Effects of Habitat Disturbance on Lizard Functional Diversity in a Tropical Dry Forest of the Pacific Coast of Mexico

4 authors:

Christian Berriozabal Islas
Universidad Politécnica de Quintana Roo
54 PUBLICATIONS **268** CITATIONS

Luis Manuel Badillo Saldaña
Autonomous University of Hidalgo
22 PUBLICATIONS **108** CITATIONS

Aurelio Ramírez-Bautista
Autonomous University of Hidalgo
277 PUBLICATIONS **2,653** CITATIONS

Claudia E. Moreno
Autonomous University of Hidalgo
157 PUBLICATIONS **5,163** CITATIONS

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Effects of Habitat Disturbance on Lizard Functional Diversity in a Tropical Dry Forest of the Pacific Coast of Mexico

Christian Berriozabal-Islas[1], Luis M. Badillo-Saldaña[1], Aurelio Ramírez-Bautista[1], and Claudia E. Moreno[1]

Abstract

Tropical dry forests are complex and diverse ecosystems threatened by multiple anthropogenic factors, such as habitat disturbance caused by land use change. We assessed species and functional diversity of lizard communities in areas with different levels of tropical dry forest disturbance in the Chamela region, Mexico. Functional richness, functional evenness, and functional dispersion were assessed considering six lizard functional traits. We recorded 415 lizards of 15 species. Species richness, species diversity, functional richness, functional dispersion, and the number of functional groups are lower in disturbed sites than in undisturbed tropical dry forest sites. On the contrary, abundance and functional evenness were higher in strongly disturbed sites. We suggest that lizard functional diversity should be studied further in order to secure the integrity of herpetofaunal communities and ecosystem processes.

Keywords

Introduction

Habitat disturbance is currently one of the most important anthropogenic factors that influence ecosystems at a very high-speed rate, which is caused by human activities in natural habitats, resulting in changes in structure, biotic composition, and resource availability (Cuarón, 2000; Hobbs, Higgs, & Harris, 2009). This disturbance negatively affects tropical forests, where biodiversity is higher than in other terrestrial ecosystems (Alvarez-Berríos et al., 2016; Gonthier et al., 2014). Particularly, tropical dry forests (TDF) are complex ecosystems that harbor an exceptionally high diversity of plants, insects, and vertebrates (Durán et al., 2002). In Mexico, however, fragmentation of this type of forest is occurring at accelerated rates, and consequently TDF remnants are commonly embedded in landscape matrices with different land use (Trejo & Dirzo, 2000). Land use change and its intensification can also modify the behavior of some species; for example, in choosing perch sites and hours of activity; while in other cases species diversity is reduced, causing direct effect on the ecosystem (Jones, 1981; Thompson, Nowakowski, & Donnelly, 2016; Wong & Candolin, 2015).

Traditional measures of species diversity (e.g., species richness, diversity, or evenness) provide limited information regarding biodiversity in a broad sense and the ecological processes in which species participate (Tsianou & Kallimanis, 2016). Alternatively, functional diversity measures account for differences in the characteristics and the functions that species perform in ecosystems, and consequently functional diversity describe the degree of functional differentiation among species (Petchey & Gaston, 2006). Functional diversity is determined by species functional traits, which are defined as phenotypic or operational characteristics that can be measured at individual or species level and that may

[1]Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, México

Corresponding Author:
Aurelio Ramírez-Bautista, Centro de Investigaciones Biológicas, Instituto de Ciencias Básicas e Ingeniería, Universidad Autónoma del Estado de Hidalgo, Pachuca, Hidalgo, Mexico.
Email: ramibautistaa@gmail.com

influence its fitness or the ecosystem processes (Weiher, 2011). Therefore, functional traits and functional diversity may be analyzed to assess the impacts of habitat disturbance on the processes and functions of the ecosystems, given that biodiversity is linked to ecosystem processes (Chapin et al., 2000; Mason, Mouillot, Lee, & Wilson, 2005). Until today, there are still few empirical studies; however, some of them have been focused on the effects that tropical forest disturbance might have on the functional diversity of animal communities (e.g., Barragán, Moreno, Escobar, Halffter, & Navarrete, 2011; García-Morales et al., 2016). In some cases, functional diversity might be strongly sensitive to habitat disturbance. For example, Flynn et al. (2009) pointed out that with greater land use intensity, species diversity, and functional diversity are reduced.

Lizard communities are good models to study the effects of habitat disturbance, not only in species richness and abundance but also in the functional diversity of ecological communities. This is because sympatric lizard species use and share the habitat niche by partitioning food resources, activity time, or microhabitat type (Pianka, 1973; Toft, 1985). Also, lizard species respond in different ways to habitat disturbances (Macip-Ríos & Muñoz-Alonso, 2008). For example, in humid tropical environments (e.g., evergreen forest), habitat disturbance reduces the species richness and abundance of these reptiles (Glor, Flecker, Benard, & Power, 2001), whereas in TDF species richness and abundance seem to increase (Suazo-Ortuño, Alvarado-Díaz, & Martínez-Ramos, 2008). In a comprehensive recent study (Suazo-Ortuño et al., 2015), lizard species richness was found to remain almost the same across different vegetation successional stages in the TDF of the Chamela region. Lizard functional diversity, however, has been poorly studied (Trimble & Aarde, 2014), especially in TDF. Reptiles play different roles in ecosystems, and lizards have ecological functions such as dispersing seeds, controlling insect populations like ants, and providing food for other animals (Cortés-Gómez, Ruiz-Agudelo, Valencia-Aguilar, & Ladle, 2015; Valencia-Aguilar, Cortés-Gómez, & Ruiz-Agudelo, 2013).

In this article, we focus on the effect that the land use change has on different functional features of the lizards (as they are expected to be affected by different levels of disturbance), but not that these traits have effects on ecosystem processes. We assume that the functional traits (and consequently the functional diversity of lizard communities) are negatively affected by habitat disturbance, and their assessment will help us to understand how ecological communities respond to disturbance (Mayfield et al., 2010; Suding et al., 2008). Thus, we expect to find a lower lizard functional diversity in strongly disturbed sites, given that the intensity of habitat disturbance may limit the presence of some functional traits, and

Table 1. Functional Traits and Attributes Used to Assess Lizard Functional Diversity.

Traits	Variable	Attribute
Diet	Categorical	1 insectivorous, 2 herbivorous, 3 omnivorous, 4 carnivorous, 5 insectivorous-carnivorous and 6 herbivorous-carnivorous
Foraging	Categorical	1 active, 2 sit and wait
Habit	Categorical	1 saxicolous, 2 fossorial, 3 terrestrial, 4 arboreal and 5 arboreal-saxicolous
Activity	Categorical	1 diurnal, 2 crepuscular, 3 nocturnal, 4 crepuscular-nocturnal, 5 diurnal-nocturnal, and 6 diurnal-crepuscular
Snout-vent length	Continuous	Mean SVL each species
Biomass	Continuous	Mean fresh body mass (g)

the environmental conditions of disturbed sites act as environmental filters for some species. Our objective was to assess species richness, abundance, and diversity, as well as functional diversity of lizard communities in areas with different levels of TDF disturbance in the Chamela region: undisturbed, moderately, and strongly disturbed sites. Our analyses of functional diversity include functional richness, functional evenness, and functional dispersion indices based on six lizard functional traits (Table 1).

Methods

Study Area

This study was carried out in the Chamela-Cuixmala Biosphere Reserve and its surroundings, in the southwestern Pacific coast (19°30′ N, 105°03′ W) of Jalisco, Mexico (Figure 1). This region has a mean annual temperature of 25°C and mean annual precipitation of 790 mm. The rainy season occurs from June to October (National Institute of Statistics and Geography [INEGI], 2009). There are some remnants of native vegetation (TDF) outside the reserve, immerse in a matrix with different land uses: grazing areas and crops (e.g., corn, squash, beans, cucumber, and chili), as well as urban areas. The reserve harbors an ample and continuous area of mature TDF. For this work, we selected nine sampling sites that represent three levels of habitat disturbance in the region (Figure 1). Sampling sites were separated at least 2 km to represent independent samples. This distance was set considering the home range (1 km²)
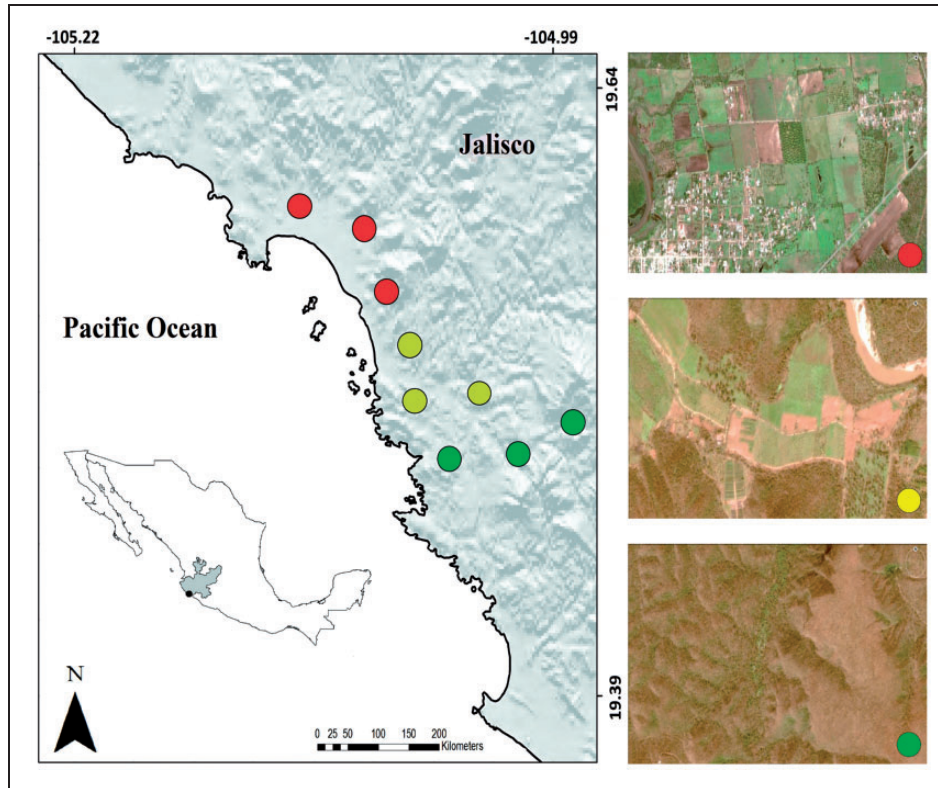
Figure 1. Location of the study area in the region of Chamela, in the coast of Jalisco, Mexico. The map of Mexico shows the location of Jalisco state and study area in black dot. The green circles represent undisturbed tropical dry forest sites, yellow circles represent moderately disturbed sites, and red circles represent strongly disturbed sites.

of *Iguana iguana* (Perry & Garland, 2002), which is the largest lizard in the area.

Undisturbed TDF Sites

We located three sampling sites within a large fragment of well preserved, continuous TDF at the Chamela-Cuixmala Biosphere Reserve (Figure 1, green circles). These areas had dense and high vegetation cover generated by old trees between 8 and 12 m high. In these areas, the canopy has a convex shape and is slightly uniform (Rzedowski, 2006). The diameter of trunks did not exceed 50 cm. The trees are branched at low altitude or near the base. There are two arboreal layers (trees and shrubs), whereas the herbaceous layer is almost nil. The selected sites presented a thick layer of soil formed by decomposing organic material (leaf litter, trunks, and branches, among others), as well as rocks.

Moderately Disturbed Sites

Three moderately disturbed sites were located at least 5 km far from forest fragments to avoid the influence of the undisturbed forest in reptile diversity. These sites represent crops and grazing areas. These sites include remnants of native and secondary vegetation, but in the sampled sites, we also found rubble and construction fragments, along with crop wastes and plastic debris. We set transects in the border between crops, grasslands, and forests, in areas that have been used by local people since the 1960s (Figure 1, yellow circles). In these sites, secondary thorn scrub patches provide an important food source for pastoral livestock (Durán et al., 2002; Rzedowski, 2006).

Strongly Disturbed Sites

We located three sampling sites in strongly disturbed areas, at least 5 km apart from those moderately disturbed. These sites were clearly disturbed by human-related activities, with presence of settlements, dirt roads, cattle, and agriculture throughout the year (Figure 1, red circles). In these areas, native woody tree species are frequently eliminated; therefore, vegetation is dominated by herbaceous plants, such as species of the Compositae family (Rzedowski, 2006). Crop fields are separated by tree fences and bounded by wooden posts. Trunks and rocks are scarce, but there is abundant rubble from buildings. We located our sampling transects in the borders between crops, paddocks, and roads.

Data Collection

Surveys took place across 400×6 m linear transects. We surveyed in 10 transects located in undisturbed TDF sites, 11 transects in moderately disturbed sites, and 11 transects in strongly disturbed sites. Three persons did surveys over 3 h in the morning, 3 h in the afternoon, and 3 h in the night, for a total of 27 h/day/person per transect, in 2012. This sampling effort was performed in June (dry season) and November (rainy season), to encompass seasonal variability. Thus, the total survey effort was 1,728 h/person.

We searched for lizards directly on the ground and up to 3 m in the trees. Each individual was measured, weighed, marked, and later released at the same site of capture, and with the same person always taking the measurements. Marked lizards were painted with a dot of non-toxic red paint on the dorsum to avoid duplicated observations. This mark is maintained only during the samplings days; we did not notice an increase of predation. Species identification was based on criteria of Wilson, Mata-Silva, and Johnson (2013) and Meza-Lázaro and Nieto-Montes de Oca (2015).

For each species, we gathered information on functional traits from field observations and published data on their natural history (Beck, 2005; Canseco-Márquez & Gutiérrez-Mayén, 2010; Castro-Franco & Bustos Zagal, 2006; García & Ceballos, 1994; Lee, 1996; Ramírez-Bautista, 1994, 2004; Ramírez-Bautista & Vitt, 1998; Ramírez-Sandoval, Ramírez-Bautista, & Vitt, 2006). Our analyses are based on six functional traits (Table 1) that reflect the interaction of lizards with their ecosystem because they are related to resource and habitat use (Casanoves, Pla, Di Rienzo, & Díaz, 2011; Rivera, Miramontes, Méndez, & Piñero, 2009; Vitt, 1981; Vitt & Congdon, 1978).

Data Analysis

Completeness of the inventories. To assess sampling completeness for each level of habitat disturbance (undisturbed, moderately, and strongly disturbed sites), we calculated the percentage of completeness based on species number and the value of the estimator Chao 1(Chao, 1984).

Species richness, abundance, and diversity. Species richness was counted as the total number of species recorded at each site. Species abundance was the number of individuals recorded. We calculated species diversity as the exponential of the Shannon entropy index, which is $q = 1$ Hill number (Jost, 2006).

Structure of communities. Composition and structure of the species for each site were assessed with rank-abundance curves, considering the proportion of the number of individuals recorded for each species, using base 10 logarithms ($\log_{10}(p_i)$) (Feinsinger, 2003; Magurran, 1998).

Species composition among habitats. We performed a permutational multivariate analysis of variance (PERMANOVA) using the Bray-Curtis distance (Anderson, 2001) to test for statistical differences in the species composition among levels of habitat disturbance (undisturbed, moderately, and strongly disturbed sites). This test was done in the R program with the package ''vegan,'' using 4,999 permutations (R Core Team, 2015). To visualize species composition patterns in communities across these sites, we performed nonmetric multidimensional scaling based on a Bray-Curtis similarity matrix.

Functional diversity. We calculated three indices that assess complementary aspects of functional diversity (Mason, Lanoiselée, Mouillot, Irz, & Argillier, 2007; Villéger, Mason, & Mouillot, 2008).

The FDc index measures functional richness as the mean length connecting any pair of species in a functional dendrogram. The FEve index measures functional evenness, that is, the relative representation of the functional traits within the community and quantifies the regularity with which species abundance is distributed in a functional space. The FDis index measures functional dispersion measured as the mean distance of individual species to the centroid of all species in the community, where the weights are species-relative abundances and traits (Laliberté & Legendre, 2010). We decided to assess functional diversity with the previously mentioned indexes because these consider multiples traits and allow to assess at the same time different features per species; these have an important advantage on other indices that only consider one trait by species (Villéger et al., 2008). We also drew functional dendrograms classifying species into functional groups according to their functional traits, for the landscape, and for each disturbance level. For all these analyses, we used Gower distances because we included both continuous and categorical data (Table 1). Functional diversity indices and dendrograms were done in the FDiversity software (Casanoves et al., 2011).

Results

We recorded 415 individuals that belong to 15 species, 13 genera, and 9 families (Table 2). The three levels of habitat disturbance showed an inventory completeness higher than 90%. In the undisturbed TDF sites, we captured 13 species, 10 in moderately disturbed sites, and 8 in the strongly disturbed sites. The highest abundance was observed in the strongly disturbed sites, but the highest species diversity (7.29 effective species) occurred in the undisturbed TDF sites (Figure 2).

Rank-abundance curves showed that species composition differed among sites (Figure 3). We also observed dominance of some species, such as *A. nebulosus*, *U. bicarinatus*, and *H. frenatus* in disturbed places

Table 2. Number of Lizards Captured by Species.

| Family	Genus	Species	Species letter	Abundance TDF	MD	SD
Dactyloidae	*Anolis*	*nebulosus*	A	2	50	12
Eublepharidae	*Coleonyx*	*elegans*	B	1		
Gekkonidae	*Hemidactylus*	*frenatus*	C		3	34
Helodermatidae	*Heloderma*	*horridum*	D	2		
Iguanidae	*Ctenosaura*	*pectinata*	E	1	13	
	Iguana	*iguana*	F	1		
Phrynosomatidae	*Phrynosoma*	*asio*	G	2		
	Sceloporus	*utiformis*	H	18	12	6
		melanorhinus	I	8	1	30
	Urosaurus	*bicarinatus*	J		31	35
Phyllodactylidae	*Phyllodactylus*	*lanei*	K	2		
Scincidae	*Marisora*	*brachypoda*	L	14	2	2
Teiidae	*Aspidoscelis*	*communis*	M	27	13	4
		lineattissima	N	27	16	27
	Holcosus	*sinister*	O	12	7	

Note. TDF = undisturbed tropical dry forest sites; MD = moderately disturbed sites; SD = strongly disturbed sites. Species letters correspond to those in Figures 3, 4, and 6.

(Figures 3 and 4). The PERMANOVA analysis showed significant differences in species composition among levels of habitat disturbance (Pseudo-$F = 5.17$, $R^2 = 0.4249$, $p < .01$). The nonmetric multidimensional scaling analysis shows these differences among sites with different levels of habitat disturbance (Figure 5).

The three aspects of functional diversity showed different trends across the levels of habitat disturbance. The undisturbed TDF sites had the highest functional richness and functional dispersion, while the strongly disturbed sites had the lowest functional richness but the highest functional evenness (Figure 2). The whole landscape includes nine functional groups of lizards (Figure 6): nine functional groups were recorded in undisturbed TDF sites, six in moderately disturbed sites, and five in the strongly disturbed sites. Also, the number of species per functional group decreases with habitat disturbance.

Discussion

This study revealed that diversity lizard species and functional diversity change with habitat disturbance in the Chamela region. Species richness, species diversity, functional richness, functional dispersion, and the number of functional groups are lower in disturbed sites than in undisturbed TDF sites. These responses might be related to several factors, for example, the lower availability and quality of microhabitats in disturbed sites
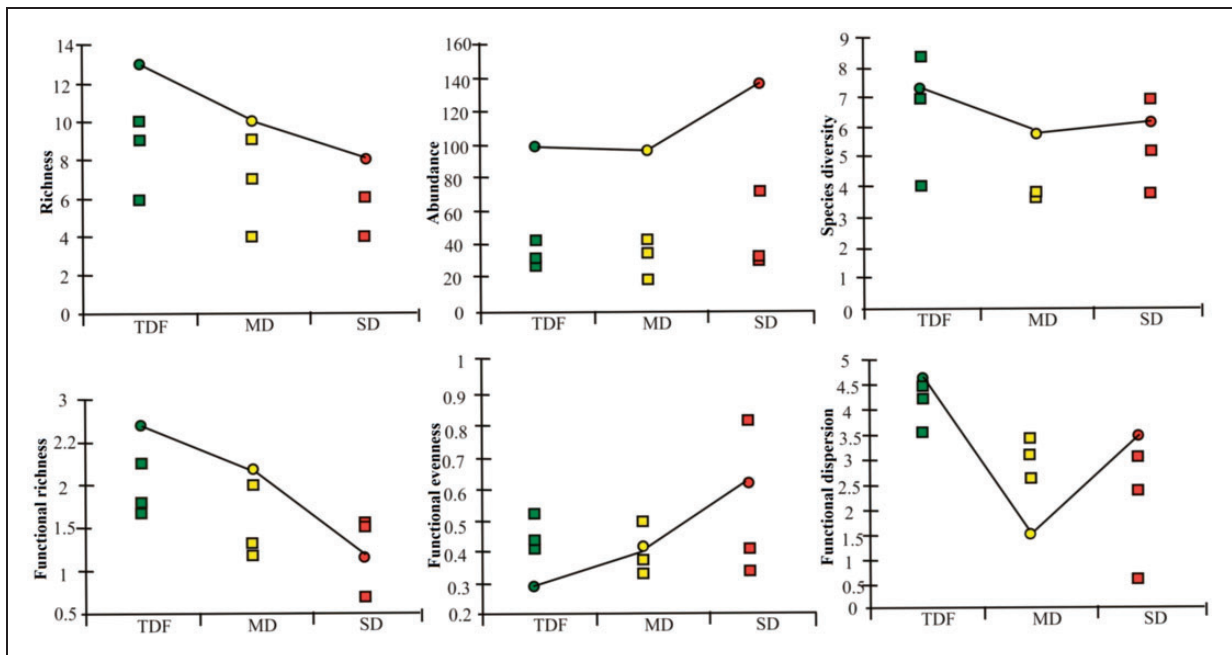
Figure 2. Species richness, abundance, and diversity (top), and values of three measures of functional diversity (below) of lizards in undisturbed tropical dry forest sites (TDF), moderately disturbed sites (MD), and strongly disturbed sites (SD). Squares show values obtained by site, while circles show the cumulative values of the three sites.
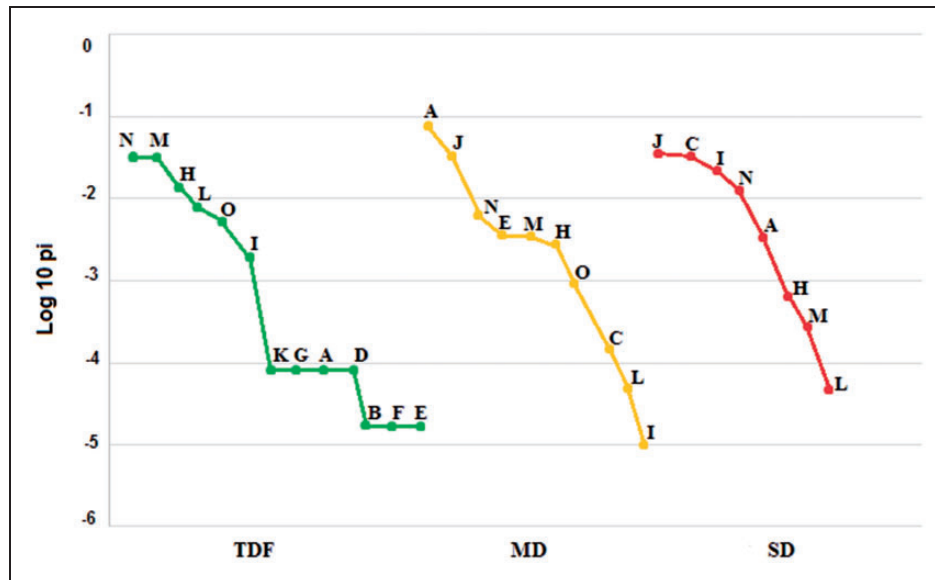
Figure 3. Rank-abundance curves of lizard communities in three levels of habitat disturbance in the Chamela region. The letters indicate lizard species, according to Table 2 and Figure 4. TDF = undisturbed tropical dry forest sites; MD = moderately disturbed sites; SD = strongly disturbed sites.
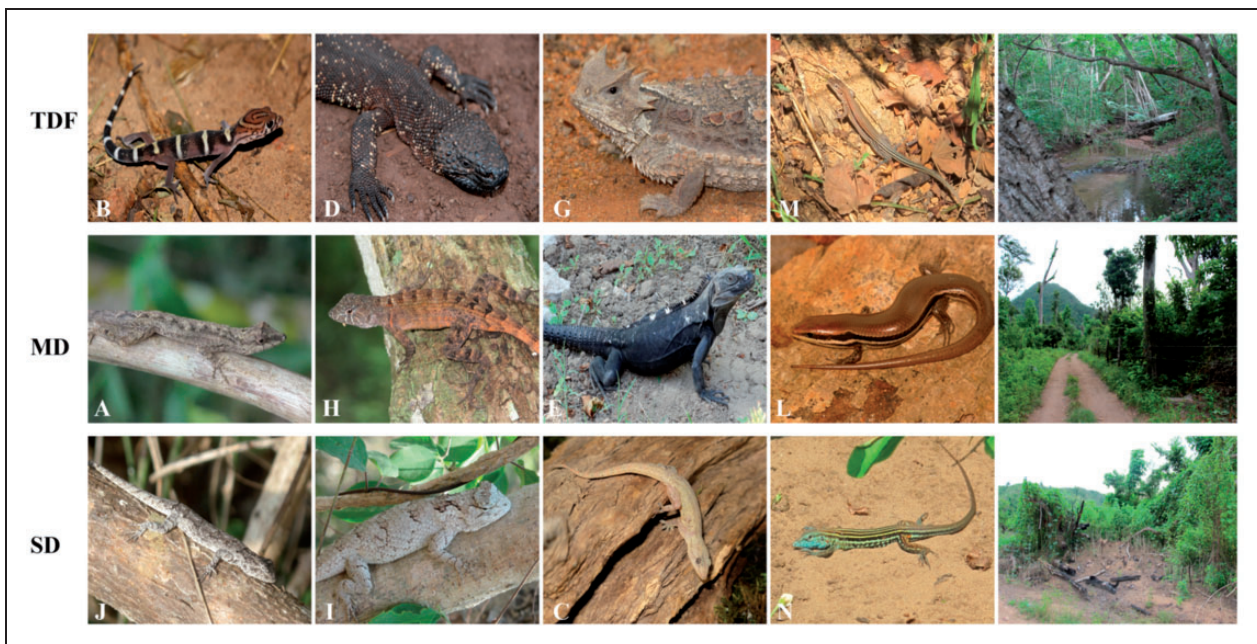

Figure 4. Photographs of the more representative species recorded in the different sites surveyed in the Chamela region. (D) *Heloderma horridum*, (E) *Ctenosaura pectinata*, (H) *Sceloporus utiformis*, (I) *S. melanorhinus*, (G) *Phrynosoma asio*, (A) *Anolis nebulosus*, (L) *Marisora brachypoda*, (B) *Coleonyx elegans*, (N) *Aspidoscelis* lineattissima, (M) *A. communis*, (C) *Hemidactylus frenatus*, and (J) *Urosaurus bicarinatus*.

(Gonthier et al., 2014). In this sense, Pianka (1966) pointed out that structural complexity of vegetation is determinative in lizard diversity, being greater species richness in more heterogeneous habitats.

On the other hand, functional characterization of the assembly was achieved by considering together the three analyzed components (FDc, FEve, and FDis), which were based on the profile of the traits each species. For example, only species with response functional traits that allow them to tolerate the new conditions generated by disturbance will remain in modified habitats, while specialist species that are less tolerant to environmental
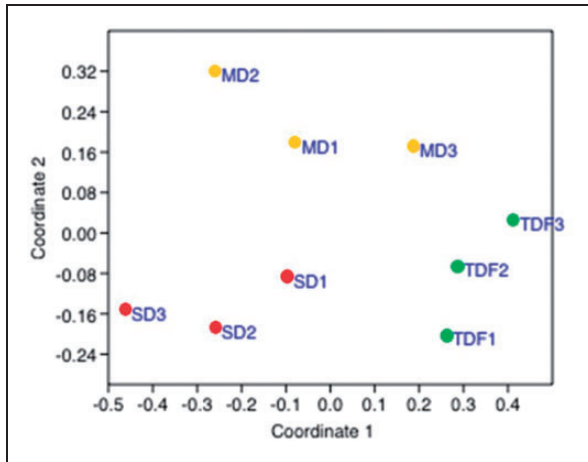
Figure 5. Nonmetric multidimesional scaling (NMDS) using the Bray-Curtis distance to show differences in species composition among undisturbed tropical dry forest (green dots), moderately disturbed (yellow dots), and strongly disturbed (red dots) sites.

changes will be more affected by habitat disturbance (Liu et al., 2015; Martínez-Abraín & Jiménez, 2016). For example, *H. horridum*, *P. asio*, *S. utiformis*, *H. sinister*, and *A. communis* have three functional traits that may limit their presence in disturbed sites: size (SVL), diet, and habit. *Heloderma horridum* is highly sensitive to habitat modifications due to its size, its microhabitat selection to forage and refuge (habit) and strict carnivorous diet (Beck, 2005; Reiserer, Schuett, & Beck, 2013). The diet of *P. asio* is almost exclusively based on ants and termites (García & Ceballos, 1994). However, Suazo-Ortuño et al. (2008) stated that lizard traits (habits, foraging strategy, and body size) in TDF do not determine differences in species between conserved and human disturbed forest areas. Our results suggest that functional traits and functional diversity may change in different habitat types.

On the contrary, for *A. nebulosus*, *H. frenatus*, and *U. bicarinatus* size, diet, and activity are traits that may allow them to use disturbed sites. Moreover, these species have more variable traits. For example, *H. frenatus* can modify its activity (diurnal, crepuscular, and nocturnal) and habits (saxicolous, arboreal, and arboreal-saxicolous) facilitating its adaptation to disturbed sites. Similar pattern was reported by Petren and Case (1998) who mentioned that behavior of *H. frenatus* is modified in open areas.

In our study, *H. frenatus* and *U. bicarinatus* were found only in disturbed sites, a response that has been previously reported (Vargas-Santamaría & Flores-Villela, 2006); therefore, these resilient species play an essential role in these modified places (Martínez-Abraín & Jiménez, 2016). For example, the lizard *H. frenatus* could be fulfilling the functions of the native species *P. lanei*.

This phenomenon of species substitution may have important consequences in the ecosystem because the distribution of traits among species, and species abundance influence partitioning of available resources among them. For example, these differences in resource use affect the values of functional evenness; which are determined by the abundance and high similarity of the functional traits of these species groups. Accordingly, when values of functional evenness are higher; in theory, it is indicated that the use of resources is maximum, while a reduction in these values means that some resources are not being used (Mouchet, Villéger, Mason, & Mouillot, 2010). Thus, our results show that lizard species in strongly disturbed sites may efficiently use even the limited resources available in those environments.

On the other hand, the values of functional richness obtained are clearly determined by species number of the community and for intraspecific variability incorporated from values for each one of the measured traits (Petchey & Gaston, 2006). Similar pattern showed in areas with greater vegetation cover in functional diversity of bats from tropical environments (García-Morales et al., 2016).

The way in which a set of extrinsic factors affect the structure of assembly will depend on the nature of the components (functional traits) because these factors could cause an increase in the dispersion of a feature or a decrease in the dispersion of another. In consequence, dispersion based in the multiple variations of traits will reflect the interactions of different factors; in other words, values of functional dispersion will reflect the great diversity of different ways of exploiting the space-food resources in environments with greater structural complexity as occurs undisturbed TDF.

The undisturbed TDF had a similar number of functional groups as that found in the whole landscape. In this sense, TDF conservation becomes more relevant because it maintains the highest lizard diversity as well as the roles the latter play in these ecosystems. For example, Flynn et al. (2009) pointed out that a higher intensification of land use reduces species richness and the function of the ecosystems. Thus, resilience in preserved environments is higher than in disturbed environments due to the higher number of functionally redundant species. Our results showed no redundant species for some functional groups, for example, *A. lineattissima* group (Güizado Rodríguez & Casas-Andreu, 2011; Figure 6), suggesting that the lizard communities may be highly sensitive to disturbances, endangering their ecological functions in this ecosystem (Martín-López, González, Díaz, Castro, & García-Llorente, 2007). However, results showed in functional dendrogram could differ due to choice of cutoff value for functional groups (Petchey & Gaston, 2002); therefore, interpretation of these dendrograms should be taken with caution. On the other hand, these dendrograms also show the functional similarities
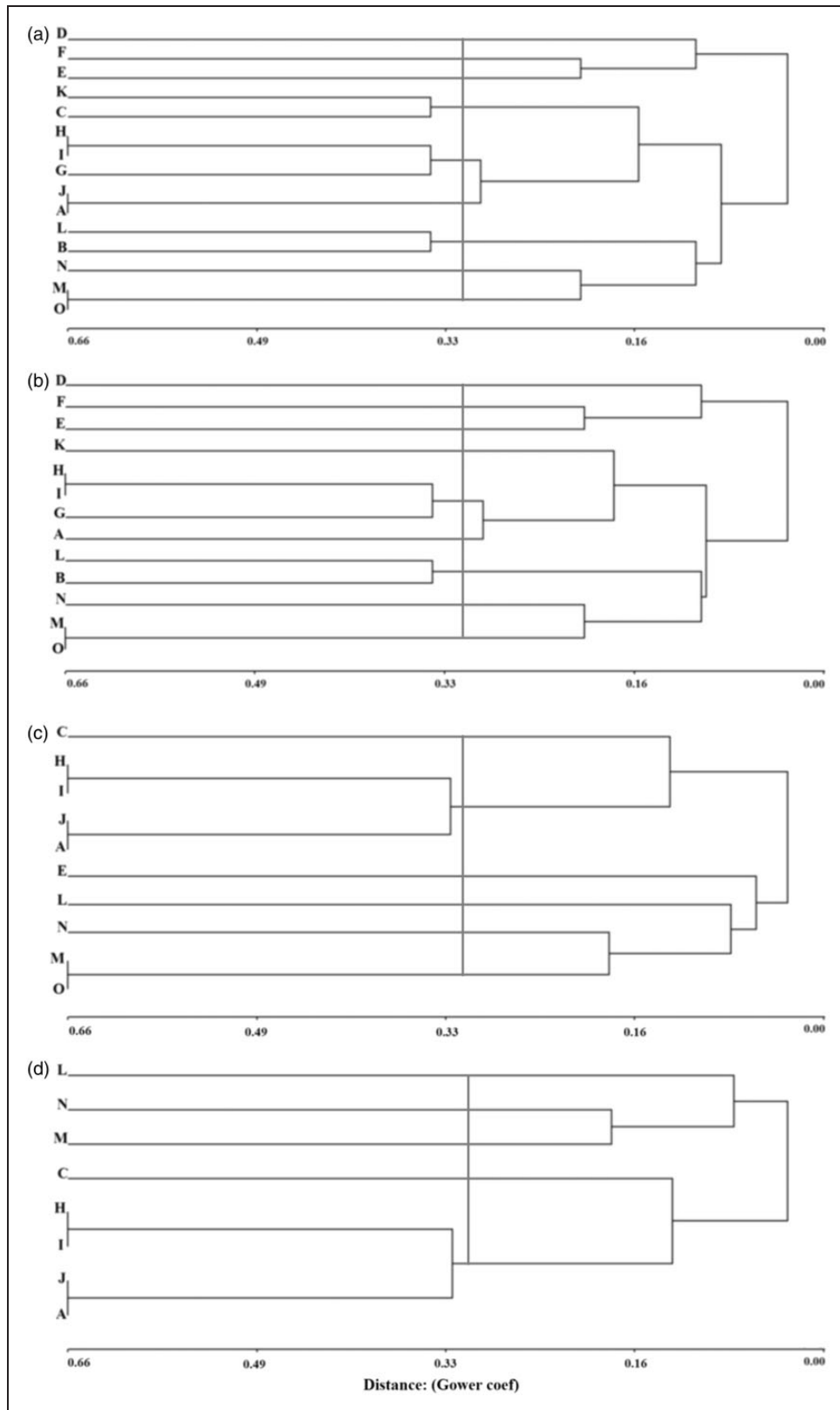
Figure 6. Functional dendrograms classifying lizard species into functional groups according to their functional traits, for the whole landscape (a), undisturbed TDF sites (b), moderately disturbed sites (c), and strongly disturbed sites (d).

of the species, and similar traits within community (Petchey & Gaston, 2006).

Despite the absence of some species in strongly disturbed sites, some species persist. For example, *S. utiformis*, *S. melanorhinus*, *A. nebulosus*, and *A. lineattissima*. This pattern is similar to another study done by Martínez-Abraín and Jiménez (2016) who pointed out that resistant or introduced species play the environmental function of the extirpated native species. Recently, Mokany, Ash, and Roxburgh (2008) noted out that the processes of ecosystems are determined by the functional traits of the abundant and common species in the communities. Our results showed that the dominant species that persist in disturbed habitats can support some ecological process. Thus, these resistant species could be involved in functional roles carried out by the species that are lost when the TDF is transformed.

Finally, we encourage the development of comprehensive studies that might consider different potential factors affecting tropical lizard diversity. In this study, we arbitrarily classified study sites into three levels of habitat disturbance, but further studies may try to account for habitat disturbance as a continuous factor, of may include other possible design factors such as ecological succession and landscape composition.

Implications for Conservation

The undisturbed TDF sites maintain the highest lizard species diversity, as well as the roles that they play in this ecosystem, while habitat disturbance due to land use intensification reduces species and functional diversity, as has been noted by Flynn et al. (2009) and García-Morales et al. (2016). Further research is needed to assess the generality of this result, evaluating lizard responses to different land use types but also to landscape composition and configuration. Our results highlight the importance of including different biodiversity aspects to provide a broad view of the impact of habitat disturbance on lizard communities beyond species numbers. Functional diversity should be considered to secure the integrity of the herpetofauna and ecosystem processes occurring in regions with undisturbed TDF, such as the Chamela region.

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