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DE SAN NICOLÁS DE HIDALGO

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Comparación del efecto de dos huracanes con diferente grado de intensidad sobre el ensamble de anfibios y reptiles en diferentes estadios sucesionales de un bosque tropical seco de Chamela, Jalisco, México.

Tesis

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1. ABSTRACT

The response of amphibian and reptile populations after a hurricane can be very varied and will depend on the intensity of the hurricanes, the frequency of hurricanes in the same region, the resilience of the populations and the habits of the species. The effect of hurricanes on amphibians and reptiles is relatively new and little is known about the responses of these groups. In this thesis we evaluated the effect of two hurricanes with different category of intensity on the region of Chamela, Jalisco in the Mexican Pacific. This region was affected by hurricane "Jova" category 2 on the Saffir-Simpson scale and maximum sustained winds of up to 165 km/h on October 11 and 12, 2011, also hurricane Patricia category 5 on the Saffir-Simpson scale impact the same coast of Jalisco on the night of October 23, 2015. Both hurricanes affected large areas of dry tropical forest. In this study we used different successional stages: Pasture (0-0), Early Forest (5-6), Young Forest (8-10), Intermediate Forest (15-17) and Old Growth Forest (>50years; (OGF). Each successional age had three replicates of 1 ha each. The sampling effort per outing post Hurricane Patricia was the same (6 person hours), 630 hours of sampling at the different stages as in the baseline work, two years before hurricane Jova and two years after Hurricane Jova. In general, the abundance of anurans, lizards and snakes was significantly lower after the hurricanes, but only for lizards and anurans was the interaction between successional stages and the hurricane significant. In addition, species richness and diversity increased for lizards and decreased for snakes after hurricanes. Although, the pattern of anuran species richness among successional stages was similar after the hurricanes, but the richness in OGF decreased markedly after hurricanes Jova and Patricia.

Keywords: tropical dry forests; human and natural disturbances; hurricanes; Herpetofauna; Sucesional Stages.

2. RESUMEN

La respuesta de las poblaciones de anfibios y reptiles después del paso de un huracán puede ser muy variada y dependerá de la intensidad de los huracanes, la frecuencia de huracanes en una misma región, la resiliencia de las poblaciones y además de los hábitos de las especies. El efecto que tienen los huracanes sobre anfibios y reptiles es relativamente nuevo y se sabe poco de las respuestas de estos grupos. En la presente tesis se evaluó el efecto de dos huracanes con diferente grado de intensidad sobre la región de Chamela, Jalisco en el Pacífico Mexicano. Esta región fue afectada por el huracán "Jova" de categoría 2 en la escala de Saffir-Simpson y vientos máximos sostenidos de hasta 165 km/h los días 11 y 12 del mes de Octubre del año 2011, además el huracán Patricia categoría 5 en las escala de Saffir-Simpson tocó tierra impactando la misma costa de Jalisco en la noche del 23 de octubre de 2015. Ambos huracanes afectaron grandes áreas de bosque tropical seco. En este estudio utilizamos diferentes edades sucesionales: Pastizal (0-0), Bosque temprano (5-6), Bosque Joven (8-10), Bosque Intermedio (15-17) y Bosque Maduro (>50años; (OGF). Cada edad sucesional tuvo tres réplicas de 1 ha cada una. El esfuerzo de muestreo por salida post huracán Patricia fue el mismo (6 horas/persona), 630 horas de muestreo en los diferentes estadios al igual que en los trabajos que se usaron como base, dos años previos al huracán Jova y dos años después del huracan Jova. En general, la abundancia de anuros, lagartijas y serpientes fue significativamente menor después de los huracanes, pero sólo para las lagartijas y los anuros la interacción de los estadios sucesionales y el huracán fue significativo. Además, la riqueza y la diversidad de especies aumentó en el caso de las lagartijas y disminuyó en el caso de las serpientes después del impacto de los huracanes. Aunque, el patrón de riqueza de especies de anuros entre los estadios sucesionales fue similar después de los huracanes, la riqueza en OGF disminuyó notablemente después de los huracanes Jova y Patricia.

Palabras Clave: Estadios sucesionales; Anfibios; Huracán; Reptiles; Chamela.

3. INTRODUCCIÓN

Las poblaciones de anfibios y reptiles están declinando a nivel global. Se considera que aproximadamente el 32% de las especies de anfibios están en peligro de extinción y el 43% en riesgo (Stuart et al., 2004), mientras que para los reptiles se considera que aproximadamente el 20% están en peligro de extinción (Böhm et al., 2013). Los factores causales de estos declives poblacionales incluyen la pérdida y modificación del hábitat, contaminación, especies invasivas, enfermedades infecciosas y el cambio climático global (Todd et al., 2010; IUCN, 2008; Lavilla, 2001 Pounds et al., 2006). Uno de los hábitats tropicales que albergan una importante diversidad de vertebrados, son los bosques tropicales secos (BTS) (Murphy y Lugo, 1986; Ceballos y García, 1995). Dentro de los bosques tropicales el BTS ocupa el 42% de la superficie tropical mundial (Murphy y Lugo, 1986) y es uno de los principales tipos de vegetación del occidente de México, cubriendo aproximadamente el 60% del área ocupada por los bosques tropicales del país (García, 2006). Este tipo de vegetación se caracteriza por una prolongada época de estiaje que puede durar hasta ocho meses, y una corta época de lluvias que por lo general ocurre entre julio y octubre. Adicionalmente, presenta una considerable variación espacial en estructura y composición de diversidad alpha y beta de especies a nivel de paisaje (Bullock et al., 1995; Trejo-Vázquez y Dirzo, 2000; Noguera et al., 2002). En la actualidad, el BTS es de los ecosistemas terrestres más amenazados (Vieira et al., 2006) y en México únicamente el 27% de estos bosques permanece intacto (Trejo-Vázquez y Dirzo, 2000).

Los bosques tropicales secos son un hábitat importante para los anfibios y reptiles ya que se ha encontrado una alta riqueza y abundancia de este grupo, además albergan una gran proporción de endemismos para este grupo en el país (Ceballos y García, 1995; Ceballos et al., 2010). La pérdida de BTS ha resultado presumiblemente en el declive de las poblaciones de anfibios y reptiles, pero la afectación a nivel de abundancia y estructura de los ensambles de anfibios y reptiles ha sido poco evaluada (Suazo-Ortuño et al., 2008; Suazo-Ortuño et al., 2015). Los paisajes antes cubiertos por BTS están ahora dominados por mosaicos agrícolas, compuestos por áreas de BTS maduros entremezclados con bloques de BTS en diferentes estadios de sucesión secundaria y parcelas agrícolas y ganaderas (Suazo-Ortuño et al., 2008).

El efecto de los estadios sucesionales se ha reportado para varios grupos, en el caso del BTS, estudios como el de Avila-Cabadilla et al. (2009), registran un incremento en abundancia y diversidad de murciélagos a medida que avanza el estadio sucesional. Los estudios que se han realizado en ecosistemas tropicales secos sobre la respuesta de anfibios y reptiles a modificaciones del hábitat se han desarrollado en el contexto de la perturbación del hábitat y la fragmentación (i.e. Suazo-Ortuño et al. 2008, Suazo-Ortuño et al., 2011). El efecto que tienen el abandono de tierras convertidas en bosques secundarios se ha documentado para anfibios y reptiles, en donde se reporta el efecto negativo de los estadios sucesionales es decir entre más perturbada o menos años de abandono tengan las áreas de estudio menor riqueza y diversidad se encuentra (Gardner et al., 2007), mientras que también se ha reportado que los bosques secundarios son refugios importantes para la herpetofauna, ya que se reportan ensambles muy parecidos o sin diferencias significativas con relación a los bosques maduros (Cáceres-Andrade y Urbina-Cardona 2009; Burbano-Yandi et al., 2015). Por consiguiente, la importancia de los bosques secundarios como facilitadores de la restauración pasiva del paisaje y la recuperación de la biodiversidad en los paisajes fragmentados por las actividades antrópicas es cada vez más reconocida (Suazo-Ortuño et al. 2008, 2015; Bowen et al., 2007; Walker et al., 2007, Chazdon, 2008; Stokstad, 2008; Brown y Lomolino, 1998; Coulson, 1993; Williams et al., 1997; Sanders y Edge, 1998).

Adicionalmente a los disturbios antropogénicos, los disturbios naturales como huracanes y tormentas tropicales pueden afectar drásticamente la estructura vegetal y por consiguiente los ensambles animales. En años recientes se han reconocido cambios severos en el clima, por lo que se han hecho diversos estudios para evaluar posibles factores causales (Crowley, 2000; Hardy, 2003; Stott et al., 2006). Los huracanes y las tormentas tropicales (H-TT) son dos fenómenos naturales que frecuentemente azotan la costa del Pacifico mexicano. Estos pueden tener impactos severos en la infraestructura costera (Salazar, 2001) y la biodiversidad (Jauregi, 1989; Jauregi et al., 1980; Walker et al., 1996; Lugo et al., 2000). Los H-TT pueden influir de manera marcada en la dinámica de los bosques de las regiones de influencia, los bosques pueden presentar modificaciones en las tasas de reclutamiento, mortalidad, crecimiento de las especies arbóreas, defoliación, daño estructural en los árboles, incluyendo desenraizamiento y pérdida de copas (Tanner *et al*., 1991; Boucher et al., 1994; Everham y Brokaw, 1996; Sánchez-Sánchez y Islebe, 1999; Salazar-Vallejo, 2002; Gerald, 2009) lo que modifica la distribución de la biomasa estructural del bosque (Lugo, 2008; Maass et al., 2017; Suazo-Ortuño et al., 2018), además favorece cambios en el microclima del bosque con la abertura del dosel (Sánchez-Sánchez y Islebe, 1999; Lugo, 2008). Debido a que los efectos de los huracanes en distintas áreas geográficas y comunidades de ambientes marinos y costeros han sido reportados desde hace muchos años, se sabe que el impacto de un huracán puede transformar en un día la distribución y abundancia de los organismos y generar patrones muy distintos a los previos (Woodley *et al.* 1981) y a largo plazo, estos episodios destructivos promueven cambios evolutivos en el ecosistema (Boero 1996; Scheffer et al. 2001). Aunque los huracanes y tormentas tropicales azotan de manera uniforme los bosques tropicales secos incluyendo las matrices en diferentes categorías de regeneración los bosques maduros son más propensos a sufrir defoliación y daño estructural en los árboles por efecto de vientos huracanados, incluyendo desenraizamiento y pérdida de copas debido a que tienen árboles notoriamente de mayores tallas que el resto de los estadios sucesionales (Tanner et al. 1991, Everham y Brokaw, 1996). Los estudios señalan que los bosques azotados frecuentemente por huracanes están adaptados a los disturbios que ocasionan dichos fenómenos, por lo que hay poca diferencia entre aquellos bosques que han sido afectados por huracanes y tormentas en épocas recientes y los abatidos por un huracán hace 24 años (Ferrando, 1998). Para la herpetofauna se ha encontrado que casi todas las especies presentes en el lugar del impacto del huracán se modifican de forma notoria (Nicoletto, 2013; Vilella y Fogarty, 2005) esto puede deberse a que se encuentran refugiadas o porque sus poblaciones y microhábitats se vieron afectados, otro de los fenómenos que se refleja tras el paso de un huracán de mayor intensidad es que las especies raras se vuelven aún más raras o desaparecen por completo (Schriever et al., 2009; Nicoletto, 2013). Algunos trabajos reportan que el efecto que tienen los huracanes y tormentas tropicales sobre el ensamble de anfibios y reptiles se da de manera diferencial dependiendo de la intensidad y duración de estos fenómenos además de la categoría de los huracanes dada por la escala Saffir-Simpson (Nicoletto, 2013; Enge, 2005; Schriever, 2009; Woolbright en 1991), Pérez et al. (2012) reportan para reptiles en Puerto Rico que las especies asociadas al litoral son más afectadas por huracanes que las especies con poblaciones alejadas del litoral. También se ha reportado que los huracanes debido a la gran cantidad de precipitación que producen pueden favorecer la abundancia, sitios de percha y microhábitat para los anfibios (Nicoletto, 2013; Enge, 2005). En un estudio donde se evaluó el ensamble de anfibios y reptiles tras el paso de dos huracanes se encontró que, aunque la abundancia y diversidad de la comunidad disminuye tras el paso del primer huracán después del segundo se vuelve una comunidad con mayor equitatividad tanto en abundancia como en diversidad (Schriever et al., 2009). Vilella y Fogarty (2005) reportan el daño antes y después del huracán George de categoría V para la cordillera central de Puerto Rico, encontrando que el paso del huracán afecta de manera diferencial a las especies de *Eleutherodactylus* presentes en la zona de impacto, algunas especies anfibios tendieron a disminuir, mientras que otras se vieron favorecidas o sin cambios tras el paso del huracán, los declives son causados por la alta especialidad del hábitat en algunas especies mientras que el aumento es aprovechado por las especies generalistas. En el caso de la herpetofauna los aspectos estructurales del hábitat, como la cobertura del dosel del bosque y la heterogeneidad, son características físicas que influyen en la estructura y composición de los ensambles de herpetofauna (Urbina-Cardona et al., 2006). Por lo que al modificar los huracanes la estructura de los bosques se ven afectados también los ensambles de anfibios y reptiles.

En la región de Chamela, Jalisco, México los bosques secundarios con diferentes edades de abandono constituyen elementos importantes en el paisaje antropizado (Suazo-Ortuño et al. 2015). Estos bosques resultados del disturbio antrópico, también sufren los embates de disturbios naturales como los huracanes, por lo que es de esperarse que los distintos estadios sucesionales del BTS, al no tener la misma estructura y composición de la vegetación respondan de manera diferencial al impacto de los huracanes y en consecuencia en la respuesta de las especies que los habitan. Por sus características biológicas los anfibios y reptiles son altamente sensibles a la perturbación del hábitat, ya sea natural o antrópica, lo cual los convierte en indicadores de la integridad de los ecosistemas (Blaustein y Wake, 1995). Hasta ahora el único estudio que evalúa cambios en los ensambles de anfibios y reptiles durante la sucesión secundaria en BTS después de un huracán es el de Suazo-Ortuño et al. (2018), quienes no encuentraron diferencias significativas en abundancia y diversidad de anfibios y reptiles a lo largo de la sucesión secundaria. El conocimiento de la respuesta funcional y estructural de los anfibios y reptiles a los efectos sinérgicos de disturbios antrópicos y naturales son esenciales para el manejo y la conservación local de los bosques y de la herpetofauna, por lo que tomando como base los estudios de Suazo-Ortuño et al., 2015, 2018a, b, se evaluaron y compararon los efectos acumulativos sobre el ensamble de anfibios y reptiles de los huracanes Jova y Patricia que azotaron con diferente intensidad los bosques secundarios del BTS de Chamela, Jalisco.

4. ARTICULO I

Effect of hurricanes on amphibians and reptiles: a review.

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Abstract

Natural disturbances modulate biodiversity dynamics depending on their frequency, severity, rotation period, and intensity. Specifically, hurricanes impact terrestrial species populations and the intensity of impact depends on return interval, seasonality, geographic location, and if it strikes an island or a continent. In the present study, we reviewed 36 studies on the effect of hurricanes on the herpetofauna. In the American continent and associated islands, 116 hurricanes have occurred from 1989 to 2018, with 37% impacting the Caribbean and Antilles. Of all studies published on the effects of hurricanes on amphibians and reptiles, 68.8% correspond to studies from the Caribbean and Antilles. Considering studies from different regions of the world on the effects of hurricanes on herpetofauna, lizards were the most studied group, with 41% of the publications, followed by herpetofauna (25%) and frogs (22%). Studies on amphibians and reptiles were conducted more frequently when higher category hurricanes occurred (60.4% on categories IV and V). The most frequently measured response variable was species abundance, which allowed ranking herpetofauna species according to their response to the impact of hurricanes: 76 species were positively affected, 87 species were negatively affected, and 85 species showed no signs of population change. These differential responses highlight the need for future research lines, including studies in trait-based ecology, ecophysiological tolerances, microhabitat use, and occupancy models. Those topics are key to better understanding the mechanisms of adaptation to disturbance regimes and environmental filter effects over herpetofauna.

Key words: bibliometrics, disturbance, frogs, herpetofauna, lizards, snakes.

1. Introduction

Hurricanes constitute a severe natural disturbance in the Caribbean, northern Pacific Ocean, Atlantic Ocean, and northern Asia (Capurro, 2001; Salazar, 2001; Yáñez-Arancibia et al., 2010; Esteves, 2017). The Saffir-Simpson Hurricane Wind Scale classifies hurricanes into categories distinguished by the intensities of their sustained wind speed (Simpson, 1971). The effect of hurricanes on islands or continents might greatly differ, as islands are generally more exposed to the deleterious effects of hurricanes and continental areas are frequently protected by bays, peninsulas, or archipelagos (McCoid, 1996; Spiller et al., 1998; Schoener et al., 2004; Schriever et al., 2009; Fickert, 2018). Depending on their frequency and intensity, hurricanes can severely impact coastal infrastructure (Salazar, 2001) and the structure and dynamics of the vegetation (Jauregi, 1989; Walker et al., 1996; Lugo et al., 2000; Van Bloem et al., 2005; Flynn et al., 2010).

Ecosystems frequently exposed to hurricanes are highly resilient, because in general, after twenty years of being impacted by a hurricane, forests tend to be structurally similar to those that have not been impacted (Ferrando, 1994, 2001). Upon hurricanes' arrival to the coast, effect on forests depends on the intensity of the sustained wind speed, the volume of precipitation, and the duration of the meteorological phenomenon (Tanner et al., 1991; Boucher et al., 1994; Van Bloem et al., 2005; Flynn et al., 2010). For example, hurricanes of a great intensity (categories IV or V) might cause (Figure 1): (1) structural changes in the vegetation, including: i) changes in the forest canopy due to strong winds that uproot and knock down medium and large sized trees (Hernández-Díaz et al., 2012), accumulating litterfall and coarse woody debris in the forest floor (Lodge et al. 1991, Zimmerman et al., 1995; Herbert et al., 1999); ii) changes in the understory due to the recruitment of a large number of seedlings caused by canopy openings (Haas-Ek, 2019); iii) changes in soil properties due to the accumulation of litterfall on the ground, and the dragging of organic matter and rocks by heavy rains (Shiels et al., 2014); iv) changes in the water bodies causing floods and the overflow of rivers and canals, carrying with them organic matter debris from other places (Hernández & Arias, 2011; Walle & Morales, 2015) and also salt water intrusion

(Schriever et al., 2009) causing major damages to breeding habitat for amphibians (Wells 2007); (2) changes in the forest micro and macroclimate (Sánchez-Sánchez & Islebe 1999; Lugo, 2008) impacting forest floor dryness following the opening of the canopy and a period of decreased rainfall after the hurricane (Joglar and Burrowes 1996; Woolbright 1997); (3) changes in animal communities (Suazo-Ortuño et al. 2018b) due to changes in species richness (Nicoletto 2013), dispersal (Censky et al., 1998, Schoener and Schoener 1983, 1984, Losos 2009) and the intrusion of fish predators (Palis 1996, Grazulis 2001); (4) Changes in trophic structure: the strength with which the winds hit the trees can affect insect composition, biomass and abundance (Dial and Roughgarden, 2004) as well as plant phenology, causing a decrease in the food supply for many vertebrate species (Angulo-Sandoval et al., 2004; Renton et al., 2018) as well as disturbing their refugees (Meshaka 2001). Finally, increasing in light availability allows for new species to colonize or establish (Waide 1991; Hoopes and Marchetti 2007; White et al. 2010), increasing breeding activity at newly created microhabitats (Meshaka 1993, 2001) (Figure. 1).

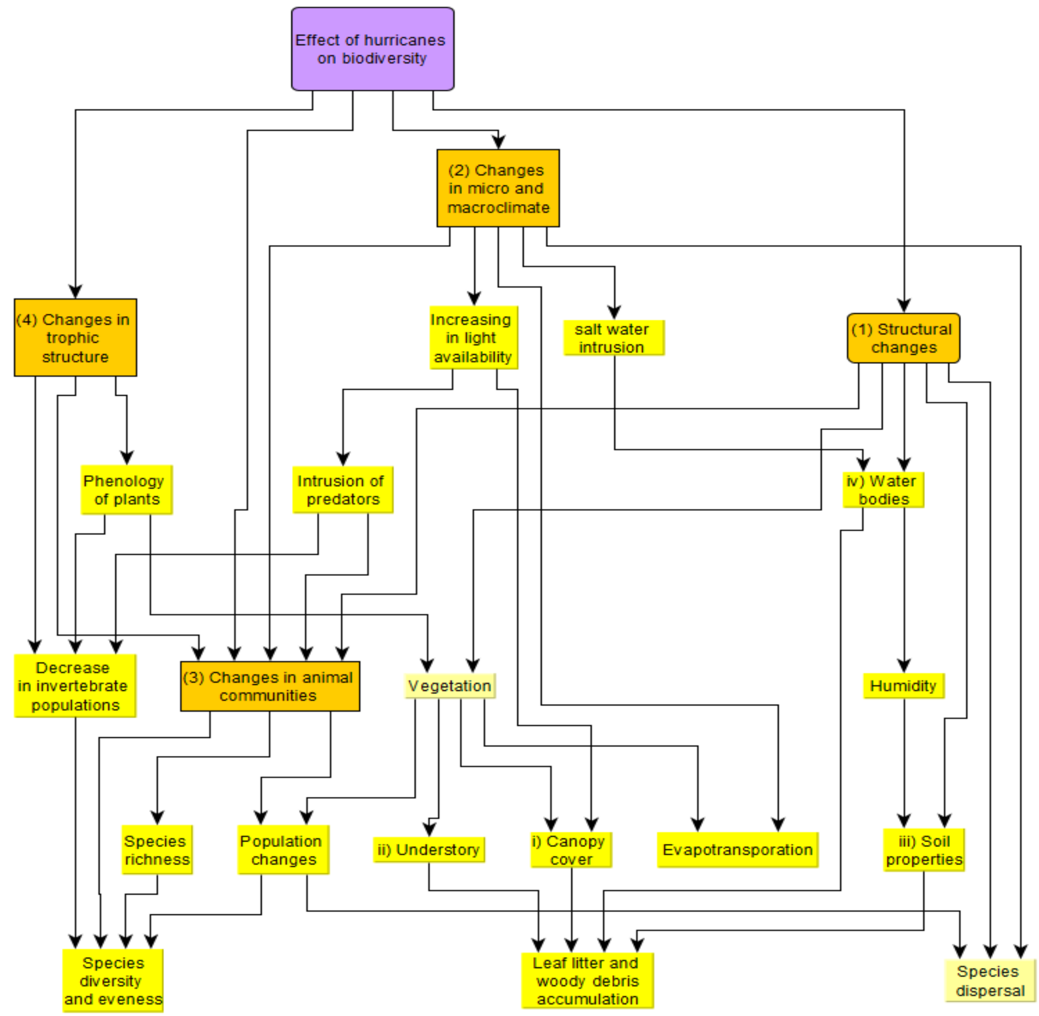


Figure. 1 Causes and effects of hurricane impact on tropical forests. Orange shapes indicate the core effects of high intensity huricanes on terrestrial habitats and animal communities. Yellow shapes are specific variables, from scientific literature, that are affected after the strike of a hurricane.

Animal species evolving in regions with frequent and intense natural disturbance regimes tend to have greater adaptation capacity to novel (anthropogenic) disturbances (Betts et al., 2019). However, due to the rise in ocean temperatures and accelerated climate change, higher-category hurricanes have become increasingly recurrent and unpredictable (Emanuel

1987; Webster et al., 2005; Emanuel, 2013), threatening the resilience of forests (Imbert et al. 2008) and associated herpetofauna communities (Marroquín-Páramo et al. 2020). Amphibians and reptiles might be markedly affected by the impact of hurricanes on their habitats due to the strong relationship between microclimate conditions and forest structure (Woolbright, 1991; Cortes-Gómez et al., 2013). The effects of hurricanes on amphibian and reptiles might disrupt key ecosystem trophic relations (Valencia-Aguilar et al. 2013), for example, it has been documented that lizard populations reduction after the strike of a hurricane modifies herbivores' assemblages and the abundance of some invertebrates such as moths and spiders (Spiller & Schoener, 2008; Spiller & Schoener, 2007).

The knowledge about the mechanisms in which amphibians and reptiles respond to hurricanes is markedly limited, even with the evident threats associated with the increased intensity and frequency of hurricanes (Marroquín-Páramo et al., 2020). It is, therefore, important to evaluate and synthesize the published information about the herpetofauna responses to hurricanes, highlighting the gaps of knowledge that might be essential for the development of conservation and mitigation strategies in response to these increasingly recurring natural disturbances. The present study aims to: (a) identify the relation between the historical incidence of hurricanes among geographical regions and the number of publications evaluating the effect of hurricanes on the herpetofauna; (b) identify patterns of geographical incidence, categories of recorded hurricanes, herpetofauna taxonomic group studied, and the response variable from studies on the effect of hurricanes on herpetofauna at a global scale; and c) identify levels of herpetofauna species vulnerability to the effects of hurricanes.

2. Methods

A search of scientific literature was carried out in four bibliographic indexation sources (Web of Science, Scopus, ScienceDirect, Google Scholar), from terms directed to title, abstract, and keywords (main sections of document indexation), within a time frame of 1980 to July 2018, with the following query string: (hurricane OR "tropical storm" OR typhoon) AND (amphib* OR toad OR frog OR salamander OR herpet* OR tadpole OR skink OR lizard OR anole OR snake OR squamata OR reptile*).

A total of 204 publications were recovered, of which 168 were excluded by three criteria: (a) 100 publications duplicated among the sources consulted; (b) 58 studies outside the disciplines of interest (e.g. engineering, hydroclimatology, medicine, among others); and (c) nine studies were not considered, as they presented the effects of hurricanes on ecosystem processes without a clear reference to amphibian or reptile species (Figure 2). The remaining 36 publications were selected after a review of their titles and abstracts to define its relevance on the effects of hurricanes on amphibian or reptile species. In addition, the literature cited section of each publication was checked on each publication to avoid overlooking any relevant document in this review, without finding any additional relevant document. The methods section of the 36 selected publications was reviewed in order to register the studied region and location (island or continent), the name and category of the hurricane on the Saffir-Simpson (SS) scale, the taxonomic group of study, and the response biodiversity variable (Table S1).

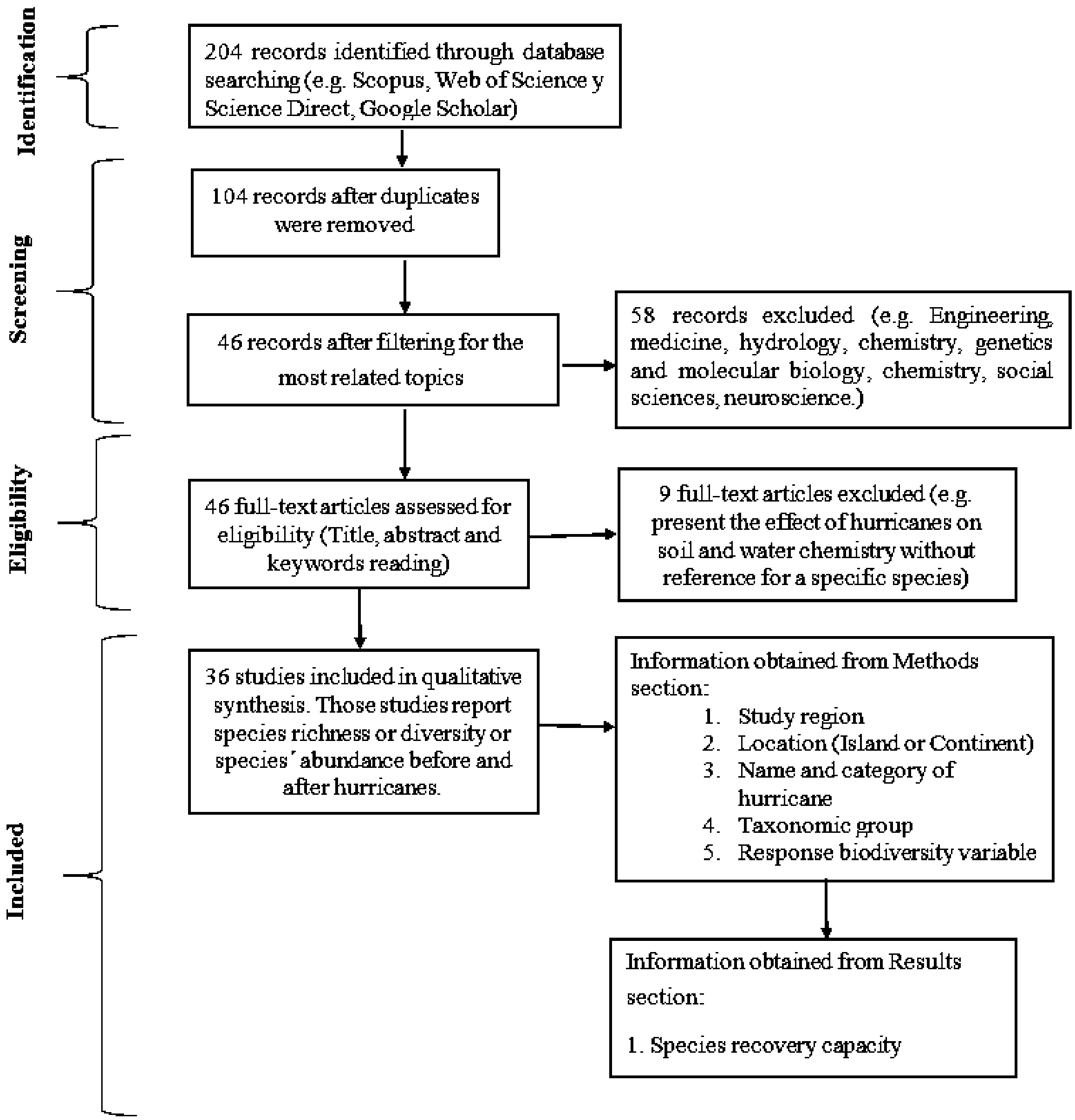


Figure. 2. Number of publications identified, filtered, and chosen for their inclusion in the analysis of the literature.

To manage the metadata of the 36 publications, we used the text mining software VantagePoint (VP) Version 10.0 which allows us to analyze and visualize information to find patterns and relationships (Search Technology Inc, 2020). Number of publications and of hurricanes per category (S-S) by country were compiled and displayed on a map in Excel with the Office 2016 PowerPivot-PowerView add-on. The response biodiversity variable per each study (i.e., species richness, species abundance, assembly structure, morphometrics or genetic structure, among others) were exported to a bibliometric visualization software called VOSviewer Version 1.6.12, which is used to construct maps of keywords based on co-occurrence data (van Eck & Waltman, 2010, p. 524). This co-word analysis is a content analysis technique that uses patterns of co-occurrence of pairs of items (i.e., words or noun phrases) in a corpus of texts to identify the relationships between ideas within the subject areas presented in these texts (He, 1999).

Additionally, we compared the incidence of hurricanes and number of studies among regions of the American continent. Hurricane incidence and intensity (SS) by impacted region in the American continent and associated islands between 1989 and 2018 was obtained by searching in the online portal Weather Underground, which has a network of weather stations, providing a unique capability to provide most local (United States) forecasts based on current weather data points (The Weather Company & IBM Business, 2020).

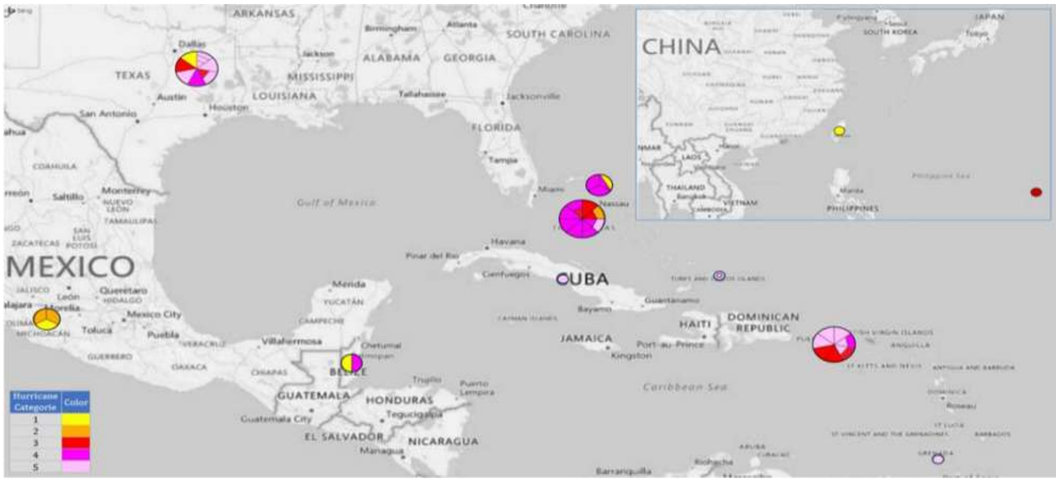
To evaluate the resilience of amphibians and reptiles to the effects of hurricanes, the results section of each of the 36 publications was reviewed to identify changes in species abundance after the strike of hurricanes. In this regard, the responses of amphibian and reptile species to hurricanes were classified, based upon changes in the number of individuals after the strike of the hurricane in the study site, as positive (their abundances increased after the impact of a hurricane on the field sampling site), negative (their abundances decreased after the impact of a hurricane on the field sampling site), or neutral (their abundances did not change after the impact of a hurricane on the field sampling site). To facilitate visualization of the species' groups based on co-occurrence data we used a modularity-based cluster that minimizes the Euclidean distances between all pairs of species. An optimization process was conducted to minimize a weighted sum of squares of those distances to properly visualize the patterns of amphibians and reptiles (network of species) (van Eck & Waltman 2013).

3. Results

3.1 Geographic incidence of hurricanes and herpetofauna studies

Studies of herpetofauna in islands and in the continent represented 68.8% and 31.3%, respectively, of the 36 reviewed publications (Figure 4a, Table S1). The Caribbean and Antilles were the most studied region with 75% of the publications, followed by the Gulf of Mexico (14%), Pacific Ocean (8.0%) and the North Atlantic (3%) (Figure 5). Most studies were on the response of herpetofauna to hurricanes of categories V (35.4%) and IV (25.4%), followed by studies of category I (12.5%), category II (6.2%), and category III (5.5%) (Figure. 3a).

a)



b)

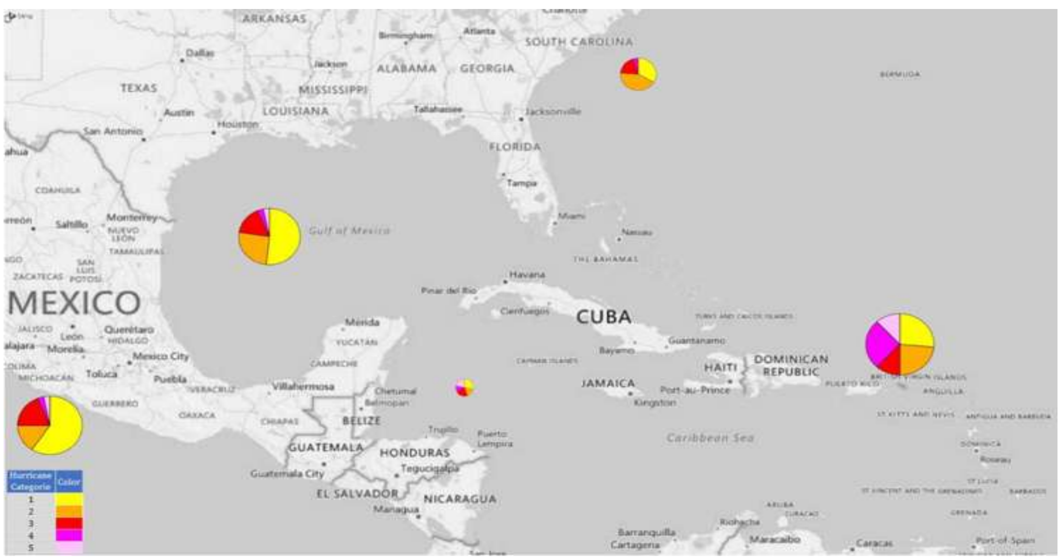


Figure. 3. Number of publications by country. The diameter of the pie graphs represents the number of publications. The divisions of the pie indicate individual publications and, when divided, each division represents the report of more than one hurricane studied in the same document (see Table S1). (a) Categories of hurricanes studied in the documents; and (b) frequency of hurricanes by region of the American continent in the last 10 years (2007-2018). The colors show hurricane category, and the diameter of the circles indicate the number of hurricanes that touched land.

Between 1989 and 2018, 116 hurricanes impacted the American continent and associated islands. Of these, 37 % occurred in the Caribbean and Antilles, 23 % in the Gulf of Mexico, 23 % in the Pacific Ocean and 17 % in the North Atlantic (Figure 3b, Table S2). Because of the warm ocean currents predominant in the Antilles, the occurrence of hurricanes is frequent in this region, and they sometimes change trajectories to other regions, such as the Gulf of Mexico, the Caribbean and the North Atlantic. Most of the hurricanes that strike the American continent (from 1989-2018) were category I and II (with 41 % and 25 %, respectively) (Table S2). The Antilles, presented the highest intensity hurricanes in the Saffir-Simpson scale (categories IV and V), followed by the Pacific Ocean and the Gulf of Mexico, where hurricanes of categories I, II and III, were more frequent (Figure 3b, Table S2).

3.2 Studies of the effect of hurricanes on herpetofauna by taxonomic group and the biodiversity variables evaluated

Of the 36 evaluated publications on the effects of hurricanes on herpetofauna, the first were published in 1991, about 41% were published between this year and 2004, and about 58.33% between 2005 and 2018 (Figure 4a-b; Table S1). The first studies reporting the effects of hurricanes on the herpetofauna were from islands, mainly considering lizards and anurans (Regan, 1991; Woolbright, 1991; Spiller et al., 1998). Lizards were the most studied taxon (15 publications), followed by the herpetofauna (8 publications), and anurans (9 publications) (Figure 4b). The least studied group was snakes, with only two publications (Liu et al., 2010; Wunderle et al., 2004). In the case of turtles and the whole clade of reptiles only one study was found for each group (Dodd et al., 2006) (Figure 4b). Regarding frogs, the main location studied was the island of Puerto Rico with a total of 62.5% of the publications (Figure. 5b), while the Pacific Oceanic (Mexico), North Atlantic, and Caribbean (Belize) regions presented 12.5% of the publications (Figure. 5a).

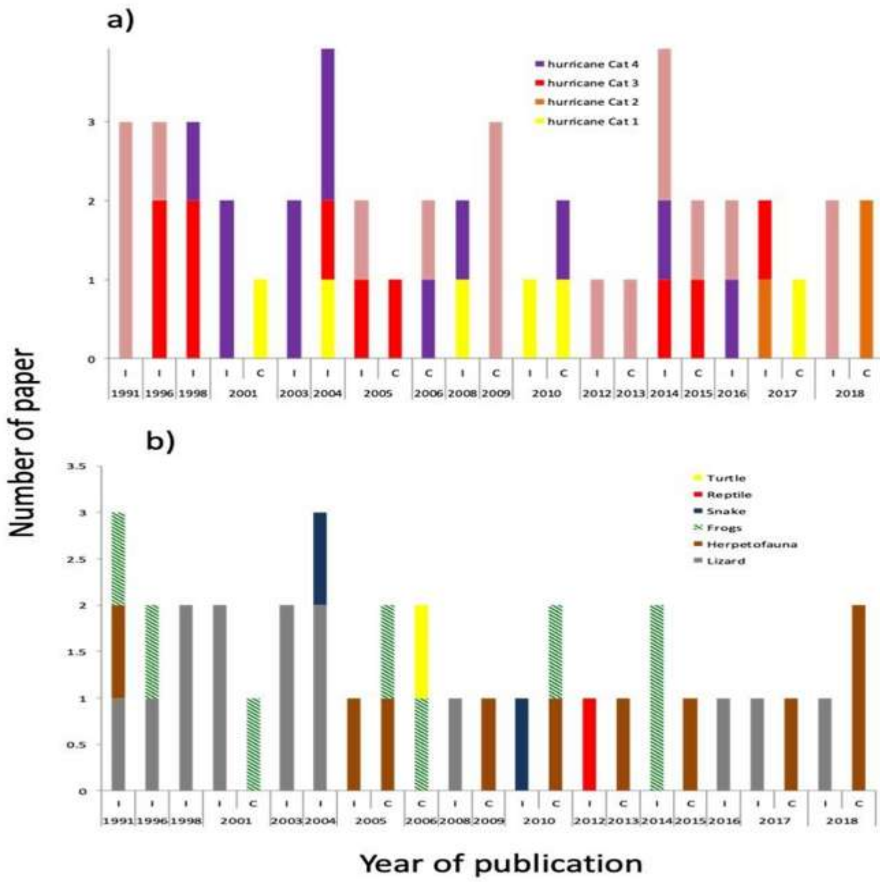


Figure. 4. Number of publications about the effects of hurricanes on the herpetofauna of islands and continental land per year: (a) Hurricanes reported by document (each document evaluated between one and three hurricanes); (b) Taxonomic groups evaluated. C= continental and I= Islands.

Although we identified 77 response biodiversity variables (Figure 6) from the 36 reviewed publications (Figure 6), our results showed that the effects of hurricanes on amphibians and reptiles were mainly evaluated through changes in population size, population dynamics, species richness and interactions (Figure 6). From all the variables, abundance presented the highest number of links (n=16) with other variables and this cluster of variables presented a greater integration within the research of the effects of hurricanes on the herpetofauna (Figure. 6).

Figure. 5 Number of publications by taxonomic group and region. The diameter of the pie graphs represents the number of publications. The divisions of the pie indicate individual publications by taxonomic group.

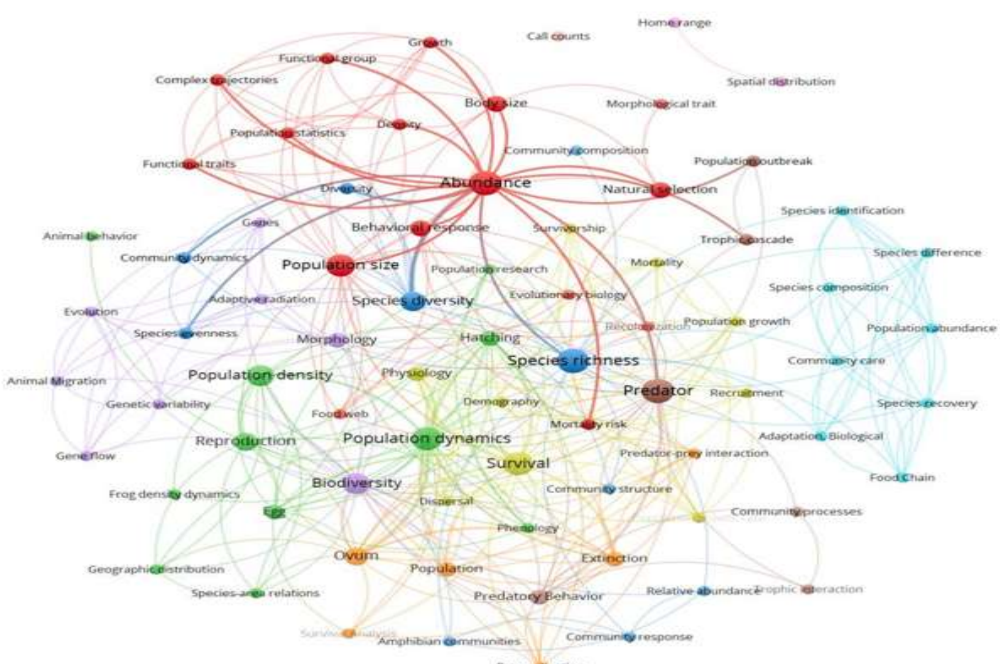


Figure. 6. Network of measured biological response variables to study the effect of hurricanes on herpetofauna. The size of the circle represents the frequency of occurrence, in which larger circles represent response variables studied in more than one document.

3.3 Hurricane effects on herpetofauna taxonomic groups

From the results of 18 publications, we found that a network of 76 herpetofauna species was positively affected. From these species, three (*Lampropeltis triangulum*, *Nerodia fasciata*, and *Eleutherodactylus coqui*) were the most frequently mentioned as positively affected (Figure 7).

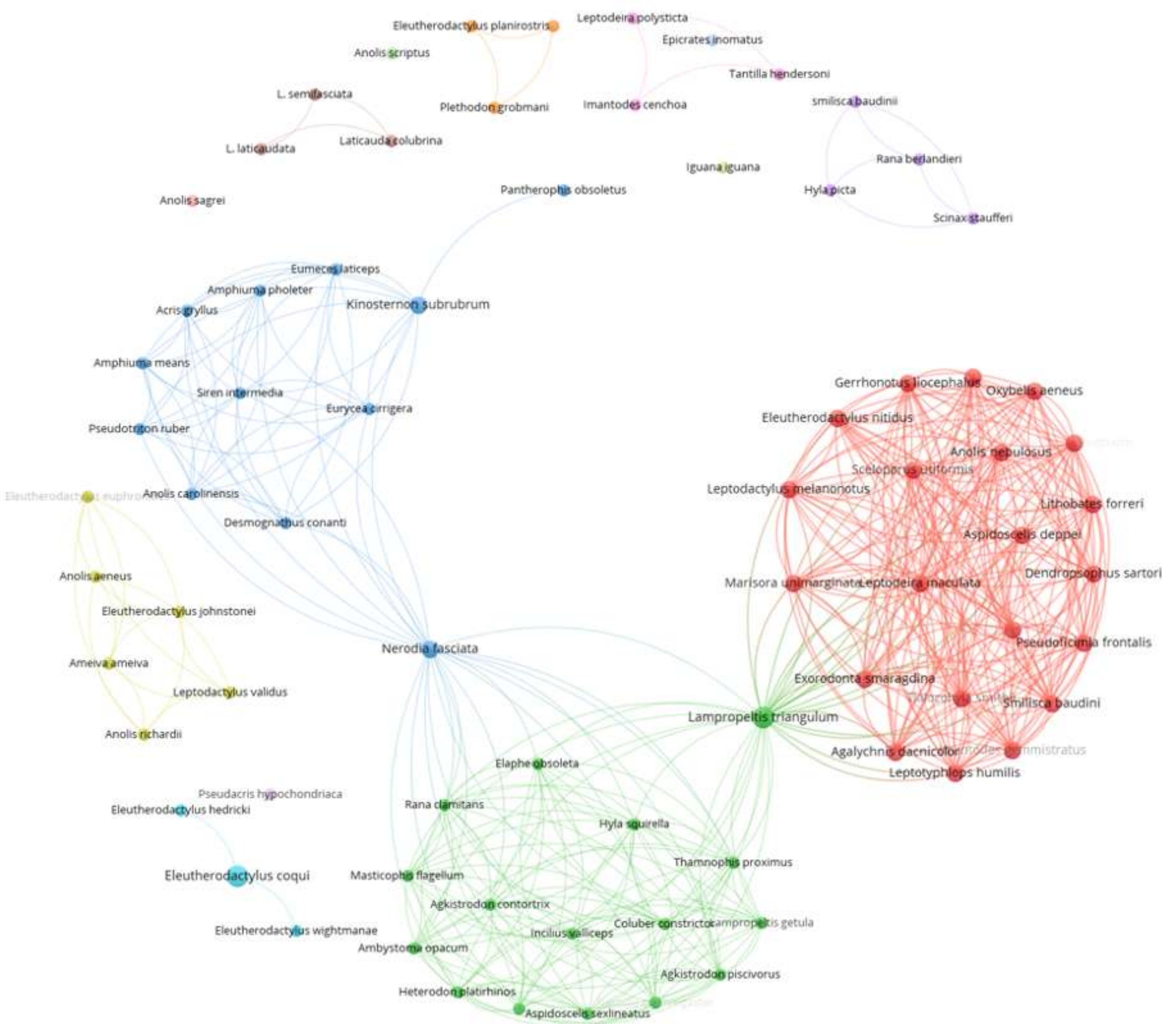


Figure. 7. Network of species positively affected by the arrival of the hurricane in their habitat. The size of the circle represents the frequency of occurrence, with larger circles representing species reported in more than one document.

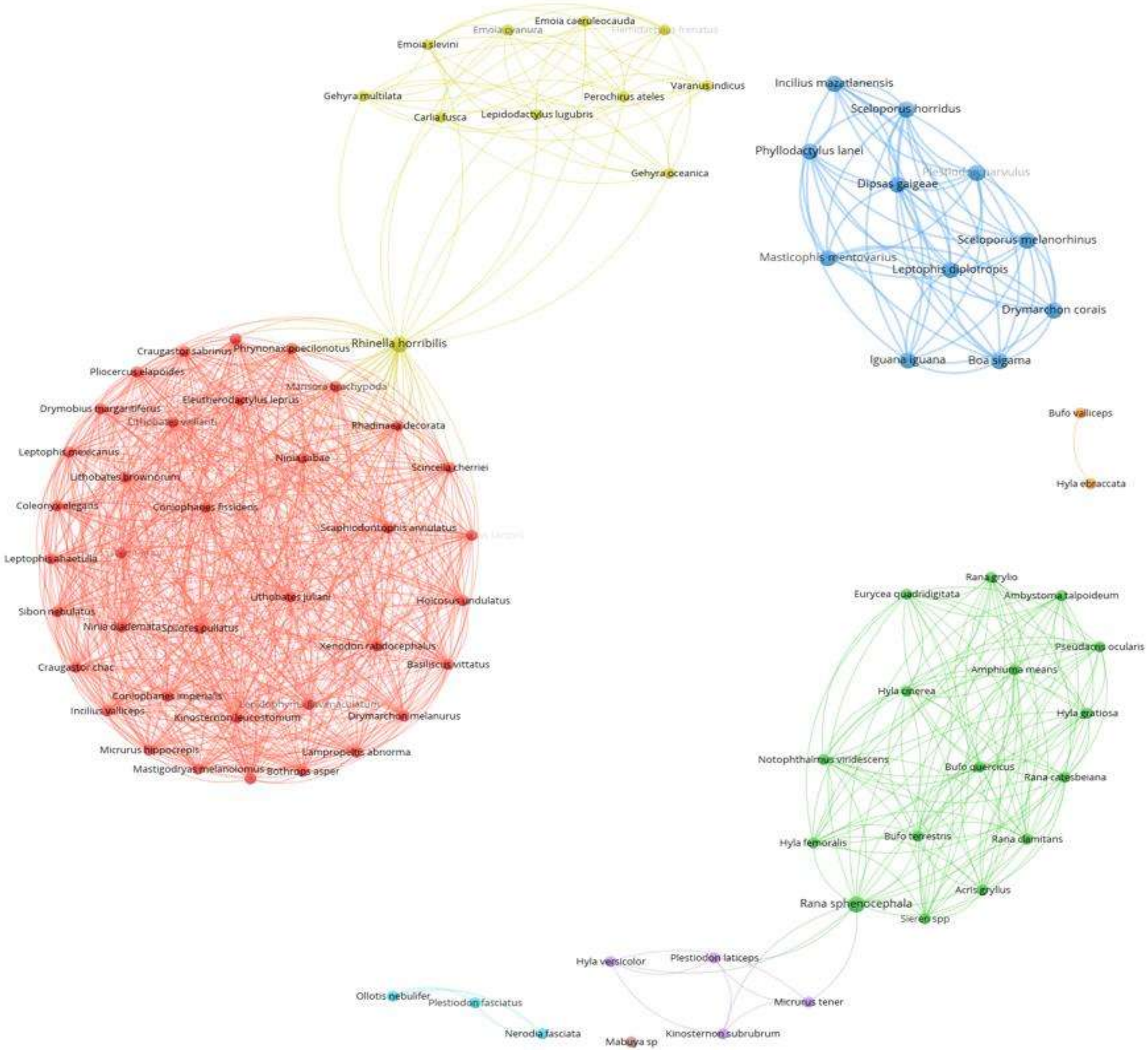


Figure. 8. Network of species negatively affected by the arrival of the hurricane in their habitat. The size of the circle represents the frequency of occurrence, with larger circles representing species reported in more than one document.

Data from 25 publications indicated that a network of 87 species was negatively affected by hurricanes (Figure 8). The most frequently reported species were *Anolis sagrei* (eight publications), A. *carolinensis* (three publications), and *Acris crepitans*, *Gastrophryne carolinensis*, *Pseudacris crucifer* (two publications each). These species were intermediate nodes in this species network (Figure. 8). We found that *Anolis* and *Eleutherodactylus* generes were most frequently mentioned as negatively affected by hurricanes. The species networks (85 species, mentioned in nine publications) which appeared to be unaffected by hurricanes formed eight clusters (Figure 9). Thirteen of the 85 species were reported in two publications to present a neutral response (Figure. 9). In this network, *Rana sphenocephala* (Gunzburger et al., 2010; Nicoletto 2013) and *Rhinella horribilis* (McCoid 1996; Gray & Strine 2017) formed intermediate nodes between two studies. The rest of the species that presented a neutral response to the effects of hurricanes had a single report (Figure 9). Most of the publications that showed negative effects of hurricanes (IV or V categories) on amphibian and reptile species also mentioned structural damage to the forest, modifying temperature and humidity patterns, microhabitat destruction and occurrence of floods (Woolbright, 1991; Schoener et al., 2001a, 2001b; Losos et al., 2003; Schoener & Spiller, 2006; Schriever et al, 2009; Gunzburger, 2010; Nicoletto 2013; Klawinski et al., 2014; Shiels et al., 2014; Suazo-Ortuño et al. 2018b). Although we found species that respond similarly to hurricanes in different publications, there were species that presented different responses among publications (e.g. *Agkistrodon piscivorus, Hyla squirella, Hyla cinerea,* and *Gastrophryne carolinensis*).

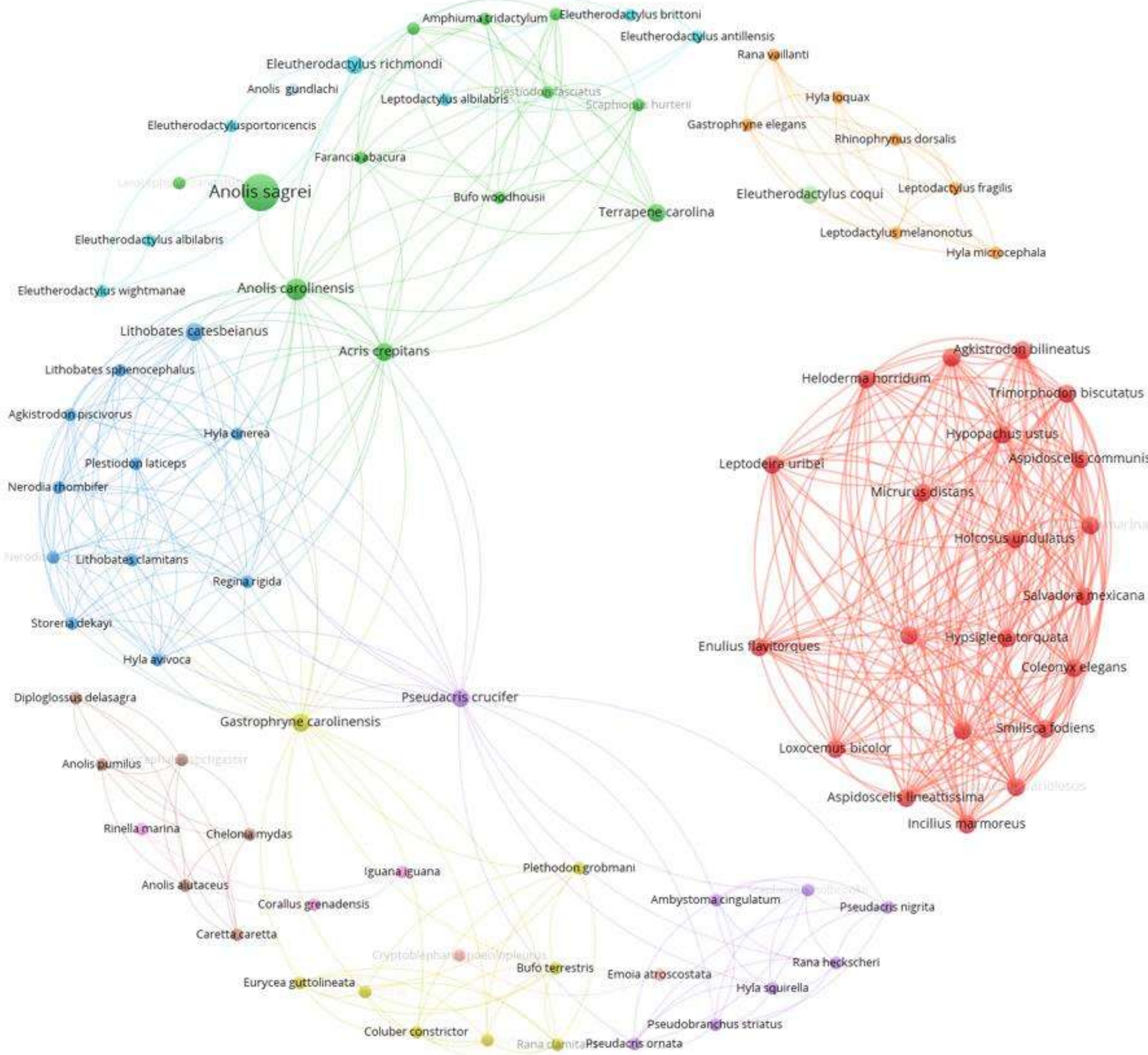


Figure. 9. Network of species without noticeable change in abundance (neutrally affected) after the arrival of the hurricane in their habitat. The size of the circle represents the frequency of occurrence, with larger circles representing species reported in more than one document.

4. Discussion

In the American continent we found an increase in the incidence of hurricanes, from a mean of 3.5 hurricanes per year in the 90´s to 4.2 hurricanes per year in the 2000´s, with some years (2005, 2010, 2012 and 2017) presenting 6 or 7 hurricanes (Table S2). Although the number of studies on the effect of hurricanes on amphibians and reptiles has been fairly constant through time (1 to 3 studies published per year; Figure 4), between January 2019 to June 2020, seven studies were published, most of these reporting the effects of category V hurricanes.

4.1 Geographic regions and herpetofauna studies

Most studies on the response of herpetofauna to hurricanes have been conducted on islands (67 %) as compared to continental regions. However, since 2009 the number of studies in continental regions have increased, probably associated with an increase in the incidence of hurricanes striking the continent (Webster et al., 2005; Schriever et al., 2009; Nicoletto, 2013; Klawinski et al., 2014; Spiller et al., 2016; Schoener et al., 2017; Suazo-Ortuño et al., 2018 a,b) (Figure. 4a; Table S2). In general, the impact of a hurricane on continental ecosystems tend to be milder than on islands as frequently hurricanes lose intensity when landing on continents (McCoid, 1996; Schriever et al., 2009). As the American continent and associated islands are one of the most affected regions by hurricanes and tropical storms in the present decade, there are efforts to understand the negative effects of these phenomena on human wellbeing and on biodiversity in this continent (Strobl, 2012; Pielke, 2003).

However, different regions within the American continent present differences in the coverage of studies on the effects of hurricanes on herpetofauna. For example, in the Pacific region, studies on this subject are few and relatively recent (Luja & Rodriguez-Estrella, 2010; Suazo-Ortuño et al., 2015, 2018a,b; Marroquín-Páramo et al., 2020), whereas the Antilles present the highest number of studies, starting in the early 1990s (Woolbright, 1991; Reagan, 1991; MCCoid, 1996), as well as the highest incidence of hurricanes.

Although the frequency of hurricanes of categories II - III has remained stable during the last thirty-five years, the frequency of hurricanes of categories IV and V notoriously increased during this period of time (Webster et al., 2005). It is also expected that in the following decades, the number of high intensity hurricanes will increase as a result of the global climate change (Emanuel 1987; Webster et al., 2005; Stanturf et al., 2007; Knutson et al., 2010; Emanuel, 2013). The increase in the frequency of high intensity hurricanes might cause damage to forests, especially in preserved forests where the older and taller trees are less resistant (Tanner et al., 1991; Everham & Brokaw, 1996).

The first publications about the effect of hurricanes on the herpetofauna were those related to Hurricane Hugo, category V, which impacted the Antilles in 1989 (Regan, 1991; Woolbright, 1991). Since 2004 the number of studies about the effects of hurricanes on wildlife, including herpetofauna, has steadily increased, possibly associated with an increment in the interest on the effects of climate change on biodiversity (Thuiller 2007; Lavergne et al. 2010; Selman, 2015; Spiller et al., 2016; Donihue et al., 2018; Suazo-Ortuño et al., 2018; Marroquín-Páramo et al., 2020). Even though there is still a debate about the importance of global warming in the intensity and frequency of hurricanes, there is evidence indicating that the hurricane regime has been affected at some regions, increasing the frequency of higher category hurricanes (Table S2; Emanuel 1987; Hoegh-Guldberg et al., 2018). The influence of climate change in the increment in frequency and intensity of hurricanes is currently a topic highly studied. For example, a search in SCOPUS for the period 2019-2020 with the keywords ("climate change" OR "global warming") AND (hurricane* OR typhoon) resulted in 300 publications. There are also studies reporting the incidence of hurricanes in places where they were previously not as frequent (Maass et al., 2017; NOOA 2017; García y Siliceo-Cantero, 2019).) such as the Mexican pacific (Suazo-Ortuño et al., 2018 a, b). Modifications to some environmental features, such as air temperature, ocean level, and water temperature, as a result of climate change, might be affecting the hurricane regime in various regions, turning them increasingly random, intense and frequent (Webster et al., 2005; IPCC-WGI, 2007; Pachauri & Jallow, 2007; Falvey & Garreaud 2009; Alfaro & Quesada Román et al., 2010; Hoegh-Guldberg et al., 2018).

4.2 Impact of hurricanes on the abundance of amphibian and reptile species

The response of herpetofauna to the effects of hurricanes is species dependent. Regarding population size, this response can be positive, negative or neutral (Nicoletto, 2013; Schriever et al., 2009, Suazo-Ortuño et al. 2018a,b). Snakes in the tropical dry forest showed a decrease in population size after the landing of high-intensity hurricanes (Suazo-Ortuño et al., 2018; Marroquín-Páramo et al., 2020). Some species can present both positive and negative responses in different locations. For example, the snake *Agkistrodon piscivorus* showed a reduction in population size in Lousiana (Schriver et. al. 2009) and Nicoletto (2003) registered an increase in abundance for this species after hurricanes in Texas. These differences in the response to hurricanes might be caused by differences in the incidence of hurricanes. In the case of Texas, population size was estimated after the impact of three hurricanes, whereas in Louisiana population size was estimated after the impact of one hurricane. Other species that showed contrasting responses depending on location was the frog *Hyla squirella* that showed a negative effect to three hurricanes category V in Louisiana (Schriever et al., 2009) and a positive effect to one hurricane category IV in Florida (Gunzburger et al., 2010). These patterns suggest that population declines (negative effect) on amphibian and reptile species might be associated with the incidence (number) of hurricanes in different locations. Additionally, the intensity of hurricanes in addition to the incidence seems to play an important role. For example, species like the frog *Gastrophryne carolinensis* presented positive effects on abundance after hurricane category IV, but negative effects after three category V hurricanes (Schriever et al., 2009; Gunzburger et al., 2010). Some species are affected negatively regardless of the hurricane intensity, such as the frog *Lithobates catesbaianus* (Schriever et al., 2009; Luja & Rodríguez-Estrella, 2010). A neutral response of one amphibian assemblage (3 salamander and 4 frog species) was registered south of the Appalachians. These species did not show significant changes in population size after being subjected to the winds associated with a hurricane of low intensity (category I) (Greenberg, 2001).

The effects of hurricanes can reorganize the structure of herpetofauna communities. For example, in southeastern Louisiana, the abundance and dominance of species in an herpetofauna community was markedly modified, after the impact of three hurricanes of high intensity (Ivan, Katrina, and Rita). After the accumulated effect of the three hurricanes, some species decreased in abundance (e.g. *A. crepitans, H. cinereal, L. clamitans, L. sphenocephalus, A. carolinensis, A. piscivorus*), whereas others disappeared (*G. carolinensis, P. crucifer, N. cyclopion, N. fascista, P. laticeps*) (Schriever, 2009) (Figure 8). Contrastingly, the abundance of species of a herpetofauna community in Village Creek, Texas increased after the impact of a single high intensity hurricane (Rita). Some species even doubled in abundance after the hurricane (*Rana clamitans, Agkistrodon piscivorus, Heterodon platirhinos, Masticophis flagellum, Nerodia erythrogaster, Thamnophis proximus*) (Figure 7) (Nicoletto, 2013).

In Puerto Rico in 1991, the effects of hurricane Hugo (category V) on the Luquillo forests was reported, finding that some generalist frog species (*Eleutherodactylus coqui* and *Eleutherodactylus hedricki*) increased in abundance a year after the hurricane, while the abundance of habitat specialists decreased after a hurricane (*Eleutherodactylus wightmanae, Eleutherodactylus richmondi* and *Eleutherodactylus albilabris*) (Figure 7, Figure 10) (Woolbright, 1991; Vilella & Fogarty, 2005). Puerto Rico was later affected by Hurricane George (category V, in 1998) and after the hurricane the populations of *Eleutherodactylus* in the Luquillo forests were evaluated. In general, the cumulative effects of both hurricanes resulted in a decrease in abundance of all species, except for the generalist species *E. coqui* that increased in abundance (Woolbright, 1991; Villela & Fogarty, 2005) (Figure 10). In the occurrence of a natural disturbance, one of the major challenges for amphibians and reptiles is recolonization as a result of their limited capacity of movement. Many of the species that were negatively affected by hurricanes in Puerto Rico presented a markedly limited vagility associated with their small size (e.g. *Eleutherodactylus richmondi and Eleutherodactylus wightmanae*) (Vredebburg & Wake 2007) and with their high specialization of microhabitat use. For species of the genus Eleutherodactylus it has been reported that changes in the structure of vegetation, rain patterns, prolonged dry periods, canopy opening and detritus deposition are factors that can negatively affect their populations (Woolbright 1991, 1996; Vilella, & Fogarty, 2005)

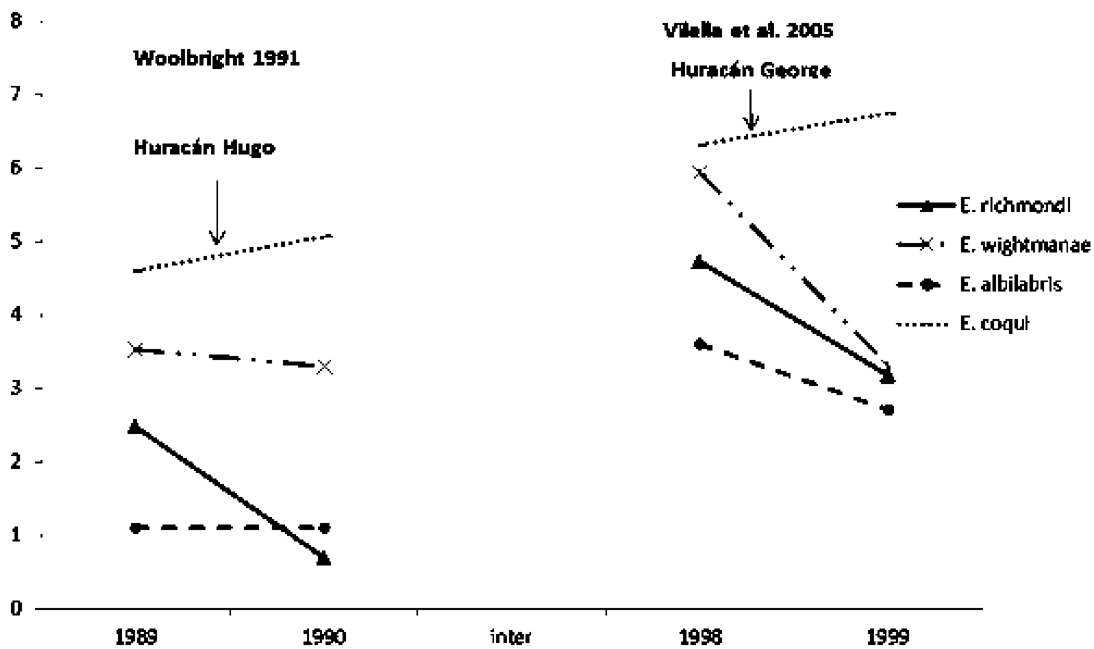


Figure. 10 Abundances (Log *n*+1) of the populations of *Eleutherodactylus* before and after hurricanes Hugo and George in the Luquillo forests in Puerto Rico (Woolbright 1991;Vilella and Fogarty 2005).

Regarding differences in habits, we found that from the total of herpetofauna species registered that were negatively affected by hurricanes in all analyzed publications, 34.1% presented aquatic or semi-aquatic habits, 32.9% terrestrial habits, 25.3% arboreal habits, and 7.5% fossorial habits. As the frequency and intensity of hurricanes increase (Table S2), the amphibians and reptiles will have to face novel challenges to survive and persist in a modified environment. Changes in availability of preferred food types and microhabitats might be particularly challenging in these modified habitats (Flores-Villela & García-Vázquez, 2014). These changes may lead to a strong competition for these resources (Willig & Camilo, 1991; Taner & Kapos, 1991). In this competing scenario, it is expected that populations of most specialized species will decrease in size or disappear locally (Dodd, 2010)

4.3 Trait-based responses of herpetofauna species to hurricanes

Due to the marked relationship between the structure of vegetation and the taxonomic composition and structure of animal assemblages it will be expected that different species will respond differently to variations in the intensity and frequency of natural disturbances (Suazo-Ortuño et al., 2018a; Martínez-Ruiz & Renton, 2018). As mentioned above, results of the reviewed publications indicate that the response of herpetofauna species to the effects of hurricanes can be negative, positive or neutral. The type of response might be related to the cascade of effects that involve microclimatic variables and changes in vegetation structure after hurricanes (Schriever, 2009; Nicoletto, 2013; Suazo-Ortuño et al. 2018 b). These differential responses of species to hurricanes might be in part mediated by differences in functional traits (Woolbright, 1991; Vilella & Fogarty, 2005; Pérez et al., 2012; Suazo-Ortuño, et al. 2018b). Therefore, information about the response of species with different functional traits to hurricanes are useful to understand the mechanisms that shape the dynamics of herpetofauna populations after a natural disturbance regime (Suazo-Ortuño et al. 2018a). For example, some lizards of the genus *Anolis* are able to tolerate the disturbance generated by floods and winds during a hurricane event (Spiller et al., 2016; Marroquín-Páramo et al., 2020) owing to adaptations like the water resistance of the eggs (Schoener et al., 2004; Losos et al., 2003) and the modification on the length of their extremities and the number of toepad lamellas, providing a better adherence on the perch during hurricanes (Dofour et al., 2019; Donihue et al., 2020; Huey & Grant 2020; Rabe et al., 2020). Depending on the publication, some lizards of the same genus presented positive or negative responses to hurricanes of low intensity (categories I to III) (Greenberg, 2001; Enge, 2005; Schoener et al., 2017). However, the response of lizard species to high intensity hurricanes (categories IV and V) was always reported as negative (Reagan, 1991; Schoener et al., 2001a, 2001b; Losos et al., 2003; Schoener & Spiller, 2004; Spiller et al., 2016). Also, it has been reported that after the strike of high impact hurricanes on some islands, lizard species completely disappeared locally and repopulation tended to be markedly slow, and even after months there were no signs of recolonization (Schoener et al., 2001a). Some lizard species that inhabit islands present traits adaptations to cope with the effects of hurricanes. For example, the eggs of some *Anolis* species from islands can resist submersion in water up to 4 hours, giving them a clear advantage to survive the effects of floods. This adaptation can also be important for the recolonization of islands by over-water dispersal (Schoener et al., 2004; Losos et al., 2003).

5. Conclusions

The effects of hurricanes on herpetofauna vary among species and taxonomic groups due to their particular traits that make them more or less vulnerable. As the frequency and intensity of hurricanes increase, the herpetofaunal assemblages frequently show higher levels of changes in structure, composition, and abundance-dominance patterns of species (eg. Marroquín-Páramo et al. 2020).

To design conservation strategies to mitigate effects of hurricanes on herpetofauna it is crucial to evaluate if populations show a level of resilience necessary to recover their pre-hurricane abundances. It is also important to estimate levels of variation in the response of different populations from different locations to hurricanes. Although some herpetofauna species can increase in population size after the strike of a low intensity hurricane, all herpetofauna species decline in abundance after the cumulative effects of a series of high intensity hurricanes. As the frequency and intensity of hurricanes increase, herpetofauna assemblages will have to confront new challenges. To evaluate the cumulative effects of hurricanes on herpetofauna species it will be important to establish long-term monitoring sites to detect changes in the assemblages' structure. As long-term studies in different regions increase, it will be possible to perform meta-analyses contrasting regions with different regimes of hurricane frequency and intensity. Natural mature habitats as well as forests in secondary natural succession also require monitoring in order to establish recovery times after the impact of a hurricane (Suazo-Ortuño et al. 2008b), their degree of vulnerability and resilience of these habitats.

Acknowledgments

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5. ARTICULO II

Cumulative effects of high intensity hurricanes on herpetofaunal assemblages along a tropical dry forest chronosequence.

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Abstract

If combined with anthropogenic disturbances and global climatic change, hurricanes may lead to major effects on animal populations and assemblages. The combined effects of cumulative natural and human disturbances on vertebrates have been little studied. There is evidence that herpetofaunal assemblages are sensitive in species richness, abundance, and diversity to anthropogenic and natural disturbances, or to their interaction. In the Pacific coast of Jalisco, Mexico, we aimed to evaluate the cumulative effects of hurricanes Jova (2011) and Patricia (2015) on herpetofaunal assemblages along tropical dry forest successional stages by comparing before and after the hurricanes. We conducted a long-term survey (2009 to 2018) on anuran, lizard and snake populations within five dry forest successional stages (from 0 to > 50 years after forest clearance), including the following: active pastures, early forests, young forests, intermediate forests, and old-growth forests as experimental controls. We hypothesized that cumulative effects of hurricanes will result in a general pattern of a decrease in abundance, richness and diversity, and an increase in evenness of anurans, lizards and snakes. We also expected that herpetofaunal diversity will decrease and evenness will increase in those stages with higher vegetation complexity, such as old-growth forest (OGF), and an increase in similarity and evenness in herpetofaunal assemblages in all successional stages. Overall, the abundance of anurans, lizards and snakes significantly decreased after hurricanes, but only for lizards and anurans the interaction of successional stage-hurricane was significant. Furthermore, species richness and diversity increased for lizards and decreased for snakes after hurricanes landed. Although, the pattern of anuran species richness among successional stages was similar after hurricanes, the richness in OGF markedly diminished after hurricanes.

Interestingly our results showed that tropical dry secondary forests, under the impact of low intensity hurricanes, might function as buffers that promote herpetofauna resilience. However, cumulative effects of hurricanes resulted in a homogenization tendency among successional stages, suggesting a negative effect for ecosystem functioning. The changes in the buffering role of secondary forests highlights the importance of these ecosystems for

conserving biodiversity in times when hurricane disturbances are increasing in frequency and intensity. Overall, we discuss how the complex interactions between human and natural disturbances such as hurricanes might be a factor that contributes to maintain biotic diversity in anthropic landscapes of tropical dry forests.

Keywords: tropical dry secondary forests; human and natural disturbances; high-intensity hurricanes; low-frequency of hurricanes.

1. Introduction

Hurricanes of greater magnitude in the Saffir-Simpson (S-S) scale have increased in frequency and intensity in the last 40 years (Webster et al., 2005; Elsner et al., 2008; Knutson, 2010; Emanuel, 2013) as a consequence of ocean global warming (IPCC-WGI, 2007; Pachauri & Jallow, 2007; Falvey & Garreaud, 2009; Hoegh-Guldberg, 2018). The effects of hurricanes on animal assemblages have been principally studied in those regions with the highest incidence of hurricanes, such as the Antilles. Contrastingly, in the central Pacific region, high-intensity hurricanes infrequently land on the continent (Salivia, 1972; Donihue et al., 2018) and studies on hurricane impact on herpetofauna are scarce. However, because of climate change, frequency of high-intensity hurricanes is increasing in these historically low-frequency hurricane regions (Webster et al., 2005; Knutson, 2010), and consequently, studies on hurricane impacts on animal assemblages in these regions become relevant.

The effects of hurricanes on animal populations vary according to species natural history (e.g., habitat type, habitat range, diet requirements, vagility; Suazo-Ortuño et al. 2018a, 2018b). For amphibians and reptiles, several studies have shown that hurricanes change species abundance, richness and diversity and also the extinction and colonization dynamics of their populations (Schriever et al., 2009; Klawinski, 2014; Suazo-Ortuño et al., 2018a, 2018b). In general, categories 4 and 5 (S-S) hurricanes cause a great decrease in amphibian and reptile populations (Schriever et al., 2009), however some species, have shown resilience to high intensity hurricanes, increasing their abundance (Enge, 2005; Suazo-Ortuño et al., 2018a, 2018b). Lizard species are among the taxa showing greater changes in abundance after hurricanes, with some species showing a marked increase in their populations, while others are driven to local extinction (MCCoid, 1996; Spiller et al., 1998 ; Schoener, 2001; Losos et al., 2003; Schoener & Spiller, 2004; Spiller et al., 2016).

Most studies regarding the effect of hurricanes on herpetofaunal assemblages have considered the effect of a single hurricane, whereas the cumulative effects of hurricanes on herpetofauna have been rarely reported in the literature. For instance, to our knowledge, there are only eight studies on the effect of two hurricanes on herpetofauna (MCCoid, 1996; Censky et al., 1998; Schoener et al., 2004; Spiller & Schoener 2008; Selman, 2015; Spiller et al., 2016 ; Schoener et al., 2017 ; Donihue et al., 2018 and one of the effect of three hurricanes (Schriever et al., 2009).

Several studies have found that after the occurrence of a hurricane, the response of the herpetofauna is variable, with some species or assemblages increasing or decreasing their abundance, richness and diversity, while others remain unchanged (Reagan, 1991; Woolbright, 1991; Schoener et al., 2001a, 2001b; Losos et al., 2003; Schoener & Spiller , 2004; Enge, 2005; Dodd, 2006; Gunzburger, 2010; Nicoletto 2013; Gray & Strine, 2017; Suazo-Ortuño et al. 2018b). However, studies of the impact of two or more hurricanes have shown a negative impacts on herpetofaunal assemblages after the second and/or third hurricane with a remarkable abundance decrease, especially for specialist species, and an abundance increase of generalist species (MCCoid, 1996; Schoener & Spiller 2004; Schriever et al., 2009; Selman, 2015; Spiller et al., 2016).

Anthropogenic disturbances, such as deforestation and fragmentation of natural ecosystems might further increase the negative effects of natural disturbances on animal populations (Betts et al., 2019). For instance, tropical dry forest landscapes in the Pacific Coast of Mexico have been cleared mostly for cattle raising activities. Thereafter, these cattle pastures are abandoned leaving a landscape composed by a mosaic of secondary forest vegetation at different stages of succession (Quesada & Stoner, 2004). Because of its geographical location, the already endangered tropical dry forest is prone to natural catastrophic disturbances, such as hurricanes, further compromising the maintenance of this diverse ecosystem (Murphy & Lugo, 1995; Scatena & Lugo, 1995; Chazdon et al., 2007; Imbert & Portecop, 2008; Lugo, 2008; Suazo-Ortuño et al., 2015, 2018a, 2018b).

In human modified tropical dry forests landscapes, secondary forests may play an important role in the conservation of animal species since the mosaic of forests at different stages of succession provides novel habitats for some native amphibians and reptiles (Dunn, 2004; Suazo-Ortuño et al., 2015, Fraga-Ramírez et al., 2017). Furthermore, in the tropical dry forest of the Chamela-Cuixmala Biosphere Reserve, after hurricane Jova (category 2 S-S), several amphibian and reptile species, exclusive of one successional stage, colonized other stages (Suazo-Ortuño et al., 2018a, 2018b; Jimenez-Rodríguez et al., 2018). The role of herpetofaunal species in the maintenance of forests' ecological integrity is relevant as they participate in various ecosystem functions, such as pollination, seed dispersal, bioturbation, insect populations regulation (Cortés-Gomez et al., 2015) and by predation of key species (e.g., rodents) that affects plant community structure (Hayward & Phillipson, 1979).

Currently, there are no studies evaluating the cumulative effects of two or more hurricanes on herpetofaunal assemblages for any tropical dry forest ecosystem. In the Pacific coast of Mexico, high category hurricanes (4 and 5 S-S) are infrequent. However, in October 2011 and October 2015 two hurricanes of different intensity made landfall (Jova, 2 S-S, and Patricia 5 S-S, respectively) along the coast of Jalisco State. These hurricanes strongly impacted biotic assemblages and several ecosystem processes (Maass et al., 2017; Jimenez et al., 2018). There is evidence of subtle effects of dry forest successional stages, hurricane Jova and their interaction on amphibian and reptile richness and diversity (Suazo-Ortuño et al., 2018b). However, marked changes have been observed in the composition of amphibian and reptile communities after hurricane Jova (Suazo-Ortuño et al., 2015; Suazo-Ortuño et al., 2018a, 2018b)

In this context, we evaluated the cumulative impact of both hurricanes (Jova and Patricia) on herpetofaunal assemblages (i.e., anurans, lizards, and snakes) in the tropical dry forest of Chamela, Jalisco, Mexico. For this, we compared the structure of herpetofaunal assemblages along contrasting successional stages. Considering the results of previous studies on the cumulative hurricane impact on herpetofauna (e.g., Schrievere et al., 2009), we hypothesized that: 1) cumulative effects of hurricanes Jova and Patricia will reflect a general pattern of a decrease in abundance, richness and diversity, and an increase in evenness of anurans and reptiles (this increase in evenness is expected because of an increase of rare species and a decrease of dominant species), 2) as successional stages present a gradient in vegetation structure complexity from lowest levels of complexity in pastures to highest in old-growth forests (OGF), we would expect that structurally more complex stages will be more impacted by the strong winds associated to hurricanes and that, therefore, herpetofaunal diversity will decrease and evenness will increase in those stages with higher complexity, such as OGF; and 3) as an increase in similarity and evenness of some animal groups in habitats within the path of maximum hurricane winds may indicate a process of biotic homogenization (McKinney & Lockwood, 1999), we expected greater similarity and evenness in herpetofaunal assemblages after cumulative effects of hurricanes in all successional stages.

2. Materials and methods

2.1 Study site

The study was conducted in the Pacific Coast of Jalisco, Mexico, within the Chamela region (19°230–19°300 N, 104°560–105°040 W) encompassing the Chamela-Cuixmala Biosphere Reserve (CHCBR, 13,142 ha) (Fig. 1). The predominant vegetation type in the study area is tropical dry forest (TDF). Mean annual temperature in the region is 25.1 °C and average annual precipitation is 788 mm (range: 453–1392 mm), which mostly occurs during the rainy season (June to October) (Bullock, 1986; García-Oliva et al., 2002; Lott & Atkinson, 2002).

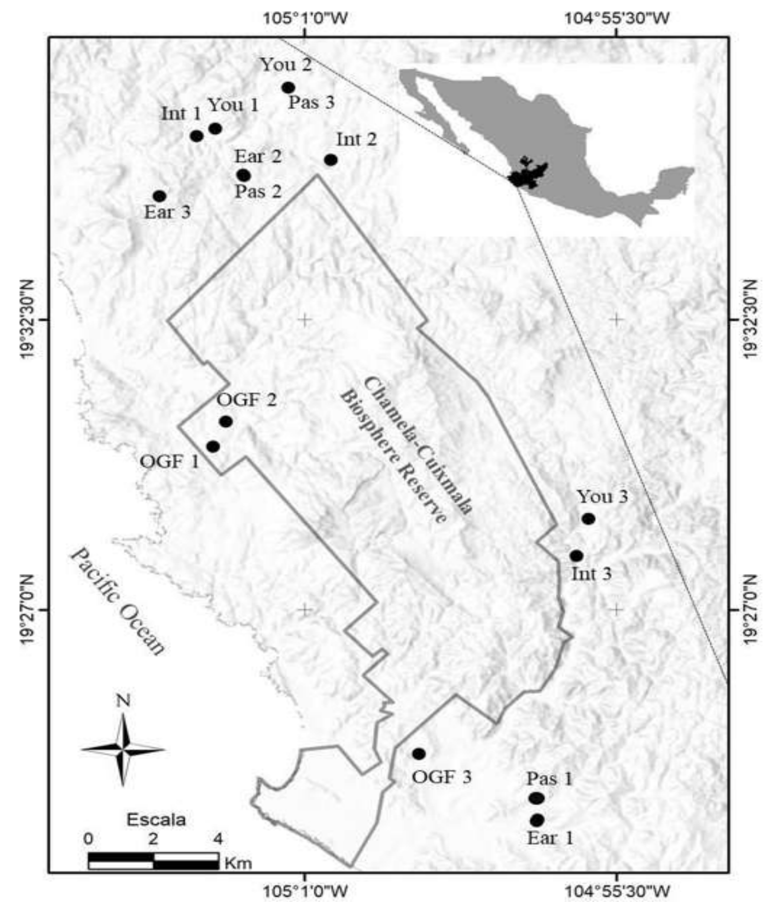

Figure 1. Distribution of the 15, 1 ha blocks representing five tropical dry forest successional stages in the Chamela-Cuixmala Biosphere Reserve in the Pacific Coast of Mexico. Pas = Pasture, Ear = Early, You = Young, Int = Intermediate, OGF = Old-growth forest.

At the beginning of the study (2009) a total of 15, 1-ha blocks (120 m x 90 m) representing five successional stages were positioned permanently to record the herpetofaunal assemblages along a chronosequence of dry forest successional stages. The 15 blocks included three replicates of each of the following successional stages: (1) active pastures (0 years of abandonment, still in use); (2) early-forests (5–6 years of abandonment); (3) young-forests (8–10 years of abandonment); (4) intermediate-forests (15–17 years of abandonment); and (5) old-growth forests (OGF) (i.e., tropical dry forest showing no evident signs of human disturbance in the last 50 years). Each of the 1-ha blocks was embedded within a matrix of vegetation of the same type, and with the exception of OGF surrounded by fire breaks and fences to keep cattle out. Because all 1-ha blocks were located at least 1 km from each other and because of the low vagility of reptiles and anurans, we assumed that our data records were not spatially correlated. The herpetofauna was sampled annually during the wet and dry seasons for eight years, (2009-2018) before and after the hurricanes as follows: pre-hurricanes (August 2009 to July 2011); post-hurricane Jova (April 2012 to August 2013); and post-hurricane Patricia (May 2016-August 2018). We carried out a total of twenty field surveys with the same sampling effort of 630 person-hours for each of the three time periods (5 successional stages x 3 1-ha blocks x 7 surveys x 5 people x 1.2 h in pre-hurricanes; 5 successional stages x 3 1-ha blocks x 6 surveys x 5 people x 1.4 h in post-hurricane Jova and 5 successional stages x 3 1-ha blocks x 7 surveys x 5 people x 1.2 h in post-hurricane Patricia). The search for anurans and reptiles was time-constrained (three hours during daytime – 09:00–16:00 – and three hours at night – 21:00–04:00 – per 1-ha block). Surveys were carried out by visually searching vegetation and the ground surface, including lifting cover objects (rocks, logs, and debris). We identified all detected individuals to species level (no heard or dead individuals were registered). To avoid counting the same individual twice during the study period, we clipped toes in frogs and lizards and ventral scales in snakes. All animals were released in the same site where they were captured.

2.2 Statistical analysis

We compared the abundance, richness, and diversity (Shannon-Wiener index) of anurans, lizards, snakes and the overall herpetofaunal assemblages (by lumping all three groups) among successional stages and disturbance conditions (pre and post-hurricanes). To evaluate the completeness of the herpetofaunal survey we used the program EstimateS (Version 9.1.0, Colwell, 2013), calculating species richness for each taxa within each successional stage and each disturbance condition using three non-parametric estimators: Bootstrap (incidence-based estimator), ACE (abundance-based coverage estimator) (Chao et al., 1993) and Chao1 (abundance-based coverage estimator) (Lee & Chao, 1994). Although ACE and Chao 1 are similar, the use of these two estimators allows a more accurate assessment regarding completeness of the inventories, and it is also assumed that both estimators similarly evaluate the species richness from each locality when their values are not substantially different (Moreno, 2001). We assessed sampling completeness by calculating the percent value of the observed species with respect to the estimated species (Soberón & Llorente, 1993).

Abundance and species richness were analyzed by fitting generalized linear mixed models (GLMM) using a Poisson error distribution (Bates et al., 2012). In the case of species diversity, we used a linear mixed model for repeated measures (LMM) with a normal distribution error type (Magurran, 2004). Sampling time of each 1-ha block was used as a repeated measure and included as a random factor (Crawley, 2013). Fixed factors were the following: successional stage (S, with five levels: pasture, early, young, intermediate and old-growth forest); disturbance condition (H, with three levels, pre-hurricane, post-hurricane Jova and post-hurricane Patricia); and the interaction between successional stages and hurricanes (S:H). We conducted the analysis using the lme4 package (Bates et al., 2012). For GLMM we used the function glmer and for LMM we used the function lmer in R 3.6.1 (R Core Team, 2019).

To evaluate whether or not the assemblage structure was affected by successional stage and hurricanes we constructed species rank-abundance plots for each herpetological assemblage at the three sampling periods: pre-hurricanes, post-Jova, and post-Patricia. We performed an analysis of covariance (ANCOVA) to test for differences in the slopes of the rank-abundance plots (R) among successional stages (S), hurricanes (H) and their interaction (R:S; R:H and R:S:H; Feinsinger, 2001; Izsák, 2006).

We explored changes in the abundances of herpetofaunal species with the Whittaker's (1952) association index across successional stages and disturbance conditions (pre-hurricanes, post-Jova, and post-Patricia) through a heatmap (Somerfield and Clarke 2013). This classification technique represented the association of the species by site based on a color palette that goes from dark red (showing the highest level of association of a species for a specific site) to pale blue when there is a low level of association. Using a similarity profile routine (SIMPROF subroutine with 9,999 Monte Carlo simulations; Clarke et al. 2014) we inspected for significant multivariate structure on the classifications between species and sites, allowing us to detect the degree of deviation of the observed profile relative to the null distribution of the permuted profiles (Clarke et al., 2008).

We used SIMPER (similarity percentage, Clarke, 1993) to determine the contribution that individual species (anurans, lizards, and snakes) made toward distinguishing differences in quantitative community structure among pre-hurricanes, post- hurricane Jova, and post-hurricane Patricia. To explore assemblage structure according to disturbance conditions and successional stages, we used a Principal Coordinates Analysis (PCoA) with Bray–Curtis resemblance measure of abundance data (Anderson & Willis, 2003). For each of the five different successional stages we explored projected patterns in species distributions (anurans, lizards and snakes) along time (7 surveys pre-hurricanes, 6 surveys post-Jova, and 7 surveys post-Patricia) by conducting a metric multidimensional scaling (mMDS), which preserves dissimilarities in the Bray–Curtis resemblance matrix as current distances, being a useful routine in ordinations with a few points (Clarke & Gorley, 2015).

3. Results

Sampling completeness and assemblage structure

Overall, we recorded a total of 4805 individuals, representing 26 families and 62 species of anurans and reptiles (Table 1). Along successional stages the number of records was as follows: in active pastures we recorded a total of 1123 individuals of 46 species; in the early stages, 821 individuals of 40 species; in young forests, 1092 individuals of 50 species; in intermediate forests, 1073 individuals of 48 species; and finally, in old-growth forest, 697 individuals of 38 species (Table 1).

Table 1. Amphibian and reptile species abundance at each of three replicates of each successional stage (pre and post-hurricanes) in the tropical dry forest of Chamela, Jalisco, Mexico. Pas = Pasture, Ear = Early, You = Young, Int = Intermediate, OGF = Old-growth forest.

	Before hurrricanes					Post hurricane Jova					Post hurricane Patricia					Overall
	Pas	Ear	You	Int	OGF	Pas	Ear	You	Int	OGF	Pas	Ear	You	Int	OGF	
ANURANS																
Bufonidae																
Incilius marmoreus	59	18	37	47	35	12	12	25	39	1	14	5	6	17	5	332
Incilius mazatlanensis	2					1					2					5
Rhinella marina	2		1	1		5		2	1		4	2				18
Craugastoridae																
Craugastor occidentalis			6	3	1			3	2				2		1	18
Eleutherodactylidae																
Eleutherodactylus nitidus						1		1				1	1	3		7
Hylidae																
Agalychnis dacnicolor	22	6	6	1		15	15	1	1		16	5	3	1		92
Dendropsophus sartori		1	3		1			5	1	2			6	2		21
Diaglena spatulata	3	79	102	57	13	2	31	59	20	4		10	20	14	4	418
Exerodonta smaragdina										8						8
Smilisca baudinii	28	4	7	7	1	14	18	16	13		6	5	14	16	7	156
Smilisca fodiens	38	10	14	15		18	13	19	8		11	6	18	2		172
Tlalocohyla smithii					8	1			1	13	1		5	1		30
Trachycephalus typhonius	9	22	8	12	3							1	4	6	3	68
Leptodactylidae																
Leptodactylus melanonotus	9					53					59					121
Microhylidae																
Hypopachus ustus	4	5		1		2		4	1		1		1	2		21
Hypopachus variolosus	20		5			6	1		1		10		2	1		46
Ranidae																
Lithobates forreri						2					1					3
LIZARDS																
Anguidae																
Gerrhonotus liocephalus										1						1
Dactyloidae																
Anolis nebulosus	53	41	59	52	35	178	143	150	99	74	4	7	6	4	2	907
Eublepharidae																
Coleonyx elegans	3		6	3	2		1	4		3	2	1	3	4		32
Helodermatidae																
Heloderma horridum			1													1
Iguanidae																
Ctenosaura pectinata	6	6	2	7	1		5	3	1	2	4	9	3	9	7	65
Iguana iguana			1	1			1					1				4
Phrynosomatidae																
Sceloporus horridus	9	4				5					3	2	1			24
Sceloporus melanorhinus	7	3	2	12	13	8	8	3	12	4	1	3	4	3	1	84
Sceloporus utiformis	43	35	95	105	47	25	46	119	135	43	42	30	35	50	12	862
Urosaurus bicarinatus	50	10	2	9	2	19	14	7	2	1	2		3	1	3	125
Phyllodactylidae																
Phyllodactylus lanei	4		1	5	16	1	3	2	7	9	8	1		2	3	62
Scincidae																
Plestiodon parvulus				1					1					1		3
Marisora brachypoda											1	2				3
Scincella assata						1					2		2	1		6
Teiidae																
Aspidoscelis communis	13	29	7	28	33	5	9	9	10	15	44	29	34	14	28	307
Aspidoscelis deppi							5	1	10	1	16	3	4	25	2	67
Aspidoscelis lineatissima	30	13	26	35	80	4	34	14	27	39	30	26	27	39	19	443
Holcosus undulatus			6	10	20			1		13		6	3	18	18	95
SNAKES																
Boidae																
Boa sigma	1			1				1	2							5
Colubridae																
Drymarchon melanurus			1	1			1		1		1					5
Lampropeltis polizona	1					2										3
Leptophis diplotropis	1	2	1	1	1		2		1	1	1					11
Masticophis mentavarius						1										1
Oxybelis aeneus	1		4	2	3	2	2	3	2	4	1	1	3	1		29
Pseudoficimia frontalis								1	1		1		1			4
Salvadora mexicana	3	1	1	1					1		1					8
Symphimus leucostomus		1	1				2									4
Tantilla bocourti		1								1	3					5
Tantilla calamarina				1	1						1	1				4
Trimorphodom biscutatus	1	1	1	1	1			2								7
Drymobius margaritiferus											1		3			4
Dipsadidae																
Dipsas gaigeae			1		1					1					2	5
Enulius flavitorques				1	3								1			5
Hypsiglena torquata	4			1		1					1					7
Imantodes gemmistratus					2		1	2	1	1			1			8
Leptodeira maculata	4		2	1		4	1	3		2	1				1	19
Leptodeira uribei	1			2	2	1	1		1					2		10
Manolepis putnami									1	2						3
Pseudoleptodeira latifasciata														1		1
Tropidodipsas philippii					2				2			1				5
Elapidae																
Micrurus distans				1	1								1		1	4
Leptotyphlopidae																
Rena humilis						1										1
Loxocemidae																
Loxocemus bicolor	2	2			1			1								6
Viperidae																
Agkistrodon bilineatus			1													1
Crotalus basiliscus	1		3	2	1						2	1	1		2	13
Overall	434	294	413	428	330	390	369	461	405	245	298	159	218	240	121	4805

Overall, pre-hurricane herpetofaunal sampling assemblage completeness varied from 46% in intermediate forests to 97% in pastures; while after the hurricanes, completeness was 53% in intermediate forest to 93% for old-growth forests after Jova; and from 64% in pastures to 91% in old-growth forests after Patricia (Table 2).

Table 2. Sampling completeness of herpetofaunal assemblages in different vegetation successional stages in the tropical dry forest of Chamela, Jalisco, México. Sampling was carried out in three periods: pre-hurricanes, post- hurricane Jova and post-hurricane Patricia.

Group	Condition	Pasture	Early Forest	Young Forest	Intermediate Forest	Old Growth Forest	Overall
Anurans	Pre-hurricane	100–100	97–100	97–100	65–77	67–73	95–97
	Post-Jova	83–95	86–100	92–97	64–79	100–100	95–98
	Post-Patricia	75-88	88-94	90-97	80-94	87-100	93-100
Lizards	Pre-hurricane	100–100	100–100	82–94	91–92	93–100	82–96
	Post-Jova	90–96	84–80	97–100	73–91	95–100	63–85
	Post-Patricia	92-97	80-89	90-100	92-96	92-100	92-95
Snakes	Pre-hurricane	51–52	44–68	38–44	37–54	67–76	93–98
	Post-Jova	53–63	58–79	68–81	57–78	58–79	84–92
	Post-Patricia	25-77	60-75	33-76	50-89	57-85	68-82
Assemblage	Pre-hurricane	85–97	80–82	64–73	46–50	67–70	93–98
	Post-Jova	68–76	73–74	88–88	53–74	85–93	81–90
	Post-Patricia	64-85	74-86	71-85	81-87	86-91	85-89

The abundance of anurans showed a significant decline after Jova (from 736 to 512 individuals) and Patricia (to 327 individuals). Overall, the decline in anuran abundance after both hurricanes was of 56 %. The greatest decline in anuran abundance occurred for early forests and the least for active pastures (Fig.2).

Table 3. Results of the statistical analysis of the assemblage of different groups of the herpetofauna at Chamela tropical dry forest. The statistics provided are as follow: values for GLMM (abundance and species richness) and for ANOVA (diversity). Stage (s), Hurricane (H) and Successional stage x hurricane disturbance condition interaction (S:H)

	Abundance			Species richness			Diversity		
Group	Stage(S)	Hurricane (H)	S:H	Stage(S)	Hurricane (H)	S:H	Stage(S)	Hurricane (H)	S:H
Anurans	12.8(4)**	8.4(2)**	1.4(8)	19.9(4)***	0.6(2)	2(8)	5.2(4)**	0.2(2)	0.5(8)
Lizards	2.2(4)	10.9(2)**	2.8(8)	2(4)	6.1(2)**	5.1(8)	1.1(4)	15.6(2)***	1(8)
Snakes	11.3(4)*	12.6(2)**	12.4(8)	4.8(4)	8(2)*	10(8)	0.5(4)	2.8(2)**	1.7(8)
Assemblage	6.8(4)	13.8(2)***	2.3(8)	9.7(4)*	1.9(2)	4.9(8)	1.7(4)**	12.3(2)**	7.3(8)

P< .05* P< .01** P< .001***

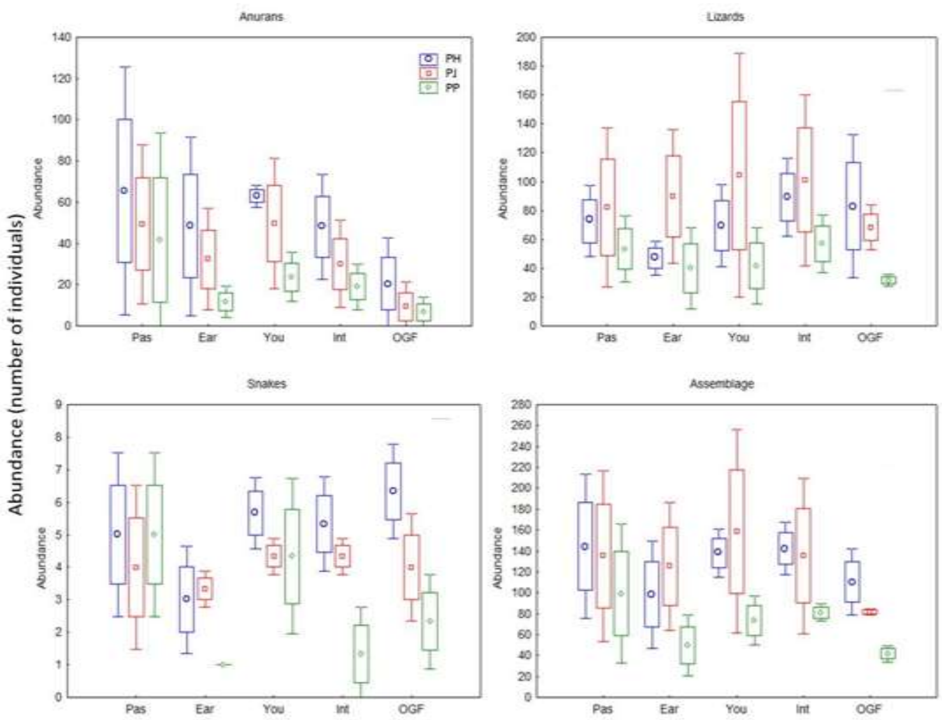

Figure 2. Changes in abundance through succession pre and post the occurrence of hurricanes Jova and Patricia at Chamela tropical dry forest. Abundance of each group and of overall herpetofauna at each of the five successional stages, box represents the standard error and whiskers represents standard deviation, figure inside the box (circle, square and diamond) represent the average. PH = pre-hurricanes, PJ = post-hurricane Jova, PP = post-hurricane Patricia. Pas = Pasture, Ear = Early, You = Young, Int = Intermediate, OGF = Old-growth forest.

Table 4. Results of the analysis of covariance of the rank-abundance curves for different groups of the herpetofauna at Chamela tropical dry forest. The statistics F, degrees of freedom, and P-values are provided.

	Anurans			Lizards			Snakes		
Group	F	df	P	F	df	P	F	df	P
Rank (R)	3892	1	<0.001	3732	1	<0.001	784	1	<0.001
Successional State(S)	4	4	<0.01	4	4	<0.01	60	4	<0.001
Hurricane (H)	92	2	<0.001	5	2	<0.05	94	2	<0.001
R:S	7	4	<0.001	3	4	<0.05	45	4	<0.001
R:H	49	2	<0.001	89	2	<0.001	7	2	<0.01
S:H	–	–	–	–	–	–	3	8	<0.01
R:S:H	–	–	–	–	–	–	–	–	–

Furthermore, the interaction successional stage x hurricane disturbance condition was significant. After Patricia, anuran abundance decreased more than 60 % in early successional forests (Table 3; Fig. 2). For lizards, there were significant differences in abundance after hurricanes Jova and Patricia (Table 3). There was a significant increase after Jova (1084 vs. 1336) but a significant decrease after Patricia (670 lizards). Successional stages showed no significant differences on lizard abundance but there was a significant successional stage x hurricane disturbance condition interaction (Table 3, Fig.2). Except for old-growth forests, lizard abundance increased after Jova but decreased after Patricia by more than 45 % for all successional stages (Table 1, Fig. 2). For snakes, there was a significant decline in abundance after hurricanes Jova (from 81 to 60 snakes) and Patricia (42 snakes) (Table 1,Table 3), but there was not a significant difference among successional stage or successional stage x hurricane interaction.

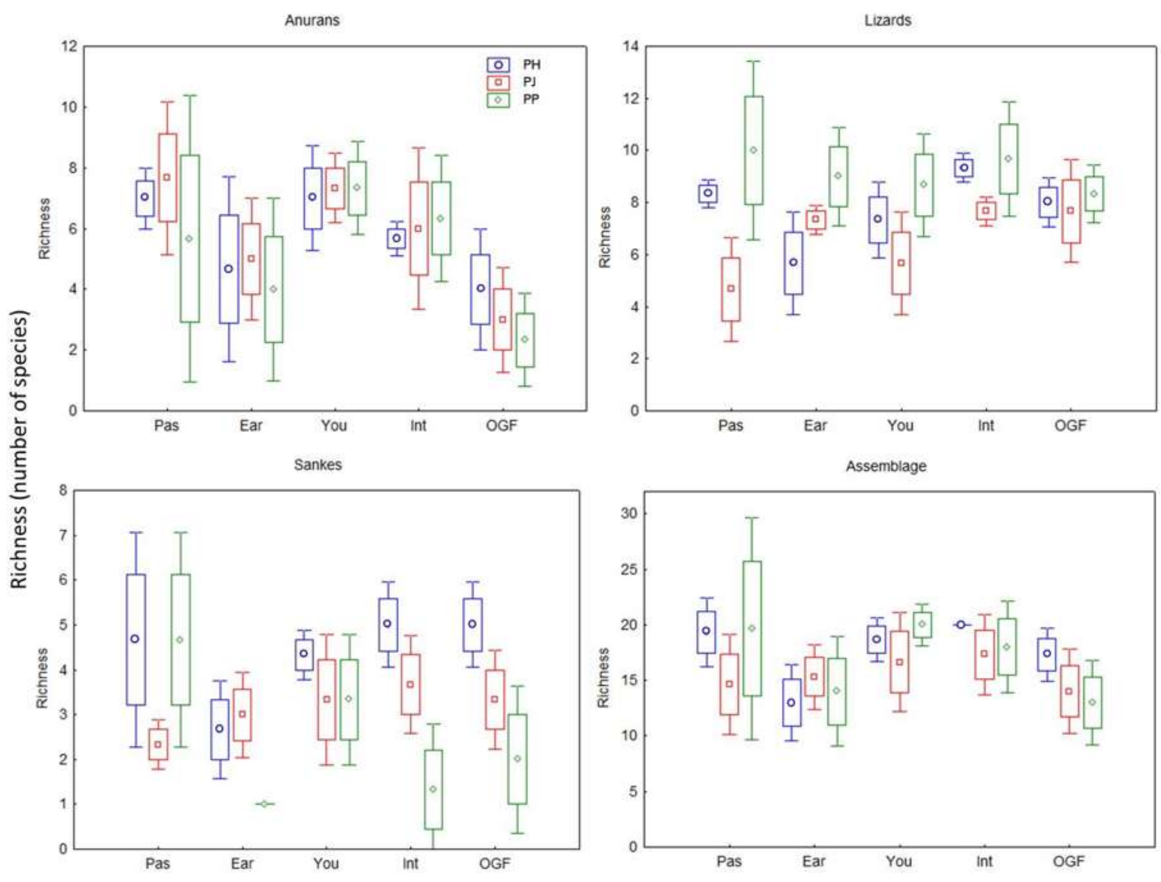

Figure 3. Changes in richness through succession pre and post the occurrence of hurricanes Jova and Patricia at Chamela tropical dry forest. Box represents the standard error and whiskers represents standard deviation, figure inside the box (circle, square and diamond) represent the average. PH = pre-hurricanes, PJ = post-hurricane Jova, PP = post-hurricane Patricia. Pas = Pasture, Ear = Early, You = Young, Int = Intermediate, OGF = Old-growth forest.

Species richness of reptiles differed significantly between hurricanes (Table 3). For lizards, species richness increased after hurricanes (14 vs. 16 species); while for snakes there was a significant decline after hurricanes (22 vs. 16 species) (Table 3, Fig. 3). After the hurricanes, anuran species richness declined significantly only for old-growth forests (Table 3; Fig. 3), and there were not significant effects of successional stage x hurricane disturbance condition interaction.

Hurricanes had a significant effect in the diversity of reptiles, but not in anurans. For lizards, species diversity declined after Jova (from H'= 1.5 to H'=1.2) but increased after Patricia (H'=1.7) (Table 3; Fig. 4). Contrastingly, species diversity of snakes strongly declined after both hurricanes (pre-Jova, H'=1.3; after Jova H'=1.02; after Patricia H'=0.7) (Table 3, Fig. 4). Successional age affected species diversity only for anurans, and no hurricane effects were detected on any group and no evidence of interactive successional stage x hurricanes was detected (Table 3; Fig. 4).

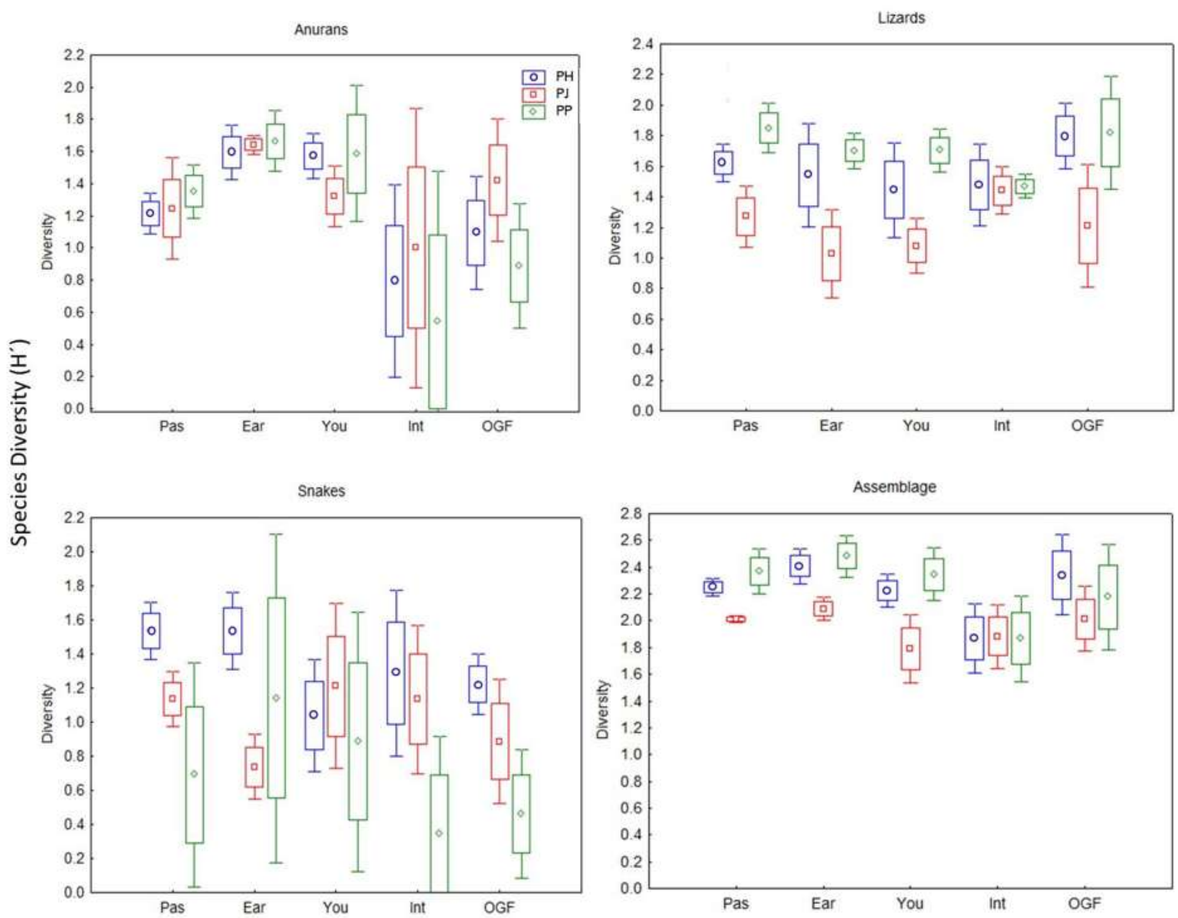

Figure 4. Changes in species diversity through succession pre and post the occurrence of hurricanes Jova and Patricia at Chamela tropical dry forest. Box represents the standard error and whiskers represents standard deviation, figure inside the box (circle, square and diamond) represent the average. PH = pre-hurricanes, PJ = post-hurricane Jova, PP = post-hurricane Patricia. Pas = Pasture, Ear = Early, You = Young, Int = Intermediate, OGF = Old-growth forest.

3.1 Assemblage evenness

Anuran species evenness changed significantly with successional stage (S) and after disturbance condition of hurricanes Jova and Patricia (H), but no interaction S:H was detected (Table 4). The slope significantly increased (became less negative) with forest succession, before and after the hurricanes; with the most negative values recorded for pastures. Before and after hurricanes, the slope gradually increased along the successional chronosequence with the least steep slopes in old-growth forests. Furthermore, after each hurricane, anuran assemblages became more evenly distributed in all successional stages, particularly after hurricane Patricia, as suggested by less negative slope values (Fig. 5).

Although *Incilius marmoreus* and *Diaglena spatulata* were the most abundant anuran species before and after the hurricanes, both showed a strong decline in their abundance after the hurricanes (by more than 50 %; Table 1, Fig. 5 and Fig. 6). Contrastingly, the anuran *Leptodactylus melanonotus* increased in abundance after the hurricanes; while *Smilisca baudinii, S. fodiens* and *Agalychnis dacnicolor* showed similar abundances before and after the hurricanes (Table 1, Fig. 6). In the case of lizards, evenness changed significantly according to successional stage (S), and after the hurricanes (H) (Table 4). There was an increment in slope through forest succession with more negative values in pastures, gradually increasing along the successional chronosequence, with highest values for old-growth forests (Fig. 5). After Jova, some lizard species became more dominant as compared to pre-hurricane conditions, whereas after Patricia lizard assemblage became more evenly distributed (Fig. 5). Overall, the lizard *Anolis nebulosus* presented a threefold increase in abundance across all successional stages after Jova (Fig. 6), being particularly high in pastures and early-forests.

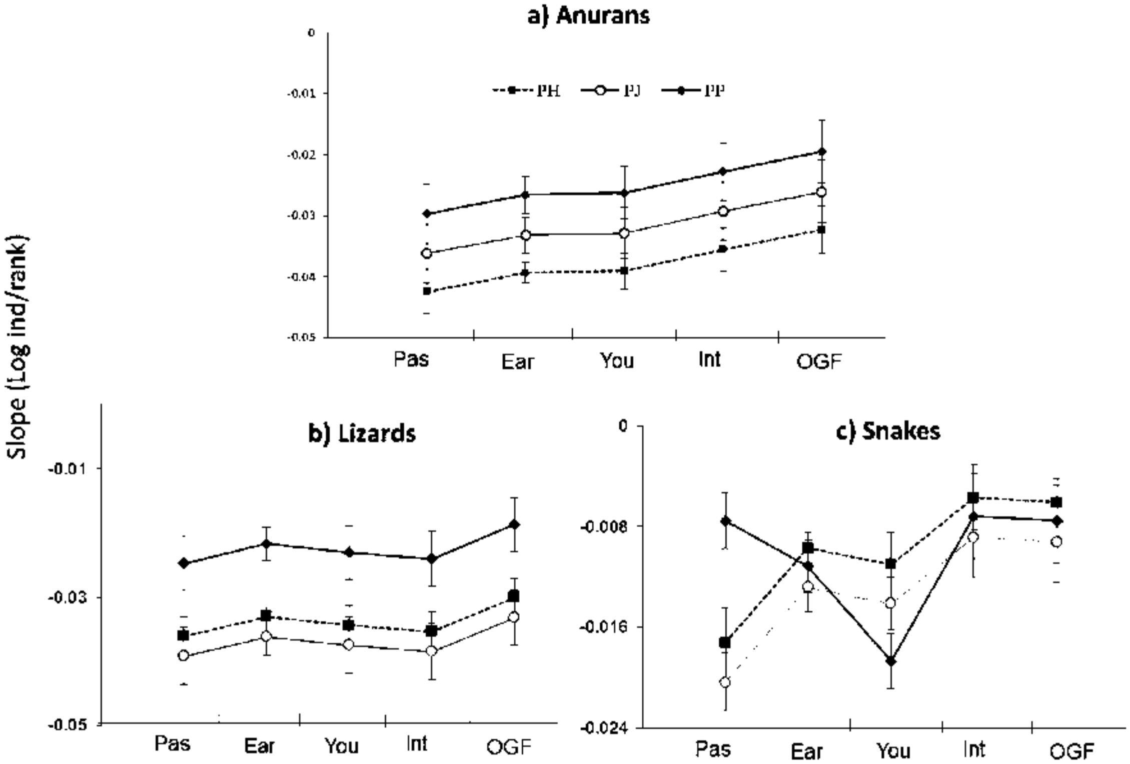

Figure 5. Slopes of the rank -abundance curves to evaluate changes in community evenness of the herpetofauna from five successional stages of the tropical dry forest in response to the occurrence of hurricanes Jova and Patricia at the coast of Jalisco, Mexico. Symbols represent the slopes and the bars represent 1SE. Square = pre-hurricanes (PH), Circles = post-hurricane Jova (PJ), Diamonds= post-hurricane Patricia (PP). Pas = Pasture, Ear = Early, You = Young, Int = Intermediate, OGF = Old-growth forest.

Contrastingly, after Patricia, the abundance of *A. nebulosus* declined by 96 % (Fig. 6). The lizard *Sceloporus utiformis* showed a 12 % increase in abundance after Jova, but a 46 % decline after Patricia (Fig. 6). The lizard *S. utiformis* became the dominant lizard species after Patricia (Fig. 6). The lizards *Sceloporus melanorhinus* and *Urosaurus bicarinatus* showed similar abundances before and after Jova; but presented a noticeable decline after Patricia, even disappearing from some successional stages such as early-forests (Table 1, Fig. 6). Snake evenness changed along successional stages (S), after both hurricanes (H), and there was a significant (S:H) interaction (Table 4).

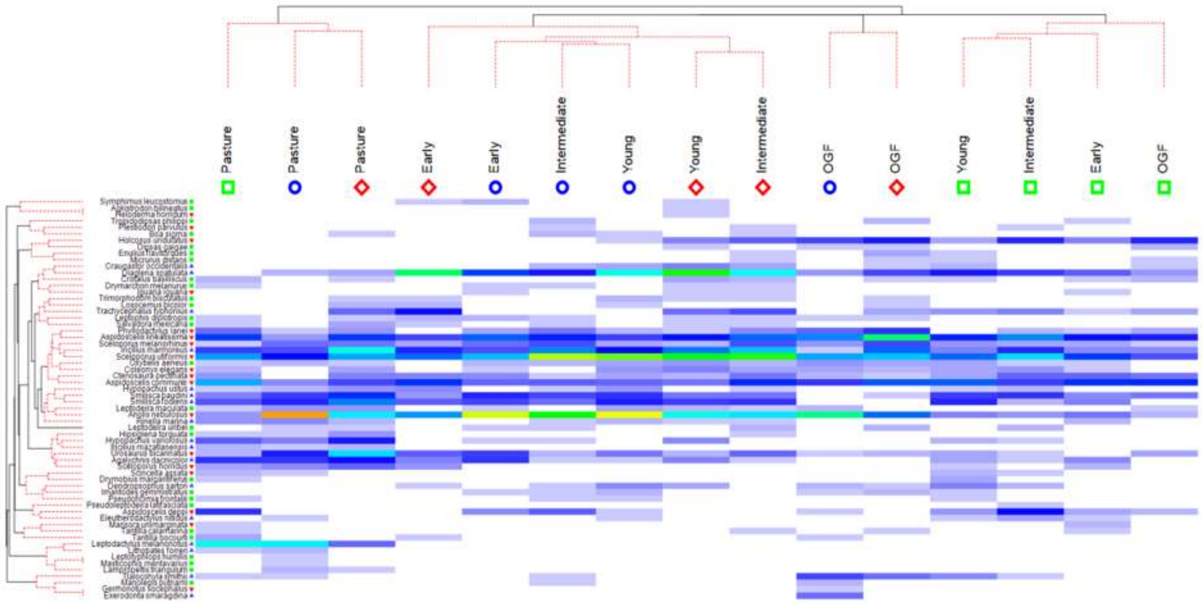

Figure. 6. A species heatmap of herpetofaunal assemblages associated with successional stages and disturbance conditions (pre-hurricanes , post-hurricane Jova and post-hurricane Patricia). For each species (left cluster) their association degree with stages and conditions (upper cluster) is represented with a color palette that goes from dark red to pale blue; the darker tones represent highest level of association of a species for a specific site. On the left cluster, the taxonomic group is shown as a different geometric figure in front of each species' name: Anurans , Lizards , and Snakes . Sites were classified in three groups, and species in 12 groups that show a different multivariate structure.

Snakes did not present the same pattern of higher evenness shown by lizards and anurans along the secondary succession gradient and after hurricanes, as the pastures exhibited a noticeable increase and young forests a decrease in snake evenness (Fig. 5). After hurricanes, the snakes *Leptodeira maculata* and *Oxybelis aeneus* lowered their dominance in pastures and *Drymobius margaritiferus* increased its dominance in young forests. In general, *O. aeneus* was the dominant snake species before and after the hurricanes, whereas *Leptophis diplotropis*, *Salvadora mexicana*, *Trimorphodon biscutatus*, *Hypsiglena torquata*, *L. maculata* and *L. uribei* declined after hurricanes. Furthermore, the snakes *Manolepis putnami*, *Symphimus leucostomus* and *Loxocemus bicolor* were not recorded at any successional stage after hurricane Patricia (Table 1, Fig. 6).

Based upon the degree of association of species on successional stages and disturbance conditions, we found 14 distinct clusters representing herpetofauna assemblages (Fig. 6). The four largest clusters included from nine to six species across taxonomic groups (anurans, lizards, and snakes). Herpetofaunal assemblages were similar in pastures before and after hurricanes, and mature forests were different from the other successional stages before and after hurricane Jova (Fig. 6). After hurricane Patricia, all successional stages (except pastures) were grouped (Fig. 6).

3.2 Cumulative effects of hurricanes on herpetofaunal assemblages

For anuran assemblages, average dissimilarity between pre-hurricanes and post-hurricane Jova was 79.05%. Five anuran species (*Diaglena spatulata*, *I. marmoreus*, *A. dacnicolor*, *S. fodiens* and *S. baudini*) accounted for 76.52% of species dissimilarity. The average dissimilarity between hurricanes Jova and Patricia was 87.56%. Five anuran species (*D. spatulata*, *S. baudini, A. dacnicolor, I. marmoreus* and *S. fodiens*) accounted for 70.1% of species dissimilarity. The average dissimilarity between pre-hurricanes and post-hurricane Patricia was 83.88%. Five anuran species (*D. spatulata*, *I. marmoreus, S. fodiens, S. baudini* and *A. dacnicolor*) accounted for 77% of species dissimilarity, showing an important discriminatory capacity between pre-hurricanes and post-hurricane Patricia (Fig. 7a). The first two axes of the PCoA explained 78.1% of the variation in anuran species distribution across successional stages before and after the hurricanes (Fig. 7a). The Metric Multidimensional Scaling Analysis showed that in all successional stages there were marked changes in assemblage structure after hurricane Patricia (MS1).

For lizard assemblages, average dissimilarity between pre-hurricanes and post-hurricane Jova was 62.79%. Five species (*A. nebulosus*, *S. utiformis*, *Aspidoscelis lineattissima*, A. communis and *U. bicarinatus*) accounted for 73.68% of species dissimilarity. The average dissimilarity between post-hurricanes Jova and Patricia was 80.77%. Five lizard species (*A. nebulosus*, *S. utiformis, A. lineattissima, A. communis and S.*

melanorhinus) accounted for 72.28% of species dissimilarity. The average dissimilarity between pre-hurricanes and post-hurricane Patricia was 78.25%. Five lizard species (*A. nebulosus*, *S. utiformis*, *A. lineattissima*, *A. communis and U. bicarinatus*) accounted for 71.02% of species dissimilarity (Fig. 7b). The first two axes of the PCoA explained 75.5% of the variation in lizard species distribution across successional stages before and after the hurricanes (Fig. 7b). The Metric Multidimensional Scaling Analysis showed that in all successional stages there were marked changes in species composition after hurricane Patricia (MS2).

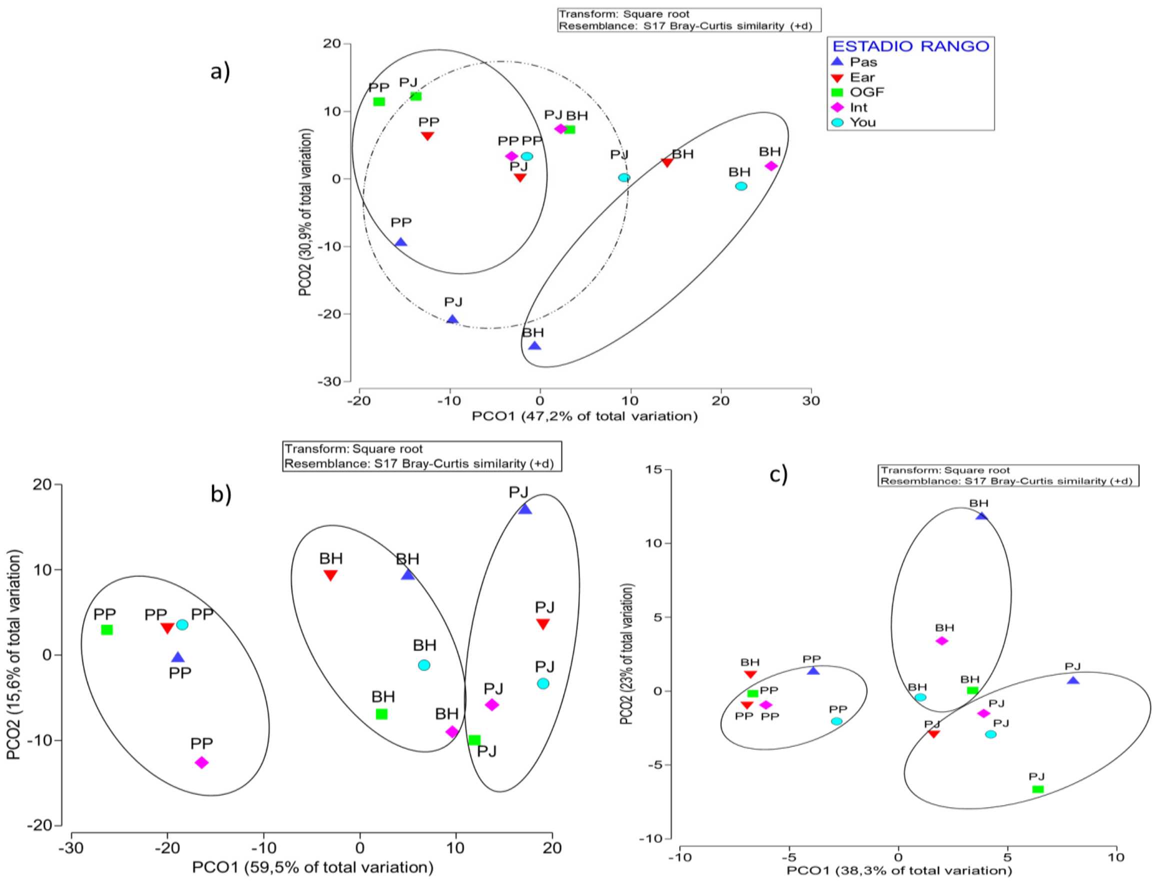

Figure 7. Principal Coordinates Analysis of species composition in the tropical dry forest of Chamela. (a) anurans, (b) lizards, (c) snakes. PH = pre-hurricanes, PJ = post-hurricane Jova, PP = post-hurricane Patricia. Pas = Pasture, Ear = Early, You = Young, Int = Intermediate and OGF = Old-growth forest.

In the case of snake assemblages, average dissimilarity between pre-hurricanes and post-hurricane Jova was 96.55%. Ten species (*O. aeneus, L. maculata, Leptophis diplotropis, T. biscutatus, Imantodes gemmistratus, Symphymus leucostomus, Loxocemus bicolor, Salvadora mexicana, Hypsoglena torquata and Coluber mentovarius*) accounted for 71.40% of species dissimilarity. The average dissimilarity between hurricanes Jova and Patricia was 98.13%. Nine species (*O. aeneus*, *L. maculata, I. gemmistratus*, *Manolepis putnami*, *L. diplotropis, Crotalus basiliscus, T. biscutatus, Pseudoficimia frontalis and Leptodeira uribei)* accounted for 70.71% of the dissimilarity. The average dissimilarity between pre-hurricanes and post-hurricane Patricia was 98.20%. Eleven snake species (*O. aeneus*, *C. basiliscus*, *L. maculata*, *S. mexicana*, *L. diplotropis, H. torquata*, *L. bicolor, T. biscutatus, Tantilla callamarina*, *L. uribei and Enulius flavitorques*) accounted for 70.34% of species dissimilarity (Fig. 7c). The first two axes of the PCoA explained 61.3% of the variation in snake species distribution across successional stages under pre and post-hurricane conditions (Fig. 7b). The Metric Multidimensional Scaling Analysis showed that pastures, early-forests, intermediate forests, and old-growth forests showed marked changes in snake species composition after hurricane Patricia (MS3).

4. Discussion

Our study considers the cumulative impact of a category 5 hurricane (Patricia) on herpetofaunal assemblages in a tropical dry forest, two years after the impact of hurricane Jova (category 2). The cumulative effects of hurricanes might cause dramatic changes in the structure of biotic assemblages within hours of landing (Wiley & Wunderle, 1993; Widmer et al., 2004; Vilella & Fogarty, 2005; Schriever et al., 2009; Wunderle & Arendt, 2011; Nicoletto 2013; Shiels et al., 2014). Although such disturbances may be a source of natural selection, their frequency and magnitude might lead some species to go locally extinct (Schoener et al., 2017). Furthermore, the decline of predatory amphibian and reptile species might alter the food chains of their communities (Spiller et al., 1998; Schoener et al., 2001a, 2001b; Spiller et al., 2016).

Overall, we found significant changes in the assemblage structure of anurans, snakes and lizards as consequence of the combined effects of hurricanes and successional stage, which is concordant with previous reports (Vecchi et al., 2008; Schriever et al., 2009; Nicoletto, 2013; Suazo-Ortuño et al., 2018b). In regard to our first hypothesis, we found a significant decline in the abundance of the herpetofauna after hurricane Patricia; while after hurricane Jova, the decline was not as evident, as some species increased in abundance, showing signs of recovery, as previously reported by Suazo-Ortuño et al. (2018a, 2018b). We also observed changes in richness and diversity of lizards and snakes after hurricanes. Contrary to our hypothesis, we did not observe a significant decline in anuran species richness and diversity despite the decline in abundance for some species at some successional stages. After hurricane Patricia anurans and lizards markedly changed in species composition in all successional stages, whereas snakes presented marked changes in all successional stages, except in young forest.

Several studies have shown a decline in species abundance, richness and diversity of herpetofaunal assemblages after hurricanes, with strong changes in community structure and composition as some species become dominant while others disappear from the community (Woolbright, 1991, Reagan, 1991; MCCoid, 1996; Spiller et al., 1998, 2016; Schoener et al., 2001a, 2001b, 2004; Vilella & Fogarty, 2005; Schriever et al., 2009; Klawinski et al., 2014; Shiels et al., 2014; Suazo-Ortuño et al., 2018a, 2018b). Contrastingly, several studies have found an increase in population abundance of herpetofauna after a hurricane (Nicoletto, 2013). Hurricanes might drive colonization and extinction dynamics of biotic populations in the regions affected (Woolbright, 1991; Vilella & Fogarty, 2005; Schriever et al., 2009).

After hurricane Patricia anuran and reptile communities showed the greatest changes in species abundance. There is evidence that abundance of some amphibian and reptile species increased after hurricanes of low intensity (categories 1 and 2 S-S) (Suazo-Ortuño et al., 2018a, 2018b; Enge, 2005; Nicoletto, 2013), whereas some specialist species showed a decline in abundance after high intensity hurricanes (Schoener et al., 2001 a, 2001b; Vilella & Fogarty, 2005; Suazo-Ortuño et al., 2018a, 2018b). In our study, after hurricane Patricia, some specialist species in OGF, specifically *Exerodonta smaragdina* and *Gerronothus liocephalus* were not found, whereas some others, such as *Tlalocohyla smithi, Phyllodactylus lanei, I. gemmistratus, M. putnami* and *Sibon philippi* markedly declined in abundance. Changes in vegetation structure lead to greater canopy openness; mainly in old-growth forest where animals become more exposed to altered environmental conditions such as increased insolation and air temperature, and a reduction in humidity (Reilly, 1991; Walker, 1991, 1996; Roth, 1992). Additionally, hurricanes can have variable ecological effects depending on their timing and severity (Schoener et al. 2004). In our study, cumulative effects of hurricanes negatively affected the abundance of most species, even those showing resilience after hurricane Jova (Suazo-Ortuño et al. 2018ab). Previous studies regarding cumulative impacts of hurricanes on herpetofauna have reported abundance declines after hurricanes (e.g., Schoener et al., 2004; Spiller et al., 2016), especially as a result of habitat destruction (Mccoid, 1996).

Regarding our second hypothesis, we found that abundance, richness and diversity of anurans changed significantly among forest successional stages. These changes were stronger in old-growth forests as shown by the PCoA, where abundance of anurans markedly declined after hurricanes. Old-growth forests are important for amphibian populations, since mature forests tend to have a greater richness, diversity and a high percentage of species endemic to these tropical dry forests (Gardner et al., 2007; Herrera-Montes & Brokaw, 2010; Hernandez-Ordoñez et al., 2015). During hurricanes, old-growth forests are more prone to defoliation and structural damage because winds can cause severe structural damage to all vertical levels of the forest, and many old-growth species, especially slow-growing plants are especially vulnerable (Tanner et al., 1991, Everham & Brokaw, 1996). Therefore, changes on vegetation structure, as consequence of natural and anthropogenic disturbances can result in changes in anuran assemblages, principally affecting species abundance, as anurans are sensitive to changes in their physical environment (Woolbright, 1996; Vilella & Fogarty, 2005; Klawinski et al., 2014; Shiels et al., 2014).

In relation to the evenness increase expected after hurricanes as stated in our first hypothesis, we found that in general, species rank in abundance changed after hurricanes in relation to baseline abundances of pre-hurricane records. As a consequence of cumulative disturbances, the herpetofaunal assemblage became more evenly distributed in detriment of some amphibian and reptile species, as has been shown for other ecosystems (Schriever et al., 2009). For instance, before hurricanes, the most abundant anurans were *D. spatulata* and *I. marmoreus*, but after hurricane Patricia, these specie decreased almost 50% in abundance. Before the hurricanes, the most abundant lizard was *S. utiformis*, and after Jova, the most abundant lizard was *A. nebulosus*, with a threefold increase in abundance, as has been reported for other *Anolis* species after hurricanes (Reagan, 1991; Enge, 2005; Schoener et al., 2017). Nevertheless, after high intensity hurricanes, some *Anolis* species showed reduction in population sizes, and some have even become locally extinct (Spiller et al., 1998; Schoener et al., 2001a). The lizard community showed the strongest changes after hurricane Patricia. Several *Anolis* species have been reported to be abundant after disturbances (Donihue et al., 2018), but not after high intensity hurricanes that have damaged their perching structures (Spiller et al., 1998; Schoener et al., 2001a). It is possible that the noticeable decline of *Anolis* abundance after category 5 (S-S) hurricane Patricia, but not after category 2 (S-S) hurricane Jova, was the high level of damage to perching sites caused by the strong winds of hurricane Patricia.

In fact, after hurricane Patricia, previously abundant species of lizards were not recorded in some successional stages. Such was the case of *U. bicarinatus* in early-forests, *Iguana iguana* and *Phyllodactylus lanei* in young-forests, and *Coleonyx elegans* and *Gerronothus liocephalus* in old-growth forests.

After hurricanes, snake's evenness increased in pastures because of a decrease in abundance of *L. maculata* and *O. aeneus*. This pattern was possibly a result of an appreciable decrease after hurricanes in abundance of the anurans *S. baudini* and *S. fodiens* and the lizard *A. nebulosus*, main prey types of these snake species. Contrastingly, after hurricanes in the young forest, snake evenness markedly decreased because of an increase in abundance of the snake *D. margaritiferus*. The increase in abundance of this species was possibly a result of an increase in abundance of the lizards *Aspidoscelis lineattisima* and *Aspidoscelis communis*, species that are part of the diet of this snake species. Furthermore, in general, because of their low abundances and secretive nature, reliable estimates of snake abundances in field studies are difficult to obtain (Duellman, 1989; Urbina-Cardona et al., 2008; Calderon- Mandujano, 2008; Luja et al., 2008).

Nevertheless, in our long-term sampling effort, we found a significant effect of hurricanes on assemblage structure of snakes. After Patricia, we found a strong decline of several snake species and the disappearance of some others, such as *Agkistrodon billineatus* and *Boa sigma*, as has been shown in other studies (Wunderle et al., 2004; Schriever, 2009). Structural changes such as tree defoliation and uprooting, as well as increase in leaf litter might alter the light regime, microclimate and heterogeneity of the forest floor (Bellingham et al., 1996). These changes can cause some habitat specialist snakes to diminish in abundance or disappear from some sites (Suazo-Ortuño et al., 2018a)

Regarding our third hypothesis, we found a significant decrease in similarity between pre-hurricanes and post-hurricane Patricia in all herpetofauna groups, and in all successional stages. Additionally, the heatmap analysis showed that after hurricane Patricia there was an increase in similarity among successional stages, except pastures. Low levels of vegetational structural complexity in pastures result in lower microhabitat availability for herpetofauna (Suazo-Ortuño et al., 2018a; Urbina-Cardona et al., 2006), but pastures allow for species movements and provide permanent availability of other resources (Driscoll et al. 2013). Therefore, amphibians and reptiles adapted to the environmental conditions of pastures are more resilient to hurricane disturbance regime than assemblages inhabiting tropical dry forest remnants. We also registered an increase in evenness in anurans and lizards after hurricane Patricia among successional stages. Our results are coincident to those reported by Martínez-Ruiz and Renton (2018) for the same study area with diurnal raptor communities. These authors report a significant increase in species evenness, and greater similarity in all habitats within the path of the eyewall of hurricane Patricia. Our results suggest that the registered increase of evenness was likely a result of a decrease in abundance of dominant species after hurricanes. Changes in resource availabilities as a result of hurricanes can be drivers of evenness (Schriever et al., 2009). The decrease in similarity of herpetofauna after hurricane Patricia was mainly a result of thirteen not previously recorded species after hurricanes (10 after Jova and two after Patricia). Herpetofauna similarities among successional stages after Patricia suggest a process of homogenization (sensu Martínez-Ruiz & Renton, 2018). Although, biotic homogenization has been associated to anthropic disturbances, and in the case of successional stages in dry tropical forest this pattern has been reported for herpetofauna groups in our study site (Suazo-Ortuño et al., 2015), scant information exists on the influence of extreme climatic events on biotic homogenization (Haslem et al., 2015). Our results suggest that the assemblages' homogenization, resulting from the cumulative effect of hurricanes might be a factor that contributes to regulate biotic diversity.

The changes in assemblage structure that were observed after hurricane Patricia in all successional stages might indicate that although some species of the herpetofauna showed a reduction in abundance or became locally extinct in some successional stages (e.g. specialist species in OGF such as *Exerodonta smaragdina*, *Tlalocohyla smithi*, *Gerronothus liocephalus*, *Phyllodactylus lanei*, *I. gemmistratus*, *M. putnami* and *Sibon philippi*) other species might be able to adapt to novel habitats that result from the interaction between secondary tropical dry forest and hurricanes. This interaction may define trajectories of ecosystems recovery and the hurricanes can be major drivers, affecting tropical dry forest herpetofaunal diversity. The findings of our study showed that hurricanes impacts on reptile and amphibian communities are modulated to some extent, by tropical dry forest successional stages.

Cumulative effects of hurricanes in tropical dry forests altered herpetofaunal abundance, species richness and assemblage structure, increasing species evenness for all successional stages, particularly in old-growth forest, possibly resetting competition relationships among species, potentially affecting long-term colonization and extinction dynamics of herpetofaunal populations and overall species interactions (Schriever et al., 2009). Additionally, our results showed few changes in the herpetofaunal community among successional stages after hurricane Jova, suggesting that tropical dry secondary forests, under the impact of low intensity hurricanes, might function as buffers that promote herpetofauna resilience. However, cumulative effects of hurricanes (a low intensity and a high intensity hurricane) resulted in a homogenization tendency among successional stages, suggesting a negative effect for ecosystem functioning. The changes in the buffering role of secondary forests highlights the importance of these ecosystems for conserving biodiversity in times when hurricane disturbances are increasing in frequency and intensity, particularly in regions with a historical record of low-frequency hurricanes (Castañeda-Moya et al., 2020). Additionally, because the amphibians and reptiles comprise a large portion of vertebrate biomass (Petranka & Murray, 2001; Pough et al., 2004) and play various ecological functions in forest ecosystems (e.g. nutrient cycling, energy flow through trophic chains as predator and prey, bioturbation, seed dispersal and pollination; Cortés-Gómez et al., 2015) they can modify forest processes such as regeneration and nutrient cycling (Felix et al., 2004). Our results indicated that the signs of recovery shown by some species after the effects of a hurricane are halted by the occurrence of a second hurricane. These results are relevant considering that the global climate change has increased the frequency and intensity of hurricanes with the consequent effects on selection pressures and survival of herpetofaunal species (Emanuel, 2005; 45 et al., 2005; Emanuel, 2013). For long-term conservation of native reptile and anuran species and their functions in the forest ecosystems, monitoring programs to evaluate the role of pulsing high-energy disturbances, such as hurricanes, in maintenance of forests biodiversity under a scenario of climate change in anthropic landscapes are necessary.

6. Credit author statement

JAMP: Conceptualization, Methodology, Investigation, Data curation and Writing- Original draft preparation. **ISO**: Conceptualization, Methodology, Resources, Writing-Reviewing and Editing, Supervision and Funding acquisition. **NUC**: Formal analysis, Writing-Reviewing, **JBM**: Visualization, Writing-Reviewing.

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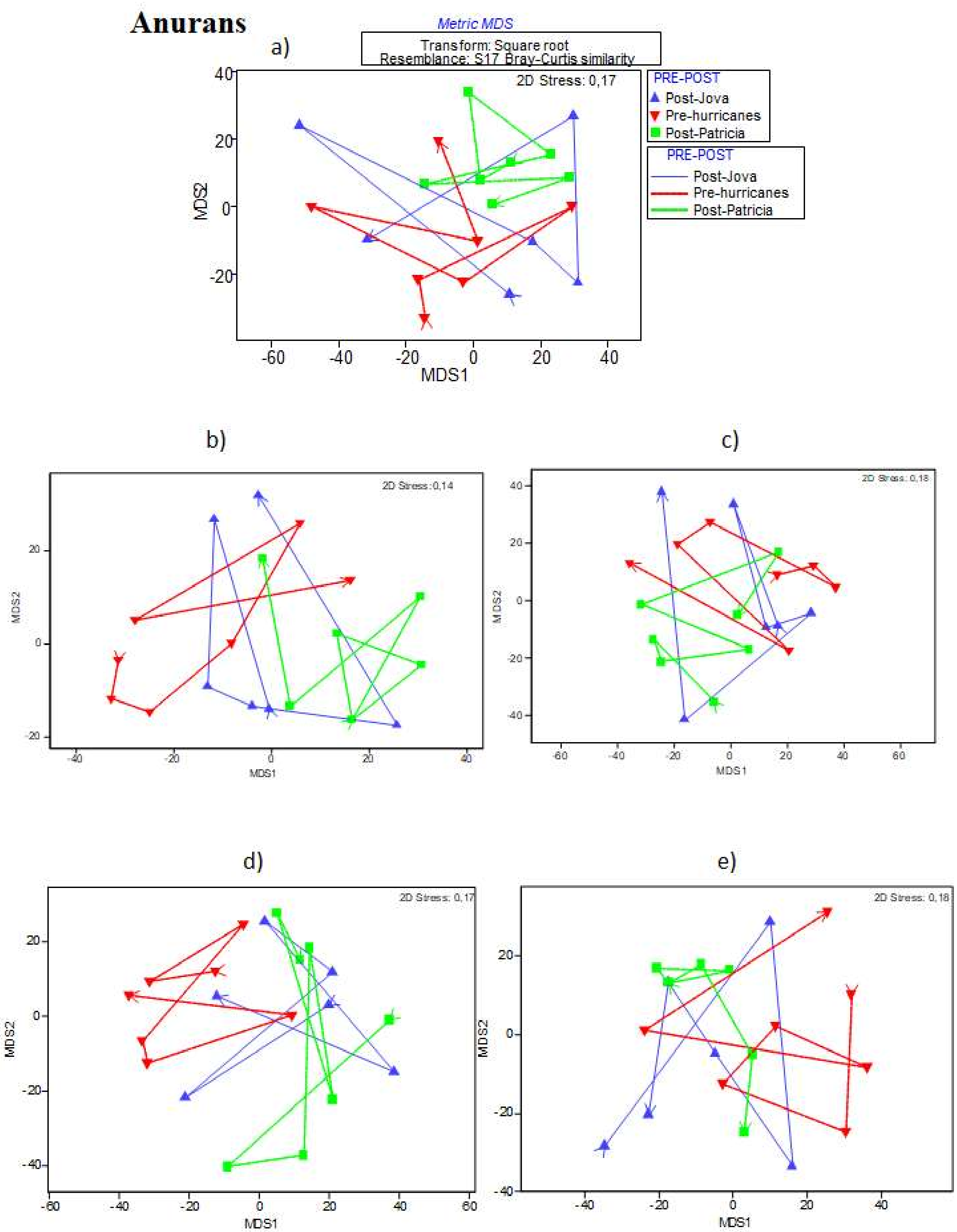
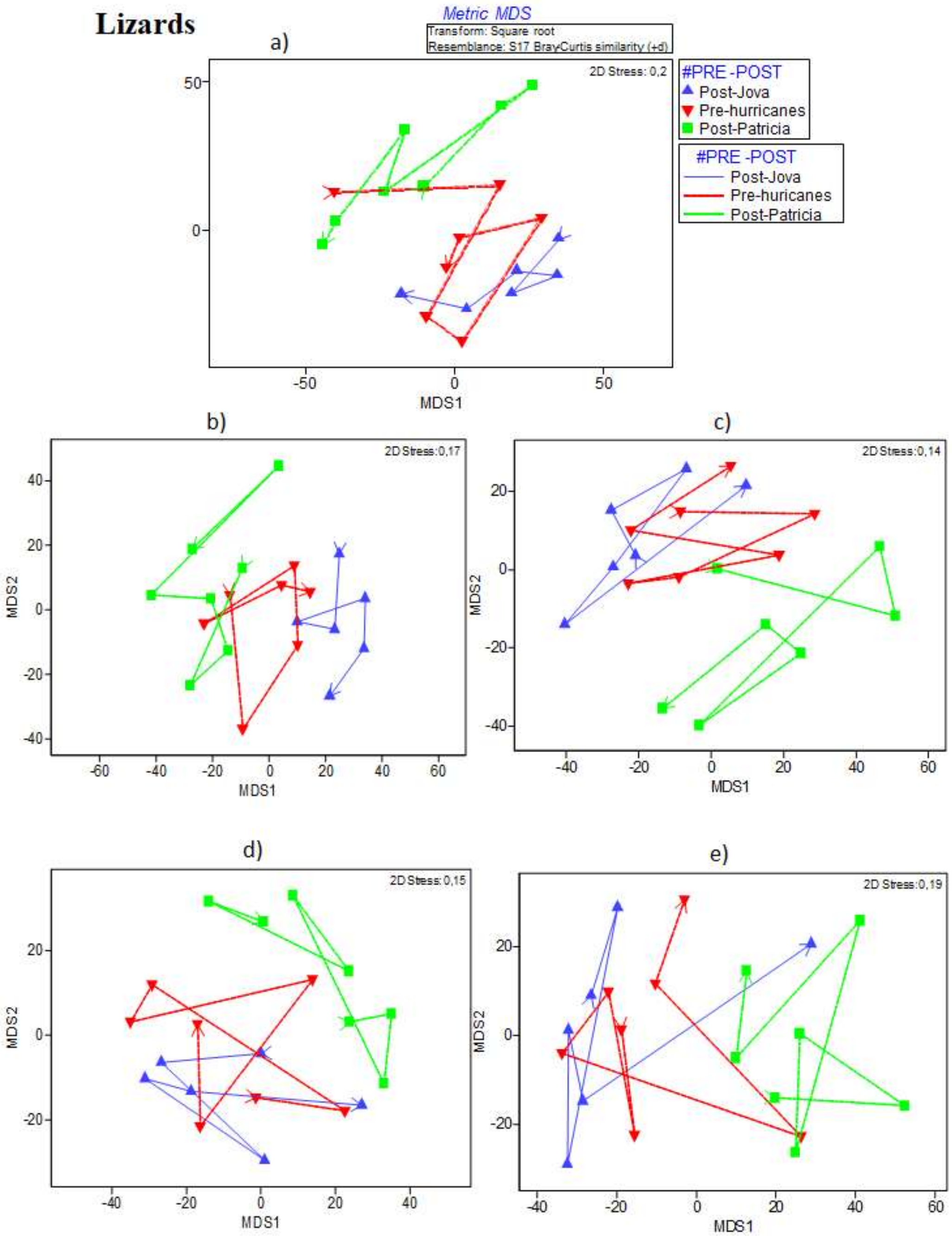
Material supplementary (MS)

MS1. Multidimensional scaling analysis of species composition of anurans in the tropical dry forest of Chamela. a) Pasture, b) Early, c) Young, d) Intermediate, e) OGF. ▼ = pre-hurricanes, ▲ = post-Jova, and ■ = post-Patricia.

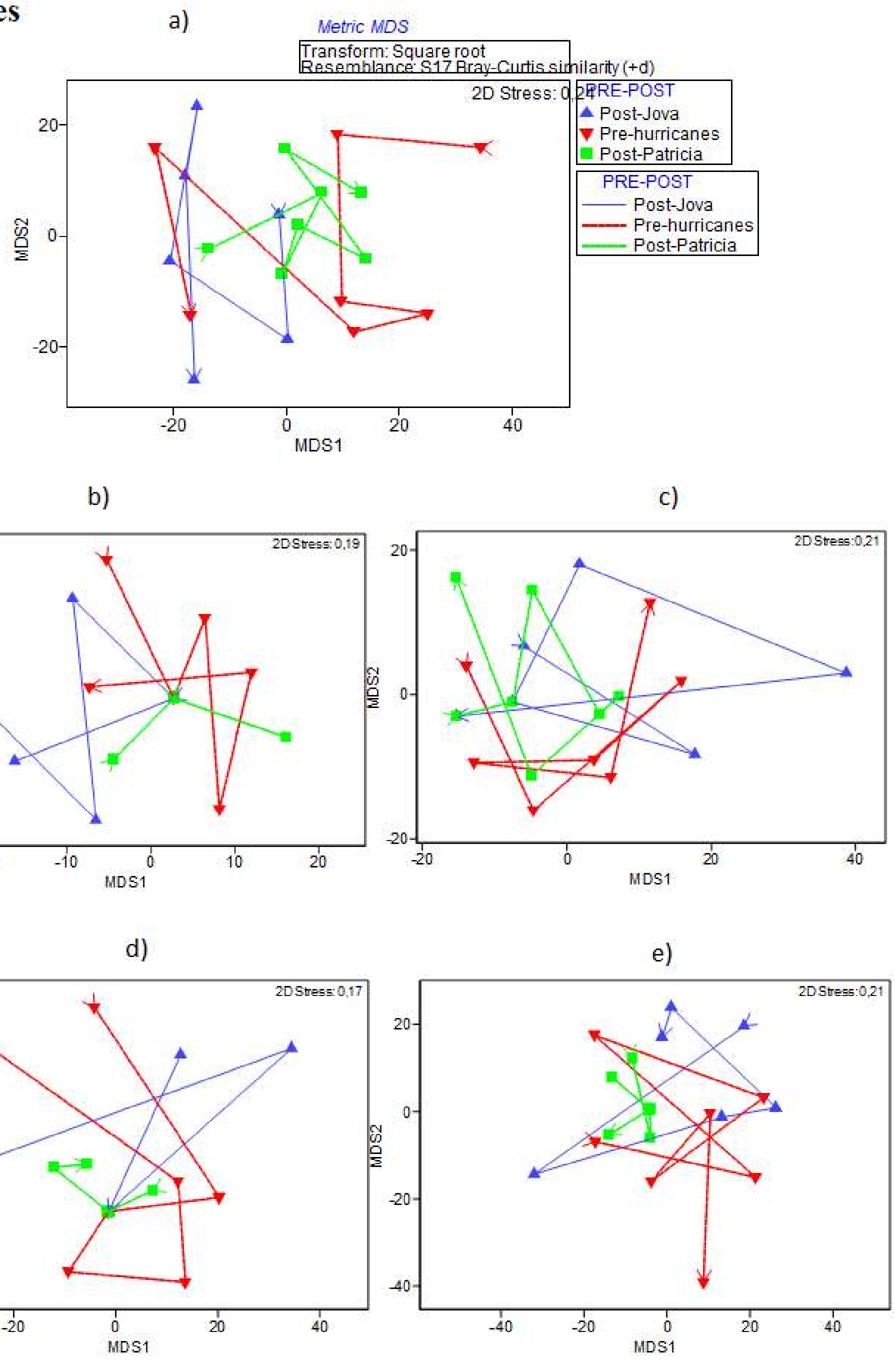


MS2. Multidimensional scaling analysis of species composition of lizards in the tropical dry forest of Chamela. a) Pasture, b) Early, c) Young, d) Intermediate, e) OGF. ▼ = pre-hurricanes, ▲ = post-Jova, and ■ = post-Patricia.



MS3. Multidimensional scaling analysis of species composition of snakes in the tropical dry forest of Chamela. a) Pasture, b) Early, c) Young, d) Intermediate, e) OGF. ▼ = pre-hurricanes, ▲ = post-Jova, and ■ = post-Patricia.

Snakes



a)
Metric MDS
Transform: Square root
Resemblance: S17 Bray-Curtis similarity (+d)
2D Stress: 0,24
PRE-POST
Post-Jova
Pre-hurricanes
Post-Patricia
MDS1
MDS2
b)
2D Stress: 0,19
c)
2D Stress: 0,21
d)
2D Stress: 0,17
e)
2D Stress: 0,21

6. ARTICULO III

Efecto de los Huracanes sobre la lagartija *Anolis nebulosus* en el bosque tropical de chamela, Jalisco, México.

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1. Abstract

In the Pacific coast of Jalisco, Mexico, we aimed to evaluate the cumulative effects of Hurricanes Jova (2011) and Patricia (2015) on on the population attributes of *Anolis nebulosus* along tropical dry forest successional stages by comparing population density and morphometric traits before and after the hurricanes. We conducted a long-term survey (2009 to 2018) on *A. nebulosus* lizards within five dry forest successional stages (from 0 to > 50 years after forest clearance), including the following: active pastures, early forests, young forests, intermediate forests, and old-growth forests as experimental controls. Our results showed an increase in abundance of more than 250% of the individuals of *A. nebulosus* after the passage of Hurricane Jova. But it decreased by more than 90% after Hurricane Patricia. In addition, hurricanes were found to promote changes in weight, snout-vent length (SVL), and perch height, among successional stages the perch height only changed in mature forest where they used higher perches.

2. Resumen

El efecto de los huracanes sobre los lagartos ha sido muy estudiado en la región del caribe principalmente para el género *Anolis*, sin embargo, en la región del pacifico se sabe poco de como afectan los huracanes a las lagartijas. Además, el régimen de huracanes en el Pacífico es muy distinto al caribe. En la región de Chamela Jalisco tocaron tierra dos huracanes el huracán “Jova” de categoría 2 en la escala de Saffir-Simpson y vientos máximos sostenidos de hasta 165 km/h los días 11 y 12 del mes de Octubre del año 2011 y el huracán Patricia categoría 5 que tocó tierra impactando la misma costa de Jalisco en la noche del 23 de Octubre de 2015. El objetivo del presente estudio fue estimar el efecto de los huracanes Jova y Patricia sobre los atributos poblacionales de *Anolis nebulosus*. Nuestros resultados mostraron un incremento en la abundancia de más del 250% de los individuos de *A. nebulosus* después del paso del huracán Jova. Pero disminuyó más del 90% después del

huracán Patricia. Además, se encontró que los huracanes promueben cambios en el peso, longitud hocico-cloaca (SVL), y el uso en la altura de la percha, además la altura de la perchas solo cambio en el bosque maduro donde las perchas fueron de mayor altura.

3. Introducción

Los efectos ocasionados por huracanes pueden llegar a modificar de manera drástica las comunidades vegetales y animales en los lugares de impacto (Jauregi, 1989; Wiley y Wunderle, 1993; Walker et al., 1996; Avila-Cabadilla et al., 2009; Pérez et al. 2012). La intensidad y frecuencia con la que los huracanes tocan tierra ha ido en aumento desde hace más de 40 años en especial los de categoría 4 y 5 (Webster et al., 2005). El pacífico es uno de los lugares con mayor actividad ciclónica pero debido a las condiciones atmosféricas y oceánicas son pocos los que llegan a tocar tierra (Reyes y Mejía-Trejo, 1991; Castro, 2010), sin embargo en las últimas décadas se ha encontrado un aumento significativo en la intensidad y frecuencia de los huracanes en el océano pacifico (Jáuregui, 2003; Maass et al., 2017; Álvarez- Álvarez-Yépiz et al., 2018). La región de la costa de Jalisco históricamente era una de las menos afectadas por huracanes (Jáuregui, 2003; Castro, 2010), a pesar de lo anterior, entre el 2011 y el 2015 esta región fue alcanzada por dos huracanes, el primero en octubre del 2011 de categoría 2 en la escala Saffir-Simpson (S-S) y el segundo de categoría 5 en octubre de 2015 ambos tuvieron un gran impacto en la biodiversidad de la región (Martínez-Yrízar et al., 2018; Martínez-Ruiz y Renton, 2018; Suazo-Ortuño et al., 2018 a,b). El incremento de este tipo disturbio ocasiona que las poblaciones estén sometidas a regímenes de disturbio/perturbación a las cueles no están acostumbradas y que pueden tener consecuencias tales como la disminución de las poblaciones, cambios en la morfología de los individuos, cambios en el microhábitat, modificación en las temperaturas, cambios en la humedad del suelo y del ambiente y extinción de especies localmente (Reagan, 1991; Schriever et al., 2009; Walker, 1996; Marroquin-Páramo et al., 2020). Aunque el estudio del efecto de los huracanes sobre las comunidades y poblaciones de herpetofauna es relativamente reciente comenzando a principio de la década de los 90's (Woolbright, 1991;

Reagan, 1991). Los estudios sobre las poblaciones cada vez son más frecuentes (Dofour et al., 2019; Walls et al., 2019; Donihue et al., 2020; Huey y Grant, 2020; Rabe et al., 2020). La herpetofauna puede ser tal vez uno de los grupos más afectados por disturbios naturales y antrópicos esto debido a que la mayoría de las especies en este grupo tienen una baja movilidad (Pough 1980; Duellman y Trueb 1994; Stebbins y Cohen 1995). Existen varios estudios que documentan el efecto de los huracanes en las comunidades de reptiles la mayoría se enfocan en los efectos a corto plazo o de un solo huracán (Dodd et al., 2006; Pérez et al, 2012; Nicoletto, 2013; Gray y Strine, 2017), son pocos los estudios que se realizan a largo plazo y que conllevan el efecto de dos o más huracanes (Spiller et al., 2016; Schoener et al., 2017; Marroquín-Páramo et al., 2020). Existen algunas especies y géneros de reptiles ampliamente estudiados tras el paso de un huracán, como es el caso de las lagartijas del género *Anolis* que ha sido uno de los más estudiados dentro del grupo de la herpetofauna, principalmente en las zonas de la Bahamas, enfocándose principalmente en la resiliencia y supervivencia de las especies después de los huracanes (Dofour et al., 2019; Donihue et al., 2020; Huey & Grant 2020; Rabe et al., 2020).

El género *Anolis* está ampliamente distribuido desde el norte de México hasta Sudamérica donde se reconocen más de 400 especies (Williams, 1992; Powell et al., 1996), pero solamente unas pocas han sido estudiadas para entender los efectos de los huracanes sobre sus poblaciones, encontrando que la modificación en las abundancias puede ocasionar cambios en la cadena trófica como el aumento de insectos modificando la herbívora de toda una isla (Schoener y Spiller, 2006; Spiller et al., 2016). Se ha demostrado que las poblaciones de *Anolis* pueden disminuir drásticamente o incluso extinguirse localmente después del paso de uno o varios huracanes de alta intensidad (Spiller et al., 1998; Schoener et al., 2001a). Sin embargo, aunque las lagartijas *Anolis* de las Bahamas son susceptibles a los efectos de los huracanes, las lagartijas han desarrollado adaptaciones evolutivas tales como la supervivencia de los huevos bajo el agua por hasta 4 horas (Schoener et al., 2004; Losos et al., 2003), el aumento en el tamaño de las extremidades y numero de lamelas que les permite aferrarse mejor a su percha y sobrevivir a vientos huracanados. Estas características les confieren una ventaja para su supervivencia volviéndolos más resilientes a estos fenómenos

(Dofour et al., 2019; Donihue et al., 2020; Huey & Grant 2020; Rabe et al., 2020). En el pacífico mexicano se sabe que, dependiendo de la intensidad del huracán, las poblaciones de *Anolis* pueden variar después de un huracán. Además, en algunas Islas de la región de estudio la densidad poblacional y la altura de la percha aumentaron después del huracán Jova (Suazo-Ortuño et al., 2018; García y Siliceo-Cantero, 2019; Marroquín-Páramo et al., 2020). Se conoce poco sobre el efecto de los huracanes en las poblaciones de lagartijas del Pacífico mexicano, por lo que es de importante conocer como responden las poblaciones a estos disturbios (Jáuregui, 2003). Además, los disturbios antrópicos, como la deforestación y el cambio de uso de suelo, las presiones a las que se ven sometidas las poblaciones de lagartijas pueden ocasionar un declive o perdida de sus poblaciones (Suazo- Ortuño et al., 2015, 2018).

El huracán Jova, categoría 2 en la escala de Saffir-Simpson (S-S), toco tierra impactando la costa de Jalisco en la madrugada del 12 de octubre de 2011 y dejó a su paso daños considerables. Los daños mayores se concentraron en la zona rurales de la costa occidente de Jalisco y en Colima. Los BTS del área de Chamela sufrieron daños notables en la estructura vegetal (Suazo-Ortuño et al., 2018 a,b). Cuatro años después, la costa de Chamela fue azotada por el huracán Patricia el día 23 de octubre, de categoría 5 en la escala de S-S a las 13:00 horas con vientos sostenidos de 325 km/h golpeando la costa de Jalisco. A partir de ese momento, el episodio fue superando todos los registros históricos de la serie contenida en el NOAA y se clasificó como el huracán más peligroso que ha golpeado la costa del Pacífico y el mayor registrado a escala global en términos de rachas de vientos de >400 km/h. Después del huracán Jova se documentaron cambios en abundancia y estructura de la herpetofauna así como cambios en sus atributos funcionales (Suazo-Ortuño et al., 2018), además en las Islas de la región se han reportado cambios en el microhábitat y un aumento en la abundancia de lagartijas (Siliceo-Cantero y García et al., 2019). El, además después del huracán Patricia se encontró un cambio en las comunidades de aves raptoras disminuyendo en los bosques donde paso directamente el huracán, además de una mayor homogenización de especies en los sitios (Martínez-Ruiz y Renton, 2017), además para los psitácidos de la región se reporta una disminución de avistamientos, del recurso alimenticio y del número de cavidades disponibles para anidación (Renton et al., 2017). El presente estudio tiene como objetivo determinar los efectos de los disturbios naturales y antrópicos en las poblaciónes de la lagartija *Anolis nebulosus* en la costa de Chamela, Jalisco. Estas poblaciones han sido monitoreada desde octubre del 2009 teniendo una amplia línea base de estudio que nos permite evaluar los cambios a través del tiempo.

4. Métodos

Los bosques tropicales son el sistema con la mayor riqueza biológica del planeta a pesar de que cubren una fracción reducida de toda la superficie terrestre (Wilson 1988; Gentry, 1995). Este tipo de vegetación se caracteriza por una prolongada época de estiaje que puede durar hasta ocho meses, y una corta época de lluvias que por lo general ocurre entre julio y octubre. Adicionalmente, presenta una considerable variación espacial en estructura y composición de especies (Bullock et al. 1995, Trejo-Vázquez y Dirzo 2000, Noguera et al. 2002). En la actualidad y a pesar de su importancia biológica, el BTS es de los ecosistemas terrestres más amenazados (Vieira et al. 2006). El área de estudio se localiza en la región de la Reserva de la Biosfera Chamela-Cuixmala y zonas aledañas a los 19º 29’ de latitud N a los 105° 03’ de longitud O, a menos de 2 km. de la costa del Pacifico en el km. 59 de la carretera federal 200 Barra Navidad-Puerto Vallarta (Figura 1). La reserva tiene una superficie aproximada de 13,142 hectáreas (DOF 1994).

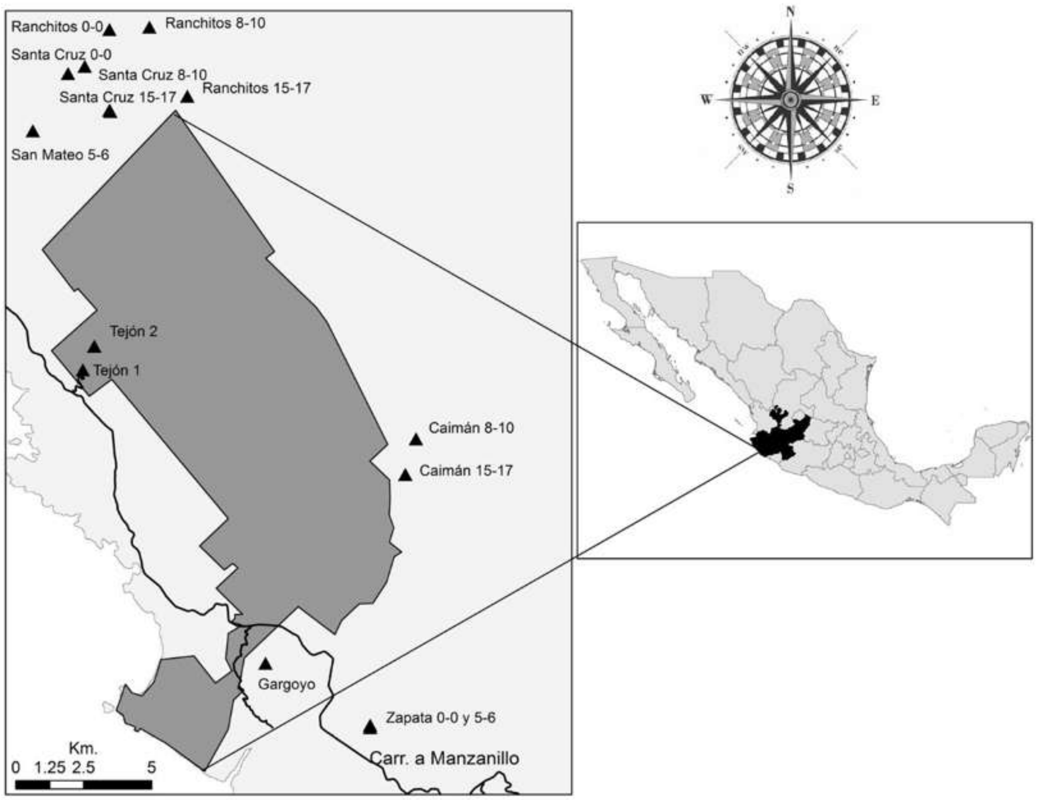

Figura 1. Ubicación de los 15 sitios en la Reserva de la Biósfera Chamela y zonas aledañas, Jalisco, México.

Se realizaron 8 salidas de campo de abril de 2016 a octubre de 2019, que abarcaron la temporada de estiaje y la temporada de lluvias en cada año de muestreo.

Para los muestreos se consideraron 15 parcelas permanentes (100 X 100 m cada una) con diferente edad de abandono después de ser modificado por actividades humanas (categoría sucesional): 3 parcelas en campos de reciente abandono con 0-5 años, 3 parcelas en campos con 5-6 años de abandono (estadio temprano), 3 parcelas en bosque secundarios de 8-10 años (bosque inicial), 3 parcelas en bosque secundario de 15-17 años (bosque intermedio) y 3 en bosque maduro (BM). Para fines de análisis, se utilizao el término categoría sucesional para agrupar los tratamientos por crono secuencia (Cook et al., 2005) esto con el fin de evaluar la influencia de la parcela y la dinámica del paisaje a través del tiempo de abandono (Martínez-Ramos et al., 2012).

La búsqueda de las lagartijas se realizó mediante el recorrido de transectos al interior de las parcelas mediante "VES" (Búsqueda por encuentro visual), ya que es un método eficiente para realizar inventarios de campo y requiere de poco equipo y puede ser usado en diversos hábitats, por lo que es la técnica comúnmente más utilizada para inventarios herpetofaunisticos. Cada parcela se muestreo dos veces por visita de campo, una en el trascurso del día y otra por la noche. El esfuerzo de muestreo por sitio fue de 6 horas/persona, por salida. El esfuerzo de muestreo por parcela se estandarizo para poder realizar las comparaciones estadísticas entre los estadios sucesionales.

Cada individuo de *A. nebulosus* capturado, fue sexado (presencia “macho” o ausencia “hembra” del abanico gular), se obtuvo la longitud hocico-cloaca (LHC), usando un vernier, y se obtuvo el peso corporal, usando una báscula de resorte de 5 y 10 g. Todos los individuos de *A. nebulosus* capturados, fueron marcados mediante ectomización de falanges, cuidando de cortar solo la punta del dedo que está libre de lamelas.

5. Análisis estadísticos.

Para comparar si existen diferencias significativas entre la abundancia, SVL, peso y la altura de la percha entre estadios sucesionales antes y después de cada huracán, usamos modelos mixtos de medidas repetidas en cada uno de los sitios. La abundancia de *A.nebulosus* se analizó ajustando un modelo lineal generalizado mixto (GLMM) utilizando una distribución de error de Poisson (Bates et al. 2012). En el caso del SVL, peso y altura de la percha, utilizamos modelos lineales mixtos (LMM) utilizando el error de distribución normal (Magurran 2004). Las medidas repetidas de cada bloque de 1 ha se incluyeron como un factor aleatorio (Faraway 2006, Pinheiro & Bates 2006, Crawley 2013). Los factores fijos fueron los siguientes: i) etapas sucesionales (S, con cinco niveles: pasture, early, young, intermediate y OGF), ii) huracán (H, con tres niveles: pre-huracan, post Jova y post Patricia), y la interacción entre estos dos factores (S x H). Realizamos el análisis utilizando el paquete lme4 (Bates et al. 2012) en R 2.13.0 (R Core Team, 2013). Además, se realizaron ANOVAS de dos vías para encontrar posibles diferencias entre la abundancia, el peso, SVL y la altura de la percha utilizada, de las lagartijas *A. nebulosus* causadas por los huracanes Jova y Patricia en los diferentes estadios sucesionales, utilizando ANOVAS de 2 vías mediante modelos lineales generalizados mixtos (MLGM) y los modelos lineales mixtos para el peso, longitud (SVL) y la altura de la percha (MLM). Para observar las diferencias arrojadas por los Anovas de dos vías se realizaron gráficos de caja y bigotes donde la caja representa el promedio ± la desviación estándar y los bigotes los valores máximos y mínimos entre los huracanes y los estadios sucesionales. Se realizó un análisis de coordenadas principales (PCA) para observar diferencias entre el peso, SVL y la altura de la percha antes y después del paso de cada uno de los huracanes, además Para estimar diferencias en el peso, SVL y la altura de la percha que se observaron en el PCA se realizó un análisis multivariado de la varianza (MANOVA). Para el análisis de estos datos se utilizó el programa Statistica 7 (Statsoft, 2000), se seleccionó el módulo modelo general lineal, y el cual cuenta con el Análisis multivariante de la varianza (MANOVA). Se empleo este análisis estadístico debido a que se cuenta con más de una variable dependiente, que en forma conjunta podrían explicar un porcentaje de la variación encontrada entre antes y después del paso de cada huracán.

6. Resultados

Después de 1890 horas de muestreo (630 horas antes de los huracanes, 630 después del huracán Jova y 630 horas después del huracán Patricia), 378 h por cada estadio sucesional y 126 h por cada sitio se encontraron un total de 907 individuos de la especie de *A. nebulosus*. El estadío sucesional con mayor abundancia fueron los pastizales (235 individuos), mientras que el estadio con menor abundancia fue el OGF (111 individuos). En el periodo de tiempo donde se encontraron una mayor cantidad total de individuos fue después del paso del huracán Jova (644 individuos) mientras que después del paso del huracán Patricia las abundancias fueron muy bajas (23 individuos) (Tabla 1).

Tabla 1. Abundancia de *A. nebulosus* por estadio sucesional antes y después del huracán Jova y Patricia.

	Pasture	Early	Young	Intermediate	OGF	Overall
Before hurrricanes	53	41	59	52	35	240
Post hurricane Jova	178	143	150	99	74	644
Post hurricane Patricia	4	7	6	4	2	23
Overall	235	191	215	155	111	907

Para las diferentes variables de respuesta de los *A. nebulosus* no se encontraron diferencias significativas entre estadios sucesionales excepto para la altura de la percha (χ^2= 13.6, df =8, p < **0**.001) (Tabla 2), lo que nos indica que *A. nebulosus* perchan a diferentes alturas a lo largo de la sucesión secundaria, mientras que para el resto de las variables podemos inferir que no existen cambios en abundancia, peso y SVL a lo largo de la sucesión secundaria. Aunque, las abundancias variaron por estadios sucesionales de valores de entre 111 (OGF) hasta 235 (Pastizales) los estadísticos no muestran una diferencia significativa (Tabla 1). Mientras que los resultados muestran un efecto significativo para las variables de abundancia (χ^2= 368.3, df =2, p < **0**.001), SVL (χ^2= 14.3, df =2, p < **0**.001) y Altura de la percha (χ^2= 25.9, df =2, p < **0**.001) entre antes y después del paso de los huracanes (pre Jova-post-Jova y post Patricia), para el peso (χ^2= 5.5, df =2, p > **0**.05) la diferencia fue marginal (Tabla 2). Podemos observar que la altura de la percha que usan los *A. nebulosus* a lo largo de los estadios sucesionales es muy parecida entre el bosque temprano (Early), el bosque joven (Young) y el bosque intermedio (intermediate), mientras que para los pastizales (Pasture) las perchas tienden a ser a nivel del suelo, por el contrario. En los OGF la altura de la percha usada es mayor que para el resto de los estadios sucesionales (Figura 1). Las abundancias fueron significativamente mayores después del paso del huracán Jova aumentando casi en 300% en comparación con antes de los huracanes, mientras que para después del paso del huracán Patricia las abundancias de *A. nebulosus* decrecieron más de 96% con respecto a antes del huracán Patricia siendo este periodo el que presenta una menor abundancia de *A. nebulosus* (Figura 2). Aunque el peso no presento una diferencia significativa entre huracanes si podemos observar que el peso fue disminuyendo conforme golpearon los huracanes la región de Chamela, presentado una media de peso más bajo en los individuos de *A. nebulosus* después del huracán Patricia. El SVL presento un comportamiento muy parecido, sin embargo, para esta variable si se encontraron diferencias significativas los individuos de *A. nebulosus* presentaron SVL significativamente menor después del huracán Jova y disminuyo aún más después del paso del huracán Patricia (Figura 2). Mientras que la altura de la percha fue significativamente menor para *A. nebulosus* después del huracán Jova y decreció aún más después del huracán Patricia presentando las perchas de menor altura en este periodo.

Tabla 2. Resultados del análisis estadístico para *A. nebulosus* en el bosque seco tropical de Chamela, Jalisco. Los estadísticos proporcionados son las siguientes: valores para GLMM (abundancia) y LMM (Peso, SVL y Altura de la percha) además de los valores de P obtenidos a partir de Anovas de dos vías. Estadio sucesional (s), huracán (H) y etapa sucesional x condición de perturbación de huracán (S: H)

Spp.	*Anolis nebulosus*		
	Stage(S)	Hurricane (H)	S:H
Abundance	7.4(4)	368.3(2)***	10.3(8)
weight	7(4)	5.5(2).	10.6(8)
SVL	3(4)	14.3(2)***	6.4(8)
Hight perch	13.6(4)***	25.9(2)***	14.4(8)

P< .05* P< .01** P< .001***

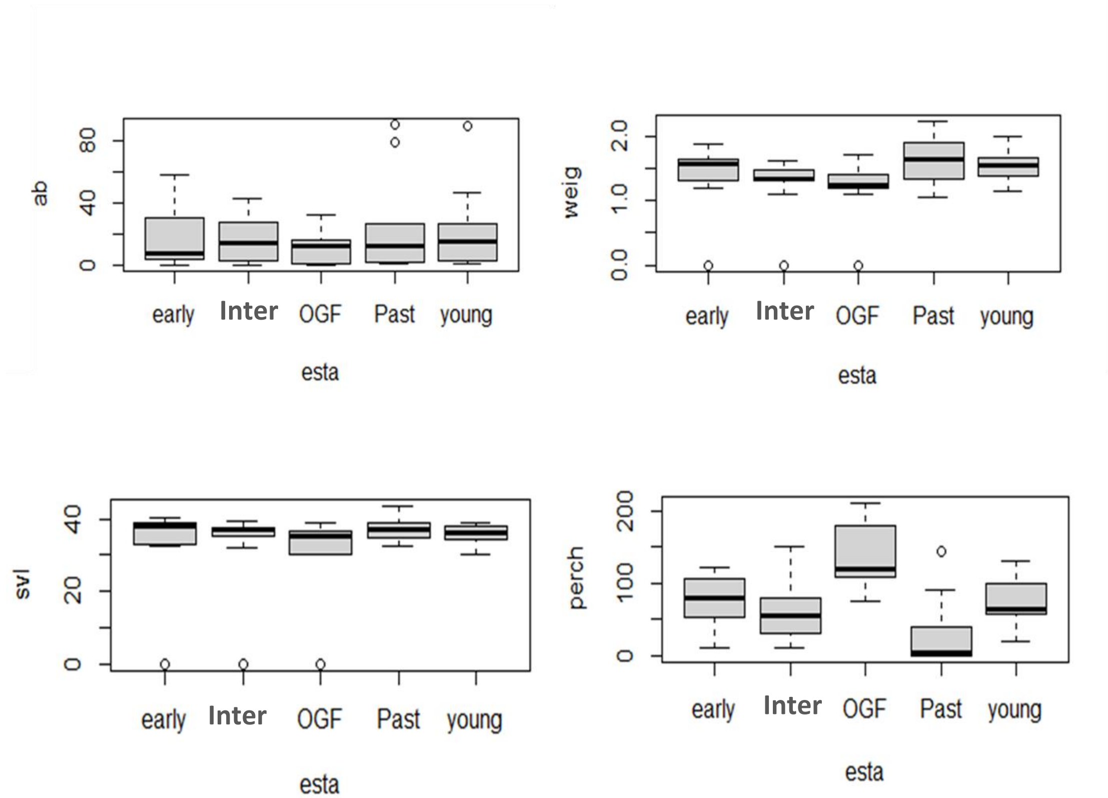

Figura 1. Cambios en abundancia, peso, SVL y altura de la percha a lo largo de los diferentes estadios sucesionales en el bosque tropical seco de Chamela, Jalisco. El cuadro representa el error estándar y los bigotes representan la desviación estándar, la línea negra dentro del cuadro representa el promedio. Past = Pastizal, Early = Bosque Temprano, Young = Bosque Joven, Inter = Bosque intermedio, OGF = Bosque maduro.

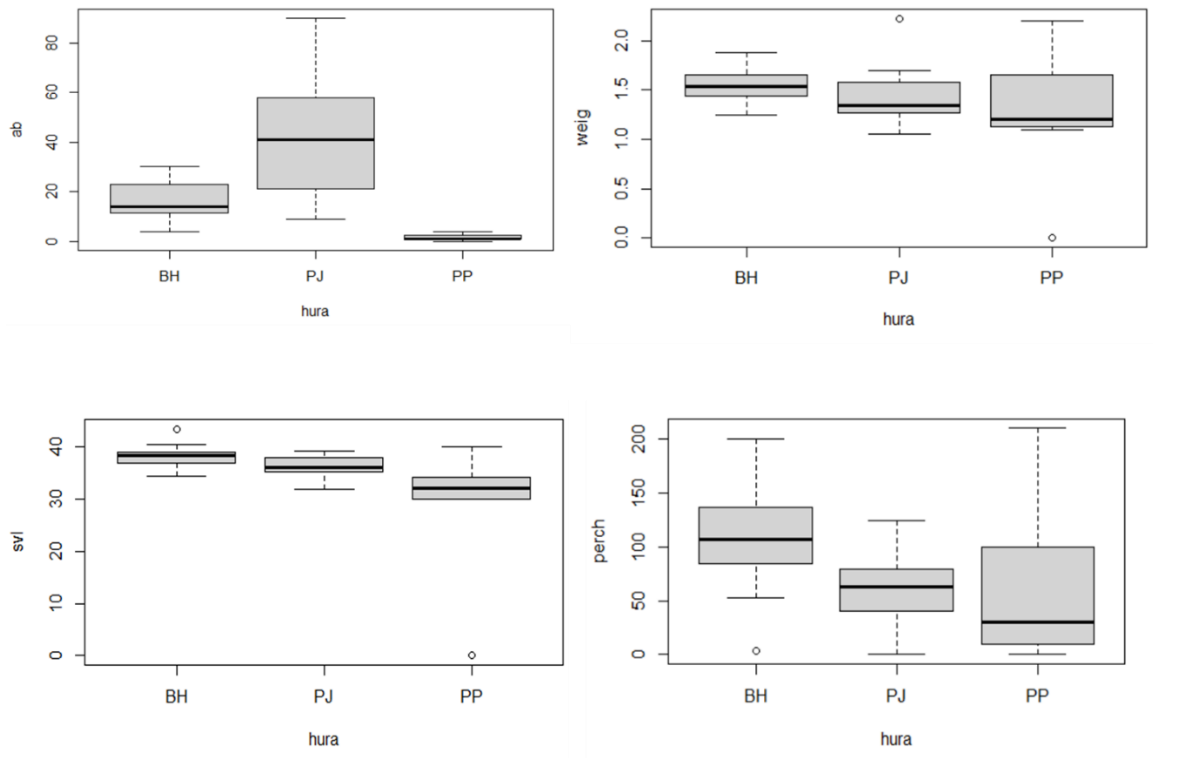

Figura 2. Cambios en abundancia, peso, SVL y altura de la percha antes de los huracanes y después del paso del huracán Jova y Patricia en el bosque tropical seco de Chamela, Jalisco. El cuadro representa el error estándar y los bigotes representan la desviación estándar, la línea negra dentro del cuadro representa el promedio. BH = pre-huracanes, PJ = post-huracán Jova, PP = post-huracán Patricia.

Las abundancias fueron menores después del paso del huracán Patricia, los individuos después de los huracanes presentaron una variación mayor en el peso y SVL además la altura de la percha que usaron los individuos encontrados de *A. nebulosus* fue diferente entre antes y después del paso de cada uno de los huracanes (Figura 3), por lo que estas principales variables separaron a los individuos entre cada uno de los momentos de estudio (antes y después del paso de cada uno de los huracanes). La diferencia más clara se encontró entre antes del paso de los huracanes y después del paso del huracán Patricia (categoría V). Sin embargo, también podemos observar una diferencia entre los individuos de *A. nebulosus* antes de los huracanes y los individuos de después del paso del huracán Jova, además el MANOVA arrojo una diferencia significativa entre los individuos de antes de los huracanes, después del Jova y después del Patricia.

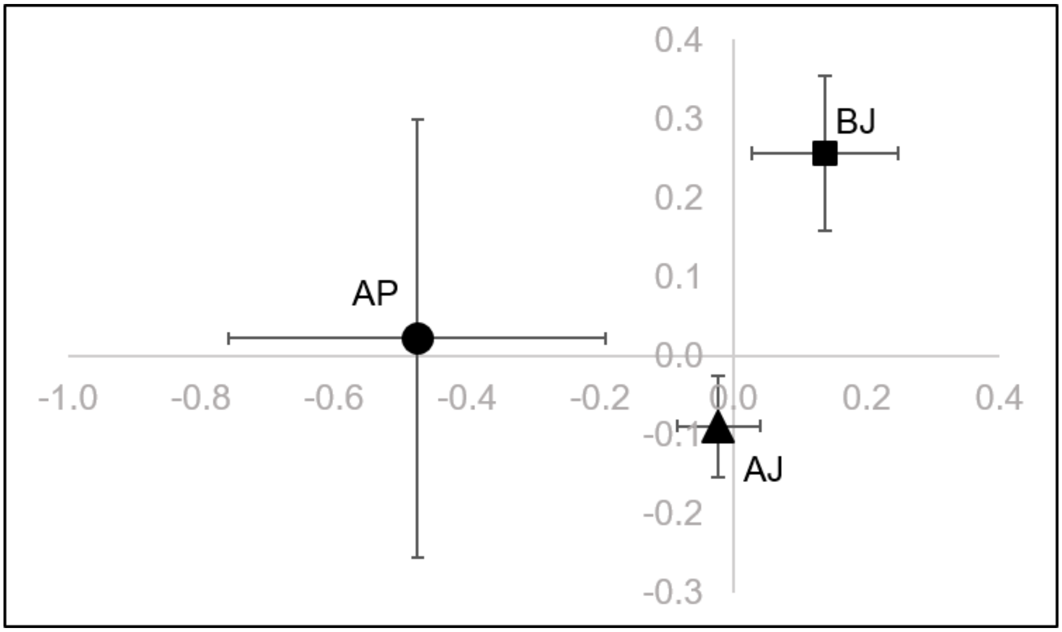

Figura 3. Análisis de coordenadas principales para *A. nebulosus* en el bosque tropical seco de Chamela Jalisco. BJ = pre-huracanes, AJ = post-huracán Jova, AP = post-huracán Patricia.

7. Discusión

Para el presente trabajo se consideraron el efecto acumulativo de dos huracanes el primero de categoría II (Jova) seguido por un huracán de categoría V (Patricia) sobre el bosque tropical seco de Chamela Jalisco. Se ha encontrado que tras el paso de un huracán la herpetofauna puede verse afectada. Por ejemplo, se ha documentado la disminución de abundancias en las poblaciones, cambios en el ámbito hogareño, además de cambios en la equitatividad de las comunidades (Schoener et al ., 2001a; Losos et al., 2003; Wunderle et al., 2004; Suazo-Ortuño et al., 2018a,b; García y Siliceo-Cantero, 2019). Nuestros resultados indicaron que tras el paso de Jova las abundancias *A. nebulosus* aumentaron, a lo largo de la sucesión secundaria, esto coincide con los resultados encontrados por Schoener y colaboradores (2017) en las Bahamas donde el aumento en la abundancia se ve relacionado con que los huracanes de categorías II y III no suelen ser tan destructivos y pueden proporcionar alimento aumentando el número de insectos, esto se ha reportado para el grupo de las aves donde el gremio de aves insectívoras aumenta tras el paso de un huracán (Wiley y Wunderle, 1993; Schoener et al., 2017). Sin embargo, después del paso del huracán Patricia las abundancias disminuyeron a niveles nunca reportados previamente para estos mismos sitios (Suazo-Ortuño et al., 2018 a,b). Estos resultados coinciden con lo reportado en varios estudios donde se reportan efectos negativos sobre las abundancias de algunas lagartijas del género *Anolis* tras el paso de huracanes de categoría IV y V, incluso en algunos casos, se reporta la extinción local y una recolonización muy lenta por crías y juveniles provenientes de huevos que sobreviven a las inundaciones (Losos y Spiller, 1999; Schoener et al., 2001a; Schoener et al., 2004; Losos et al., 2003). También se encontró que las variables morfológicas como el peso y el SVL disminuyeron tras el paso de cada uno de los huracanes por lo que los organismos tendieron a ser de tallas más pequeñas, además se encontró una diferencia significativa entre la altura de la percha. Adicionalmente, se encontró que el efecto de Patricia potencializa los cambios, por ejemplo, la altura de la percha, ya que la altura a la que percharon los organismos de *A. nebulosus* fue menor tras el segundo huracán en comparación con antes o después del huracán Jova. Los cambios en la altura de la percha ocasionados por huracanes han sido reportados para esta especie de lagartija en un estudio en las islas de la bahía de Chamela, estos resultados muestran un aumento en la altura de la percha, contrarios a los que se encontraron en nuestro trabajo (Garcia y Siliceo-Cantero, 2019). La disminución en la altura de la percha puede deberse a que los árboles de mayor altura son más sensibles a los vientos ocasionados por huracanes (Cooper-Ellis et al., 1999; Boutet y Weishampel, 2003) por lo que después del paso de cada uno de los huracanes los árboles de mayor talla fueron derribados o descopados y la altura a la que perchaban se vio afectada obligando a los individuos a perchar a menor altura. Los vientos causados por el huracán Patricia fueron notoriamente mayores que los del huracán Jova por lo cual los sitios de percha después del huracán Patricia fueron más bajos que después del huracán Jova . Variables como es el caso del peso y SVL de *A. nebulosus* disminuyeron después del paso de cada huracán, los cambios morfológicos están relacionados con disturbios naturales en las comunidades de lagartijas. Para las lagartijas de genero *Anolis* se han reportado cambios en el SVL tras el paso de huracanes de alta intensidad en las Islas del Caribe, por ejemplo, para un estudio en Dominica después del huracán María se encontraron diferencias morfológicas en las lagartijas de la especie *A. cristatellus* y *A. oculatus* el tamaño corporal fue significativamente mayor después del paso del huracán (Dofour et al., 2019). En nuestro estudio encontramos una diferencia significativa en el SVL pero no en el peso, lo que podría indicar que los organismos presentan un SVL menor pero que puede verse compensado con un tamaño de extremidades mayor, ya que cambios en las extremidades tanto anteriores como posteriores pueden ayudarles a aferrarse mejor a las perchas tras el paso de vientos huracanados (Schoener et al., 2017; Dofour et al., 2019; Donihue et al., 2020), los cambios en los hábitos y en la morfología tras el paso de los dos huracanes en la zona son evidentes. Se ha reportado que los eventos de disturbio naturales tales como los huracanes tienen la capacidad de efectuar cambios evolutivos en las especies a escalas contemporáneas y geológicas (Rabe et al., 2020), estudios han encontrado que la sobrevivencia de las poblaciones del género *Anolis* tras de un huracán están directamente relacionadas con la morfología de las mismas, los individuos con mejores adaptaciones como el tamaño de las extremidades y el número de lamelas por área en las falanges les sirven para aferrarse a las perchas y mantenerse fijos durante los vientos causados mientras golpean los huracanes, es por esta razón que estas adaptaciones son un factor determinante para subsistir a los embates de los huracanes (Donihue et al., 2018; Huey y Grant 2020; Rabe et al., 2020). Aunque no medimos el tamaño y numero de lamelas por extremidad creemos que al ser chamela un lugar con un registro histórico bajo en cuanto a huracanes, los lagartos no presentan una morfología tan variada en cuanto al tamaño de las extremidades. Lo que también se traduce en que el número de lamelas por individuo debería de ser muy parecido en toda la población, la poca variabilidad morfológica de esta población pudo ser una un factor importante en la disminución de la población de *A. nebulosus* ya que tras el paso de un huracán categoría V pocos individuos presentan adaptaciones necesarias para sostenerse a las perchas y sobrevivir a vientos de tal magnitud. Se ha demostrado para más de 180 especies de *Anolis* que el tamaño de los dedos y por lo tanto el numero de lamelas esta estrechamente relacionado con el numero de huracanes a los cuales sus poblaciones han sido expuestas (Huey y Grant, 2020), por lo que lo anterior también explicaría por qué se encontraron organismos con un SVL menor pero sin diferencia significativa en el peso, ya que muy probablemente los organismos sobrevivientes presentan un SVL menor pero patas más grandes que para poder aferrarse mejor a sus sitios de percha como se ha reportado en estudios previamente. La destrucción del hábitat ocasionada por los fuertes, vientos, inundaciones, descope y caída de los árboles son factores que cambian las condiciones ambientales y estructurales de los bosques aumentando la temperatura y disminuyendo la humedad (Willig y Camilo 1991; Lugo et al., 2005) ocasiona cambios en las abundancias de las poblaciones de lagartos, se ha demostrado que algunas lagartijas del género *Anolis* pueden aumentar sus abundancias tras huracanes de baja intensidad (Enge, 2005; Schoener et al., 2017) esto debido a que la gran mayoría de las especies de este género son consideradas como especies generalistas (Losos, 2009) lo que coincide con nuestros resultados ya que tras el paso del huracán Jova de categoría 2 los lagartos *A. nebulosus* aumenten sus abundancia adaptándose a los cambios estructurales y aprovechan los nichos vacíos de las especies que no se adaptaron a los cambios, aunque los cambios en los hábitos fueron notorios ya que tras la caída y muerte de los árboles de mayor talla los lagartos fueron forzándolos a perchar a una menor altura, sin embargo, no fueron capaces de sobrevivir y adaptarse a los cambios ocasionados por el huracán Patricia de categoría V ya que los cambios fueron más abruptos, esto se ha reportado para varias especies de reptiles ya que el impacto de varios huracanes en un periodo corto de tiempo ocasiona el declive en sus poblaciones (Spiller y Schoener, 2004; Schriever et al., 2009), por lo que después del huracán Patricia las abundancias disminuyeron y los pocos organismos encontrado estuvieron perchando a alturas menor que después del paso del huracán Jova. Es necesario llevar a cabo estudios a largo plazo para evaluar el impacto de los huracanes sobre las poblaciones de lagartos en los bosques tropicales secos conservados y los bosques secundarios para poder establecer estrategias de monitoreo y conservación de estos reptiles.

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7. DISCUSIÓN GENERAL

Se ha documentado que los huracanes de categorías 4 y 5 en la escala de Saffir-Simpson han aumentado en los últimos años (Webster et al. 2005; Elsner et al. 2008; Knutson et al. 2010, Emanuel, 2013). Estudios han comprobado que el aumento de huracanes está directamente relacionado con el aumento en le temperatura superficial de los océanos, este aumento ha sido de por lo menos .5 °C en los últimos 40 años (Emanuel 2005 y Webster et al. 2005).

En el siglo XXI se volvió más frecuente el estudio del efecto de huracanes sobre la hepetofauna, esto podría tener relación también con que a partir del año 2000 se comenzó a tomar más en cuenta el aumento de CO_2 en el planeta, una de las pautas más importantes puede ser tal vez que el Grupo Intergubernamental de Expertos sobre Cambio Climático (2002) manifiestan que, durante el año 2000, los indicadores de concentración de gases de invernadero como del CO_2 y metano, se han incrementado un 31% y 151% respectivamente, con respecto a los valores que se tenían registrados anteriores al siglo XIX. En el reporte más reciente de 2018 aún existe un gran debate sobre si el calentamiento global ha tenido un efecto sobre la intensidad y frecuencia de los huracanes, aunque existen fuertes evidencias que demuestran que el régimen de huracanes para algunos sitios se ha visto afectado aumentando sobre todo los huracanes de categorías más intensas (IPCC 2018), además existen estudios donde se reporta la incidencia de huracanes en lugares donde no era tan frecuente este régimen de disturbio (NOOA 2017; Suazo-ortuño et al 2018).

Uno de los lugares con mayor incidencia de huracanes es el Océano Pacífico junto con las Antillas, en las Antillas la incidencia de huracanes de categoría IV y V es mayor que en el resto del mundo. Existen zonas como la región del pacifico que han presentado un aumento en intensidad y frecuencia de huracanes en los últimos años (Jáuregui, 2003; Álvarez-Yépiz y Martínez-Yrízar, 2015; Maass et al., 2017). Al aumentar la intensidad y frecuencia de estos eventos, las comunidades de anfibios y reptiles se ven forzadas a enfrentar nuevos retos en la búsqueda de recursos, desde el microhábitat que se ve afectado hasta la búsqueda de recursos alimenticios, ya que la gran mayoría de los anfibios y reptiles son carnívoros (Flores-Villela y García-Vázquez 2014), esto da paso además, a una fuerte competencia por los recursos alimenticios, ya que los recursos que consumen principalmente pequeños insectos hasta algunos vertebrados se ven afectados por los huracanes(Willig y Camilo 1991; Taner y Kapos 1991), disminuyendo sus poblaciones y por lo tanto forzando a una competencia donde las poblaciones de especies de hábitos más especializados se ven condenadas a disminuir o desaparecer localmente, lo que lleva a una pérdida de variabilidad genética y, por supuesto, a la pérdida de la diversidad ecológica(IUCN 2018). Aunque los primeros reportes de cómo afectan los huracanes a la herpetofauna datan de los años 90's con trabajos sobre el efecto de huracanes de categoría V en las Antillas para Anfibios y lagartos (Reagan, 1991; Woolbright, 1991), en realidad el auge de estos estudios comenzóa finales de los 80's, a partir de que se le dio una mayor importancia al cambio climático y las consecuencias que este fenómeno puede acarrear (Houghton y Woodwell, 1989; Holt, 1990), a partir de ese momento los estudios comenzaron a evaluar como respondían las comunidades a los huracanes con estudios enfocados en diferentes grupos desde los arrecifes, insectos, anfibios, reptiles, aves, hasta mamíferos de talla pequeña y grande, el aumento en este tipo de estudios relacionados con todos estos grupos es inminente (Taner et al., 1991; Woolbright 1991; Wiley y Wunderle 1993; Mccoid 1996).

Para la región de Chamela se registró el huracán Jova de categoría II, seguido por el huracán Patricia de categoría V apenas 4 años después. Esto es un notorio incremento debido que en casi 50 años se registraron menos de 10 huracanes en el estado de Jalisco (Jáuregui, 2003), estos huracanes resultaron en daños en las comunidades vegetales, aves, anfibios y reptiles solo por mencionar algunos (Martínez-Ruiz y Renton 2018; Suazo-Ortuño et al., 2018; García y Siliceo-Cantero, 2019), el efecto sobre las comunidades de anfibios y reptiles en diferentes estadios sucesionales del a zona fue notorio, desde la disminución en las poblaciones, hasta la desaparición de especies en algunos estadios y sitios donde se habían registrado anteriormente, la completitud del muestreo también vario entre antes de los huracanes, después del paso del huracán Jova y después del paso del huracán Patricia. Antes de los huracanes la completitud de anfibios fue de entre 65 % (Intermediate forest) y 100% (pasture and early forest), mientras que despues del paso del huracán Jova vario entre 64%

(Intermediate forest) y 100 % (Early and OGF), la representatividad para este grupo vario mucho menos despues del huracán Jova entre 75% (pasture) y 100% (OGF; Table. 1). Para las lagartijas la representatividad varío entre 82% (Young Forest) y 100% (Pasture, Early y OGF) antes de los huracanes, después del huracán Jova la representatividad del muestreo vario entre 73% (Intermediate Forest) y 100 % (Young and OGF), mientras que después del huracán patricia vario entre 80% (Early) y el 100% (Young y OGF; Table. 1). Para el grupo de las serpientes la representatividad vario entre 37%(Intermediate) y 76% (OGF) antes de los huracanes, después del huracán Jova entre 53% (Pasture) y 81% (Young) y para después del huracán Patricia entre 25 % (Pasture) y entre 89 % (Intermediate), estos porcentajes de completitud se comparan o incluso son superiores a los que se han encontrado en trabajos relacionados con herpetofauna y estadios sucesionales como el de Gardner et al. (2007) quienes reportan una completitud de entre 22% y 96% para anfibios y lagartijas y el de Burbano-Yandi et al. (2015) donde se reporta una completitud de entre 67% y 87% para anfibios, también es comparable al de trabajos con un esfuerzo de muestreo parecido en los Tuxtlas se logró una completitud de entre 88% y 93% para anfibios y reptiles respectivamente (Urbina-Cardona et al. 2006), además, para la misma región se reporta una completitud de entre 78% en anfibios y 64% en reptiles (Salvatore 2006). Mientras que para la región de Chamela Jalisco Fraga-Ramírez et al. (2017) reporta para anfibios y reptiles entre 33% y 100%, en esta región Suazo-Ortuño et al. (2015) para los mismos sitios reportan una completitud de entre 82 y 100% para anfibios y reptiles.

Encontramos diferencias significativas en la estructura de la comunidad de anfibios, lagartijas y serpientes, entre el paso de los huracanes, además las abundancias de lagartijas y anfibios disminuyeron significativamente después del paso del huracán Patricia. Las abundancias después del huracán Patricia fueron significativamente más bajas para todos los grupos y a nivel de herpetofauna podemos observar una disminuciónen en sus abundancias comparadas con la de los estudios previos (Suazo-Ortuño et al., 2015, 2018 a,b). Las abundancias de las poblaciones de herpetofauna antes y después del paso del huracán Jova no mostraron una disminución evidente, incluso en estos mismos sitios algunas poblaciones tendieron aumentar después del huracán (Suazo-Ortuño et al. 2018 a,b) mientras que después del huracán Patricia las abundancias de la gran mayoría de las poblaciones de anfibios y reptiles disminuyeron, encontramos diferencias significativas marcadas tanto en riqueza como en diversidad lo cual difiere completamente con el trabajo anterior para esta zona donde no se registraron diferencias en riqueza mientras que en nuestro estudio todos los grupos excepto los anfibios presentaron una disminución en riqueza tras el paso del Huracán Patricia y para lagartijas solo la diversidad tuvo diferencia significativa después del paso del huracán Jova (Suazo-Ortuño et al. 2018), aunque para anfibios no fue significativo en cuanto a riqueza y diversidad si podemos observar una disminución de especies presentes en algunos estadios. Este efecto acumulativo de los huracanes puede llegar a tener una perdida significativa en abundancia, riqueza y diversidad si los huracanes siguen azotando cada vez con más frecuencia e intensidad como se ha visto en los últimos años (Webster et al., 2005; Vecchi et al., 2008; Emanuel, 2013).

Después del paso de un huracán los patrones en la estructura de la vegetación cambian (Tanner et al., 1991; Everham y Brokaw, 1996; Van Bloem et al. 2006) y uno de los retos mayores para los anfibios y reptiles es su limitada capacidad de movimiento y recolonización. Esta limitación ecológica se debe a restricciones fisiológicas, como la relativa baja movilidad que presenta este grupo de vertebrados (Duellman y Trueb 1994, Stebbins y Cohen 1995). Al aumentar la intensidad y frecuencia de estos eventos (Material suplementario 1), las comunidades de anfibios y reptiles se ven forzadas a enfrentar nuevos retos en la búsqueda de recursos, desde el microhábitat que se ve terriblemente afectado hasta la búsqueda de recursos alimenticios, ya que la gran mayoría de los anfibios y reptiles son carnívoros (Flores-Villela y García-Vázquez 2014), esto da paso además, a una fuerte competencia por los recursos alimenticios, ya que los recursos que consumen principalmente pequeños insectos hasta algunos vertebrados se ven afectados por los huracanes(Willig y Camilo 1991 Taner y Kapos 1991), disminuyendo sus poblaciones y por lo tanto forzando a una competencia donde las poblaciones de especies de hábitos más especializados se ven condenadas a disminuir o desaparecer localmente, lo que lleva a una pérdida de variabilidad genética y, por supuesto, a la pérdida de la diversidad ecológica (IUCN 2018), por lo que la baja movilidad que presenta este grupo, el efecto acumulado de más de un huracán y además el cambio en los recursos disponibles y la fuerte competencia por ellos intra e interespecífica son posiblemente los factores causales que influyeron en la marcada disminución de las diferentes especies de herpetofauna a lo largo de los diferentes estadios sucesionales, ya que se ha reportado que el paso que incluso el paso de un huracán de baja intensidad en los bosques secos es capaz de disminuir las poblaciones de algunas especies de herpetofauna, como es el caso de *D. spatulata* donde después del paso del huracán Jova de categoría II se reporto que sus abundancias se redujeron cerca del 50% y otras aumentaron más del 300% como es el caso del *L. melanonotus* (Suazo-Ortuño et al., 2015), este efecto ya se ha reportado previamente para algunas comunidades de anfibios en Puerto Rico mientras que algunas especies disminuyen debido a los efectos de los huracanes otras especies generalistas aumentan aprovechando los nichos vacíos (Woolbright 1991; Vilella y Fogarty 2005), esto mismo ha sido reportado para lagartos de la región de chamela en la isla San Agustín donde después de un huracán los *A. nebulosus* disminuyen y los lagartos de la especies *Urusaurus bicarinatus* aumentan (Siliceo-Cantero et al., 2020). Para las poblaciones de distintas especies de *Anolis* se han reportado los efectos causados por huracanes sobre todo en el área de las Antillas encontrando que son especies altamente vulnerables a los efectos de los huracanes sobre todo a los de alta intensidad (cat IV y V), provocando disminución de sus poblaciones, extinción local en algunas islas, y cambios en el uso del microhábitat. Sin embargo, también se ha encontrado que este grupo de especies presenta varias adaptaciones para hacer frente a los efectos de los huracanes por ejemplo se ha encontrado que los huevos de estas especies pueden resistir entre 3 y 4 horas bajo el agua lo que les permite repoblar los lugares donde los individuos de sus especies han desaparecido (Losos et al., 2003; Schoener et al., 2004). Además se ha encontrado que las especies que habitan en lugares con una alta incidencia de huracanes presentan un mayor tamaño de los dedos y una mayor cantidad de lamelas, lo que los ayuda a aferrarse con mayor firmeza a las perchas y sobrevivir a los vientos y lluvia ocasionados por los huracanes (Dofour et al., 2019; Huey y Grant, 2019). La estrategias que desarrollan algunas especies como es el caso de varias especies del género

Anolis les han permitido sobrevivir y evolucionar en lugares con una alta incidencia de huracanes pero en lugares donde las comunidades no están sometidas a estos regímenes de disturbio, el efecto acumulativo de más de un huracán puede tener efectos notables como las poblaciones, cambios en la dominancia de especies, disminución de riqueza y diversidad y la extinción local de algunas especies (Schriever et al., 2009; Marroquín-Páramo et al., 2020). Por lo que es de vital importancia establecer estrategias para el monitoreo y la conservación de la herpetofauna y conocer el efecto que tienen los regímenes de disturbio tanto naturales como antrópicos dentro de su hábitat.

8. CONCLUSIONES

El efecto acumulado de los huracanes sobre anfibios y reptiles ha sido mayormente reportado en islas de las Antillas con huracanes de categoría 4 y 5 en la escala de S-S.

En cuanto al efecto de los huracanes sobre la herpetofauna las lagartijas son el grupo mayormente estudiado sobre todo el género *Anolis.*

En este estudio referente al efecto de los huracanes sobre la herpetofauna los principales resultados están relacionados con cambios en la abundancia, riqueza, diversidad, equitatividad y dominancia de las especies.

Después de los huracanes la abundancia de los anfibios, lagartijas y serpientes disminuyeron significativamente en todos los estadios sucesionales.

El efecto acumulativo los huracanes sobre una misma zona cambia la estructura y composición de las comunidades y poblaciones de herpetofauna.

La comunidad de herpetofauna presento una mayor equitatividad después del paso de los huracanes. Después de los huracanes existió una homogenización biótica como resultado de las perturbaciones naturales y antrópicas.

La abundancia de *A. nebulosus* aumento un 250% después del paso del Jova, mientras que después del huracán Patricia disminuyo más del 90%.

Los huracanes pueden promover cambios en el peso y longitud hocico-cloaca de *A. nebulosus* además de cambios en la altura a la que perchan.

9. LITERATURA CITADA

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