y sobrevivencia y que dependen de procesos que actúan en escalas temporales cortas (i.e. abundancia). Por otra parte, se espera que la escala del efecto sea mayor para las respuestas multi-especies que dependen de procesos que actúan en escalas de tiempo mayores (i.e. riqueza de especies, diversidad beta).

#### **Objetivos:**

- Definir la escala del efecto para la diversidad de rapaces del bosque seco
- Determinar si la escala del efecto es diferente para grupos de especies de rapaces con distinto grado de especialización del hábitat y dieta
- Determinar si la escala del efecto es diferente entre variables de respuesta y variables de la estructura del paisaje

## **Capítulo IV. Landscape structure influences diurnal raptor diversity in the tropical dry forest of Mexico**

**Hipótesis:** La estructura del paisaje influye en la diversidad, composición y estructura de las comunidades. De acuerdo con los patrones observados, se espera que las variables de composición del paisaje (i.e. cantidad de hábitat) tengan mayor efecto en la diversidad de rapaces diurnas que aquellas variables de la configuración del paisaje (i.e. densidad de parches, densidad de borde).

Asimismo, el efecto de la estructura del paisaje puede ser diferente de acuerdo con distintos rasgos biológicos de las especies, como el nivel de especialización. En particular se espera que la cantidad de bosque tenga mayor influencia para las rapaces especialistas del bosque, que para aquellas rapaces asociadas a áreas abiertas. Además, se espera que las rapaces especialistas del bosque estén influenciadas negativamente por la fragmentación del hábitat. Por el contrario, se espera que las rapaces con menor grado de especialización del hábitat estén menos influenciadas por la cantidad de bosque, e influenciadas positivamente por la fragmentación del hábitat.

### **Objetivos:**

- Evaluar la influencia relativa de la composición y configuración del paisaje en la diversidad de rapaces diurnas con distinto grado de especialización del hábitat



# **CAPÍTULO I. HABITAT HETEROGENEITY FACILITATES RESILIENCE OF DIURNAL RAPTOR COMMUNITIES TO HURRICANE DISTURBANCE**

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# Habitat heterogeneity facilitates resilience of diurnal raptor communities to hurricane disturbance<sup>☆</sup>

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## ABSTRACT

The response of avian communities to hurricane disturbance may differ according to their specific requirements or functional groups, but little is known regarding the response of top-predator birds of prey to these disturbances. We aimed to evaluate the influence of the major Hurricane Patricia on the diversity of diurnal raptors in tropical dry forest, along the coast of Jalisco, Mexico. We conducted raptor surveys at 13 sites located within the eyewall radius of maximum hurricane winds along the path of the hurricane, and 16 sites located outside the hurricane eyewall. We compared the density and species richness of raptors among four habitats of tropical deciduous and semi-deciduous forest, mangroves, and agricultural fields, within the hurricane eyewall and outside the radius of maximum winds. Our results demonstrated a reduction in raptor density in tropical forests within the radius of maximum hurricane winds, where raptor density was significantly lower in deciduous forests within the hurricane eyewall compared to deciduous forests outside the eyewall. Species richness of diurnal raptors was similar among habitats and conditions with the exception that mangroves within the hurricane eyewall had significant higher raptor species richness compared to mangroves outside the eyewall. There was also a significant increase in species evenness, and decrease in similarity, of raptor communities in mangroves and deciduous forest sites within the hurricane eyewall compared to sites outside the eyewall. The reduced density of diurnal raptors in tropical forest sites within the path of the hurricane probably reflects the impact of hurricane winds on forest structure, whereas the increase in species richness and evenness of raptor communities in mangroves within the hurricane eyewall suggests that these habitats could provide a refuge for diurnal raptors following hurricane disturbance. Our results highlight the importance of maintaining landscape heterogeneity of native vegetation to provide alternate habitats for wildlife communities following major disturbance, and facilitate their resilience to extreme climatic events such as hurricanes.

## 1. Introduction

Hurricane impacts have increased in frequency and intensity over the last decades (Webster et al., 2005; Elsner et al., 2008; Emanuel, 2013), provoking changes in the physical environment with impacts on animal communities (Emanuel, 2005). Strong winds associated with hurricanes can provoke structural damage of bird habitats, with more severe hurricane damage in large trees and mature forests, while open habitats may be less impacted (Gresham et al., 1991; Varty, 1991; Roth, 1992; Wauer and Wunderle, 1992). The response of avian species to hurricane disturbance may differ according to their specific requirements or functional groups, making it important to evaluate the vulnerability of organisms to such natural disturbances.

In avian communities, terrestrial species that rely on plants for food

are likely to be more affected by hurricane impacts. Eight months after landfall by Hurricane Hugo in the Caribbean, Wauer and Wunderle (1992) found significant declines in abundance for 76% of primary consumer species that rely on plant resources of fruits, seeds, or flowers, compared to 46% of secondary consumers. Various studies have determined a decline in frugivorous and nectarivorous birds 4–8 months after hurricane disturbance, whereas insectivorous birds may increase in abundance as they are able to forage for insects in areas opened-up by hurricanes (Lynch, 1991; Wauer and Wunderle, 1992; Wunderle et al., 1992; Wiley and Wunderle, 1993; Wunderle, 1999; Wunderle and Arendt, 2011). This diet-related population response suggests that hurricanes have significant indirect effects on avian communities through loss of food resources, nest-sites, and habitat, rather than direct mortality (Wiley and Wunderle, 1993). However, few studies have

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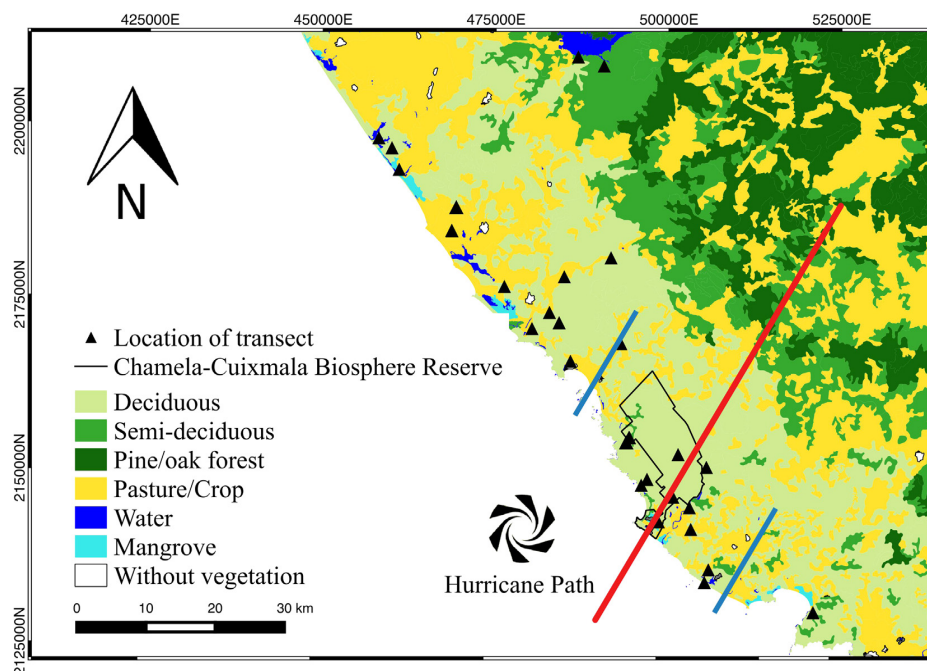


Fig. 1. Map of the study region along the coast of Jalisco, Mexico, showing the location of survey sites in each habitat type within the main path of Hurricane Patricia, and outside the boundaries of maximum hurricane winds. Red line indicates the track of Hurricane Patricia obtained from historical hurricane tracks of the National Oceanic and Atmospheric Administration (<https://coast.noaa.gov/hurricanes/>). Blue lines represent the boundaries of maximum hurricane winds estimated from data published by Kimberlain et al. (2016).

evaluated the influence of hurricane disturbance on bird groups with distinct functional requirements, such as raptors that are primarily carnivorous and function as top-predators in avian communities (Newton, 1979).

Wauer and Wunderle (1992) found that whereas 70–92% of nectivore and fruit/seed eating bird populations declined in abundance, only 25% of raptor populations demonstrated a decline 8 months after hurricane landfall. In particular, most populations of the Red-tailed Hawk (*Buteo jamaicensis*) and American Kestrel (*Falco sparverius*) remained unchanged after landfall by Hurricane Hugo (Wauer and Wunderle, 1992), possibly due to an increase in detectability of their prey. Similarly, in the Yucatán Peninsula of Mexico, Lynch (1991) found no significant response of the Roadside Hawk (*Rupornis magnirostris*) to landfall by Hurricane Gilbert, although the Ferruginous Pygmy-Owl (*Glaucidium brasilianum*) showed a significant decline with no recovery up to a year-and-a-half after hurricane impact. However, no studies have specifically evaluated the response of a raptor community to hurricane disturbance, particularly on the Pacific coast of the continental Neotropics, even though a greater number and percent of hurricanes occur and make landfall along the Neotropical Pacific coast compared to the Atlantic (Jáuregui, 2003).

In the 2015 hurricane season (June–November), the largest and strongest hurricane ever recorded, category 5 Hurricane Patricia, made landfall as a category 4 major hurricane on the Pacific coast of Jalisco in Mexico (Kimberlain et al., 2016). Hurricane Patricia had estimated maximum winds of 241 km/h over an eyewall (wall of clouds that surround the eye of the hurricane and where the most damaging winds and intense rainfall is found) radius of 5 nautical miles (9.3 km), producing a narrow swath of severe damage to buildings and forest structure (Kimberlain et al., 2016). It is not yet known what impact this hurricane landfall may have had on the rich biodiversity of the tropical dry forest in the region. Therefore, in the present study we aimed to evaluate the potential influence of this hurricane disturbance on the diversity of diurnal raptors in the tropical dry forest along the Pacific coast of Mexico. We specifically aimed to determine whether there were

differences in density, species richness, and community structure of diurnal raptors in habitats within the hurricane eyewall of severe damage compared to habitats outside the main path of hurricane impact. Evaluating the response of species or functional groups to hurricanes enables us to assess their potential vulnerability to disturbance produced by environmental change, with important implications for conservation.

## 2. Methods

### 2.1. Study area

The study was conducted in the tropical dry forest on the coast of Jalisco in western Mexico, specifically in the coastal municipalities of La Huerta and Tomatlán. The region has a warm, semi-humid climate with a mean annual temperature of 26 °C (García, 2004). Mean annual rainfall is 788 mm (range 453–1393), the majority of which occurs during the rainy season from June to October, with a prolonged dry season from November to May (Bullock, 1986; García-Oliva et al., 2002). The dominant vegetation is dry deciduous forest, located mainly on the hills (Lott and Atkinson, 2002), which has a canopy height of 12 m, a dense understory, and is characterized by a loss of leaf cover for 5–8 months in the dry season (Rzedowski, 2006). Common tree species in deciduous forest are *Croton pseudoniveus*, *Lonchocarpus constrictus*, *Trichilia trifolia*, and *Cordia alliodora*, (Lott et al., 1987). Semi-deciduous forest occurs in humid valleys from sea-level to 1000 m asl, and is characterized by larger trees of 25 m canopy height that maintain their foliage through most of the year (Rzedowski, 2006). This forest has a large proportion of trees  $\geq 30$  cm diameter at breast height (dbh), with common tree species of *Thouinidium decandrum*, *Capparis verrucosa* and *Astronium graveolens* (Lott et al., 1987). Wetlands with mangrove vegetation also occur along the coast, and are dominated by short, evergreen trees of *Laguncularia racemosa*, *Rhizophora mangle*, and *Avicennia germinans* (Durán et al., 2002). In some low-lying areas of community lands along the coast, tropical dry forest has been replaced by cattle

pastures, and agricultural systems with sorghum and maize crop fields, as well as Papaya, Mango, and Tamarind tree orchards (Maass, 1995, Maass et al., 2005).

Hurricane Patricia made landfall along the coast of Jalisco on 23 October 2015, with the main path of the hurricane entering the continent at Playa Cuixmala, and moving inland along the watershed of the Rio Cuitzmala. We determined the boundaries of maximum hurricane winds based on the estimated 5 nautical mile (9.3 km) radius of maximum winds on the weaker western side of the hurricane (Kimberlain et al., 2016), and from observations on-the-ground of the extent of severe hurricane damage in the days immediately following landfall by Hurricane Patricia (K. Renton pers. obs.). This showed that most severe damage occurred within the boundaries of maximum hurricane winds over a narrow area along the coast from southeast of Arroyo Seco to northwest of Arroyo Chamela, heavily impacting the Chamela-Cuixmala Biosphere Reserve (Fig. 1).

Given that no raptor surveys have previously been conducted in the region, there is an absence of data on density and richness of diurnal raptors prior to hurricane impact. Therefore, to evaluate the influence of hurricane landfall on raptor communities, we selected 29 survey sites, with 13 survey plots located within the radius of maximum hurricane winds, and 16 survey plots located outside the hurricane eyewall (Fig. 1). For each of these two hurricane conditions, we established survey plots in four main habitat types of tropical deciduous and semi-deciduous forest, mangroves, and agricultural fields. These represent the principal land covers along the coast of Jalisco (Sánchez-Azofeifa et al., 2009), and are the main habitats used by the raptor assemblage in the region. Most raptor species are associated with forest habitats, while generalist species may favor open areas of agricultural fields (del Hoyo et al., 1994; Ferguson-Lees and Christie, 2005), and a few raptor species specialize in hunting around waterbodies and associated vegetation in mangrove estuarine systems (Jullien and Thiollay, 1996; Loures-Ribeiro and dos Anjos, 2006). The track of Hurricane Patricia impacted a large area of conserved, mature forest in the Chamela-Cuixmala Biosphere Reserve (Fig. 1), therefore we selected comparable survey plots in mature forests outside the radius of maximum winds. Raptors are also wide-ranging species whose occurrence tends to be influenced by landscape-level features of habitat or vegetation types and land-use (Jullien and Thiollay, 1996; Sánchez-Zapata and Calvo, 1999; Buji et al., 2013), rather than microhabitat structural differences, such as may occur in secondary forests.

Within the boundaries of maximum hurricane winds, the majority of trees in deciduous and semi-deciduous forests suffered severe damage of broken branches, snapped trunks, and uprooted or inclining trees (Fig. 2a and c), with an extensive loss of canopy cover (Parker et al., this issue). Mangroves showed less visible signs of damage, with a few trees having broken branches and snapped trunks, but mostly we observed inclined trees in these areas after hurricane impact (Fig. 2e). Hurricane Patricia also caused severe damage to crops in agricultural areas within the hurricane path, particularly in the case of tree orchards where many fruit trees suffered defoliation, broken branches, snapped trunks, or were removed (Fig. 2g). Outside the boundaries of maximum hurricane winds, forests and mangroves were not visibly affected by Hurricane Patricia, with trees showing little signs of wind damage, and canopy cover remaining intact (Fig. 2b, d, f). Crops and tree orchards also remained intact in agricultural areas outside the boundaries of maximum hurricane winds (Fig. 2h).

## 2.2. Raptor surveys

In each of the 29 survey plots, we established a 1.5 km length transect to survey the community of diurnal raptors, with each transect surveyed only once. We did not consider vultures in the surveys because of their carrion-feeding behavior, but focused our surveys on Accipitriformes and Falconiformes who actively search for prey. We conducted surveys five months after landfall by Hurricane Patricia

during March-May 2016, with most surveys conducted in April 2016, corresponding to the first raptor breeding season after hurricane impact.

To estimate density of diurnal raptors, we applied distance sampling for line transect surveys (Thomas et al., 2010). We commenced surveys 60 min after daybreak, walking at a steady, slow pace of approximately 1.5 km/h in one direction along the transect. On detecting a raptor, we measured distance from the observer to the bird with a laser range-finder (TruePulse 200), as well as the angle from the transect central line to the bird. This data was used to calculate the perpendicular distance of each bird from the transect line, and generate distance models of diurnal raptor density (Buckland et al., 2001).

To estimate species richness of diurnal raptors along the survey transect, we used data on number of individuals of each species detected during the distance sampling surveys, and complemented this by returning along the same transect conducting playbacks of raptor vocalizations to detect additional species not recorded during the initial surveys. The use of vocal stimulus increases detectability of raptors given their territorial behavior (Fuller and Mosher, 1987). Playbacks of pre-recorded vocalizations of species reported for the region were conducted at three points separated by 750 m along the transect. At each point, we played two 30 s cycles of each raptor species vocalization, spaced with 40 s of silence to await a response. We only used playback of vocalizations of raptor species not detected during the transect survey. We used a MIPRO MA-202 amplifier for playbacks, which was orientated in different directions around the playback station (Barnes et al., 2012). If we obtained a vocal response from a raptor species, we suspended playback of vocalizations for that species for the rest of the survey on that transect.

## 2.3. Data analysis

### 2.3.1. Raptor density

We estimated the density of diurnal raptors detected along survey transects using the program Distance 6.2 (Thomas et al., 2010), which calculates a probability function and effective detection radius to estimate the number of individuals in the area surveyed (Buckland et al., 2001). We used a stratification approach with each habitat as a different stratum to analyze survey data by habitat type and minimize heterogeneity in detection probabilities (Buckland et al., 2001). We determined raptor density for each habitat and hurricane condition surveyed, and selected the model with best fit to the data based on the corrected form of the Akaike's Information Criterion (AICc) recommended for small sample sizes (Burnham and Anderson, 2002).

We selected models based on a low AICc of delta AICc < 2, and that also had the lowest number of parameters and coefficient of variation. To determine whether raptor density differed significantly among habitats we compared 84% confidence intervals for each density estimate from the best-fitting model, as this robustly mimics significance values from statistical tests (MacGregor-Fors and Payton, 2013). Hence, we considered density estimates as significantly different where confidence intervals did not overlap.

### 2.3.2. Species richness

We estimated species richness of diurnal raptors using rarefaction analysis with the program EstimateS 9.1.0 (Colwell, 2013). We established a cut-off value of 97 individuals to calculate an estimated species richness ( $S_{est}$ ) for the two hurricane conditions of within and outside the hurricane eyewall of maximum winds, based on the lowest accumulated abundance recorded in either of these two hurricane categories. To calculate species richness for each habitat category in each hurricane condition, we established a cut-off value of 16 individuals, which was the lowest abundance recorded for any habitat/hurricane condition category. We determined significant differences in species richness among habitats and hurricane conditions by comparison of 84% confidence intervals for each richness estimate (MacGregor-Fors



**Fig. 2.** Habitat types where surveys were conducted along the coast of Jalisco. Semi-deciduous forest within the path of Hurricane Patricia (a) and outside the boundaries of the hurricane eyewall of maximum winds (b). Deciduous forest within the path of the hurricane (c) and outside the maximum winds (d). Mangroves within (e) and outside (f) the boundaries of maximum hurricane winds. Agricultural sites affected by Hurricane Patricia (g) and unaffected agricultural sites outside the hurricane eyewall (h).

and Payton, 2013).

### 2.3.3. Community structure and composition

We generated rank-abundance curves representing the abundance distribution of species in the community (Magurran, 2004), to evaluate community structure of diurnal raptors in each of the habitats and hurricane conditions. Rank-abundance curves with a pronounced slope represent communities dominated by a few species with high abundance, whereas curves with more gradual slopes represent more even communities where a number of species have similar abundances (Magurran, 2004). Data on number of individuals of each species recorded in surveys was transformed to a logarithmic scale ( $\log_{10}$ ) to facilitate comparisons (Magurran, 2004). We applied ANCOVA to compare the slopes of rank-abundance curves for each habitat between the two hurricane conditions of within and outside the hurricane eyewall. Statistical analyses were conducted using R (R Core Team, 2015) with Bonferroni adjusted alpha value of  $P < 0.012$ .

Finally, we calculated Bray-Curtis similarity indices to compare

community composition of diurnal raptors for each habitat type between the two hurricane conditions of within and outside the hurricane eyewall of maximum winds (Magurran, 2004). We also applied Bray-Curtis multivariate cluster analysis with simple linkage using the Bio-Diversity Pro software (McAleece et al., 1997), to assess similarity of diurnal raptor communities among habitat types for each hurricane condition.

## 3. Results

### 3.1. Raptor surveys

Over all surveys we registered 192 individuals, comprising 20 species of diurnal raptors: 13 species from the family Accipitridae; 6 species of Falconidae; and 1 species of Pandionidae (Table 1). Five of the 20 species were winter migrants, while the rest of the species were resident in the region (Table 1).

**Table 1**

Total number of individuals of each diurnal raptor species registered in surveys conducted during March–May 2016 along transects located within the main path of Hurricane Patricia, and outside the boundaries of the hurricane eyewall of maximum winds. \* = Migrant species. <sup>1</sup> = Forest specialist, <sup>2</sup> = around water, <sup>3</sup> = open areas, <sup>4</sup> = diet specialist, <sup>5</sup> = generalist. Habitat associations and main dietary specialization were obtained from del Hoyo et al. (1994), Ferguson-Lees and Christie (2005), and species accounts in Whitacre (2012).

Scientific name	Common name	Number of individuals	
		Hurricane path	Outside eyewall
<b>Accipitridae</b>			
<i>Accipiter striatus</i> *	Sharp-shinned Hawk <sup>1</sup>	2	0
<i>Busarellus nigricollis</i>	Black-collared Hawk <sup>2</sup>	0	1
<i>Buteo albonotatus</i> *	Zone-tailed Hawk <sup>3,5</sup>	2	0
<i>Buteo brachyurus</i>	Short-tailed Hawk <sup>5</sup>	3	5
<i>Buteo jamaicensis</i>	Red-tailed Hawk <sup>3,5</sup>	1	0
<i>Buteo plagiatus</i>	Gray Hawk <sup>5</sup>	24	23
<i>Buteogallus anthracinus</i>	Common Black Hawk <sup>2</sup>	8	8
<i>Buteogallus urubitinga</i>	Great Black Hawk <sup>1</sup>	6	3
<i>Chondrohierax uncinatus</i>	Hook-billed Kite <sup>4</sup>	1	9
<i>Elanus leucurus</i>	White-tailed Kite <sup>3,5</sup>	0	1
<i>Geranospiza caerulescens</i>	Crane Hawk <sup>1</sup>	9	4
<i>Parabuteo unicinctus</i>	Harris's Hawk <sup>3,5</sup>	0	1
<i>Rupornis magnirostris</i>	Roadside Hawk <sup>3,5</sup>	8	16
<b>Falconidae</b>			
<i>Falco peregrinus</i> *	Peregrine Falcon <sup>3</sup>	1	0
<i>Falco rufigularis</i>	Bat Falcon <sup>1</sup>	3	0
<i>Falco sparverius</i> *	American Kestrel <sup>3</sup>	0	1
<i>Caracara cheriway</i>	Crested Caracara <sup>3,5</sup>	5	17
<i>Herpotheres cachinnans</i>	Laughing Falcon <sup>4</sup>	6	1
<i>Micrastur semitorquatus</i>	Collared Forest-falcon <sup>1</sup>	13	8
<b>Pandionidae</b>			
<i>Pandion haliaetus</i> *	Osprey <sup>2,4</sup>	1	1

**3.2. Raptor density**

We determined an overall density of 32.6 diurnal raptors/km<sup>2</sup> in the region. There was slightly higher density of 36.8 raptors/km<sup>2</sup> (84% CI: 29.9–45.3) in areas outside the eyewall radius of maximum winds of Hurricane Patricia, compared with 26.3 raptors/km<sup>2</sup> (84% CI: 19.8–34.8) for sites within the path of the hurricane eyewall, although the large overlap in confidence intervals means that this was not statistically significant. Highest raptor density of 74.5 raptors/km<sup>2</sup> (84% CI: 48–115.7) was recorded in semi-deciduous forest outside the hurricane eyewall of maximum winds, with a markedly lower 37.8 raptors/km<sup>2</sup> (84% CI: 28.7–49.8) in semi-deciduous forest within the path of the hurricane eyewall. However, this was only marginally significant due to the large confidence intervals for surveys in semi-deciduous forest sites outside the hurricane eyewall (Fig. 3). Deciduous forest outside the hurricane eyewall had significantly higher 40.3 raptors/km<sup>2</sup> (84% CI: 29.7–54.7), compared to 14.5 raptors/km<sup>2</sup> (84% CI: 8.8–23.8) in deciduous forest sites within the path of the hurricane eyewall (Fig. 3). In general, raptor density tended to be lower in mangroves and agricultural fields than in forest sites, but did not differ significantly between hurricane conditions (Fig. 3).

**3.3. Raptor species richness**

Species richness of diurnal raptors was similar between hurricane conditions (Hurricane eyewall path: S<sub>est</sub> = 16 species, 84% CI: 13.6–18.3; Outside eyewall: S<sub>est</sub> = 14.9 species; 84% CI: 10.9–18.6).

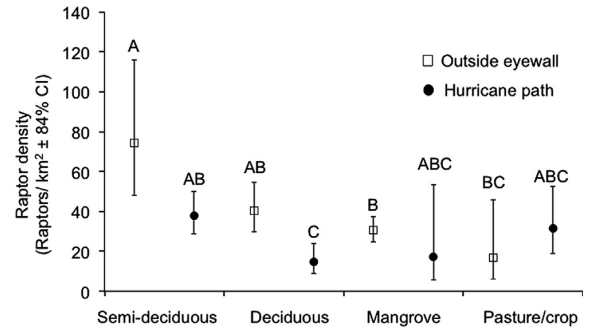


Fig. 3. Density estimates per km<sup>2</sup> for diurnal raptors, with 84% confidence intervals, in each habitat type located within the main path of Hurricane Patricia, and outside the boundaries of the hurricane eyewall of maximum winds. Capital letters indicate statistically significant differences among groups.

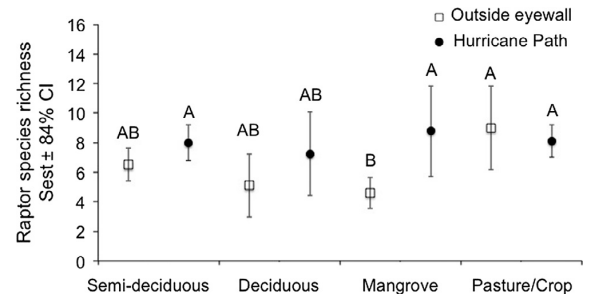


Fig. 4. Estimated species richness with 84% confidence intervals for each habitat type within the main path of Hurricane Patricia, and outside the boundaries of the hurricane eyewall of maximum winds. Capital letters indicate statistically significant differences among groups.

Species richness was also similar among habitats, ranging from estimated richness values of 4.6–9 species of diurnal raptors (Fig. 4). Lowest species richness of diurnal raptors was estimated for mangroves outside the hurricane eyewall of maximum winds (S<sub>est</sub> = 4.6; 84% CI: 3.5–5.6; Fig. 4). This was significantly lower than species richness in semi-deciduous forest within the hurricane path (S<sub>est</sub> = 6.5, 84% CI: 5.3–8.4), and for agricultural fields within and outside the hurricane eyewall of maximum winds (Fig. 4). Mangroves were also the only habitat to show significant differences in species richness between hurricane conditions, with significantly higher species richness of diurnal raptors in mangroves within the path of the hurricane eyewall of maximum winds (S<sub>est</sub> = 8.8; 84% CI: 7.4–13.5) compared to mangroves outside the hurricane eyewall (Fig. 4).

**3.4. Community structure**

The most dominated raptor community occurred in mangroves outside the hurricane eyewall (Fig. 5), which were dominated by the Crested Caracara (*Caracara cheriway*), Roadside Hawk and Common Black Hawk (*Buteogallus anthracinus*). Deciduous forests outside the hurricane eyewall also had relatively dominated diurnal raptor communities, where the most common species were the Gray Hawk (*Buteo plagiatus*), and the Roadside Hawk (Fig. 5). In both these habitats community structure differed significantly between the two hurricane conditions (mangroves: ANCOVA F<sub>1,17</sub> = 32.6, P < 0.001; Deciduous forest: ANCOVA F<sub>1,16</sub> = 5, P = 0.04). In both cases, community structure of diurnal raptors was more even for sites located within the path of the hurricane compared to sites outside the hurricane eyewall (Fig. 5). By comparison, community structure of diurnal raptors in semi-deciduous forest and agricultural fields did not differ significantly between the two hurricane conditions (Fig. 5).

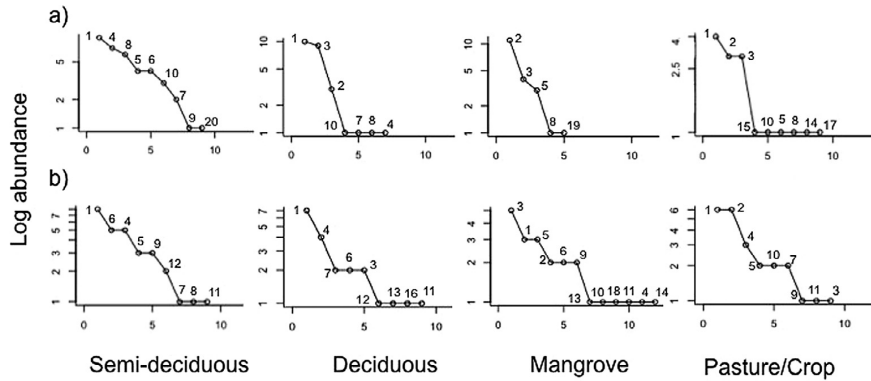


Fig. 5. Rank-abundance curves for the diurnal raptor communities in each habitat located (a) outside the boundaries of the hurricane eyewall of maximum winds, and (b) within the main path of Hurricane Patricia. Numbers represent the following species: 1 = Gray Hawk; 2 = Crested Caracara; 3 = Roadside Hawk; 4 = Collared Forest-falcon; 5 = Common Black Hawk; 6 = Crane Hawk; 7 = Great Black Hawk; 8 = Hook-billed Kite; 9 = Laughing Falcon; 10 = Short-tailed Hawk; 11 = Bat Falcon; 12 = Sharp-shinned Hawk; 13 = Zone-tailed Hawk; 14 = Osprey; 15 = Black-collared Hawk; 16 = Red-tailed Hawk; 17 = White-tailed Kite; 18 = Peregrine Falcon; 19 = American Kestrel; 20 = Harris's Hawk.

3.5. Community composition

The Gray Hawk was the most abundant species in all habitats except mangroves (Fig. 5). However, community composition differed among habitats and between hurricane conditions. Of habitats outside the path of the Hurricane Patricia eyewall, semi-deciduous forest separated as having the most distinct diurnal raptor community at 41% similarity (Fig. 6a), where the Hook-billed Kite (*Chondrohierax uncinatus*), Collared Forest-falcon (*Micrastur semitorquatus*), Common Black Hawk, Crane Hawk (*Geranospiza caerulescens*), and Great Black Hawk (*Buteogallus*

*urubitinga*) were common species that were rarely encountered in the other habitats (Fig. 5). Outside the hurricane eyewall, the habitat types with most similar diurnal raptor communities were deciduous forest and agricultural fields (57%; Fig. 6a), where the Gray Hawk, Crested Caracara, and Roadside Hawk were all common species (Fig. 5). Mangroves outside the hurricane eyewall separated from these previous two habitats at 44% similarity (Fig. 6a), having communities of a few, abundant species (Fig. 5).

By comparison, within the hurricane eyewall all habitats presented greater similarity in diurnal raptor communities (> 50%; Fig. 6b). Of

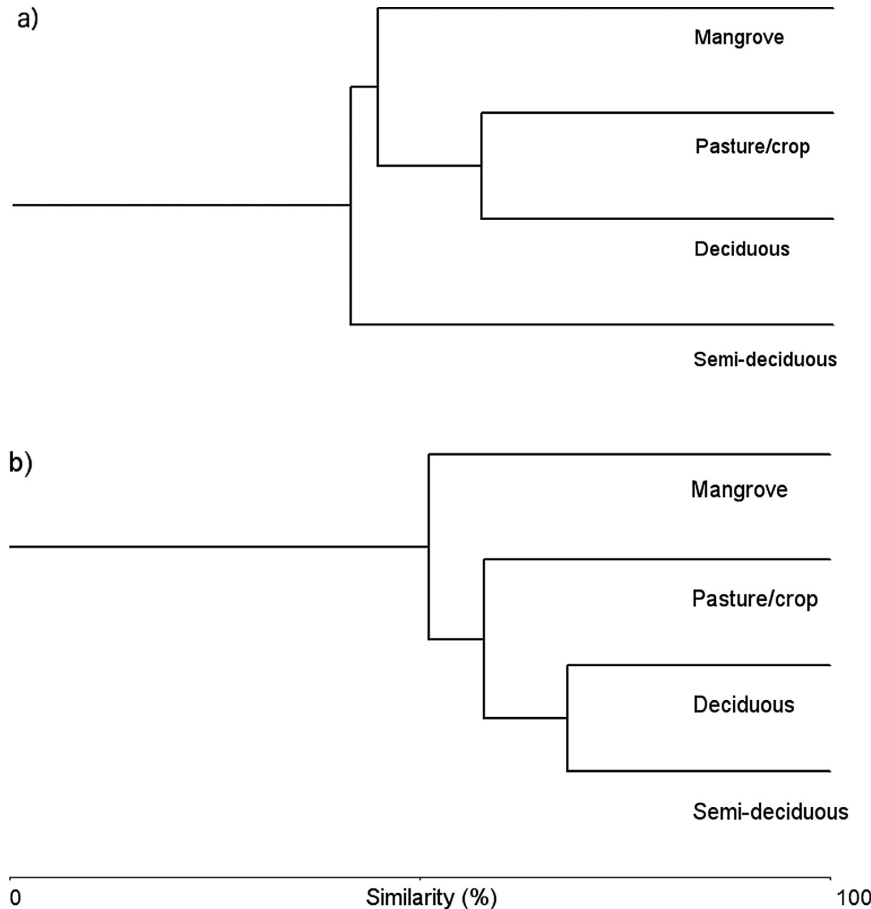


Fig. 6. Dendrograms of Bray-Curtis multivariate cluster analysis for diurnal raptor communities among habitats (a) outside the path of the eyewall of Hurricane Patricia, and (b) within the eyewall of maximum hurricane winds.

these, mangroves separated at 51% similarity in raptor communities, and was the only habitat within the hurricane eyewall where the Roadside Hawk was an abundant species (Fig. 5). In the path of the hurricane eyewall, semi-deciduous and deciduous forests presented greatest similarity in raptor communities (68%), separating from agricultural fields at 58% similarity (Fig. 6b). The Collared Forest-falcon was among the most abundant species in all three of these habitats, whereas outside the path of the hurricane eyewall the Collared Forest-falcon was only abundant in semi-deciduous forest (Fig. 5).

All habitats differed in community composition of diurnal raptors between hurricane conditions (Fig. 5). In particular, Bray-Curtis indices demonstrated low similarity in species composition between the two hurricane conditions for mangroves (Bray-Curtis = 0.418) and deciduous forest (Bray-Curtis = 0.468). Mangroves occurring within the path of the hurricane had a greater number of species with similar abundances compared to mangroves outside the hurricane eyewall (Fig. 5). In particular, the Gray Hawk, Crane Hawk, and Laughing Falcon (*Herpetotheres cachinnans*) were abundant species in mangroves within the path of the hurricane that did not occur in mangroves outside the hurricane eyewall (Fig. 5). Mangroves within the path of the hurricane also had a large number of rare species (1 individual each) that were not encountered in mangroves outside the hurricane eyewall (Fig. 5): Zone-tailed Hawk (*Buteo albonotatus*), Peregrine Falcon (*Falco peregrinus*), Short-tailed Hawk (*Buteo brachyurus*), Collared Forest-falcon (*Micrastur semitorquatus*), Bat Falcon (*Falco ruficularis*), and Osprey (*Pandion haliaetus*).

Deciduous forest within the path of the hurricane had a greater number of relatively abundant raptor species compared to deciduous forest outside the hurricane eyewall (Fig. 5). The Collared Forest-falcon, Great Black Hawk, and Crane Hawk became more abundant in deciduous forest within the path of the hurricane compared to deciduous forest outside the hurricane eyewall (Fig. 5). There were also a number of additional species with low abundance in deciduous forest within the hurricane path, such as the Sharp-shinned Hawk (*Accipiter striatus*), Zone-tailed Hawk, Red-tailed Hawk (*Buteo jamaicensis*), and Bat Falcon (Fig. 5).

Semi-deciduous forest on the other hand showed high similarity in species composition of diurnal raptors between hurricane conditions (Bray-Curtis = 0.727). There were only a few differences in species composition between hurricane conditions with the Laughing Falcon being more abundant, and the Hook-billed Kite (*Chondrohierax uncinatus*) relatively rare, in semi-deciduous forest within the path of the hurricane (Fig. 5).

Finally, agricultural fields had moderate similarity in species composition of diurnal raptors between hurricane conditions (Bray-Curtis = 0.5). In particular, the Common Black Hawk and Collared Forest-falcon were relatively abundant in agricultural fields within the path of the hurricane compared to those outside the hurricane eyewall (Fig. 5). On the other hand, the Black-collared Hawk (*Busarellus nigricollis*), Hook-billed Kite, Osprey, and White-tailed Hawk (*Elanus leucurus*) were registered albeit rarely in agricultural fields outside the hurricane eyewall, but not in agricultural fields within the path of the hurricane (Fig. 5).

## 4. Discussion

### 4.1. Density of diurnal raptors

We found significant differences in density of diurnal raptors between hurricane conditions five months after landfall by Hurricane Patricia, particularly for tropical forest habitats where raptor density was markedly lower for forests within the path of maximum hurricane winds. These results differ from that found in other studies which determined little change in abundance of particular raptor species 4–8 months after hurricane impact (Lynch, 1991; Wauer and Wunderle, 1992). However, previous studies did not evaluate the raptor

community specifically, and are based on estimates of relative abundance or percent occurrence in survey plots rather than density. The three raptor species evaluated in these previous studies are also widespread, common, generalist species (del Hoyo et al., 1994) that may be more adaptable to changing environmental conditions. By contrast, our findings for the diurnal raptor community within the path of the hurricane eyewall agree with the patterns observed for other bird groups, which demonstrate a decline in abundance 4–6 months after hurricane impacts (Lynch, 1991; Wauer and Wunderle, 1992; Wunderle et al., 1992; Wiley and Wunderle, 1993).

Furthermore, the fact that we recorded greatest declines in raptor density in forest habitats within the path of the hurricane concurs with reports of more severe hurricane damage in mature forest compared to open habitats (Wauer and Wunderle, 1992). Large, tall trees are more susceptible to branch breakage or uprooting by hurricane winds than smaller trees (Gresham et al., 1991; Reilly, 1991; Varty, 1991; Walker, 1991; Roth, 1992), and severe conditions of structural damage to trees were observed in the forest transects that we surveyed within the path of the hurricane. The strong winds of Hurricane Isabel caused the loss of nest-trees for the Bald Eagle (*Haliaeetus leucocephalus*) in Chesapeake Bay, with a significant negative effect on reproductive performance of eagles in the breeding season after the hurricane (Watts and Byrd, 2007). Many of the diurnal raptor species in our study have been recorded nesting and perching in tall, emergent trees of mature forests, including the Hook-billed Kite, Crane Hawk, Great Black Hawk, Collared Forest-falcon, and Laughing Falcon (Gerhardt et al., 2012; Parker et al., 2012; Sutter, 2012; Thorstrom, 2012; Whitacre and Vásquez, 2012). The migratory Sharp-shinned Hawk is also associated with mature forests (Reynolds et al., 1982; Woltmann, 2001). Therefore, the lower density of diurnal raptors in deciduous and semi-deciduous forest within the path of Hurricane Patricia may respond in part to the structural damage caused to large trees that provide perching, roosting, and nesting sites for raptors.

### 4.2. Species richness and community structure

Species richness of diurnal raptors was similar among habitats and varied little between hurricane conditions, except in the case of mangroves. The similarity in species richness for sites within the path of the hurricane and those outside the hurricane eyewall of maximum winds suggests that diurnal raptor species continue using the same areas after hurricane impact, although they may be more dispersed and wandering, resulting in lower densities. The territoriality of many raptor species may ensure some fidelity to areas previously used, even under conditions of high disturbance (Watts and Byrd, 2007; Martínez-Ruiz et al., 2016).

Many raptor species may be able to persist after hurricane disturbance due to a potential increase in detectability of small prey in areas opened by hurricane damage (Wiley and Wunderle, 1993). In particular, various diurnal raptor species in our study area have broad dietary niches, and occur in a variety of habitats throughout their distribution. Some species are even able to exploit a wide variety of prey from different taxa. Diurnal raptors such as the Gray Hawk, Crane Hawk, Great Black Hawk, Common Black Hawk, Collared Forest-falcon, Roadside Hawk, Bat Falcon, and Short-tailed Hawk are known to consume a variety of species of reptiles, amphibians, birds, mammals, and insects (del Hoyo et al., 1994; Gerhardt et al., 2012; Panasci, 2012; Parker and Whitacre, 2012; Sutter, 2012; Thorstrom, 2012). Some diurnal raptor species may include carrion in their diet and are considered opportunistic foragers, such as the Crested Caracara and Great Black-Hawk (del Hoyo et al., 1994; Ferguson-Lees and Christie, 2005; Gerhardt et al., 2012). Outbreaks of insect populations have been recorded following hurricane disturbance (Torres, 1992; Beuzelin et al., 2009), and these form part of the diet of a number of species of diurnal raptors at our study site. Small, insectivorous birds that are potential prey species for raptors may also increase in abundance following



hurricane disturbance (Waide, 1991; Wauer and Wunderle, 1992).

Only in the case of mangroves did species richness of diurnal raptors vary significantly between hurricane conditions, where mangroves within the path of Hurricane Patricia had significantly higher raptor species richness than mangroves outside the boundaries of maximum hurricane winds. This may be because mangroves within the eyewall of maximum hurricane winds showed less visible damage, with few up-rooted trees or snapped trunks, which may be due to the low structural complexity of large, tall trees in mangroves of tropical dry life zones (Pool et al., 1977). Species susceptibility to wind is the determinant factor influencing hurricane damage in structurally homogeneous mangrove stands, where Red Mangrove (*Rhizophora mangle*) is far more susceptible to hurricane damage than the other mangrove species (Imbert et al., 1996; Sherman et al., 2001). Furthermore, mangroves show a rapid plant regeneration and forest recovery after hurricane disturbance, with almost half of trees well-foliated 17 months after landfall by Hurricane Joan in Nicaragua (Roth, 1992). This resilience of mangroves may enable them to provide food resources and shelter for raptors after hurricane disturbance.

Finally, we recorded a low number of migratory raptor species in our surveys, with species such as the Peregrine Falcon and American Kestrel that are usually considered common, being represented with just one individual each in surveys. The spring migration of raptors returning to their North American breeding grounds occurs from mid-February to late May (Goodrich and Smith, 2008). Our raptor surveys were conducted in the months of March to May during the period when raptors may be on spring migration, however there should still have been migratory raptors in the region during the surveys. Timing of migration is highly variable among species and individuals, as well as according to region or migratory route (Goodrich and Smith, 2008). Some species or individuals migrate later in the season, such as west coast Peregrine Falcons that return north between late April and late May (Dekker, 1984), but only one individual of this species was recorded in our surveys. The Cooper's Hawk (*Accipiter cooperii*) also returns later in the season from mid-March to early May (Goodrich and Smith, 2008), similar to the Zone-tailed Hawk and Sharp-shinned Hawk, but was not recorded in the region during our surveys. Hurricanes have the potential to disrupt migratory routes, arrival dates, or winter survival of migratory birds (Wiley and Wunderle, 1993). Wunderle et al. (1992) found that migrant insectivorous birds showed similar population declines as resident insectivores four months after landfall by Hurricane Gilbert in Jamaica, although Lain et al. (2017) found no significant influence of hurricanes Rita and Ike on the community of migratory songbirds stopping over along the northern Gulf of Mexico. In the case of raptors, the Peregrine Falcon has been observed to make changes in movements during migration when faced with adverse climatic conditions (McGrady et al., 2006). Hurricane Patricia impacted the region during the fall migration for raptors travelling to their wintering grounds, which occurs in September to October (Goodrich and Smith, 2008). Therefore, it may be that many individuals of migrating raptors altered their routes, moved on to other areas, or reduced the time they spent in the region, resulting in the scarcity of migratory species recorded in our surveys.

#### 4.3. Habitat expansion in response to hurricane disturbance

Our results suggest that raptor communities within the path of maximum hurricane winds may have modified their habitat use in response to hurricane disturbance. We determined significantly lower density of raptors in forest habitats within the path of the hurricane compared to forests outside the hurricane eyewall. Our rank-abundance data also showed that raptor species characteristic of closed-forest, such as the Collared Forest-falcon, Great Black Hawk, and Crane Hawk, were found to be relatively abundant in a number of habitats within the path of the hurricane eyewall, but outside the range of maximum hurricane winds these species were only abundant in semi-deciduous forest.

Raptor communities of semi-deciduous forest may be particularly affected by hurricane disturbance due to the greater structural damage caused by strong winds to trees of larger size (Gresham et al., 1991; Reilly, 1991), and in our study region deciduous and semi-deciduous forests within the path of the hurricane eyewall suffered a severe loss of canopy cover (Parker et al., this issue). Therefore it may be that raptors of forest habitats affected by maximum hurricane winds have expanded their activity areas to explore and exploit alternative habitats in search of food resources, resulting in habitat expansion in response to hurricane disturbance.

In particular, the raptor community within the path of the hurricane eyewall may be exploiting resources in mangroves as we determined a significantly higher species richness of diurnal raptors in mangroves within the path of the hurricane compared to mangroves outside the range of maximum hurricane winds. The separation of the diurnal raptor community in mangroves from that of other habitats within the hurricane eyewall further suggests that mangroves may serve as habitat refuges for many raptor species following hurricane disturbance. This use of mangroves by additional raptor species may not have resulted in a significant increase in raptor density as forest or diet-specialist species tend to occur at low densities, and may be more dispersed and wandering in the hurricane disturbed landscape. By comparison mangroves outside the path of the hurricane had raptor communities dominated by generalist species, such as the Crested Caracara and Roadside Hawk, which are abundant resident species.

Mangroves along the coast of Jalisco are restricted to habitat patches in a narrow strip along the coastline, and may be used as seasonal or marginal habitats by raptors and other bird species. Various studies in Australia have determined that most bird species associated with mangroves are more abundant in other adjacent habitats (Noske, 1996; Kutt, 2007; Mohd-Azlan et al., 2011). Similarly, in West Africa Altenburg and Spanje (1989) found that most of the birds recorded in mangroves were more common in adjoining forests and crops. The diurnal raptor assemblage determined in our study does not include mangrove-dependent species, although species such as the Common Black Hawk and Collared Forest-falcon have been reported to occur in mangroves and estuarine ecosystems in other parts of their distribution (del Hoyo et al., 1994). Noske (1996) in northern Australia also reports that raptors are rare in mangrove habitats. Therefore, the greater species richness of raptors in mangroves within the path of Hurricane Patricia but not in mangroves outside the hurricane eyewall, suggests that more raptor species are visiting and using mangroves following the structural damage caused to adjacent forest habitats. This highlights the importance of considering potentially overlooked habitats such as mangroves in management strategies to conserve avian communities.

#### 4.4. Biotic homogenization

All habitats within the path of the hurricane eyewall showed greater similarity in diurnal raptor communities, whereas outside the hurricane eyewall semi-deciduous forest had the most distinct diurnal raptor community. We also found greater evenness of diurnal raptor communities in mangroves and deciduous forests occurring within the path of the hurricane. The few studies of hurricane impacts on raptors have not evaluated potential effects on community structure, but hurricane impacts in Louisiana, USA, were found to result in increased evenness of herpetofauna communities (Schriever et al., 2009).

The increased similarity and evenness of raptor communities in habitats within the path of maximum hurricane winds may indicate a process of biotic homogenization (McKinney and Lockwood, 1999), referred to as an increase in taxonomic similarity of biotas (Olden, 2006). This process usually involves an increase in generalist, widespread species and loss of specialist, endemic species, but various ecological mechanisms may give rise to biotic homogenization, being greatest when similar species invade communities, with or without local extinctions (Olden and Poff, 2003). Biotic homogenization is

driven by anthropogenic activities (McKinney and Lockwood, 1999; Olden, 2006), and homogenized avian communities are generally associated with human-induced urbanized or fragmented landscapes (Devictor et al., 2007; van Rensburg et al., 2009; Villegas-Vallejos et al., 2016; Vázquez-Reyes et al., 2017). Little information exists on the influence of extreme climatic events on biotic homogenization, although Haslem et al. (2015) determined that severe drought in southeastern Australia increased turnover-related differentiation of woodland avifauna, particularly in human-modified landscapes. Notably, landscapes with more native forest vegetation had more stable avian communities in response to severe drought events (Haslem et al., 2015). No studies have evaluated the influence of severe storms on biotic homogenization, but models of human-induced climate change predict an increase in the frequency and intensity of hurricanes making landfall (Walsh and Pittcock, 1998; Goldenberg et al., 2001; Webster et al., 2005), with greater destructive potential (Emanuel, 2005). Our results suggest that this may lead to habitat expansion, and invasion of biotas with species from other communities, potentially increasing similarity of biotas.

It should be noted that biotic homogenization refers to a change in biotas over time, but as no raptor surveys have previously been conducted in the region, we lack data on species composition of diurnal raptor communities prior to hurricane impact. This limits our conclusions as spatially separated habitats within and outside the range of maximum hurricane winds may not be directly comparable. Nevertheless, raptors have large area requirements (Newton, 1979), and are more influenced by landscape features rather than local habitat characteristics (Jullien and Thiollay, 1996; Sánchez-Zapata and Calvo, 1999; Buij et al., 2013). Therefore, we consider that comparing diversity of diurnal raptors within and outside the path of maximum hurricane winds in the same region allows us to make inferences regarding the influence of these extreme climatic events on the diurnal raptor community. Our results highlight the importance of maintaining landscape heterogeneity of native vegetation to ameliorate the impact of disturbance by extreme climatic events.

## 5. Conclusions

To our knowledge, this is the first study that evaluates the influence of hurricane disturbance on a community of diurnal raptors. We found that Hurricane Patricia had differing effects on the diurnal raptor community depending on habitat type. Raptor density was markedly lower in forests within the path of the hurricane, whereas species richness and evenness of raptor communities was higher in mangroves within the hurricane path. This suggests that while raptors in forest habitats may be more greatly impacted by hurricane disturbance, raptors may be resilient to hurricane disturbance because of their high mobility, enabling them to move among different habitats. However, we have yet to determine whether there may be long-term or delayed effects of hurricane impact on the resident and migratory raptor community in each habitat type. Furthermore, the position of raptors at the top of the trophic chain means that changes observed in raptor density among habitats within and outside the path of hurricane landfall may have consequences for top-down control of prey communities.

Our results further highlight the importance of alternate habitats such as mangroves, which may serve as refuge habitats for diurnal raptors following hurricane impact. The biogeographical distribution of mangroves is confined to tropical and subtropical regions (Giri et al., 2011), largely coinciding with the global distribution of occurrence of tropical cyclones and hurricanes (Laing and Evans, 2011). This means that mangroves can provide an important first line of defense against landfalling hurricanes. Nevertheless, despite the potential importance of mangroves in providing environmental services (Costanza et al., 1997; Kathiresan and Bingham, 2001), these ecosystems have declined considerably mainly due to human activities of aquaculture, deforestation, and urban development (Valiela et al., 2001). It is estimated that by 2001, there had been a loss of 35% of mangroves worldwide

(Valiela et al., 2001), with the continued exploitation of mangroves putting at risk the persistence of these forests, and the environmental services they provide (Alongi, 2002; Duke et al., 2007). This is of particular concern in tropical developing countries where rates of loss of mangroves are increasing more rapidly (FAO, 2003).

Mexico is the fourth most mangrove-rich country worldwide (Giri et al., 2011), and mangroves are protected by Mexican law (SEMARNAT, 2010). Mangroves are scarce and patchily distributed, and restoration efforts can take many years when possible, but often the loss of this forest is total or irreversible (Imbert et al., 2000; Duke et al., 2007). Along the coast of Jalisco, mangroves occur as small patches of trees around the mouth of estuaries, with only 180 ha of mangroves located within protected areas (CONABIO, 2009), and cutting of mangroves still occurs in the region (M. Martínez Ruiz pers. obs.). Therefore, monitoring and surveillance programs are required to regulate mangrove exploitation, particularly in coastal areas where these habitats can provide important refuges for wildlife after hurricane disturbance. The results of our study highlight the importance of maintaining environmental heterogeneity for the diurnal raptor community, and other avian groups with specific ecological requirements, to withstand the increasing pressures of global change. Managers aiming to conserve wildlife communities need to incorporate strategies to maintain alternate habitats in the landscape, which although less preferred by the target species or community, may have greater resilience to disturbance, thereby providing alternative habitats for wildlife communities following extreme climatic events.

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## **CAPÍTULO II. VARIACIÓN ESPACIO-TEMPORAL DE LA DIVERSIDAD DE RAPACES DIURNAS EN EL BOSQUE TROPICAL SECO BAJO INFLUENCIA DE UN EVENTO CLIMÁTICO EXTREMO**

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## RESUMEN

Poco se sabe con respecto a la respuesta de las aves rapaces a la estacionalidad de los bosques tropicales secos o a la perturbación de disturbios como huracanes. En este estudio, evaluamos la variación espacio-temporal de la diversidad de rapaces diurnas en el bosque tropical seco de México. Durante dos años llevamos a cabo muestreos de rapaces durante la época seca y húmeda en 29 transectos que representan 4 hábitats del bosque seco. Los transectos se distribuyeron dentro y fuera del radio de vientos máximos del Huracán Patricia de categoría 4. La estacionalidad del bosque seco influyó en la abundancia y riqueza de rapaces diurnas, tanto en el área afectada como en el área no afectada por el paso del huracán, con mayor diversidad de rapaces en la época seca. Los hábitats más estacionales como el bosque deciduo y las áreas agrícolas mostraron variación temporal significativa en la densidad de rapaces, tanto en áreas afectadas como no afectadas por el huracán. Sin embargo, los hábitats con menor grado de estacionalidad como los humedales y el bosque semideciduo solo mostraron variación temporal en la densidad de rapaces en las áreas afectadas por los vientos máximos del huracán. Asimismo, en las áreas afectadas por el huracán, los ensambles de rapaces solo fueron distintos entre hábitats durante la época seca, sin un agrupamiento claro por hábitat durante la época húmeda, mientras en áreas no afectadas por el huracán los hábitats mostraron ensambles distintos, tanto en la época seca como en la húmeda. Nuestros resultados muestran que la perturbación de un huracán de alta intensidad puede modificar la dinámica espacio-temporal del ensamble de rapaces diurnas con posibles efectos en cascada en diferentes hábitat de los bosques tropicales secos.

*Palabras clave:* estacionalidad, disturbios, bosque seco, depredadores tope, huracanes

## INTRODUCCIÓN

En los bosques tropicales secos, las aves frugívoras, granívoras y nectarívoras pueden presentar altas fluctuaciones espacio-temporales en abundancia dado que son consumidoras primarias sobre recursos vegetales que son temporalmente variables (Levey, 1988; Arizmendi and Ornelas, 1990, Loiselle and Blake, 1991, Renton, 2001), asimismo, en dichos bosques se ha determinado variación estacional en la abundancia y diversidad de aves residentes (Ornelas et al., 1993, Corcuera and Butterfield 1999, Almazán-Núñez et al. 2018), donde las aves insectívoro-frugívoras y omnívoras presentaron significativamente mayor abundancia durante la época seca (Almazán-Núñez et al. 2018). En particular, en el bosque seco de la costa de Jalisco, el bosque deciduo es el hábitat más estacional, y presenta mayor riqueza de especies de aves durante la época húmeda (Ornelas et al., 1993).

En comparación con las aves frugívoras y nectarívoras, las aves rapaces son consumidores secundarios en las comunidades de aves y son depredadores tope en los ecosistemas (Newton, 1979). Sin embargo, algunas especies de aves rapaces usan hábitats particulares durante periodos específicos del año y los movimientos que realizan están estrechamente relacionados con la disponibilidad de presas (Newton, 1979). Asimismo, se ha reportado variación en abundancia y/o riqueza de rapaces en humedales y ambientes riparios del Neotrópico, con mayor riqueza de rapaces diurnas durante la época húmeda (Hayes 1991, Carmona et al. 2017). Por otro lado, (Jensen et al., 2005) determinaron mayor riqueza de especies de rapaces en la época húmeda en áreas dominadas por sabana, pero en el área dominada por uso agropecuario y parches de bosque la riqueza fue mayor durante la época seca (Zilio et al., 2014). Adicionalmente, se han reportado respuestas especie-específicas en abundancia de rapaces relacionadas con la variación estacional en climas subtropicales de Sudamérica, donde especies residentes de rapaces fueron más abundantes durante los meses correspondientes a primavera-verano (noviembre-febrero), cuando hay menor precipitación (Zilio et al., 2014). Otras especies del ensamble de rapaces fueron más abundantes durante el otoño-

invierno, cuando ocurre la concentración de las lluvias en la región, mientras algunas otras no mostraron diferencias en abundancia entre épocas (Zilio et al., 2014).

Los disturbios causados por eventos climáticos como huracanes también pueden influir sobre la dinámica de las comunidades de aves, particularmente en los consumidores primarios, los cuales disminuyen en abundancia después del paso de huracanes, mientras las aves insectívoras y omnívoras pueden incrementar en abundancia (Wiley and Wunderle, 1993). Para otros grupos funcionales, como las rapaces, se ha reportado que ocurren cambios mínimos en la abundancia de especies particulares de 4-8 meses después del impacto de huracanes (Lynch, 1991; Wauer and Wunderle, 1992). Por ejemplo, en el bosque tropical seco de México, hubo menor densidad de rapaces diurnas en los bosques ubicados en el radio de vientos máximos del Huracán Patricia de 2015 (categoría 4), comparado con los bosques ubicados fuera de esta área (Martínez-Ruiz and Renton, 2018). Por otra parte, la riqueza de especies y equitatividad de las comunidades de rapaces diurnas fue significativamente mayor en los humedales con vegetación de manglar en el área afectada por dicho huracán a 5 meses del disturbio (Martínez-Ruiz and Renton, 2018).

El incremento en la frecuencia e intensidad de disturbios naturales como huracanes durante las últimas décadas (Emanuel, 2005; Webster et al., 2005) resalta la importancia de evaluar la influencia de estos eventos climáticos en la biodiversidad. Asimismo, eventos asociados al cambio climático podría modificar los patrones estacionales de los ecosistemas tropicales secos (Murray-Tortarolo et al., 2017), por lo que es necesario determinar la dinámica espacio-temporal en las comunidades de los bosques tropicales secos, los cuales se encuentran altamente amenazados por presiones antropogénicas (Janzen, 1988; Miles et al., 2006). En particular, se conoce poco acerca de la estacionalidad de las rapaces en los ambientes secos tropicales. En este estudio nuestro objetivo fue evaluar si existe variación estacional en la diversidad de rapaces diurnas del bosque tropical seco de Jalisco, así como determinar si el paso de un huracán de alta intensidad tiene consecuencias a largo plazo (2 años) en la dinámica de los ensambles de rapaces diurnas en el bosque seco.



## MÉTODOS

### *Área de estudio*

El estudio se llevó a cabo en el bosque tropical seco del oeste de México (19° 41'N, 105° 03'W) en el estado de Jalisco. Los bosques tropicales secos se caracterizan por una marcada estacionalidad, presentando en el año una prolongada sequía de entre 4-7 meses (Miles et al., 2006; Mooney et al., 1995) y en donde la precipitación es el principal factor que influye en la fenología y productividad de la vegetación (Martínez-Yrizar et al., 1996). El clima de la región corresponde a la clasificación Aw (caliente subhúmedo con lluvias en verano) con una temperatura media anual de 26°C (García, 2004). La región presenta un marcado patrón estacional en la precipitación, el 86% del promedio anual (770 mm) ocurre durante los meses de junio a octubre en la denominada época húmeda, con una prolongada época seca de noviembre a mayo (Bullock, 1986). El tipo de vegetación predominante es el bosque deciduo, localizado en las partes altas, donde los árboles presentan una copa de hasta 12 m de altura y sotobosque denso (Lott and Atkinson, 2002) y se caracterizan por la pérdida foliar en la época seca (Rzedowski, 2006). Por otra parte, el bosque tropical semideciduo se ubica en los valles húmedos o cañadas desde el nivel del mar hasta los 1000 msnm, donde los árboles presentan mayor talla de hasta 25 m de altura y mantienen el follaje la mayor parte del año (Rzedowski, 2006). Estos dos tipos de vegetación se encuentran de forma continua en el paisaje, pero difieren en composición florística y en su fenología (Lott, 1987; Martínez-Yrizar et al., 1996). Por la costa también se encuentran áreas de humedales con vegetación de manglar, compuesta de árboles bajos de mangle blanco (*Laguncularia racemosa*), mangle rojo (*Rhizophora mangle*) y mangle negro (*Avicennia germinans*) (Durán et al., 2002; Rzedowski, 2006) y en algunos ocurre la presencia de Majagua (*Heliocarpus donnell smithii*). En las tierras privadas y en las regidas por ejidos, el bosque deciduo ha sido removido para la agricultura de cultivos anuales y perennes, y pastizales para ganado (Maass, 1995).

En la costa del Pacífico mexicano se ha registrado que en promedio un huracán toca tierra cada 10 años, aunque estos han sido tormentas de menor categoría (NOAA,

2018). Sin embargo, se ha reportado un incremento en la frecuencia de huracanes en la costa del Pacífico (Blake et al., 2009; Jáuregui E., 2009). Recientemente, en el 2011, el huracán menor Jova (categoría 2 en la escala de Saffir Simpson) tocó tierra en la región de Chamela-Cuixmala por la costa Jalisco, mientras en 2015, el huracán Patricia (categoría 4) tocó tierra en la Reserva de la Biósfera Chamela-Cuixmala (NOAA, 2015). El huracán Patricia provocó severos daños en las áreas urbanas y en los bosques ubicados en el área de vientos máximos (Kimberlain et al., 2016). Ambos huracanes dejaron lluvias atípicas asociadas a su paso en la región (Parker et al., 2018); los efectos más visibles del paso de los huracanes Jova y Patricia en el bosque tropical seco fueron la pérdida de follaje en el dosel, así como la pérdida de árboles y ramas (Martínez-Yrizar et al., 2018; Parker et al., 2018).

#### *Transectos de muestreo*

Determinamos los límites del área afectada por el huracán Patricia con base en la distancia (9.3 km) del radio de vientos máximos del huracán (Kimberlain et al., 2016) y con observaciones en el campo después del paso del huracán Patricia (Martínez-Ruiz and Renton, 2018). A lo largo de 97 km de la costa, seleccionamos 29 transectos de estudio, 13 localizados en el área de paso de vientos máximos del Huracán Patricia, y 16 sitios localizados fuera del rango de los vientos máximos (Martínez-Ruiz and Renton, 2018). Los transectos fueron distribuidos en los hábitats presentes en la región que son de relevancia para las rapaces diurnas: bosque deciduo, bosque semideciduo, humedales y áreas de uso agropecuario.

#### *Muestreo de rapaces diurnas*

Realizamos muestreos de rapaces diurnas (familias Accipitridae, Falconidae y Pandionidae) durante 4 temporadas en el área de estudio (húmeda 2016, seca 2017, húmeda 2017 y seca 2018). En cada uno de los 29 transectos de estudio, se realizó un muestreo de rapaces diurnas para obtener el número de individuos y el número de especies de rapaces en cada transecto. Cada transecto tuvo 1.5 km de longitud y fueron visitados una vez en cada una de las 4 temporadas. Los muestreos se llevaron a cabo

solo en condiciones climáticas favorables, evitando condiciones de lluvia y viento que pudieran influir en la detectabilidad de los individuos (Bibby et al., 2000).

Para estimar la densidad de rapaces diurnas utilizamos muestreo de distancias para transectos lineales (Thomas et al., 2010). Los muestreos comenzaron 60 minutos después del amanecer y tuvieron una duración aproximada de 3.5 horas. Durante el recorrido en el transecto, medimos la distancia del observador a cada ave observada con un range-finder láser (TruePulse 200), así como el ángulo desde la orientación del transecto al ave observada. Dichos datos se usaron para calcular la distancia perpendicular de cada ave respecto a la línea del transecto y poder generar modelos de densidad (Buckland et al., 2001).

Para estimar la riqueza de especies de rapaces diurnas, usamos los datos del número de individuos de las especies detectadas en el transecto de observación y registros adicionales de respuesta a provocaciones auditivas (playback). A lo largo del transecto, establecimos 3 estaciones de provocaciones auditivas, separadas por 750 m entre sí. En cada estación de playback, se reprodujeron dos ciclos de 30 s del llamado de una especie de rapaz, seguido de 40 s de silencio en espera de respuesta. Solo usamos las vocalizaciones pre-grabadas de las especies de rapaces que no se detectaron durante el transecto inicial de observación. Usamos un game-caller marca FOX-PRO modelo Crossfire para reproducir las vocalizaciones pre-grabadas de las rapaces. El reproductor fue orientado en diferentes direcciones alrededor de la estación de provocación auditiva (Barnes et al., 2012). Cuando se obtuvo respuesta vocal de las aves, se suspendió la provocación auditiva para esa especie durante el resto del muestreo.

### *Análisis estadístico*

Evaluamos la variación espacio-temporal en la comunidad de rapaces mediante modelos lineales generalizados mixtos (GLMM), con errores tipo Poisson (adecuados para datos provenientes de conteos) y la función de enlace log para determinar si el número de individuos y número de especies de rapaces diurnas por transecto está influenciado por el hábitat (semideciduo, deciduo, humedal y agropecuario) y la temporada de muestreo

(4 muestreos) o la estacionalidad (época seca y húmeda), así como la interacción de estos dos factores (hábitat\*temporada y hábitat\*estacionalidad). Para los modelos, el hábitat y la temporada o estacionalidad fueron considerados como factores fijos, mientras cada transecto de observación de rapaces fue considerado como factor aleatorio. Además, con el propósito de determinar diferencias significativas entre subgrupos (hábitats, temporadas, épocas), elaboramos modelos anidados al remover factores fijos y aplicamos pruebas post-hoc de comparaciones múltiples por pares utilizando la función “lsmean” (package lsmean; (Lenth, 2016) con ajuste de Tukey-Kramer para obtener los valores de alfa. Consideramos un valor de  $P < 0.05$  como un factor significativo. Los análisis GLMM fueron realizados en R 3.5.1 (R Development Core Team 2017), utilizando la función “glmer” del paquete lme4 (Bates et al., 2015). Se crearon modelos anidados para sitios ubicados dentro y fuera del radio de vientos máximos del huracán Patricia.

Adicionalmente, estimamos la densidad de rapaces en los diferentes hábitats del bosque seco en las 4 temporadas de estudio (húmeda 2016, seca 2017, húmeda 2017, seca 2018) en transectos afectados y no afectados por el Huracán Patricia usando el programa Distance 6.2 (Thomas et al., 2010) para modelar la densidad. Igualmente, se estimó la riqueza de especies de rapaces en los diferentes hábitats y temporadas de estudio mediante rarefacción usando el programa EstimateS 9.1.0 (Colwell, 2013). Determinamos la variación espacio-temporal en densidad y riqueza de rapaces mediante la comparación de los intervalos de confianza al 84% (MacGregor-Fors and Payton, 2013).

Por último, determinamos si hubo variación espacio-temporal en la composición de los ensamblajes de aves rapaces aplicando análisis de similitud ANOSIM (Clarke, 1993) para evaluar si existen diferencias significativas en la similitud de ensamblajes de rapaces en los diferentes hábitats en la época seca y lluviosa y en áreas afectadas y no afectadas por el paso del Huracán Patricia. Usamos los plots de rangos de similitud para evaluar las diferencias intra-grupos de los análisis de similitud cuando fueron significativos. Posteriormente, usamos un agrupamiento jerárquico para representar gráficamente la similitud de los ensamblajes de rapaces diurnas en términos de su composición y abundancia. Usamos las funciones “anosim” y “hclust” de la paquetería vegan de R.

## RESULTADOS

En conjunto, registramos un total de 604 individuos de rapaces diurnas, pertenecientes a 20 especies de las familias Accipitridae, Falconidae y Pandionidae (Tabla 1). Particularmente, en el área no afectada por los vientos máximos del Huracán Patricia se registró un total de 302 individuos, con 176 individuos en la época seca y 126 en la época húmeda. Igualmente, en el área afectada por el Huracán Patricia, se registró un total de 302 individuos, con 187 individuos en la época seca y 115 individuos para la época húmeda (Tabla 1).

### *Variación espacio-temporal en abundancia y densidad de rapaces diurnas*

Los modelos GLMM indicaron influencia significativa de la temporada de muestreo en el número de individuos de rapaces registrados por transecto, tanto en el área fuera del radio de vientos máximos de Huracán Patricia (GLMM temporada:  $X^2_3=8.1$ ,  $P = 0.04$ ), como en el área afectada por el huracán (GLMM temporada:  $X^2_3=14.91$ ,  $P = 0.001$ ). De igual manera, la estacionalidad de época seca y húmeda tuvo influencia significativa sobre la abundancia de rapaces tanto en el área no afectada por vientos máximos del huracán Patricia (GLMM estacionalidad:  $X^2_1=6.62$ ,  $P = 0.01$ ) y en el área afectada por el huracán (GLMM estacionalidad:  $X^2_1=12.9$ ,  $P = 0.0003$ ). En general, hubo mayor número de rapaces registrados en los transectos durante las dos épocas seca de 2017 y 2018 comparada con los muestreos en la época húmeda (Fig 1). En particular, el incremento en registros de rapaces diurnas fue significativo para la temporada seca 2017 comparado con la temporada húmeda 2017 en el área fuera del radio de vientos máximos de Huracán Patricia ( $Z = 2.65$ ,  $P = 0.03$ ), mientras en el área afectada por el huracán la estacionalidad fue más marcada con diferencia significativa entre la época húmeda 2016 y secas 2017 ( $Z = -2.8$ ,  $P = 0.02$ ), y entre la época húmeda 2017 con secas 2018 ( $Z = 3.433$ ,  $P = 0.003$ ). Por otro lado, el hábitat no tuvo influencia significativa en el número de individuos por transecto dentro de cada temporada de muestreo o época del año. Tampoco hubo interacción significativa de hábitat\*temporada, o de hábitat\*estacionalidad sobre el

número de rapaces en los transectos, tanto en el área afectada como no afectada por el huracán.

Sin embargo, al modelar la densidad de rapaces se determinó variación temporal significativa en los hábitat más estacionales del bosque seco, es decir el bosque deciduo y áreas de uso agropecuario, ambos en el área no afectada por el huracán y en el área impactada por el huracán (Fig 2b y 2d). En estos dos hábitat, las estimaciones de densidad tienen intervalos de confianza amplios, aunque en el bosque deciduo fueron menores en la primera temporada de muestreo (Fig 2b), mientras para las áreas agropecuarias fueron menores durante las lluvias de 2016 en el área afectada por el huracán y lluvias de 2017 en el área no afectada (Fig 2d). En general, el bosque deciduo presentó significativamente menor densidad de rapaces durante la primera época húmeda 2016 (Fig 2b), aunque en el área no afectada por el huracán esto solo fue significativamente menor que la estimación de densidad de rapaces en la época húmeda de 2017, cuando se presentó la mayor densidad de rapaces (Fig 2b). Por otra parte, en el área afectada por el huracán, el bosque deciduo (Fig 2b) y los transectos en las áreas de uso agropecuario (Fig 2d) mostraron significativamente menor densidad de rapaces durante la primera época húmeda de 2016, en comparación con las subsecuentes temporadas.

Contrario a esto, los hábitat más húmedos y perennes (bosque semideciduo y los humedales) en el área fuera del radio de vientos máximos del huracán presentaron ligeras fluctuaciones en densidad de rapaces, aunque la variación no fue significativamente distinta entre temporadas (Fig 2a y 2c). Notablemente, el bosque semideciduo impactado por el Huracán Patricia mostró variación estacional significativa en densidad de rapaces con mayor densidad en la época seca comparado con la época húmeda (Fig 2a). De forma similar, los humedales afectados por el huracán presentaron variación temporal, con mayor densidad durante las primeras dos temporadas de muestreo y una marcada declinación en densidad de rapaces en las últimas dos temporadas (Fig 2c). Cabe destacar que en el bosque semideciduo los intervalos de confianza para las estimaciones de densidad fueron más amplios en la época seca en el área afectada por el huracán y en la época húmeda para el área fuera del rango de vientos máximos del huracán (Fig

2a). En cambio, para los humedales hubo mayor variación para las estimaciones de densidad durante las primeras dos temporadas de muestreo comparado con las últimas dos temporadas, cuando las estimaciones de densidad presentaron mayor confianza (Fig 2c).

#### *Variación espacio-temporal en riqueza de rapaces*

Para el número de especies de rapaces diurnas registradas por transecto, los modelos GLMM mostraron una influencia significativa de la temporada de muestreo únicamente en el área afectada por el Huracán Patricia (GLMM:  $X^2_3 = 8.2$ ,  $P = 0.04$ ), mientras que la temporada de muestreo en los transectos fuera del radio de vientos máximos del huracán no fue significativa. Sin embargo, la estacionalidad de época seca y húmeda tuvo una influencia significativa sobre el número de especies de rapaces diurnas registrados en los transecto, tanto fuera del radio de vientos máximos de Huracán Patricia (GLMM:  $X^2_1 = 4.8$ ,  $P = 0.028$ ) como en el área impactada por el huracán (GLMM:  $X^2_1 = 7.3$ ,  $P = 0.006$ ), con mayor número de especies de rapaces durante la época seca (Fig 3). En todos los casos, no hubo un efecto significativo de hábitat, o de la interacción hábitat\*temporada y hábitat\*estacionalidad sobre el número de especies de rapaces registradas en los transectos.

Por otro lado, la estimación de riqueza de especies de rapaces mostró una diferencia significativa entre las cuatro temporadas de muestreo para los humedales (Fig 4c) y áreas de uso agropecuario (Fig 4d), tanto en el área fuera del radio de vientos máximos de Huracán Patricia como en el área impactada por el huracán. En el área afectada por el huracán, los humedales presentaron significativamente mayor riqueza de rapaces en la época seca de 2017 con una subsecuente declinación en riqueza de rapaces en la época húmeda de 2017 (Fig 4c). En las áreas de uso agropecuario hubo un incremento inicial en riqueza de especies en la temporada seca 2017, con una subsecuente declinación en riqueza para los transectos no afectados por el huracán Patricia, mientras que el área impactada por el huracán hubo mayor riqueza de rapaces durante la época seca comparado con la época húmeda (Fig 4d).

El bosque deciduo no mostró variación temporal significativa en riqueza de especies de rapaces, tanto en el área afectada, como no afectada por el huracán Patricia (Figs 4b). En cambio, el bosque semideciduo mostró variación temporal significativa en áreas afectadas y no afectadas por el huracán (Fig 4a). En el área no afectada se observó menor riqueza de rapaces en la época húmeda 2016 comparado con secas 2018 (Fig 4a). A diferencia de esto, en el área afectada por el huracán se observó una marcada declinación en riqueza de rapaces en el bosque semideciduo durante la época húmeda de 2017 comparado con las temporadas anteriores, seguido de un incremento considerable en riqueza para la época seca de 2018 (Fig 4a). En general, las estimaciones de riqueza tuvieron intervalos de confianza mayores durante las primeras dos temporadas de muestreo, demostrando mayor confianza para la estimación de riqueza en el segundo año de estudio (Figs 3a-d).

#### *Composición de especies de rapaces en las épocas seca y húmeda*

El análisis de similitud mostró diferencias significativas en la composición de especies de rapaces diurnas entre los diferentes hábitat del bosque seco en el área no afectada por el Huracán Patricia, tanto en la época seca (ANOSIM  $R=0.476$   $p=0.001$ ) como en la época húmeda (ANOSIM  $R=0.402$ ,  $p=0.007$ ). Asimismo, la agrupación jerárquica mostró que en el área no afectada por el huracán, la mayoría de los transectos de muestreo se agruparon de acuerdo con el hábitat durante la época seca, con agrupación de los bosques semideciduo y deciduo, mientras los humedales quedaron separados de los demás hábitats (Fig 5i). Esto indica que los ensambles de rapaces de los dos tipos de bosque son similares durante la época seca en el área no afectada por el huracán, mientras los humedales tienen una composición de especies más distinta a la del resto de los hábitat muestreados. En la época húmeda para el área no afectada por el huracán, solo se mantuvo la agrupación por hábitat para los humedales (Fig 5ii), mientras que la composición de rapaces fue similar entre el bosque deciduo, el bosque semideciduo y las áreas de uso agropecuario. Por el contrario, en el área afectada por el huracán Patricia, hubo diferencia significativa en la composición de rapaces entre hábitats únicamente durante la época seca (ANOSIM  $R=0.499$ ,  $p=0.001$ ), de nuevo los humedales se



agruparon (Fig 5 iii). En la época húmeda no hubo diferencias entre hábitat en la composición de la comunidad de rapaces (ANOSIM  $R=0.204$ ,  $p=0.08$ ) aunque se mantiene la agrupación de los humedales (Fig 5 iv). Por último, para cada uno de los hábitats, no hubo diferencias en la composición de especies de rapaces entre épocas seca y húmeda, ni en áreas afectadas o no afectadas por el paso del Huracán Patricia.

## DISCUSIÓN

### *La estacionalidad del bosque seco influye en la diversidad de rapaces diurnas*

Nuestros resultados muestran que la estacionalidad del bosque tropical seco influye en la abundancia y riqueza de rapaces diurnas, con mayor diversidad de rapaces diurnas en la época seca. La influencia de la estacionalidad es significativa en transectos dentro y fuera del rango de los vientos máximos del Huracán Patricia. Parte de nuestros resultados concuerdan con lo reportado en otros estudios, donde se ha encontrado variación en la abundancia de rapaces en distintos ecosistemas estacionales de América (Carmona et al., 2017; Hayes, 1991; Jensen et al., 2005; Zilio et al., 2014).

La mayor abundancia y riqueza de especies de rapaces diurnas en la época seca podría atribuirse a una mayor presencia de las especies de rapaces migratorias durante los muestreos en los meses de marzo a mayo (época seca), cuando la mayoría de las rapaces migratorias inician su regreso a los sitios de reproducción en el norte. Por otro lado, los muestreos que realizamos en la época húmeda (agosto-septiembre) coinciden con el inicio de la migración norte-sur de las rapaces migratorias, por lo que pudieran no estar representadas en nuestros muestreos durante estos meses. Esto se ha sugerido en otros estudios, donde el ensamble de rapaces en la temporada seca está definido por la presencia de especies migratorias en pastizales de Argentina (Blendinger et al., 2004). Asimismo, en Marismas Nacionales, en el oeste de México, las especies de rapaces migratorias se encuentran mejor representadas en los muestreos durante los meses de noviembre a febrero, en comparación con otros meses del año que coinciden con la concentración de la precipitación (Carmona et al., 2017). Nosotros encontramos que especies de rapaces migratorias como *Accipiter cooperii*, *Elanus leucurus* y *Falco*

*peregrinus* solo fueron registradas durante la época seca. La variación en densidad de rapaces en los bosques deciduos puede ser una respuesta a la estacionalidad que presentan las comunidades de sus presas en el bosque tropical seco. Diferentes estudios han demostrado que la abundancia de mamíferos (Stoner and Timm, 2011), aves (Almazán-Núñez et al., 2018; Nassar et al., 2014), artrópodos (Hanson, 2011; Pescador-Rubio et al., 2002) y anuros y reptiles (García and Cabrera-Reyes, 2008) presentan fluctuaciones estacionales entre las épocas húmedas y secas en los bosques tropicales secos. Por otra parte, las fluctuaciones en densidad de rapaces en las áreas de uso agropecuario pueden relacionarse al tipo y manejo de cultivos presentes, ya que los cultivos en la región son temporales y esto puede influir en la disponibilidad temporal de presas como aves y roedores. Por otra parte, la riqueza de especies de rapaces no presentó variación temporal, indicando que las rapaces asociadas a los bosques usan este hábitat de forma continua a pesar de las afectaciones por el disturbio.

Nuestros resultados también demostraron que la composición de especies de rapaces diurnas fue distinta entre hábitats, tanto en la época seca como en la época húmeda en el área fuera del rango de vientos máximos del huracán. Sin embargo, en el área afectada por el huracán, solo hubo disimilitud entre hábitats en ensambles de rapaces durante la época seca, mientras para la época húmeda las especies de rapaces fueron similares entre hábitats y solo hubo agrupamiento para los humedales con base en la composición de especies de rapaces. Esto coincide con lo observado por Martínez-Ruiz and Renton (2018), quienes a 5 meses después del Huracán Patricia encontraron mayor similitud en comunidades de rapaces entre hábitats en el área afectada por el huracán, así como mayor equitatividad en humedales afectados por huracán. Nuestros resultados muestran que los efectos del paso de un huracán mayor pueden ser prolongados, con efectos en los ensambles de rapaces hasta dos o tres años después del disturbio.

La similitud en ensambles de rapaces entre diferentes hábitats en el área afectada puede ser causa de una reorganización de las comunidades animales que forman parte de la dieta de las rapaces, como resultado de la llegada a tierra de un huracán mayor (Waide, 1991). Las aves frugívoras, granívoras y nectarívoras disminuyen en abundancia

tras el paso de huracanes, mientras las aves insectívoras podrían incrementar en abundancia (Brown et al., 2011; Johnson and Winker, 2010; Waide, 1991; Wiley and Wunderle, 1993). Asimismo, en cuanto a la herpetofauna, se ha observado que los anuros decrecen en abundancia, mientras los reptiles pueden verse beneficiados (Schriever et al., 2009; Suazo-Ortuño et al., 2018), y los ensambles de anuros y reptiles también presentan cambios en equitatividad después de un huracán (Suazo-Ortuño et al. 2018). Por otro lado, puede haber incrementos y/o reducción en la abundancia de invertebrados (insectos, caracoles) después de disturbios como huracanes (Torres, 1992; Willig and Camilo, 1991). Estos cambios en las comunidades de presas de las rapaces, aunado a las modificaciones al hábitat causadas por el huracán, podrían promover una mayor expansión en las áreas de actividad de las aves rapaces en búsqueda de recursos alimenticios (Martínez-Ruiz y Renton 2018). Esto podría ser aún mayor en la época húmeda en la región, la cual coincide con el fin de la temporada reproductiva de al menos 8 especies de rapaces residentes (Whitacre, 2017), permitiendo a las rapaces desplazarse en áreas más grandes y resultando en mayor similitud en la composición de rapaces diurnas entre hábitats durante la época húmeda.

#### *Influencia del huracán sobre la variación espacio-temporal de rapaces*

Nuestros resultados indican que el paso de un huracán mayor puede alterar la dinámica espacio-temporal en los ensambles de rapaces. Los bosques deciduos y áreas de uso agropecuario afectados por el huracán presentaron menor densidad de rapaces en la primera temporada de muestreo en este estudio (húmeda 2016), con un incremento significativo en densidad en temporadas subsecuentes. Debido a los daños estructurales del bosque deciduo (Parker et al., 2018) y de áreas de cultivo (Martínez-Ruiz and Renton, 2018) a causa de los vientos asociados al huracán Patricia y a los cambios reportados en la abundancia de algunas presas (Mason-Romo et al., 2018; Suazo-Ortuño et al., 2018), se sugiere que las rapaces diurnas usaron hábitats alternos ubicados dentro o fuera del área afectada en el año después del paso del huracán. El amplio margen de error en las estimaciones de densidad puede deberse a cambios en la distribución espacial de los individuos que podrían estar posicionados en recursos agregados en los

bosques deciduos afectados por el huracán y usando hábitat alternos, sugiriendo movimientos de las rapaces entre épocas en éstos hábitat.

El estudio previo de Martínez-Ruiz y Renton (2018) mostró la influencia del paso del Huracán Patricia en la comunidad de rapaces diurnas a 5 meses del disturbio, donde el bosque deciduo afectado por el huracán tuvo menor densidad de rapaces comparado con el bosque deciduo no afectado por el disturbio. La variación temporal durante dos años en densidad de rapaces en los bosques afectados por el huracán sugiere que la influencia de este tiene un efecto prolongado de al menos 2 años sobre las rapaces. La influencia del Huracán Patricia se ve reflejada en la variación temporal y estacional de la densidad de rapaces en los hábitats más húmedos y perennes del bosque tropical seco en el área afectada por el huracán. La variación temporal en densidad de rapaces en humedales afectados se detectó hasta 18 meses del paso del huracán con una subsecuente declinación en densidad, y esto coincide con lo observado en el estudio previo donde la riqueza de rapaces en humedales fue significativamente mayor en las áreas afectadas por el Huracán Patricia (Martínez-Ruiz and Renton, 2018). Los autores sugieren que distintas especies de rapaces habrían usado los humedales como hábitat alternativo tras el disturbio (Martínez-Ruiz and Renton, 2018). Esto podría relacionarse con la menor estabilidad en la estimación de densidad (reflejada en la amplitud de los intervalos de confianza) en los humedales durante los primeros 18 meses tras el impacto del huracán, y menor variación en las estimaciones a 2 años del paso del huracán. Esto reafirmaría el uso temporal de humedales como hábitat refugio para las rapaces, de acuerdo con lo sugerido por Martínez-Ruiz y Renton (2018).

En cambio, la variación temporal significativa en densidad y riqueza de rapaces en el bosque semideciduo dentro del área afectada por el huracán podría relacionarse al mayor impacto que tienen los vientos de huracán en los bosques maduros con árboles grandes y altos, que son más susceptibles a daños por vientos asociados a los huracanes (Reilly, 1991; Walker, 1991). En el área de estudio, se reportó que la estructura del dosel del bosque cambió radicalmente tras el paso del huracán Patricia en 2015 (Parker et al., 2018). La densidad y riqueza de rapaces diurnas decrece en el tiempo en el bosque semideciduo dentro del área de vientos máximos del huracán Patricia, y la densidad es

particularmente menor en época lluviosa a dos años después del paso del huracán Patricia. Esto puede estar relacionado con la baja resiliencia en la fenología del bosque semideciduo ante el paso de huracanes, lo cual puede provocar efectos en cascada para algunas especies animales (Renton et al., 2018). Tanto las modificaciones estructurales al hábitat, como la modificación de los patrones de fenología y la consecuente modificación en disponibilidad de recursos podrían influir en una menor densidad y riqueza de rapaces en el bosque semideciduo a dos años después del paso del huracán Patricia. Por otra parte, dada la capacidad que tienen las rapaces para desplazarse en grandes áreas, estas aves pueden aprovechar hábitats alternos de alta resiliencia ante disturbios, como los humedales (Martínez-Ruiz and Renton, 2018) o el bosque deciduo, el cual muestra mayor resiliencia en la fenología ante disturbios de huracanes comparado con el bosque semideciduo (Renton et al., 2018). Esto explicaría el incremento en densidad de rapaces en el bosque deciduo cuando la densidad y riqueza fue menor en el bosque semideciduo. Es posible que la baja producción de hojarasca en el bosque seco tras el paso de Huracán Patricia (Martínez-Yrizar et al., 2018) genere un incremento en la detectabilidad de algunas presas para las aves rapaces. Se sugiere que varias especies de rapaces persisten después de los disturbios debido a un incremento potencial en la detectabilidad de presas pequeñas en áreas modificadas por daños de huracanes (Wiley and Wunderle, 1993).

Nuestros resultados muestran que la diversidad de rapaces diurnas es influenciada por la estacionalidad del bosque tropical seco. La ocurrencia de eventos climáticos extremos podría acentuar el efecto de la estacionalidad al provocar cambios en los ensambles de rapaces a través de la modificación del hábitat y de los cambios en las comunidades de presas de las rapaces diurnas. La estabilidad en riqueza de rapaces diurnas sugiere que las especies son resilientes a los cambios en el bosque seco, pero con variación en densidad, la cual se ve influenciada a largo plazo por el paso de un evento climático extremo.

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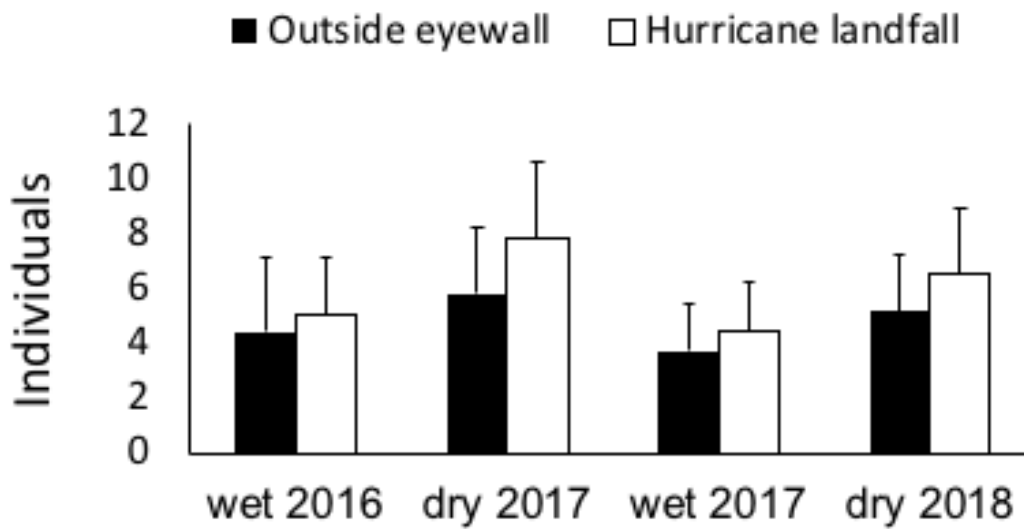
**Tabla 1.-** Número de individuos de las especies de rapaces diurnas registradas en la época de secas y húmedas y en transectos ubicados fuera y dentro del rango de vientos máximos del Huracán Patricia. \* Indica especies migratorias.

Species	Common name	Number of individuals			
		Outside eyewall		Hurricane landfall	
		Wet	Dry	Wet	Dry
<b>ACCIPITRIDAE</b>					
<i>Accipiter cooperii</i> *	Cooper's hawk	0	1	0	0
<i>Accipiter striatus</i> *	Sharp-shinned Hawk	0	1	1	4
<i>Buteo albonotatus</i> *	Zone-tailed hawk	3	2	2	3
<i>Buteo brachyurus</i>	Short-tailed hawk	4	4	4	1
<i>Buteo jamaicensis</i>	Red-tailed hawk	0	1	0	4
<i>Buteo plagiatus</i>	Gray Hawk	27	44	30	47
<i>Buteogallus anthracinus</i>	Common Black Hawk	3	5	4	7
<i>Buteogallus urubitinga</i>	Great Black-Hawk	6	10	1	10
<i>Chondrohierax uncinatus</i>	Hook-billed Kite	1	2	4	1
<i>Elanus leucurus</i>	White-tailed Kite	1	0	0	0
<i>Geranospiza caerulescens</i>	<u>Crane Hawk</u>	2	4	10	15
<i>Geranoaetus albicaudatus</i> *	White-tailed Hawk	0	2	0	0
<i>Rupornis magnirostris</i>	<u>Roadside hawk</u>	30	35	17	19
<b>FALCONIDAE</b>					
<i>Falco peregrinus</i> *	Peregrine Falcon	0	1	0	3

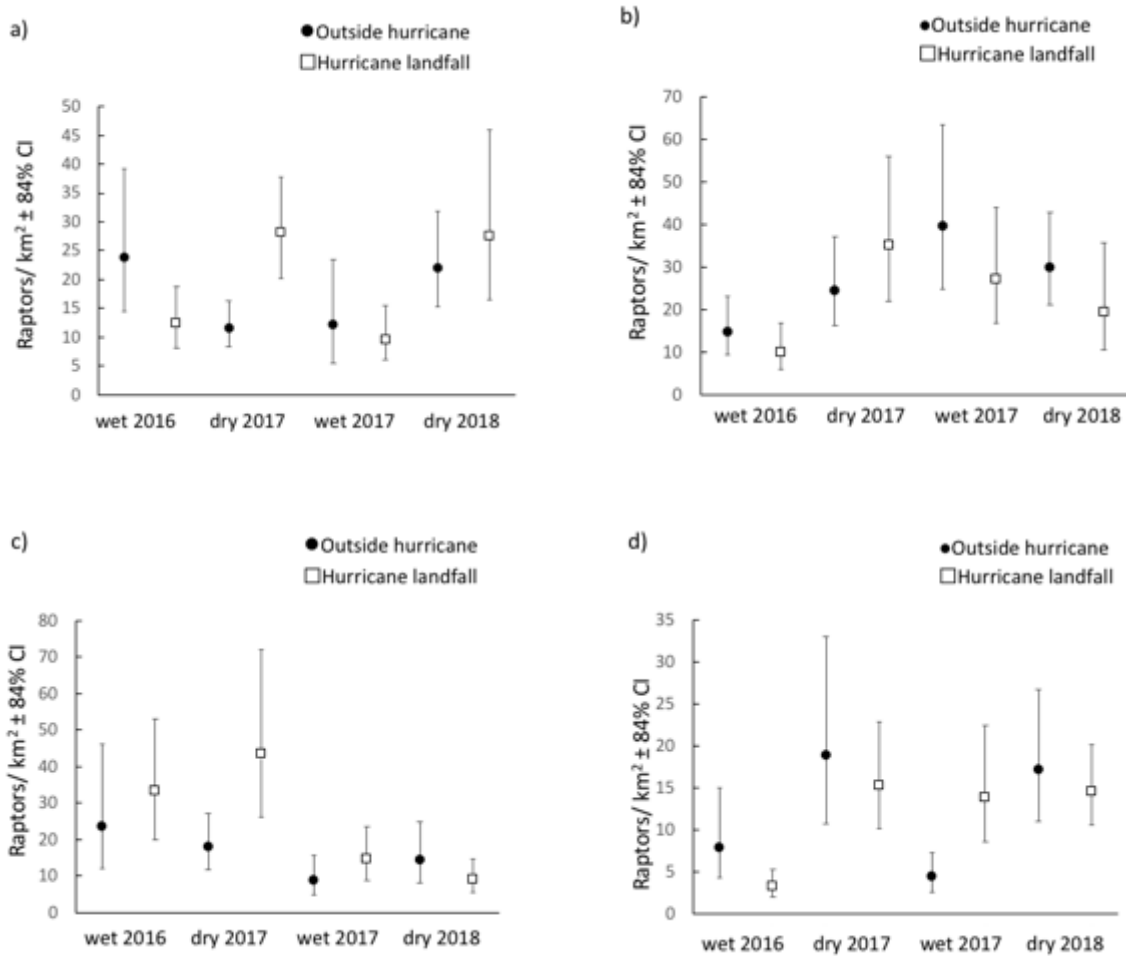
<i>Falco ruficularis</i>	Bat Falcon	4	11	1	11
<i>Falco sparverius</i> *	American Kestrel	1	4	0	2
<i>Caracara cheriway</i>	Crested Caracara	9	25	7	10
<i>Herpetotheres cachinnans</i>	Laughing falcon	10	5	8	13
<i>Micrastur semitorquatus</i>	Collared Forest- Falcon	23	17	21	31
PANDIONIDAE					
<i>Pandion haliaetus</i> *	Osprey	2	2	5	6

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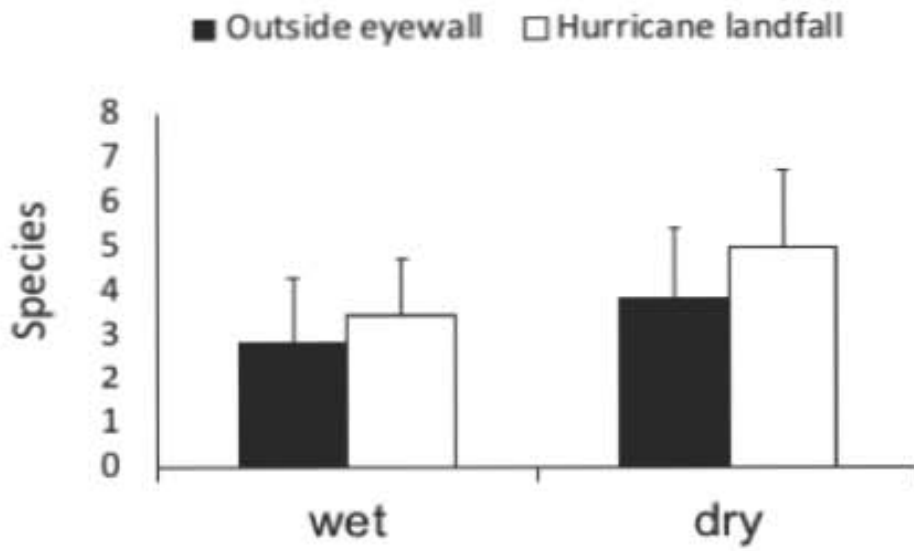
**Figura 1.** Promedio (+SD) de individuos de rapaces diurnas registradas por transecto en el área fuera del radio de vientos máximos del huracán Patricia y en el área afectada por Patricia.



**Figura 2.** Variación temporal en la densidad (84% IC) estimada de rapaces diurnas en los hábitat de a) bosque semi-deciduo, b) bosque deciduo, c) humedales y d) área de uso agropecuario en el área fuera del radio de vientos máximos de Huracán Patricia (círculos negros) y en el área afectada por el huracán (cuadros blancos) por la costa de Jalisco.

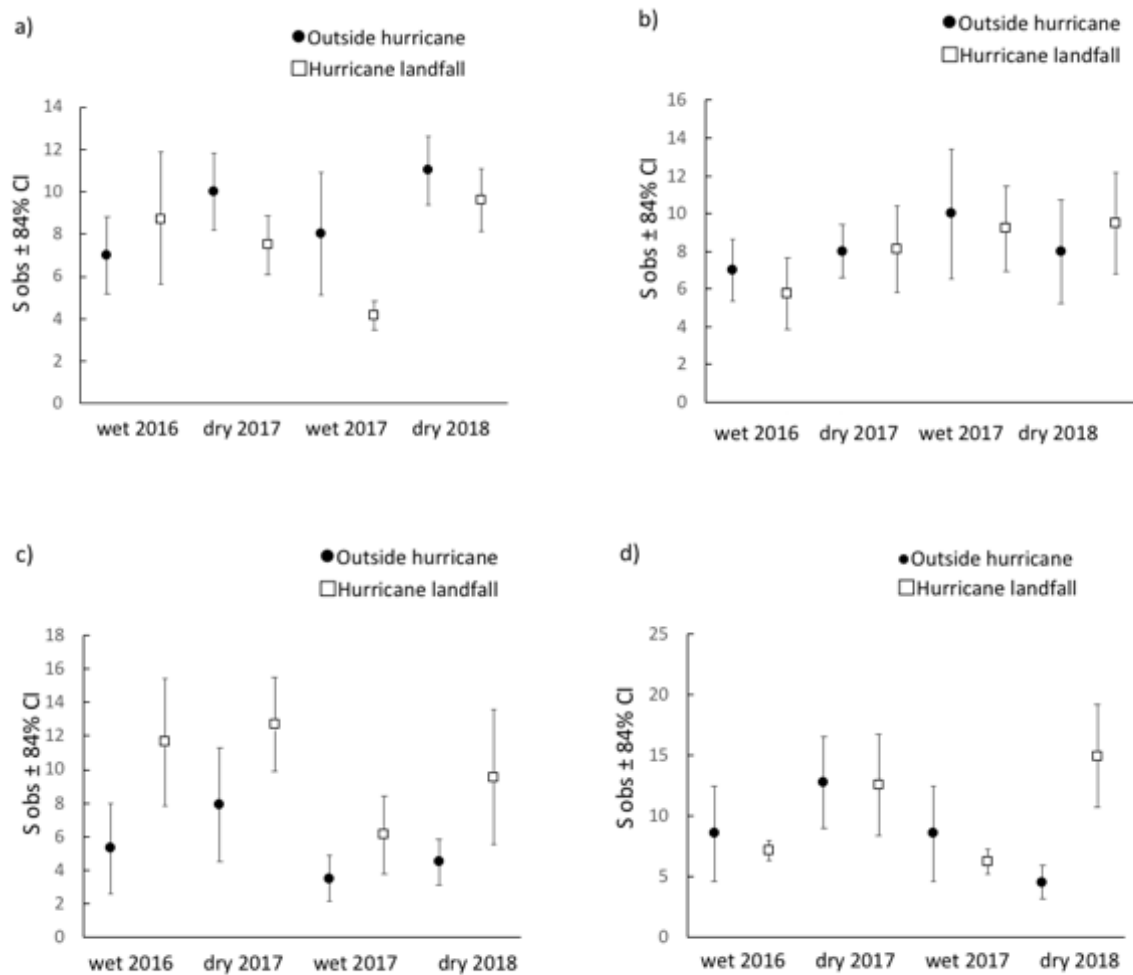


**Figura 3.** Promedio (+SD) del número de especies de rapaces por transecto registrados en la época lluviosa y seca, en el área dentro y fuera del radio de vientos máximos del Huracán Patricia.

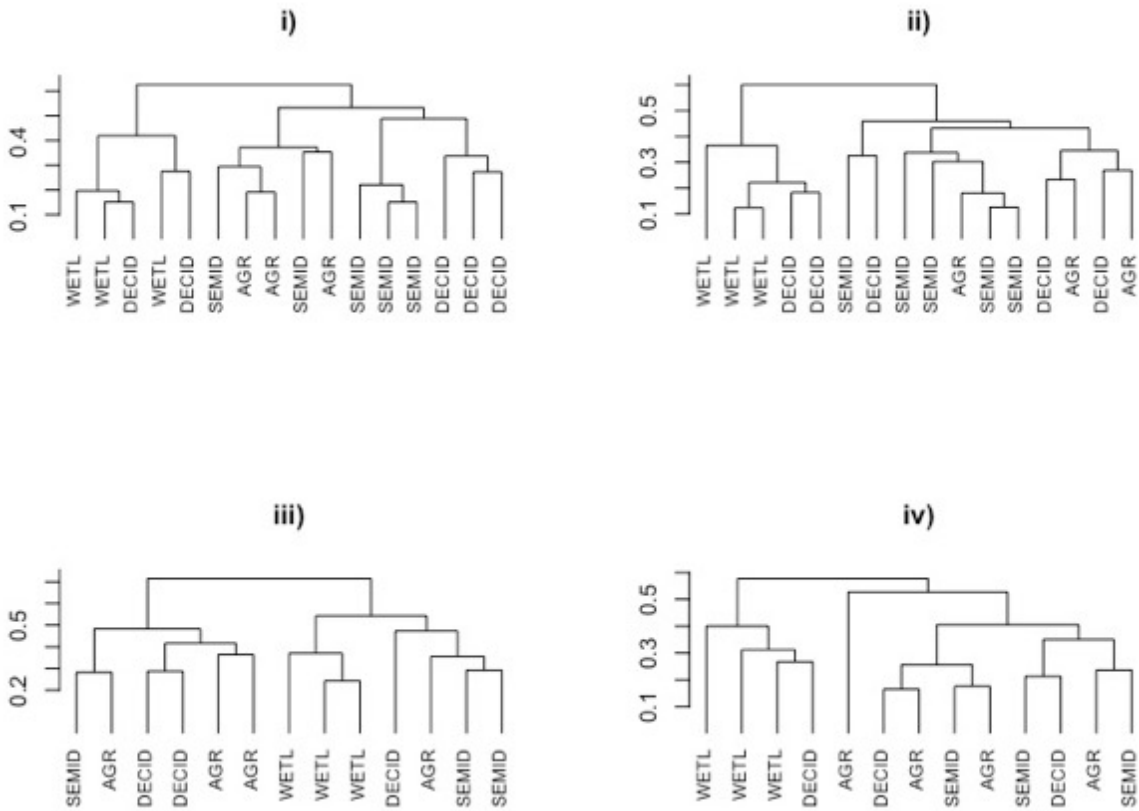




**Figura 4.** Variación temporal en riqueza estimada (IC 84%) de especies de rapaces diurnas en los hábitat de a) bosque semideciduo, b) bosque deciduo, c) humedales y d) uso agropecuario en el área fuera del radio de vientos máximos de Huracán Patricia (círculos negros) y en el área afectada por el huracán (cuadros blancos) por la costa de Jalisco.



**Figura 5.** Agrupación jerárquica de los ensambles de rapaces diurnas en los distintos hábitat del bosque seco, en el área no afectada por el huracán durante i) la época seca y ii) la época húmeda, y en el área afectada por huracán durante iii) la época seca y iv) la época húmeda. Abreviaciones: AGR= agrícola, DECID=Deciduo, SEMID=semi-deciduo, WETL=wetland.



**CAPÍTULO III. PATTERNS AND DRIVERS OF THE SCALE OF LANDSCAPE  
EFFECT ON DIURNAL RAPTORS IN A FRAGMENTED TROPICAL DRY FOREST**

(en revisión *Landscape Ecology*)

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**Patterns and drivers of the scale of landscape effect on diurnal raptors in a fragmented tropical dry forest**

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## **Abstract**

*Context* Theoretical models propose that the spatial extent at which landscape structure best predicts community responses depends on species traits, landscape metrics, and response variables, but empirical support for this is scarce.

*Objectives* We tested for differences in scale of effect (SoE) among ecological traits of diurnal raptors, landscape metrics, and response variables.

*Methods* We conducted 1.5 km transect surveys to determine individual abundance, species richness and temporal beta diversity of raptors at 26 sites in the tropical dry forest biome of western Mexico. We measured landscape metrics of forest cover, matrix hardness, forest patch density, and edge density in 16 concentric landscapes of 400 to 3400 ha around each survey site. We then assessed the landscape size at which each landscape metric best predicted each response variable (SoE), and applied ANOVA to test for differences in SoE among raptor ecological groups, landscape metrics, and response variables.

*Results* SoE differed significantly among landscape metrics, being higher for forest cover than matrix hardness and edge density. Both forest cover and matrix hardness decreased with increasing landscape size, where forest cover best predicted raptor responses at mean 2800 ha landscape, and matrix hardness at 800 ha. On the other hand, SoE did not differ significantly among species traits or response variables.

*Conclusions* SoE was mainly driven by spatial metrics, with diurnal raptors being more strongly associated with forest cover measured over larger scales. This supports findings for other taxa and suggests that forest cover influences dispersal success across larger scales.

**Keywords:** Chamela-Cuixmala Biosphere Reserve · Multiscale approach · Scale of response · Scale dependency · Species traits · Tropical raptors

## Introduction

In recent decades, an increasing number of studies have demonstrated the key role played by landscape structure in shaping biotic populations and assemblages (Fahrig 2003; Galán-Acedo et al. 2019). However, such a role cannot be detected if landscape metrics are measured at suboptimal scales, within too small or too large spatial extents (Fahrig 2013). Therefore, landscape metrics need to be measured across several spatial scales to identify the scale that yields the strongest species-landscape relationship (Jackson and Fahrig 2012, 2015), the so-called scale of effect (SoE). Identifying the SoE is not merely a methodological protocol in landscape studies, but it can provide key information on the way species perceive and use territory (Suárez-Castro et al. 2018; Moraga et al. 2019; San-José et al. 2019). In fact, SoE reflects the spatial extent at which ecological patterns, processes and mechanisms that drive a given response variable operate (Miguet et al. 2016) thereby informing as to the spatial scale that is relevant for the ecological phenomenon under study. In this context, several hypotheses have been proposed as to how the SoE may be influenced by species traits, response variables, and landscape metrics (Miguet et al. 2016; Martin 2018a), but there is still scarce empirical support for such hypotheses.

Miguet et al. (2016) propose that SoE should depend strongly on species traits, especially on those associated with individual mobility, such as dispersal distance and home range size. In particular, the SoE should be higher in more mobile species because they are expected to use resources over larger spatial scales, and thus, they should be influenced by landscape metrics measured across larger scales (Miguet et al. 2016). Regarding landscape metrics, the SoE should be larger for landscape predictors influencing dispersal success (habitat cover, matrix quality) than for predictors such as edge density, and fragmentation that may influence foraging efficiency and breeding resource availability (Miguet et al. 2016). Following a similar rationale, ecological responses that are influenced by long-distance dispersal, such as species richness, should have a larger SoE than responses (e.g. abundance of individuals) that are more nearly affected by local processes such as fecundity and survival over shorter temporal scales (Miguet et al. 2016).

Unfortunately, the few empirical tests of these predictions are not conclusive (Gestich et al. 2010; Galán-Acedo et al. 2018; Martin 2018a, b; San-José et al. 2019), so additional studies are needed to better understand the way species interact with landscape features across different spatial scales. This information is particularly valuable for raptors (birds of prey), not only because of their key ecological role in ecosystems, but also because of their delicate conservation status.

Among birds, raptors are considered as indicators of environmental health because they are sensitive to anthropogenic disturbance due to their position as top-predators in the trophic chain (Newton 1979; Donázar et al. 2016), and they provide important ecosystem services (O'Bryan et al. 2018). Tropical regions contain the majority of raptor species (Mindell et al. 2018), and tropical forest raptors are more likely to be threatened with extinction and have declining populations than non-tropical species (McClure et al. 2018). Despite the importance of this avian group, there is a lack of knowledge on how landscape structure influences raptors. Some studies have addressed the influence of particular landscape features on raptors by assessing more than one spatial scale in Europe (Sánchez-Zapata and Calvo 1999), Africa (Anadón et al. 2010), and North America (Wright et al. 1997; Finn et al. 2002). However, to our knowledge, the influence of landscape structure on raptor communities in tropical forests has never been investigated.

Here we assessed the SoE of landscape structure on diurnal raptors in a tropical dry forest of western Mexico. Particularly, we assessed the spatial scale at which landscape metrics best-predicted ecological responses of raptors, separately assessing raptors grouped by ecological traits of habitat and dietary specialization. Following Miguet et al. (2016), we expected that SoE would be higher for habitat amount (landscape forest cover) and matrix hardness than for landscape metrics associated with habitat fragmentation (patch density, and edge density). Regarding ecological responses, we expected a smaller SoE for individual abundance than for species richness and temporal species turnover (i.e. temporal variation in species composition within a given site). Finally, regarding species' ecological traits, variation in SoE with habitat or dietary specialization would depend on whether specialists disperse farther than generalists or the opposite (Miguet et al. 2016).

## Methods

### Study area

We conducted the study in and around the Chamela-Cuixmala Biosphere Reserve within the tropical dry forest biome along the coast of Jalisco, Mexico (Fig. 1). The climate in the region is warm, with a mean annual temperature of 26 °C (García 2004), and annual rainfall averaging 788 mm, the majority of which occurs during the rainy season (June to October), with an extended dry season from November to May (Bullock 1986). Vegetation is primarily deciduous forest, located mainly on the hills, and is characterized by a canopy height of 8-12 m and loss of leaf cover for 5-8 months in the dry season (Lott and Atkinson 2002; Rzedowski 2006). Discontinuous patches of semi-deciduous forest occur in humid valleys from sea-level to 1000 m asl, and have large, tall trees with a canopy height of 15-30 m, where the majority of trees maintain their foliage through most of the year (Rzedowski 2006). Wetlands with mangrove vegetation also occur along the coast. In some low-lying areas, tropical dry forest has been converted to agricultural systems and cattle pastures (Maass 1995).

### Study sites and raptor surveys

We selected 26 survey sites along the coast of Jalisco (Fig. 1), distributed in 4 different land cover types (habitats): semideciduous forest (7 survey sites), deciduous forest (6 survey sites), agricultural land (7 survey sites), and wetlands (6 survey sites). In each of the 26 sites, we established a 1.5 km length transect to survey the community of diurnal raptors (Accipitridae, Falconidae). We conducted surveys over four periods, corresponding to the dry (March-April) and wet (August-September) seasons of 2017 and 2018. We used a combination of line-transect observations and playback methods to estimate abundance and richness of raptors in each of the four habitats along the coast (Fuller and Mosher 1987; Bibby et al. 2000). Further details of raptor survey techniques can be found in Martínez-Ruiz and Renton (2018).



## Response variables

We recorded 19 species of diurnal raptors, which were grouped according to habitat and dietary specialization (Table S1). Habitat specialization included three categories: (i) forest raptors (species associated with broad extensions of deciduous or semideciduous forest, and to specific resources from old-growth forests); (ii) forest-edge raptors (species that require forest cover but that use and are frequently found at forest edges); and (iii) open-area raptors (species associated with open-habitats, like agricultural fields). Dietary specialization also included three categories: (i) specialist raptors (species that concentrate the diet on one or two taxa); (ii) mid-generalists raptors (species that fed on 3-4 taxa); and (iii) generalists raptors (species that consume  $\geq 5$  taxa). Such classifications were based on available literature (del Hoyo et al. 1994; Ferguson-Lees and Christie 2005; Clark and Schmitt 2017; Whitacre 2017).

For each group and for the entire raptor community, we evaluated three response variables: (i) individual abundance (average number of individuals observed per transect over the 4 survey periods); (ii) species richness (accumulated number of species per transect over the entire survey period); and (iii) temporal beta diversity (Whittaker index,  $\beta_w = \gamma/\bar{\alpha}$ , where  $\gamma$  is the accumulated number of species per transect, and  $\bar{\alpha}$  is the mean number of species per survey period). We measured the latter response as a proxy of temporal dynamics of communities, which may be shaped by temporal changes in resource availability and landscape connectivity.

## Landscape metrics

We used a site-landscape approach (sensu Fahrig 2013) where the response variables described above were recorded at the site scale, but landscape structure was measured within 16 concentric buffers (landscapes) at 200 ha intervals from 400 ha (1128 m radii) to 3200 ha (3289 m radii) at each survey site (Fig. 1). To obtain landscape metrics, we first used Spring 5.2.2 (Câmara et al. 1996) to develop a land cover map from a high resolution (10 m) satellite image (Sentinel 2 A) taken in the dry season (March) of 2016. We defined eight land-cover types: water, crops, pastures, tropical deciduous forest, tropical semi-deciduous forest, wetlands with

mangrove vegetation, beach with bare sand, and human settlements. The accuracy assessment of the map followed the procedure proposed by Olofsson et al. (2014), where the certainty level was 80% with errors derived mainly from faults in the differentiation between crops and pastureland, and between tropical deciduous and semi-deciduous forest. We used the Patch Analyst extension of ArcGis 10.5 to calculate four landscape metrics within each buffer that are widely assessed in landscape studies, and that can be of critical relevance for different taxa (Gestich et al. 2010; Sánchez-de-Jesús et al. 2016; Galán-Acedo et al. 2018; Arce-Peña et al. 2019; San-José et al. 2019) including birds (Carrara et al. 2015). In particular, we measured landscape forest cover as the percentage of the landscape covered by forest (semi-deciduous + deciduous). Also, we calculated forest patch density as the number of forest patches in the landscape divided by landscape area because this is a typical measure of habitat fragmentation (Fahrig 2017). We also estimated forest edge density as the total perimeter length of all forest patches within the landscape divided by landscape area (m/ha). This spatial metric depends strongly on shape complexity of all forest patches in the landscape. Finally, following previous landscape studies (San-José et al. 2019), we measured matrix hardness as the proportion of non-forest land covers in the matrix (cattle pastures, urban settlements and bare ground), as these land cover types show highest contrast to native forest cover. Matrix hardness was calculated considering the area covered by all land covers in the matrix, and not by total landscape area, to make the metric independent of forest cover (Garmendia et al. 2013).

### *Data analyses*

We used the *ape* package (Paradis et al. 2004) and *letsR* package (Vilela and Villalobos 2018) for R (R Development Core Team 2017) to compute correlogram plots based on Moran's Index to test for spatial independence of our samples. We only found significant spatial autocorrelation in 18 of 84 (21%) of our models. Nevertheless, these autocorrelations showed very small Moran's Index values (<0.17, in all cases; Table S2), suggesting that they could be spurious correlations

(Fortin et al. 2002). Therefore, we considered all survey sites as independent samples in subsequent analyses.

To assess the SoE, we used generalized linear models (GLM) to quantify the relationship between each landscape metric (forest cover, patch density, edge density, matrix hardness) and each response variable (abundance, richness, turnover) at each scale. Then, following Fahrig (2013) we plotted the percent deviance explained by the models (a measure of goodness-of-fit of the models) as a dependent variable against landscape size to identify the spatial extent that yields the best-fitted associations (i.e. those associated with a smaller error) between each response and predictor.

We estimated 108 SoE values (3 response variables x 4 landscape metrics x 3 dietary specialization groups x 3 habitat specialization groups). Then, after verifying that residuals followed a normal distribution (Shapiro-Wilk  $W = 0.971$ ,  $p = 0.104$ ), we applied three-way ANOVA to determine whether SoE differed among landscape metrics, ecological responses, and ecological traits of raptors (San-José et al. 2019). All analyses were conducted using the R statistical software (R Development Core Team 2017).

## Results

### Differences in landscape structure across scales

Most landscape structure metrics gradually changed across scales. In particular, both mean forest cover (Fig. 2a) and mean matrix hardness (Fig. 2b) decreased with increasing landscape size. Regarding landscape configuration, forest edge density did not differ among landscape sizes (Fig. 2c), but mean patch density decreased with increasing landscape size, especially in landscapes > 2400 ha (Fig 2d).

### Scale of landscape effect on diurnal raptors

During our two-year survey, we recorded a total of 558 individuals of 19 species of diurnal raptors from the families Accipitridae and Falconidae (Table S1). Based on the percent deviance explained by the models, mean SoE for the entire raptor community was 1633.3 ha (95%CI = 773.4 - 2493.2 ha), although this varied for

raptor communities grouped by ecological traits. In particular, forest-specialist raptors had large SoE values either above 2600 ha or between 600 ha to 1400 ha (Supplementary material Fig S1). By comparison, most SoE for forest-edge and open-area raptors tended to be smaller (400- to 800-ha landscapes), except for edge density where SoE was higher (1400-2000 ha; Fig. S1). Interestingly, species with a specialized diet showed a very high variation in SoE, ranging from 400 ha to 3400 ha (Fig. S1). Similarly, when considering dietary generalists, SoE occurred at either the smallest (400 ha) or the largest (3400 ha) landscapes (6 out of 24 relationships tested; Fig S1), suggesting that the true SoE of landscape structure on dietary specialists and generalists raptors may fall outside the range of landscape sizes considered in the present study. Despite this, we found no significant differences in SoE among ecological traits of raptors ( $F_{(5,61)} = 0.89$ ,  $p = 0.49$ ; Fig. 3a, 3b).

On the other hand, SoE differed significantly among landscape metrics ( $F_{(3,61)} = 3.4$ ,  $p = 0.022$ ). In particular, forest cover had a significantly higher mean SoE of  $2433.3 \pm 1056.6$  ha (95% CI = 1869.9 – 2996.6 ha) compared to the matrix hardness with a mean SoE of  $1500 \pm 880.8$  ha (95% CI = 781.6 – 2218.3 ha), while edge density and patch density had intermediate values (Fig. 3c). Finally, SoE did not differ among ecological responses ( $F_{(2,61)} = 0.33$ ,  $p = 0.72$ ; Fig. 3d).

## Discussion

To our knowledge, this is the first study to assess the spatial extent that best predicts the response of diurnal raptors to different landscape structure metrics. Our findings revealed that the mean scale of landscape effect (SoE) of diurnal raptors was 1633 ha (landscapes of 2279-m radius). Most SoE values fell within the range of landscape sizes considered in this study, suggesting that raptor-landscape relationships were adequately estimated (Jackson and Fahrig 2015). As expected, SoE varied with landscape metric, being higher for forest cover than for matrix hardness and edge density. Yet, contrary to expectations, SoE did not differ among ecological groups or response variables. These results highlight the need for a multiscale approach when evaluating raptor responses to different spatial metrics.

Below we discuss these findings in the light of previous theoretical and empirical studies.

Our findings point out that the scale of landscape effect mainly depends on spatial metrics. This is consistent with previous studies on the topic (Galán-Acedo et al. 2018; San-José et al. 2019). In particular, diurnal raptors are affected by forest cover measured over larger scales, whereas responses to matrix hardness and edge density were more evident when measuring these metrics at smaller scales. This supports theoretical models (Miguet et al. 2016) and previous empirical studies on birds (Smith et al. 2011), and suggests that forest cover may influence dispersal success across larger scales, whereas matrix hardness and edge density are probably related to local-scale processes such as edge effects (Miguet et al. 2016). Some studies on birds have demonstrated that forest cover in the landscape increased forest bird movements (Bélisle et al. 2001), and individual birds chose transience paths and settlement areas with greater forest cover during the dispersal process (Cox and Kesler 2012). Moreover, forest-raptors species rarely cross large-expanses of open landscapes, which may indicate a reduced dispersal capacity when forest cover is low (Thiollay 1989b), particularly for those species that do not soar (e.g. Collared Forest-falcon, Hook-billed Kite, Crane Hawk). Additionally, raptors are prone to human persecution, some species being particularly vulnerable because they are considered agricultural pests (Thiollay 1989a; Sarasola et al. 2018). In this sense, we believe that forest cover in the landscape should most strongly influence dispersal success for raptors by reducing mortality of individuals during the dispersal process.

On the other hand, matrix hardness and edge density are probably related to local-scale processes such as edge effects. Many diurnal raptor species (e.g. the Hook-billed Kite, Crane Hawk, Great Black Hawk, Laughing Falcon, and Collared Forest-falcon) use large emergent trees for perching and nesting (Gerhardt et al. 2013; Parker et al. 2013; Sutter 2013; Thorstrom 2013; Whitacre and Vásquez 2013). Therefore, local edge effects such as the increased mortality of emergent trees (Laurance et al. 2000) may be stronger when the matrix is composed of treeless areas (Mesquita et al. 1999). The fact that raptors were more strongly

related to matrix hardness when measured across smaller spatial extents indicates that this landscape variable drives raptor communities through its impact on local processes such as feeding and reproductive success.

Surprisingly, we found no significant differences in SoE among response variables. Miguet et al. (2016) propose that the number of individuals should be related to spatial features of relatively smaller landscapes because this response is associated with local patterns (e.g. resource availability) and processes (e.g. fecundity and survival). In contrast, species richness and temporal changes in species composition (temporal beta diversity) should depend more on the structure of relatively larger landscapes because these responses are expected to be shaped by long-distance dispersal. Previous studies support these predictions (Cushman and McGarigal 2004; Jackson and Fahrig 2014; San-José et al. 2019). The lack of differences in SoE among ecological responses found in the present study suggests that in this avian group the abundance of individuals, species richness, and temporal species turnover are all influenced by forces acting over similar spatial and temporal scales; a finding probably associated with the relatively high mobility of raptors compared to other avian groups. Other studies have also found no differences in SoE among ecological patterns (Galán-Acedo et al. 2018), most probably because the number of individuals not only depends on local patterns, but it can also be related to long-distance dispersal (Kareiva and Wennergren 1995; Fahrig 2001; Lindenmayer and Fischer 2006). Similarly, species richness and temporal beta diversity not only depend on large-scale processes, but they can also be affected by local patterns and processes, such as intra- and inter-specific interactions (Morin 2011). In fact, temporal beta diversity (calculated using Whittaker's index) is given by the association between total (gamma) diversity and local (alfa) diversity (Halffter and Moreno 2005), so it is reasonable to expect that it is shaped by processes across different spatial scales.

Although we did not detect significant differences in SoE among ecological traits of raptors, we observed a differing pattern of SoE of landscape structure on diurnal raptors when raptor species were grouped by ecological traits of habitat or dietary specialization. In particular, forest raptors had strongest relationships of

ecological responses to landscape structure at larger spatial scales compared to forest-edge or open-area raptors that may represent a lesser degree of habitat specialization. Forest raptors probably have larger SoE because they need to move over larger areas to include sufficient forest habitat within their home ranges. Some raptor species have larger home ranges (Tella et al. 1998; Glenn et al. 2004; Forsman et al. 2005) and territories (Martínez-Ruiz et al. 2016) in landscapes with lower forest cover. Other bird species have also been observed to increase territory size or home range in fragmented habitats so as to include more of the optimal or preferred habitat (Wiens et al. 1985; Rolstad 1991). This would support the hypothesis that SoE should be higher in more mobile species that need to use available resources over larger spatial scales (Miguet et al. 2016). Among the drivers of SoE, dispersal distance has been proposed as the main determinant of the SoE (Jackson and Fahrig 2012). Simulation studies support this idea (Jackson and Fahrig 2012; Ricci et al. 2013), but dispersal estimates are rare in the literature which makes it difficult to make further suggestions.

The high mobility of raptors may also explain why we did not detect significant differences in SoE among species with different habitat specialization. Most raptor species have large home ranges and often exhibit large dispersal distances (Newton 1979). For example, mean natal dispersal distances for American kestrels is ~8 km (Miller and Smallwood 1997), and ~6.4 km and 23.4 km for Crested Caracara (male and female individuals, respectively; Nemeth and Morrison 2002). According to Jackson and Fahrig (2012), the SoE should be at least 4 times the dispersal distance for individuals, thus suggesting that further studies need to incorporate a wider range of spatial scales in order to properly evaluate differences in SoE among ecological groups of tropical raptors.

We could have expected that dietary-specialist raptors would show larger SoE since they may have to move further to obtain the specialized food resources they require. However, it may be that the smaller SoE for dietary specialist raptors is associated with limited prey mobility and distribution rather than dispersal distance of raptors. Prey mobility may vary for different species of raptor dietary specialists. The Sharp-shinned Hawk and the Peregrine Falcon are bird-eating specialists (del

Hoyo et al. 1994), while the Hook-billed Kite and the Laughing Falcon specialize on consuming snails and snakes, respectively (Parker et al. 2013; Whitacre and Vásquez 2013). Given that raptors are top-down predators, we believe that landscape structure effects on ecological responses of dietary specialists may be more associated with prey mobility rather than dispersal capacity of raptors, thus resulting in the opposite SoE to that found for habitat specialization in raptors.

Considering the mean SoE found in our study, we can recommend 1600 ha as an appropriate landscape size for future studies to accomplish meaningful research on this avian group and in this ecosystem. Our results may therefore serve as an aid to future studies that aim to evaluate raptor responses to landscape predictors, enabling researchers to adequately space survey points and reduce the elevated costs that field work on raptors usually implies. Furthermore, since SoE did not differ significantly among raptor ecological groups and response variables, we may be confident that different raptor species are likely to have similar responses to the same landscape metric, at least in the dry forest assemblage.

Our results determined that SoE for a highly mobile avian group was mainly driven by spatial landscape metrics. This supports findings for other taxa and suggests that forest cover influences dispersal success across larger scales, probably by reducing mortality of diurnal birds of prey. Our results indicate that management and planning strategies can be conducted over the same spatial scale for different diurnal raptor species and biological responses. In particular, the preservation of large extensions of forest cover in the landscape should be of great importance for diurnal raptor dispersal success in the dry forest.

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## Figure legends

**Figure 1.** Location of study sites along the coast of Jalisco, Mexico. Points represent the center of each 1.5 km survey transect, and circles around each point represent the largest landscape size considered in our study (3400 ha). A landscape representation of the 16 concentric buffers (at 200-ha intervals) around the center of each transect is indicated at the bottom-left side of the map.

**Figure 2.** Landscape metrics of (a) forest cover, (b) matrix hardness, (c) edge density, and (d) patch density for each landscape size (400 ha to 3400 ha). Horizontal lines show the median of each landscape metric, the bottom and top of each box are the first and third quartiles respectively. Upper and lower whiskers represent the highest and lowest values within 1.5 times the interquartile range. Dots beyond whiskers represent outliers.

**Figure 3** Scales of landscape effects on diurnal raptors. We separately indicate the scale of effect for (a) raptors grouped by habitat specialization, (b) raptors grouped by dietary specialization, (c) different ecological responses, and (c) different landscape structure metrics. Boxplot indicate the median (thick black line), 1<sup>st</sup> and 3<sup>rd</sup> quartiles (box), and the range of observed values (whiskers). The white circle indicates the mean. Abbreviations: FC = forest cover, ED = edge density, PD = patch density, MH = matrix hardness.



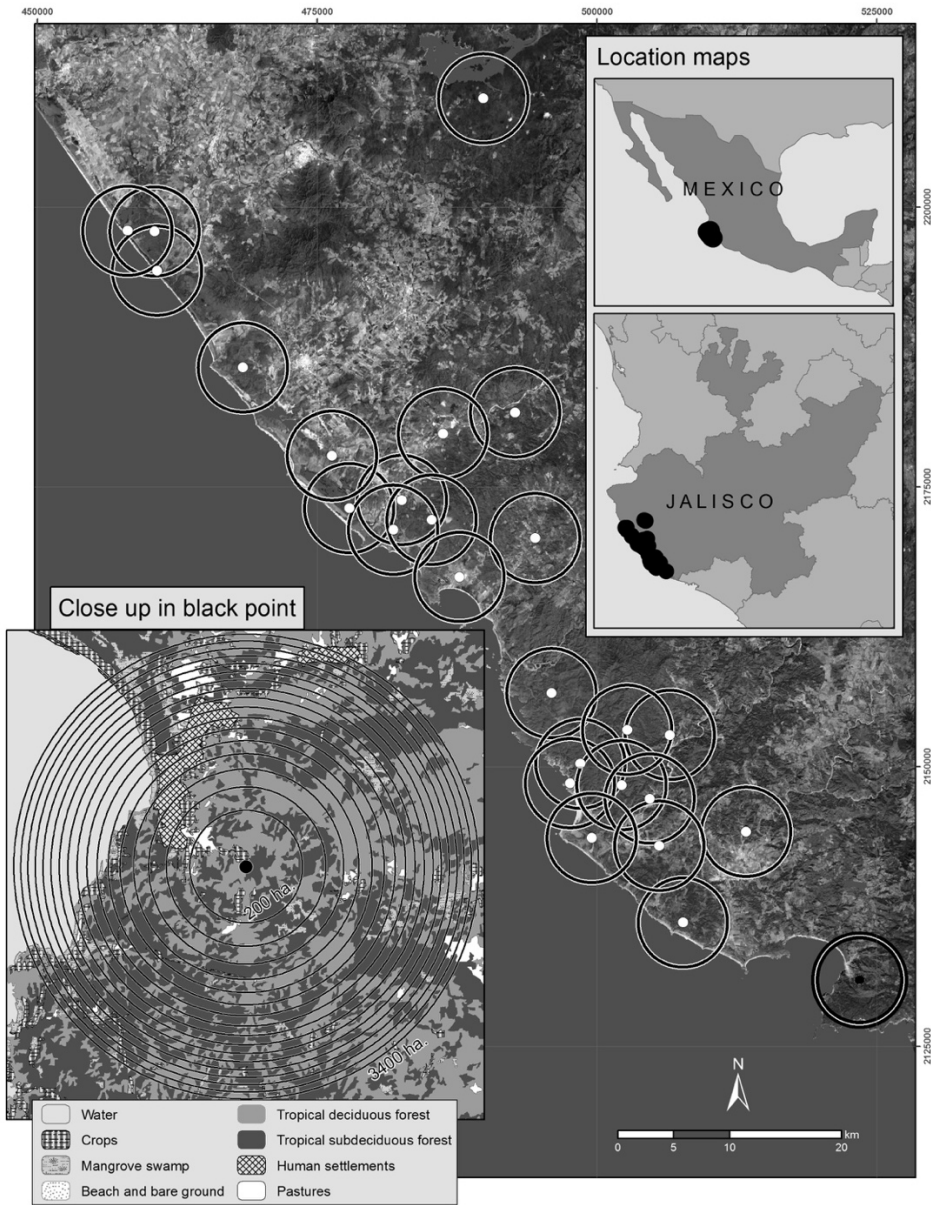


Figure 1

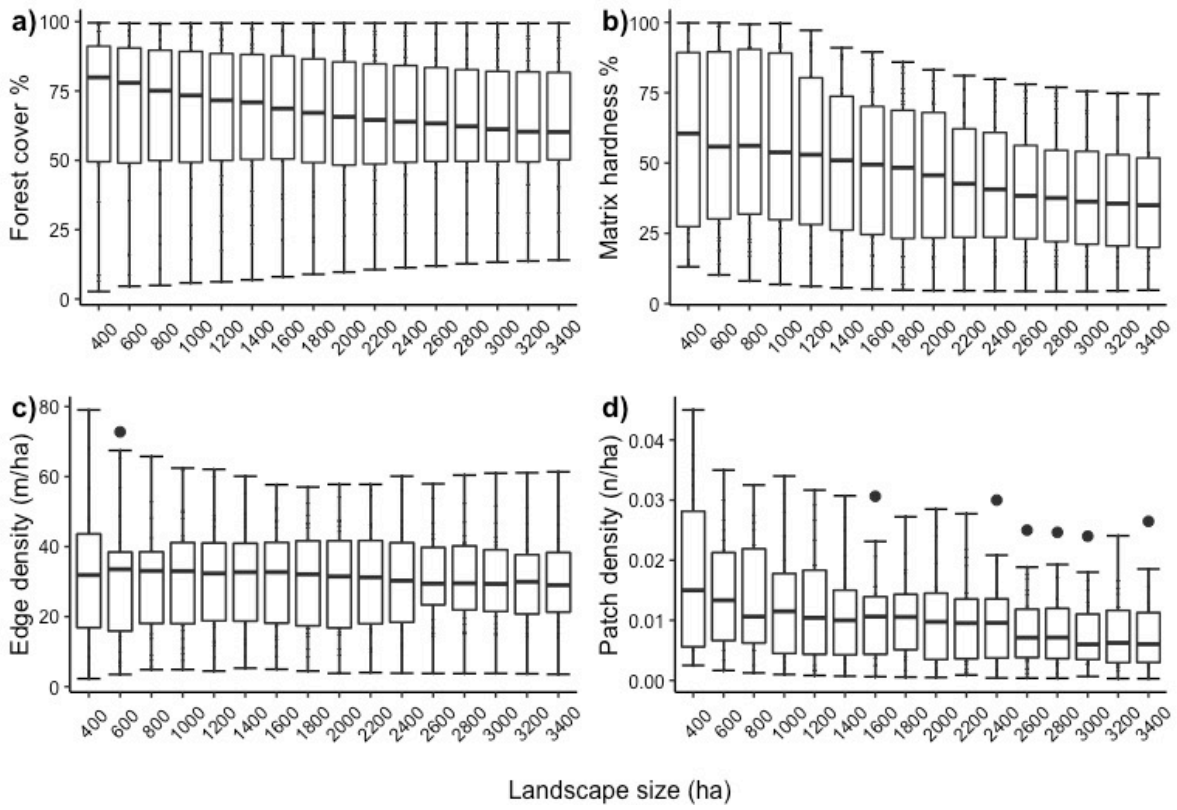


Figure 2

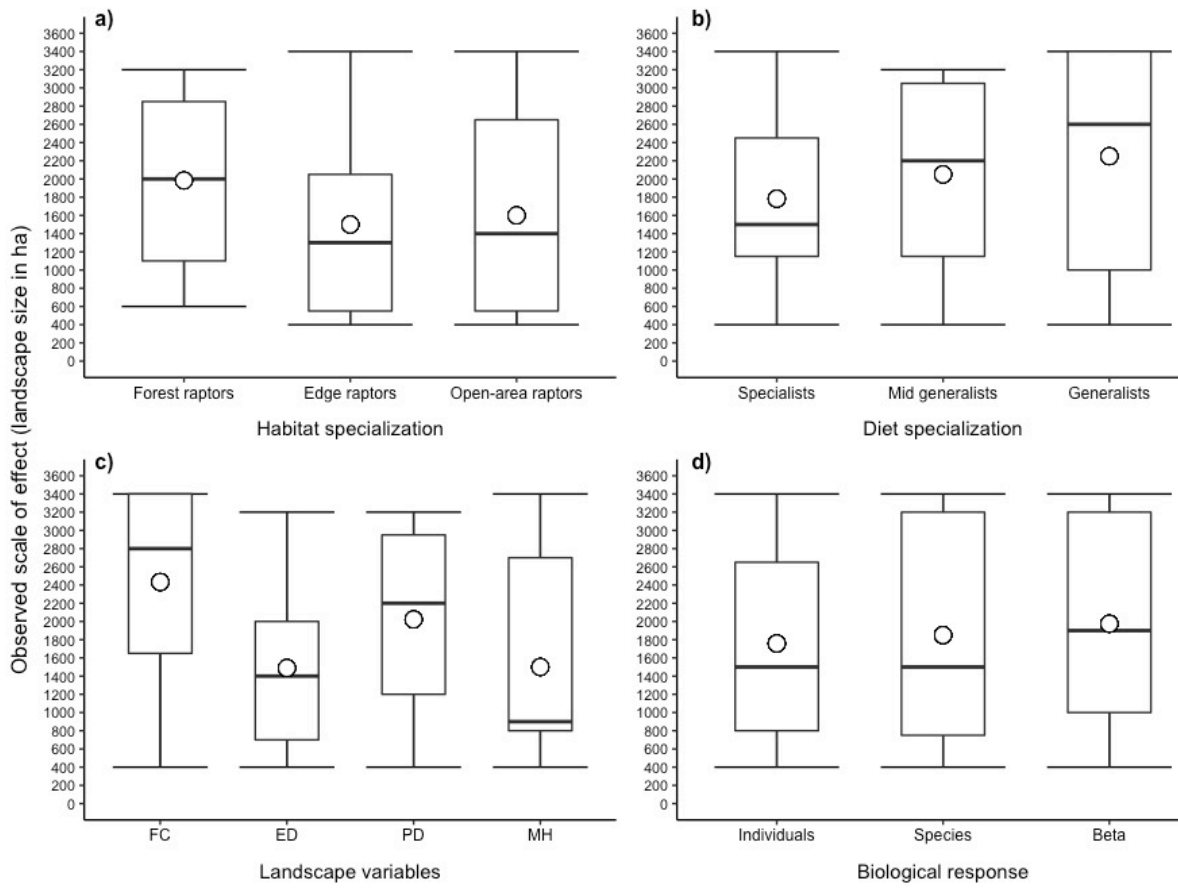


Figure 3

## Supplementary Materials for:

Martínez-Ruiz M, Arroyo-Rodríguez V, Franch I, Renton K. Patterns and drivers of the scale of landscape effect on diurnal raptors in a fragmented tropical dry forest. *Landscape Ecology*

**Table S1.** Raptor species of the tropical dry forest grouped according to habitat and dietary specialization

Raptor species	Common name	Habitat specialization			Dietary specialization		
		Fores t	Forest-edge	Open-area	Specialis t	Mid generalist	Generalis t
<i>Accipiter cooperii</i>	Cooper's Hawk		X			X	
<i>Accipiter striatus</i>	Sharp-shinned Hawk		X		X		
<i>Buteo albonotatus</i>	Zone-tailed Hawk		X			X	
<i>Buteo brachyurus</i>	Short-tailed Hawk		X			X	
<i>Buteo jamaicensis</i>	Red-tailed Hawk			X			X
<i>Buteo plagiatus</i>	Gray Hawk		X			X	
<i>Buteogallus anthracinns</i>	Common Black Hawk		X			X	
<i>Buteogallus urubitinga</i>	Great Black Hawk		X				X
<i>Chondrohierax uncinatus</i>	Hook-billed Kite	X			X		
<i>Elanus leucurus</i>	White-tailed Kite			X		X	
<i>Geranospiza caerulescens</i>	Crane Hawk	X					X

<i>Geranoaetus albicaudatus</i>	White-tailed Hawk			X				X
<i>Rupornis magnirostris</i>	Roadside Hawk		X					X
<i>Falco peregrinnus</i>	Peregrine Falcon			X		X		
<i>Falco ruficularis</i>	Bat Falcon	X					X	
<i>Falco sparverius</i>	American Kestrel			X			X	
<i>Caracara cheriway</i>	Crested Caracara			X		X		
<i>Herpetotheres cachinnans</i>	Laughing Falcon		X			X		
<i>Micrastur semitorquatus</i>	Collared Forest-falcon	X					X	

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**Table S2.** Moran's spatial autocorrelation index for 26 survey sites, and  $p$  values for the residuals of the best models for number of individuals (Ind), species richness (sp), and temporal species turnover (beta diversity) of diurnal raptors as a function of each landscape predictor at the selected scale of effect in tropical dry forest, western Mexico. Significant values are indicated in bold ( $p < 0.05$ ). Sub-indices indicate the landscape size (ha) at which scale of effect was detected.

Model	Moran's Index	$P$ -value
<u>Raptor community</u>		
Ind~Forest cover <sub>400</sub>	-0.0579	0.7360
Ind~Edge densityge density <sub>400</sub>	-0.00681	0.5332
Ind~Patch density <sub>400</sub>	-0.00599	0.5204
Ind~Matrix hardness <sub>800</sub>	-0.0606	0.6957
Sp~Forest cover <sub>3400</sub>	-0.0008	0.4696
Sp~Edge densityge density <sub>400</sub>	0.1031	<b>0.0088</b>
Sp~Patch density <sub>1600</sub>	0.1494	<b>0.0005</b>
Sp~Matrix hardness <sub>3400</sub>	0.0395	0.1403
Beta~Forest cover <sub>400</sub>	0.0631	<b>0.0561</b>
Beta~Edge densityge density <sub>3200</sub>	0.0027	0.4236
Beta~Patch density <sub>1800</sub>	0.0050	0.3988
Beta~Matrix hardness <sub>3400</sub>	-0.0519	0.8203
<u>Forest raptors</u>		
Ind~Forest cover <sub>3000</sub>	-0.0792	0.4676
Ind~Edge density <sub>1400</sub>	0.0679	<b>0.0464</b>
Ind~Patch density <sub>2600</sub>	0.0627	0.0609
Ind~ Matrix hardness <sub>800</sub>	-0.0527	0.8121
Sp~Forest cover <sub>3200</sub>	0.0771	<b>0.0296</b>
Sp~Edge density <sub>1400</sub>	0.1765	<b>0.0001</b>
Sp~ Patch density <sub>3200</sub>	0.1611	<b>0.0002</b>
Sp~ Matrix hardness <sub>600</sub>	0.0681	<b>0.0432</b>
Beta~Forest cover <sub>2800</sub>	-0.0771	0.5633
Beta~Edge density <sub>1200</sub>	-0.0833	0.4912
Beta~ Patch density <sub>2800</sub>	-0.0836	0.4884

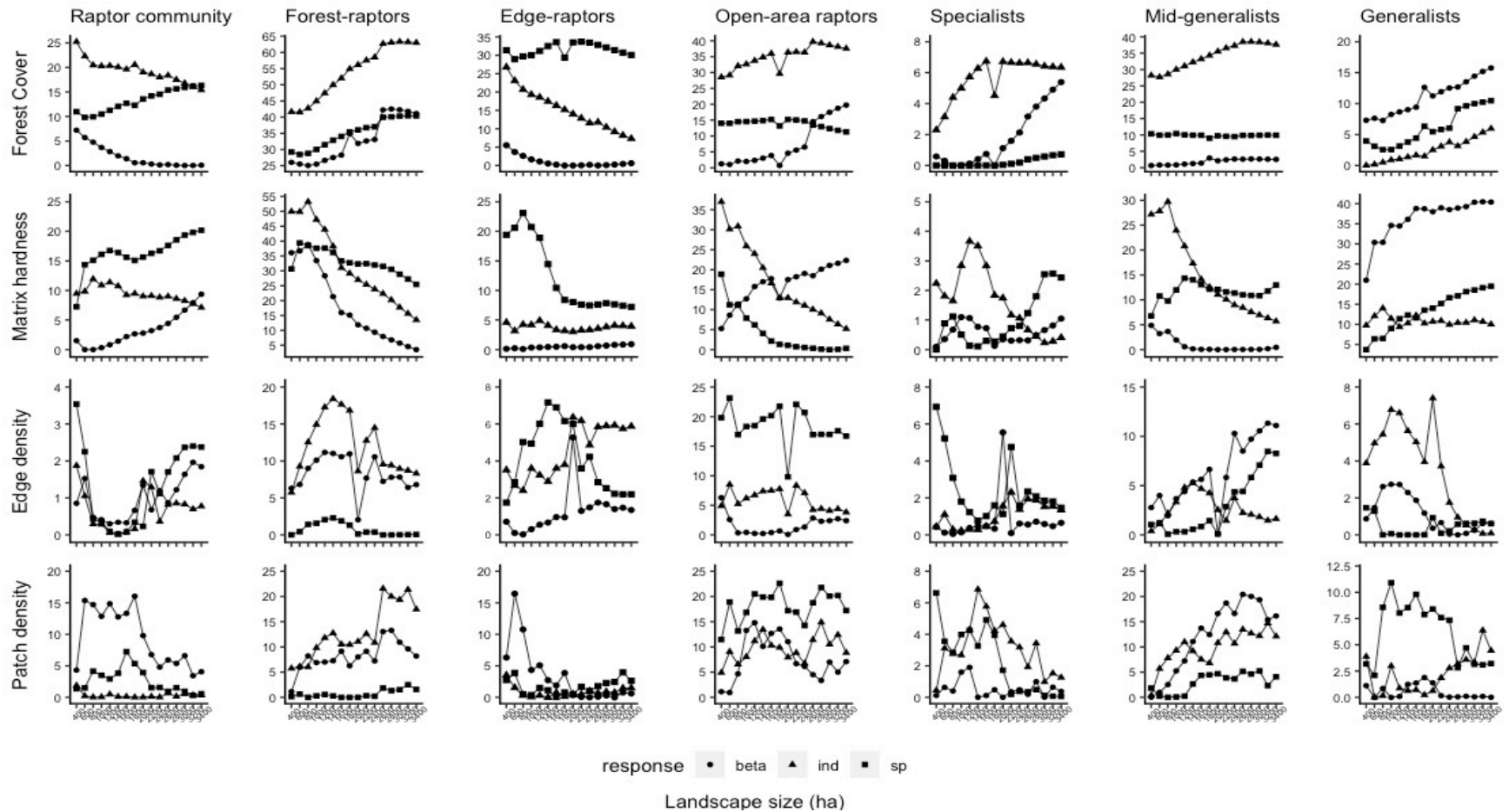
Beta~ Matrix hardness <sub>800</sub>	-0.0766	0.5603
<u>Forest-edge raptors</u>		
Ind~Forest cover <sub>400</sub>	-0.0590	0.7254
Ind~Edge density <sub>2000</sub>	-0.0391	0.9864
Ind~ Patch density <sub>400</sub>	-0.0673	0.6037
Ind~ Matrix hardness <sub>1200</sub>	-0.0853	0.3911
Sp~Forest cover <sub>2200</sub>	0.0025	0.4279
Sp~Edge density <sub>1400</sub>	0.1120	<b>0.0039</b>
Sp~ Patch density <sub>3200</sub>	0.0892	<b>0.0149</b>
Sp~ Matrix hardness <sub>800</sub>	-0.0146	0.6382
Beta~Forest cover <sub>400</sub>	0.0617	<b>0.0361</b>
Beta~Edge density <sub>2000</sub>	0.0064	0.2997
Beta~ Patch density <sub>600</sub>	0.0040	0.3289
Beta~ Matrix hardness <sub>3400</sub>	-0.0119	0.5222
<u>Open-area raptors</u>		
Ind~Forest cover <sub>2600</sub>	-0.0680	0.6043
Ind~Edge density <sub>600</sub>	0.0785	<b>0.0134</b>
Ind~ Patch density <sub>2800</sub>	0.0525	0.0630
Ind~ Matrix hardness <sub>400</sub>	-0.0616	0.6781
Sp~Forest cover <sub>1600</sub>	-0.0413	0.9814
Sp~Edge density <sub>600</sub>	-0.0285	0.8338
Sp~ Patch density <sub>1800</sub>	0.0009	0.4563
Sp~ Matrix hardness <sub>400</sub>	-0.0211	0.7298
Beta~Forest cover <sub>3400</sub>	-0.0419	0.7801
Beta~Edge density <sub>400</sub>	-0.1382	0.2029
Beta~ Patch density <sub>1200</sub>	-0.1282	0.2595
Beta~ Matrix hardness <sub>3400</sub>	-0.0872	0.6452
<u>Dietary specialists</u>		
Ind~Forest cover <sub>1600</sub>	-0.0861	0.3952
Ind~Edge density <sub>2200</sub>	-0.0595	0.7089
Ind~ Patch density <sub>1400</sub>	-0.0458	0.9123
Ind~ Matrix hardness <sub>1200</sub>	-0.0848	0.4037
Sp~Forest cover <sub>3400</sub>	-0.0187	0.6766
Sp~Edge density <sub>400</sub>	-0.0165	0.6559

Sp~ Patch density <sub>400</sub>	-0.0064	0.5253
Sp~ Matrix hardness <sub>3200</sub>	-0.0229	0.7352
Beta~Forest cover <sub>3400</sub>	0.0061	0.4179
Beta~Edge density <sub>2000</sub>	0.0797	<b>0.0438</b>
Beta~ Patch density <sub>1200</sub>	0.1009	<b>0.0176</b>
Beta~ Matrix hardness <sub>1000</sub>	0.0462	0.1425
<u>Mid-generalist diet</u>		
Ind~Forest cover <sub>2800</sub>	0.0057	0.3618
Ind~Edge density <sub>1400</sub>	0.1194	<b>0.0030</b>
Ind~ Patch density <sub>3200</sub>	0.0728	<b>0.0388</b>
Ind~ Matrix hardness <sub>800</sub>	0.0026	0.3843
Sp~Forest cover <sub>1000</sub>	0.0435	0.1144
Sp~Edge density <sub>3200</sub>	0.1398	<b>0.0010</b>
Sp~ Patch density <sub>3000</sub>	0.1637	<b>0.0002</b>
Sp~ Matrix hardness <sub>1200</sub>	0.0305	0.1861
Beta~Forest cover <sub>1800</sub>	-0.0683	0.5968
Beta~Edge density <sub>3200</sub>	-0.0764	0.4963
Beta~ Patch density <sub>2600</sub>	-0.0306	0.8623
Beta~ Matrix hardness <sub>400</sub>	-0.0551	0.7781
<u>Generalist diet</u>		
Ind~Forest cover <sub>3400</sub>	-0.0811	0.4515
Ind~Edge density <sub>2000</sub>	-0.0528	0.8147
Ind~ Patch density <sub>3200</sub>	-0.0597	0.7181
Ind~ Matrix hardness <sub>800</sub>	-0.0850	0.4074
Sp~Forest cover <sub>3400</sub>	-0.0571	0.7503
Sp~Edge density <sub>400</sub>	-0.0479	0.8833
Sp~ Patch density <sub>1000</sub>	-0.0540	0.7924
Sp~ Matrix hardness <sub>3400</sub>	-0.0858	0.4023
Beta~Forest cover <sub>3400</sub>	-0.0490	0.9000
Beta~Edge density <sub>1000</sub>	0.0130	0.3472
Beta~ Patch density <sub>1800</sub>	-0.0015	0.4903
Beta~ Matrix hardness <sub>3200</sub>	-0.1213	0.1554

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**Figure S1** Percentage of explained deviance (y-axis) in biological responses of individual abundance (ind), species richness (sp), and temporal turnover (beta) of diurnal raptors for each landscape metric (forest cover, matrix hardness, edge density, patch density) at 200-ha incremental spatial scales of landscape sizes (200-3400 ha) in tropical dry forest.



## **CAPÍTULO IV.- LANDSCAPE STRUCTURE INFLUENCES DIURNAL RAPTOR DIVERSITY IN THE TROPICAL DRY FOREST OF MEXICO**

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## ABSTRACT

Landscape structure is modified by land use change due to anthropogenic activities, being land-use change one of the main threats to biodiversity. Nevertheless, the effects of landscape structure on biodiversity may differ for species with different degree of habitat specialization; therefore, understanding the effects of landscape attributes on biodiversity is needed to design effective conservation strategies. For two years, we surveyed diurnal raptors in 26 sites located in the tropical dry forest of western Mexico. We used a multi-model inference approach to assess for the relative effects of landscape composition (forest cover and matrix hardness) and configuration (forest cover and matrix hardness) on individual abundance, species richness and temporal turnover of diurnal raptors with different degree of habitat specialization. We found that landscape structure strongly influences diurnal raptor diversity in the dry forest, being forest cover the most important landscape variable for forest raptors, confirming that habitat loss is an important threat to forest raptor species in the dry forest. Both landscape composition and configuration had a similar influence on the diversity of habitat generalist raptors. Interestingly, habitat fragmentation had mainly positive effects on the abundance and richness of diurnal raptors, independent of their habitat-associations. Our findings support previous studies of positive effects of fragmentation on biodiversity. Higher forest cover in the landscape resulted in a more stable assemblage of forest-raptors over time, which may be related to the maintenance of raptors territories when forest cover is higher. On the other hand, habitat generalists increased temporal species turnover with greater forest cover, probably due to greater landscape heterogeneity within the matrix.

*Key words:* birds of prey, fragmentation effects, landscape composition and configuration, species turnover

## INTRODUCTION

Conversion of natural ecosystems, mainly as a result of agricultural activities, is one of the major pressures and threats to biodiversity (Haddad et al., 2015; Newbold et al., 2015). Land use change is a landscape process that results mainly in the reduction and/or fragmentation of habitats, but also changes the amount, type and spatial arrangement of other land covers in the landscape (Fahrig, 2003). Habitat loss generally has negative and strong effects on diversity, relative to weaker effects of habitat fragmentation per se, which can have either positive or negative effects on biodiversity (Fahrig, 2003). In fact, empirical studies have found mostly positive ecological responses to habitat fragmentation (Fahrig, 2017), however at present, there is no general consensus concerning the relative importance and directional effect of landscape fragmentation on biodiversity (Fahrig, 2018; Fahrig et al., 2019; Fletcher et al., 2018). Thus, additional studies conducted at the landscape level are required to clarify the effects of habitat fragmentation.

Several studies have evaluated the relative importance of landscape composition and configuration on bird diversity. Studies in temperate zones have found that habitat amount has stronger effects on bird presence and abundance, while landscape configuration can have positive, negative, or neutral effects (Betts et al., 2006; McGarigal and McComb, 1995; Quesnelle et al., 2013; Smith et al., 2011; Trzcinski et al., 1999). A recent study found that species richness of temperate birds was strongly related to habitat amount but showed no relationship to fragmentation (De Camargo et al., 2018). Various studies have also determined that forest cover (habitat amount) is more important than habitat configuration for forest birds in the Neotropics (Carrara et al., 2015; Cerezo et al., 2010), the Mediterranean (Mortelliti et al., 2010; Touhiri et al., 2017), and Australia (Radford and Bennett, 2007).

Among avian groups, birds of prey (hereafter raptors) are considered to be highly sensitive to disturbance because of their higher trophic level (Donazar et al., 2016; Newton, 1979), and some raptor species are known to provide important ecosystem services (O'Bryan et al., 2018). However, there is a lack of research on raptor

communities, particularly for tropical raptors (Buechley et al., 2019), even though 90% of diurnal raptors occur in these regions, many of which are endemic (Bildstein et al. 1998). To our knowledge, no studies have evaluated how landscape composition and configuration influence diversity of tropical raptor communities.

In this study we assessed the effects of landscape structure on the diversity of top-predator diurnal raptors in a fragmented tropical dry forest landscape in western Mexico. Since the impact of landscape structure variables on species may vary according to habitat specificity of species (Hatfield et al., 2017), we separately assessed the response of raptors with different habitat specialization. In particular, we evaluated the relative effect of landscape composition (forest cover and matrix hardness) and configuration (edge and patch density) on response variables of individual abundance, species richness and temporal beta diversity of forest-raptors, edge-raptors and open-area raptors in tropical dry forest. Since forest-raptors and edge-raptors depend to some extent on forest resources, we predicted that forest-raptor and edge-raptor abundance and richness would be positively and strongly related to forest cover in the landscape, while open-area raptors might be positively and strongly influenced by matrix hardness. We also predicted that forest-raptors would be negatively associated with fragmentation metrics (edge density, patch density), since these species are specialized to forest interior. On the other hand, we expect that forest-edge raptor abundance and richness would be positively related to both forest cover and edge density, with forest cover being the most important predictor. Finally, we hypothesized that open-area raptors would be positively influenced by predictor variables associated with fragmentation. Given the lack of studies on raptor community dynamics, we had no a priori prediction for temporal beta diversity of raptors or how this responds to landscape structure.

## METHODS

### *Study area*

We conducted the study in the tropical dry forest of the Pacific coast of Jalisco in western Mexico, specifically in the municipalities of La Huerta and Tomatlán. The region has a warm semi-humid climate with a mean annual temperature of 26°C (García, 2004). Weather in the region has a marked seasonality, mean annual rainfall is 788 mm, the majority of which occurs during the rainy season from June to October, with a prolonged dry season from November to May (Bullock, 1986). The dominant vegetation in the region is deciduous forest, which is located mainly on the hills, and is characterized by a canopy height of 8-12 m and loss of leaf cover for 5-8 months during the dry season (Durán et al., 2002; Rzedowski, 2006). Common tree species in the deciduous forest are *Croton pseudoniveus*, *Lonchocarpus constrictus*, *Trichilia trifolia* and *Cordia alliodora* (Lott, 1987). The semi-deciduous forest occurs in humid valleys from sea-level to 1000 masl, and is characterized by tall trees of 25 m canopy height that maintain their foliage through most of the year (Rzedowski, 2006). Trees in semi-deciduous forest have  $\geq 30$  cm diameter at breast height (dbh), with common tree species such as *Thouindium decandrum*, *Capparis verrucosa*, and *Astronium graveolens* (Lott, 1987). Wetlands with mangrove vegetation occur along the coast, and are dominated by short, evergreen trees of *Laguncularia racemosa*, *Rhizophora mangle*, and *Avicennia germinans* (Durán et al., 2002). In low-lying areas of community lands along the coast, the tropical dry forest have been replaced by agricultural systems and cattle pastures where the dominant crops are sorghum, maize, watermelon as well as papaya, mango, and tamarind tree orchards (Maas, 1995; Maas et al., 2005). During the period from the 70s to mid-90s, land-use change to agricultural fields resulted in the reduction by 25% of deciduous forest and 50% of semi-deciduous forest along the coast (Flores-Casas and Ortega-Huerta, 2019).

### *Raptor surveys*

We selected 26 survey sites along the coast that were spatially separated by at least 5 km. At each survey site, we established a 1.5 km length transect to survey diurnal raptors,

mainly Accipitriformes and Falconiformes. Each transect was surveyed four times over the two years from 2016-2018, covering two dry and two rainy seasons. We commenced surveys 60 min after daybreak, walking at slow pace of approximately 1.5 km/h in one direction along each transect. During each survey, we detected raptors by sight or vocalization, and we used these data to estimate individual abundance. Given the low detectability of raptors, species richness was estimated using a combination of methods, using data of number of individuals of each species and complementing this with vocal stimuli to increase the response of raptors highly territorial raptors (Fuller and Mosher, 1987). After the initial raptor survey, we established three playback points separated by 750 m along each survey transect, where we generated pre-recorded vocalizations of species reported for the region. Each playback consisted of two 30 s cycles of each raptor species vocalization, spaced with 40 s of silence to await a response. We only used playback of vocalizations for those raptor species that were not detected during the initial transect survey. We used a Fox Pro digital game caller for playbacks, which was orientated in different directions around the playback point (Barnes et al., 2012). When we obtained a vocal response from a raptor species, we suspended playbacks for that particular species for the rest of the survey on that transect.

### *Biological traits of raptors*

We grouped 19 diurnal raptor species registered in our surveys according to habitat specialization under the assumption that this trait is an indicator of mobility (Miguet et al., 2016). We considered three categories of habitat specialization: i) Forest raptors, associated with broad forest (deciduous or semideciduous) cover extensions and to specific resources from mature forests; ii) Edge raptors, species requiring forest cover or elements from mature forests, but also use and are frequently found in forest-agricultural edges; and iii) Open-area raptors, that are species associated with open-habitats such as agricultural areas. Raptor species were grouped by habitat categories based on information from available literature; in particular, we compiled information from reference materials in the Handbook of the Birds of the World (del Hoyo et al., 1994) and its recent online version, Raptors of the World (Ferguson-Lees and Christie, 2005), Raptors of

Mexico and Central America (Clark and Schmitt, 2017), and Neotropical Birds of Prey (Whitacre, 2017).

### *Response variables and landscape metrics*

We determined three response variables of diurnal raptor communities in each of the three habitat categories: i) Individual abundance, the mean number of individuals recorded for a survey transect over the four surveys; ii) Species richness, the total number of species of diurnal raptors recorded for a survey transect considering all four surveys; and iii) Temporal beta diversity ( $\beta_w$ ) of the compositional difference between years in a two-year period, which was calculated as the total number of raptor species recorded in each transect ( $\gamma$ ) divided by the mean number of raptor species ( $\alpha$ ) in each transect. To calculate landscape metrics, a land-cover map was developed from a high resolution (10 m) satellite image from the year 2016 (Sentinel 2 A). We used Spring 5.2.2 (Câmara et al., 1996) to define 8 land-cover types: water, crops, pastures, deciduous forest, semi-deciduous forest, wetlands with mangrove vegetation, beach/bare ground, and human settlements (Fig 1). Accuracy assessment of the map followed the procedure proposed by Olofsson et al., (2014), with a certainty level of 79.6%. We generated 16 concentric buffers at 200 ha intervals around the center of each survey transect to measure landscape structure. The smallest landscape size was 400 ha (1128 m radii), and the largest was 3400 ha (3289 m radii). Within each landscape size, we calculated four metrics of landscape structure that we considered of importance for diurnal raptors: 1) Forest Cover, calculated as the proportion of landscape covered by forest (deciduous + semi-deciduous), 2) Forest patch density, calculated as the number of forest patches in the landscape divided by landscape area, 3) Forest edge density, determined by first measuring the total perimeter length of all forest patches in the landscape, which was then divided by landscape area (m/ha). Finally, the landscape matrix was defined by the remaining land covers that were not deciduous or semideciduous forest within the landscape, and 4) Matrix hardness was thereby calculated as the percent of those land covers that are most contrasting with deciduous or semi-deciduous forest, this is the



proportion of agricultural fields, cattle pastures, human settlements and beach/bare ground within the matrix. All of the landscape metrics were calculated using the Patch analyst extension in ArcGis 10.5. In a prior study, we evaluated the scale of effect of each landscape metric (Jackson and Fahrig, 2015) to determine the landscape size that best predicts raptor responses to landscape structure (Martinez-Ruiz et al. Capítulo III). We then used these optimal spatial scales for statistical analyses in the present study.

### *Statistical analysis*

We first computed Moran's Index to test for spatial independence of our samples. We used the *ape* package (Paradis et al., 2004) and *letsR* package (Vilela and Villalobos, 2018) for R (R Development Core Team, 2017). We found significant spatial autocorrelation in 12 of 48 models. In all cases we observed very small Moran's I values ( $<0.17$  in all cases), suggesting that they can be related to spurious correlations (Fortin et al., 2002). We therefore considered all study sites as independent samples in subsequent analyses. To avoid multi-collinearity problems between the predictor variables (landscape structure), we estimated the variance inflation factor (VIF) of each predictor using the "car" package for R 3.3.3 (Fox and Weisberg, 2011). A  $VIF > 4$  indicates possible collinearity, and a  $VIF > 10$  indicates severe collinearity (Neter et al., 1996). All of our VIF values were  $<7$ , which indicated some collinearity among predictors.

We used generalized linear models (GLM) to test the effects of landscape composition and configuration on response variables for each raptor habitat group. We then used a multimodel averaging approach to assess the relative effect of each landscape predictor on each response variable (Burnham and Anderson, 2002). For each response variable we constructed 8 models representing all combinations of explanatory variables plus the null model. For each model, we computed Akaike's Information Criterion corrected for small samples (AICc), and we then ranked the models from best to worst according to AICc values. We then calculated the sum of Akaike weights ( $\sum w_i$ ) of the models in which each landscape metric appeared, the sum of Akaike weights represents the probability that each variable is contained in the true best model, and it

was used to obtain model-averaged parameter estimates (Burnham and Anderson, 2002). A given landscape metric was considered as an important predictor for a given response variable if it showed a high  $\Sigma wi$ , and if the model-average unconditional variance was lower than the model-averaged parameter estimates (error bars Fig 1). All models were built using the package “MuMIn” (Bartón, 2019) for R (R Development Core Team, 2017).

## RESULTS

### *Raptor surveys*

Over all surveys we registered 558 individuals, comprising 19 species of diurnal raptors: 12 species from the family Accipitridae, and 6 species of Falconidae (Appendix 1). Four of the 19 species were winter migrants, while the rest were resident in the region (Appendix 1).

### *Responses of raptors to landscape structure*

For the group of forest raptors, the response variable of individual abundance showed the strongest association with landscape structure variables, and explained 47.2% of deviance in the complete model. The other two response variables of species richness and temporal beta diversity of forest raptors both explained about a third of deviance each (33.28 – 37.22%). In particular, the landscape variable of forest cover was the most important predictor for all three response variables of forest raptors (number of individuals  $\Sigma wi = 0.672$ , species richness  $\Sigma wi = 0.327$ , and temporal beta diversity  $\Sigma wi = 0.437$ ). Greater forest cover had positive effects on both individual abundance and species richness of forest-raptors, but we found lower species temporal turnover of this group with greater forest cover in the landscape (Fig 3a). The matrix hardness was the second important predictor for forest raptors, having greater weight for the response variable of temporal beta diversity of forest raptors ( $\Sigma wi = 0.422$ ). However, matrix hardness had a negative effect on number of individuals, and positive effect on species richness, with little change in temporal beta diversity of forest raptors (Fig 1a). The landscape metrics of patch density and edge density that are had lower weight in complete models for forest raptors,

which suggests that forest raptors are more dependent on changes in landscape composition than landscape configuration. We observed positive effects of habitat fragmentation (edge and patch density) on the number of individuals and species richness of forest-raptors, with negative effects of fragmentation on temporal beta diversity of forest raptors (Fig 1a).

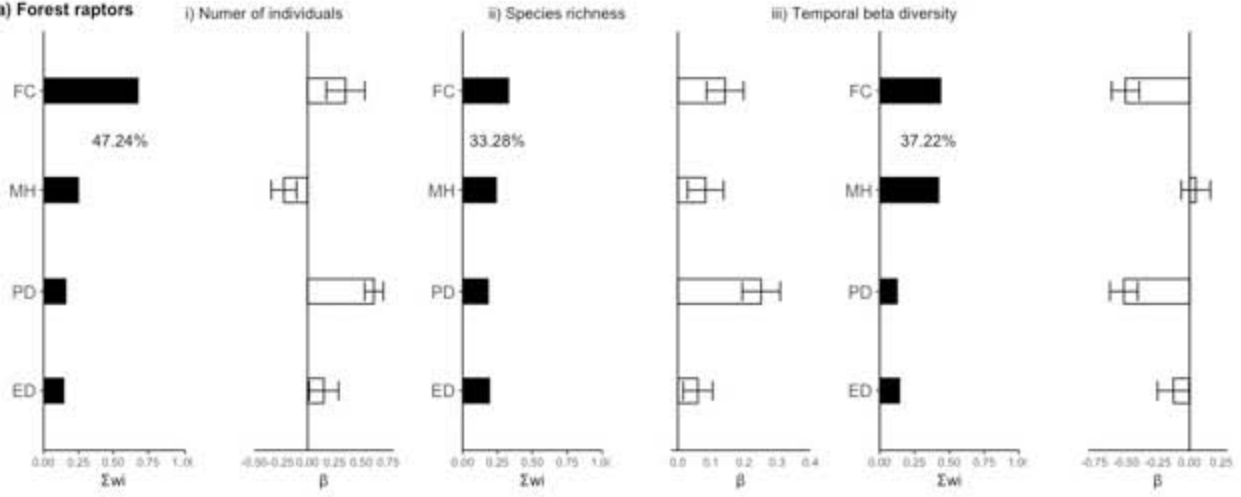
Regarding the group of forest-edge raptors, our results showed that temporal beta diversity of forest-edge raptors was strongly associated with landscape metrics, explaining 82.05% of deviance in the complete model. Landscape metrics associated with fragmentation were the most important predictors for temporal beta diversity of edge-raptors (Edge Density:  $\sum wi = 0.983$ ; Patch Density:  $\sum wi = 0.904$ ). Interestingly, forest cover also had a strong influence on temporal beta diversity of forest-edge raptors ( $\sum wi = 0.876$ ). However, whereas temporal beta diversity of forest-edge raptors was positively associated with edge density and forest cover, this response variable had a negative association with patch density (Fig 1b). Species richness of forest-edge raptors explained 53.41% of deviance in the complete model, and was positively influenced by landscape variables associated with fragmentation (patch density and edge density), but negatively affected by landscape composition variables (forest cover, matrix hardness), although all landscape metrics had low weight in the complete model (Fig 1b). Finally, the response variable of individual abundance was positively associated with all landscape metrics (Fig 1b), but explained little of the deviance (20.62%) in the complete model for forest-edge raptors.

In the case of open-area raptors, all three response variables were similarly associated with landscape variables, explaining 41.79% to 45.22% of deviance in the complete model. However, landscape metrics had differing importance and effect for each of the response variables of open-area raptors (Fig 1c). Individual abundance of open-area raptors was most influenced by landscape composition metrics of forest cover ( $\sum wi = 0.662$ ) and matrix hardness ( $\sum wi = 0.496$ ), being negatively associated with forest cover and positively associated with matrix hardness (Fig 1c). Species richness of open-area raptors was strongly influenced by the fragmentation metrics of patch density ( $\sum wi = 0.626$ ) and edge density ( $\sum wi = 0.498$ ), as well as matrix hardness ( $\sum wi = 0.625$ ). However,

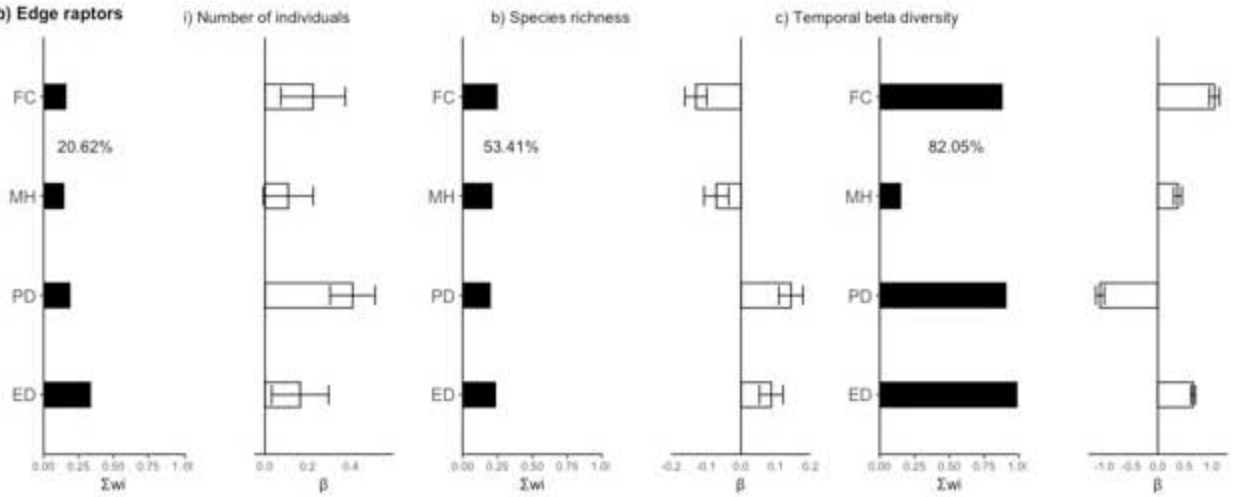
whereas species richness of open-area raptors was positively associated with fragmentation metrics (patch density, edge density), this response variable was negatively associated with matrix hardness and forest cover (Fig 1c). Finally, temporal beta diversity of open-area raptors was most influenced by forest cover ( $\sum w_i = 0.665$ ) and patch density ( $\sum w_i = 0.551$ ), being positively associated with both these landscape metrics (Fig 1c).

Fig 1.- Effect of landscape metrics on the response variables of number of individuals (i), species richness (ii), and temporal beta diversity (iii) of a) forest raptors, b) forest-edge raptors, and c) open-area raptors of the tropical dry forest in western Mexico. The importance of each landscape variable is shown by the sum of Akaike weights ( $\sum w_i$ ) (black bars). Parameter estimates ( $\beta$ ) are shown indicating the positive or negative effects of each landscape metric on each response variable. We indicate values of pseudo- $R^2$  (the percentage of explained deviance by the complete model) for each response variable.

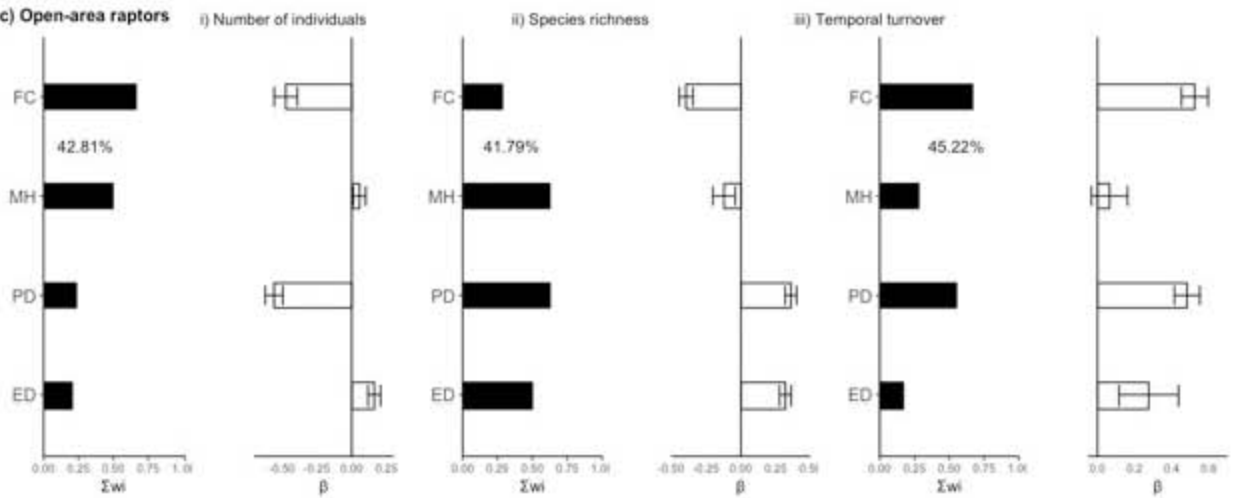
**a) Forest raptors**



**b) Edge raptors**



**c) Open-area raptors**



## DISCUSSION

### *Influence of landscape composition and configuration on diurnal raptor diversity*

We determined that landscape structure influenced diurnal raptors in the tropical dry forest of western Mexico, and that the response of raptor communities to landscape composition and configuration varied depending on the type of habitat specialization shown by different raptor groups. Our results demonstrated that forest raptors were most strongly influenced by forest cover, particularly in terms of number of individuals of forest raptors. Temporal beta diversity, or species turnover, of forest-edge raptors was influenced by forest cover, and the fragmentation metrics of patch and edge density. Finally, all response variables of open-area raptors were equally associated with landscape structure, but landscape metrics had differing importance and effect for each response variable of open-area raptors. To our knowledge, this is the first study to assess the influence of landscape composition and configuration on diurnal raptor diversity of a tropical system.

The importance of forest cover as a landscape predictor for forest raptor species is consistent with our predictions, and supports similar results obtained for other biological groups (Fahrig, 2017). Diversity of forest specialist birds has also been found to be strongly associated with increased forest cover in other studies (Carrara et al., 2015; Fahrig, 1998; Smith et al., 2011). Forest specialist species may be expected to be more vulnerable to changes in the amount of habitat available (Fahrig, 1998; Newbold et al., 2014). This is further supported by the negative effect of forest cover, and the fragmentation metrics of patch and edge density, on temporal beta diversity of forest-raptors, where increased forest cover or increased fragmentation of the landscape leads to low species turnover. This may reflect the stability of this raptor community in large extensions of forests. Raptors show high fidelity to territories that they maintain over a number of years, even in seasonal environments (Newton, 1979; Panasci, 2013; Sutter, 2013; Thorstrom, 2013). Many tropical birds also defend territories throughout the year rather than just in the breeding season (Stutchbury and Morton, 2001). Therefore, we believe that the resident forest raptor community may show low species turnover due to the species'

high fidelity to their territories over time. Contrary to expectation, species richness of forest-raptors increased with matrix hardness of the landscape. This may be explained by how we defined matrix hardness in our study based on land covers that are less similar to forest cover. These dissimilar land covers included agricultural fields and cattle pastures, which although distinct to forest cover still maintain features that have forest elements, such as isolated trees, living fences, and water bodies, that can provide resources used by forest raptors. These potentially wildlife friendly elements could explain the positive effect of matrix hardness on species richness of forest raptors. Indeed, forest raptors such as the Collared Forest-falcon (*Micrastur semitorquatus*) and Hook-billed Kite (*Chondrohierax uncinatus*) were observed foraging in forest-farmland edges during our study (M. Martinez Ruiz pers. obs.). Thus, it is important to consider the heterogeneity of land covers within the matrix as a measure of matrix quality for raptors, since several studies have shown that the matrix may present different degree of suitability for the occurrence, species richness, individual abundance, and dispersal of distinct bird species (Antongiovanni and Metzger, 2005; Gobeil and Villard, 2002; Kennedy et al., 2010; Renjifo, 2001).

Contrary to our predictions, forest cover was not the most important predictor for forest-edge raptor species, where temporal species turnover and species richness of this raptor group were strongly associated with landscape metrics. We determined that fragmentation metrics of patch and edge density had higher or similar weight for response variables of forest-edge raptors as habitat amount of forest cover in the landscape. This is contrary to a recent study that found a strong association of species richness of temperate birds to habitat amount in the landscape, but not to fragmentation (De Camargo et al., 2018). Bird diversity of habitat generalists in a tropical rainforest also had a weak association with landscape configuration (Carrara et al., 2015). Our findings suggest that species richness and turnover of forest-edge raptors may be influenced by both landscape composition and configuration (Fahrig, 2003).

We hypothesized that open-area raptors would be more strongly influenced by landscape metrics associated with fragmentation, however, our results showed differing effects of landscape structure depending on the response variable being

evaluated. Landscape composition most strongly influenced individual abundance of open-area raptors, but both composition and fragmentation metrics influenced species richness and turnover of this raptor group. In accordance with our prediction, individual abundance and species richness of open area raptors decreased with greater forest cover, and increased with higher fragmentation of the landscape. This suggests that the break-up of forest cover in the landscape benefits habitat generalist raptors, supporting more generalist species.

The strong influence of both forest cover and landscape fragmentation on temporal beta diversity of forest-edge and open-area raptors suggests that a landscape matrix of forest cover and agricultural fields may offer a variety of resources for edge and open-area raptors. Higher forest cover, greater edge density, and the presence of wildlife friendly elements within the matrix hardness may facilitate movement of raptors among different habitat patches, thus enabling landscape complementation dynamics (Dunning et al., 1992) for generalist raptors. The strong association of temporal species turnover with landscape structure for forest-edge and open-area raptors may be an indication of local species sorting processes (Leibold et al., 2004), the model predicts that species composition in a locality is determined partly by habitat tolerances, but temporal fluctuations should emerge when environmental conditions are highly variable (Chase and Leibold, 2003). We believe that more fragmented landscapes may support higher temporal beta diversity of habitat generalist raptors due to the heterogeneity caused by the presence of different land covers. Moreover, the variability of annual crops in agricultural lands, and seasonality of the tropical dry forest create a highly variable environment thus increasing temporal turnover (Leibold and Chase, 2018).

#### *Positive effects of landscape fragmentation on diurnal raptor diversity*

Our results showed that landscape fragmentation had a consistent positive effect on species richness of the three raptor groups evaluated in this study. These findings are consistent with previous studies that showed positive effects of fragmentation on diversity of different taxonomic groups (Fahrig 2017). Particularly, we found that edge density had positive constant effect on both individual abundance



and species richness of forest raptors, forest-edge raptors, and open-area raptors. This is consistent with the study by Carrara et al. (2015) who determined that forest edge density positively influenced diversity of forest specialist birds. The positive responses of individual abundance and species richness of forest raptors to habitat fragmentation are also consistent with other studies that found positive responses of species richness of specialists, rare and/or threatened species to habitat fragmentation (Fahrig 2017). This result is not surprising for forest-edge raptor species, since fragmented landscapes have more forest edge (Fahrig, 2003). We believe that the positive influence of edge density on the three groups of raptors is associated with positive effects of edges, functional connectivity in the landscape, and complementation/supplementation dynamics (Dunning et al., 1992). The presence of several small forest patches in the landscape may facilitate successful movement of individuals to encounter another forest patch via landscape supplementation (Dunning et al., 1992), as forest raptor species could supplement resource intake by using resources in forest patches nearby. This may be important for forest raptors that do not soar, such as the Collared Forest-falcon, Hook-billed Kite, and Crane Hawk (*Geranospiza caerulescens*), and may be reluctant to cross long distances among habitat patches. Forest-edge raptor species such as the Gray Hawk (*Buteo plagiatus*), and Laughing Falcon (*Herpetotheres cachinnans*), are known to use resources from different elements in the landscape, as they usually prefer to nest in the forest, but roost and forage at the edge and in the surrounding matrix (Parker et al., 2013; Sutter, 2013). Fragmentation might be particularly beneficial for forest-edge raptors, since edges between forest and agricultural fields would facilitate movement between these two habitats, allowing forest-edge raptors to use resources from different landscape covers via landscape complementation (Dunning et al., 1992).

A higher density of generalist predators at forest edges is also the proposed explanation for the increased avian nest predation found at forest-farmland edges (Andr n, 1992; Flaspohler et al., 2001; Marini et al., 1995; Rudincky and Hunter, 1993) and in smaller habitat patches (Paton, 1994). Activity of large predators has also been found to increase with fragmentation (Keyser et al., 2001), suggesting

that forest-edge raptors may benefit by foraging in fragmented landscapes. This may be true also for open-area raptors, which also use resources from the matrix and edges. Among fragmentation variables, only patch density had a negative effect on individual abundance of open-area raptors. This makes sense since a greater density of forest patches in the landscape would decrease the amount of open area in the matrix, reducing the preferred habitat and availability of resources for open-area raptor species.

## **CONCLUSIONS**

Our findings demonstrated that landscape structure influences diurnal raptor diversity in the tropical dry forest. As expected, forest cover was the most important predictor for forest raptors, confirming that habitat loss is an important threat to forest raptor species in the tropical dry forest. Both landscape composition and configuration had a similar influence on the diversity of diurnal forest-edge and open-area raptors. Fragmentation had mainly positive effects on individual abundance and species richness of diurnal raptors, whether they were habitat specialists or generalists. This supports previous studies that demonstrate positive effects of habitat fragmentation on diversity. Higher forest cover in a fragmented landscape resulted in a more stable assemblage of forest raptors over time. However, the opposite was true for habitat generalists, where greater forest cover and edge density increased temporal species turnover of forest-edge and open-area raptors, probably due to greater landscape heterogeneity within the matrix.

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## DISCUSIÓN GENERAL Y CONCLUSIONES

Los resultados de la presente tesis nos permitieron entender como las rapaces diurnas responden ante disturbios naturales como los huracanes. Además, mostramos que las rapaces diurnas también responden a la estacionalidad de distintos hábitat, y a la composición y configuración del paisaje en el bosque tropical seco de la costa de Jalisco.

En el capítulo I de la presente tesis, demostramos que un huracán mayor tuvo influencia distinta en los ensambles de rapaces diurnas dependiendo del hábitat. La menor densidad de rapaces en los bosques afectados por el huracán podría estar asociada con los daños estructurales a los bosques maduros que causan los vientos de huracán (Wauer and Wunderle 1992). Los resultados de este capítulo sugieren que las rapaces en áreas afectadas por el huracán modificaron el patrón de uso del hábitat en respuesta a los daños ocasionados al hábitat por los vientos de un huracán mayor. Concluimos que los humedales pueden funcionar como hábitat refugio para varias especies de rapaces diurnas tras el disturbio de un huracán, ya que la riqueza y equitatividad del ensamble de rapaces diurnas fue mayor en los humedales afectados por el huracán, y distintas especies de rapaces asociadas a los bosques fueron observadas en los humedales a 5 meses del paso del huracán Patricia (Martínez-Ruiz and Renton 2018). La alta movilidad de las rapaces diurnas les permitiría desplazarse entre diferentes hábitats, y la heterogeneidad de hábitats en el paisaje ayudaría a la resiliencia de las rapaces diurnas en el bosque tropical seco ante disturbios naturales de los huracanes. En este sentido, nuestros resultados destacan la importancia de mantener hábitat alternos en el paisaje, como los humedales, que muestran alta resiliencia ante disturbios de huracanes (Kathiresan and Bingham 2001). Esto cobra mayor importancia ante el reciente incremento en intensidad y frecuencia de huracanes de mayor categoría (Emanuel 2005). De esta forma, en este capítulo contribuimos al conocimiento de la respuesta de un grupo de alto nivel trófico ante los disturbios naturales de huracanes.

En el capítulo II determinamos la respuesta de la diversidad de rapaces diurnas a la estacionalidad en los hábitat del bosque tropical seco, y si la influencia

de la estacionalidad es diferente en las áreas afectadas y no afectadas por un huracán de alta categoría. Nuestros resultados mostraron que la estacionalidad del bosque tropical seco influye en la diversidad de rapaces diurnas, con mayor diversidad de rapaces durante la época seca. Estos resultados concuerdan con lo reportado en otros estudios, donde se ha encontrado variación en la abundancia de rapaces en otros ecosistemas estacionales de América (Hayes 1991; Jensen et al. 2005; Zilio et al. 2014; Carmona et al. 2017). La variación temporal en diversidad de rapaces sugiere que se deben evaluar respuestas biológicas de este grupo en más de una temporada anual en los ecosistemas estacionales.

En este capítulo encontramos que aquellos hábitat con mayor temporalidad, como el bosque deciduo y las áreas agrícolas, mostraron variación temporal significativa en la densidad de rapaces diurnas, en áreas afectadas y no afectadas por el Huracán Patricia. Por otra parte, los hábitat perennes, del bosque subcaducifolio y los humedales, solo mostraron variación en densidad de rapaces en las áreas afectadas por el huracán. Esto indica que el paso de un huracán mayor puede alterar la dinámica espacio-temporal en los ensamblajes de rapaces en el bosque tropical seco. La variación temporal en densidad de rapaces en humedales afectados se detectó hasta 18 meses después del paso del huracán, y esto coincide con lo observado en el Capítulo I, donde la riqueza y equitatividad de rapaces diurnas en los humedales fue significativamente mayor en las áreas afectadas por el Huracán Patricia (Martínez-Ruiz and Renton 2018). Por otro lado, la variación temporal durante dos años en densidad de rapaces en los bosques afectados por el huracán sugiere que la influencia de este tiene un efecto prolongado sobre las rapaces. En este sentido, la ocurrencia de eventos climáticos extremos, como un huracán mayor, podrían acentuar el efecto de la estacionalidad al provocar cambios en los ensamblajes de rapaces mediante la modificación al hábitat, y cambios en las comunidades de presas de las rapaces. La estabilidad en la riqueza de rapaces durante los dos años y medio de muestreo sugiere que las rapaces son resilientes a los cambios en el bosque tropical seco, pero con variación en densidad, la cual se ve influenciada a un plazo de dos años por el disturbio de un huracán de alta categoría. De esta forma, los resultados del capítulo II mostraron que los efectos del

paso de un huracán mayor pueden ser prolongados para los ensambles de las rapaces diurnas.

Por otra parte, en el capítulo III de esta tesis usamos un enfoque multi-escalar para determinar la escala del efecto a lo cual la estructura (composición y configuración) del paisaje mejor predice las respuestas biológicas de las rapaces diurnas (Jackson y Fahrig 2012). La mayoría de escalas del efecto detectadas estuvieron dentro del rango de escalas espaciales consideradas en nuestro estudio, lo que sugiere que las relaciones entre las rapaces diurnas y la estructura del paisaje fueron estimadas adecuadamente (Jackson and Fahrig 2015). Nuestros resultados arrojaron una escala del efecto de 1633 ha para el ensamble de rapaces diurnas del bosque seco, esta medida se puede usar como una escala espacial adecuada para futuros estudios en rapaces del bosque tropical seco. Esto cobra importancia ya que se carece de información acerca del área adecuada para el estudio de aves rapaces las cuales tienen territorios grandes y esto ha sido una limitante en el estudio de este grupo.

Además, nuestros resultados mostraron que la escala del efecto para las rapaces diurnas depende principalmente de las métricas del paisaje consideradas, lo cual es consistente con otros estudios en el tema (Galán-Acedo et al. 2018; San-José et al. 2019). Nuestros resultados sugieren que las rapaces diurnas del bosque tropical seco son afectadas por la cobertura forestal medida en escalas espaciales mayores mientras que las respuestas a la dureza de la matriz y la densidad de borde fueron más evidentes en escalas espaciales más pequeñas. Estos resultados dan soporte a los modelos teóricos (Miguet et al. 2016) y evidencia empírica (Smith et al. 2011) en el tema, sugiriendo que la cobertura forestal está más relacionada con el éxito de dispersión en escalas espaciales mayores (Miguet et al. 2016), mientras que la densidad de borde y la dureza de la matriz podrían limitar la dispersión de rapaces en paisajes más pequeños. No encontramos diferencias en escalas del efecto entre respuestas biológicas de las rapaces diurnas, lo que sugiere que la abundancia, riqueza de rapaces y diversidad temporal beta medida durante dos años, están influenciadas por fuerzas que actúan en escalas espaciales y temporales que son similares. La abundancia de individuos no depende solo de

procesos locales, pues también puede estar relacionada con la dispersión a grandes distancias (Fahrig 2001; Lindenmayer and Fischer 2006). Asimismo, la riqueza de especies y la diversidad beta temporal no solo dependen de procesos a escala mayor, sino que también pueden estar afectadas por procesos locales como las interacciones intra e interespecíficas (Morin 2011).

La estimación de la escala del efecto nos permitió evaluar adecuadamente la influencia de variables de composición y configuración del paisaje en la diversidad de rapaces diurnas del bosque tropical seco. En el capítulo IV de esta tesis, usamos las métricas del paisaje medidas en la escala del efecto para rapaces diurnas. Determinamos que las respuestas a la composición y configuración del paisaje son diferentes para rapaces diurnas con distinto grado de especialización en el hábitat. De acuerdo a lo esperado, encontramos que la cobertura forestal fue la variable del paisaje con mayor importancia para las rapaces forestales, lo cual es consistente con otros grupos biológicos (Fahrig 2017) y aves especialistas del bosque (Smith et al. 2011; Carrara et al. 2015). La cobertura forestal y fragmentación del bosque tuvieron un efecto negativo en la diversidad beta temporal de las rapaces forestales, probablemente por una mayor estabilidad en los territorios de las rapaces forestales en grandes extensiones de bosque. La densidad de borde fue la variable más importante para las especies de rapaces asociadas a los bordes. Esto contrasta con un análisis reciente donde se muestra que la riqueza de aves en zonas templadas está fuertemente relacionada con la cantidad de hábitat en el paisaje, pero no con la fragmentación del mismo (De Camargo et al. 2018). Nuestros resultados sugieren que la abundancia de rapaces del borde depende más de la configuración del paisaje que de la composición del mismo, mientras que la riqueza de especies está influenciada de forma similar por la composición y configuración del paisaje. Contrario a lo observado para las rapaces forestales, la diversidad beta temporal de rapaces asociadas a bordes y áreas abiertas estuvo influenciada positivamente por la cobertura forestal, y además por la dureza de la matriz y densidad de borde. Concluimos que el mantenimiento de extensiones grandes de bosque, los bordes y la presencia de elementos “amigables” para las rapaces en la dureza de la matriz facilitarían el movimiento de rapaces generalistas entre diferentes parches hábitat,

permitiendo dinámicas de complementación del paisaje (Dunning et al. 1992). Concluimos que procesos como *species sorting* (Leibold et al. 2004) y condiciones variables en el ambiente como estacionalidad del bosque y variabilidad anual en cultivos determinarían la composición de especies y la alta beta temporal para las rapaces generalistas del hábitat (Chase and Leibold 2003).

Nuestros resultados mostraron que la fragmentación del bosque tiene un efecto positivo constante en la riqueza de especies de rapaces asociadas a borde y rapaces asociadas a áreas abiertas, estos resultados son consistentes con estudios previos que muestran efectos positivos de la fragmentación en la diversidad de distintos taxa (revisado en (Fahrig 2017). Consideramos que la influencia positiva de la fragmentación del bosque está relacionada con los efectos positivos asociados a los bordes, la conectividad funcional del paisaje y dinámicas de complementación (para rapaces generalistas de hábitat) y suplementación del paisaje (Dunning et al. 1992).

En esta tesis presentamos el primer estudio que determina la influencia de un disturbio natural mayor en aves depredadores tope, para las cuales no se tenía información acerca de su respuesta ante eventos de huracanes. Asimismo, contribuimos al conocimiento acerca de la influencia de la estacionalidad del hábitat en este grupo de aves, el cual no se había evaluado para ensamblajes de rapaces en el bosque seco. Finalmente, evaluamos la respuesta de las rapaces diurnas ante los cambios en el paisaje, considerando y evaluando por primera vez la escala del efecto del paisaje en las rapaces diurnas. El obtener la escala del efecto permitió develar adecuadamente las relaciones de la estructura del paisaje con la diversidad de rapaces diurnas en el bosque seco.

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