

Amphibian diversity in Serranía de Majé, an isolated mountain range in eastern Panamá

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Abstract

Eastern Panamá is within the Mesoamerican biodiversity hotspot and supports an understudied amphibian fauna. Here we characterize the amphibian diversity across an elevational gradient in one of the least studied mountain ranges in eastern Panamá, Serranía de Majé. A total of 38 species were found, which represent 17% of all species reported for Panamá. Based on expected richness function and individual-based rarefaction curves, it is estimated that this is an underestimate and that at least 44 amphibian species occur in this area. Members of all three amphibian orders were encountered, represented by ten families and 22 genera, including five species endemic to Central America. Estimated species richness decreased with elevation, and the mid-elevation site supported both lowland and highland species. Our study provides a baseline for understanding the distribution pattern of amphibians in Panamá, for conservation efforts, and for determining disease-induced changes in amphibian communities.

Keywords

Altitudinal diversity, amphibian species inventory, Panamá

Introduction

Mesoamerica is a global biodiversity hotspot (Johnson et al. 2015). Within this region, Panamá has the second greatest number of reptile and amphibian species, containing 26% of all amphibian species reported for Mesoamerica (Jaramillo et al. 2010). However, a substantial portion of eastern Panamá has been understudied. Geographically, eastern Panamá comprises the northernmost part of the Chocó biogeographical region (Duque-Caro 1990), and it is part of the Tumbes-Chocó-Magdalena global biodiversity hotspot (Mittermeier et al. 1999). This region includes a number of relatively low mountain ranges, including the Serranía de San Blas + Serranía del Darién on Caribbean side, the inland Serranía de Pirre + Altura de Nique + Altos de Quía, Serranía de Majé, and the Serranía de Sapo + Serranía de Jingurudó + Altos de Aspavé + Cordillera de Juradó along the Pacific Ocean (Duque-Caro 1990; Batista et al. 2016).

Whitfield et al. (2016) analyzed regional trends and reported that eastern Panamá has a very small number of recognized species in relation to its geographic area, which reflects the limited number of field surveys in the area. A sharp increase in the number of field surveys during the last decade has led to the discovery of several new amphibian species with restricted distribution ranges (e.g., Ibáñez and Crawford 2004; Crawford et al. 2010a; Batista et al. 2014a, 2014b, 2016) supporting the hypothesis that eastern Panamá is a region with a high endemic amphibian diversity. This is in contrast to the claim that it was mainly a dispersal route during the Great American Biotic Interchange (Webb 2006), and was colonized by species groups from the north and South America (Vanzolini and Heyer 1985; Pinto-Sánchez et al. 2012).

One reason to establish baseline estimates of amphibians is to assess changes following loss caused by disease epidemics. The pathogenic fungus *Batrachochytrium dendrobatidis* (*Bd*) causes population declines and extinctions of many amphibian species worldwide, particularly in the Neotropics (James et al. 2015, Lips 2016). *Bd* has caused dramatic declines of amphibian communities in the highlands of western and central Panamá (Lips 1999; Lips et al. 2006; Crawford et al. 2010b). Importantly, to our knowledge, at the time of sampling there were no published data reporting the presence of *Bd* in the region – though the amphibian species present at this region can either represent the original community or a subset as a consequence of an undetected *Bd* epidemic. Here, we describe the results from field surveys to characterize α and β diversity along an altitudinal gradient in the isolated Serranía de Majé of eastern Panamá.

Materials and methods

Study sites

During the wet season, from June 23 to July 2 2007, we conducted field surveys at three study sites located at a low, middle, and high elevations in the Serranía de Majé. This mountain range is located on the Pacific coast, previously known as Serranía de Cañazas (Myers 1969), and is isolated from others mountainous areas by the Chepo

and Chucunaque Rivers (Figure 1; Angehr and Christian 2000). Its highest point, Cerro Chucantí (1,489 m), stands on the eastern end of the mountain range, at the boundary of the Panamá and Darién provinces (Angher and Christian 2000).

The three study sites were located in Lowland Wet/Moist Forest (LWM) below 600 m, and Premontane Rain Forest/Wet Forest (PRW) above 600 m (Holdridge 1967). The sites were: a low elevation site, Centro Cristo Misionero (8.96N, 78.457W) at 120–150 m elevation; a mid-elevation site, located within the Reserva Natural Privada Cerro Chucantí (8.79N, 78.451W) at 797 m elevation; and, the high elevation site, also located in the Cerro Chucantí private natural reserve (8.80N, 78.462W), near the top of the Cerro Chucantí, at 1,240–1,365 m elevation. The approximate airline distances between the study sites were 19, 18, and 2 km for lowland-mid-elevation, lowland-highland and mid-elevation-highland sites, respectively.

Data collection

The surveys were conducted using the sampling technique “free and unrestricted search”, which is considered to be one of the most efficient methods to record a high number of species in a relatively short amount of time (Rueda et al. 2006). Different types of habitat such as forest, streams, ponds, and open areas with grass were surveyed during the day and night. Species identification and individual counts were performed using the techniques ‘visual encounter survey’ (VES) and ‘acoustic encounter survey’ (AES). In addition, the search effort invested (in person-hours) at each sampling site was calculated by multiplying the search time by the number of observers, and the catch per unit of search effort for each site was calculated by dividing the number of post-metamorphic amphibians encountered by the search effort at the respective site as estimated by Kilburn et al. (2011).

A few specimens of each species were collected as voucher specimens (Suppl. material 1: Table S1), photographed, and deposited in the reference Collection of Herpetology (specimen tags CH and AJC) at the Smithsonian Tropical Research Institute, and in the Museo de Vertebrados de la Universidad de Panamá (tags MVUP). Amphibians to be preserved were first euthanized using Orajel (benzocaine 20%) or occasionally 10% ethanol. Before fixation, liver samples were taken from each specimen and preserved for future phylogenetic and phylogeographic analyses (Seutin et al. 1991). Vouchers were then fixed in 10% formalin in a position that facilitates examination. To verify the identification of specimens we used all relevant literature available on the amphibians of Panamá (e.g., Ibáñez et al. 1999a), and compared specimens with those in the CH reference collection. The identification of anuran advertisement calls was facilitated by audio recordings of Panamanian frogs (Ibáñez et al. 1999b).

Data analyses

We calculated α diversity based on all post-metamorphic amphibians captured at each site (Hortal et al. 2006), using the software EstimateS 8.0.0 (Colwell 2006). We calcu-

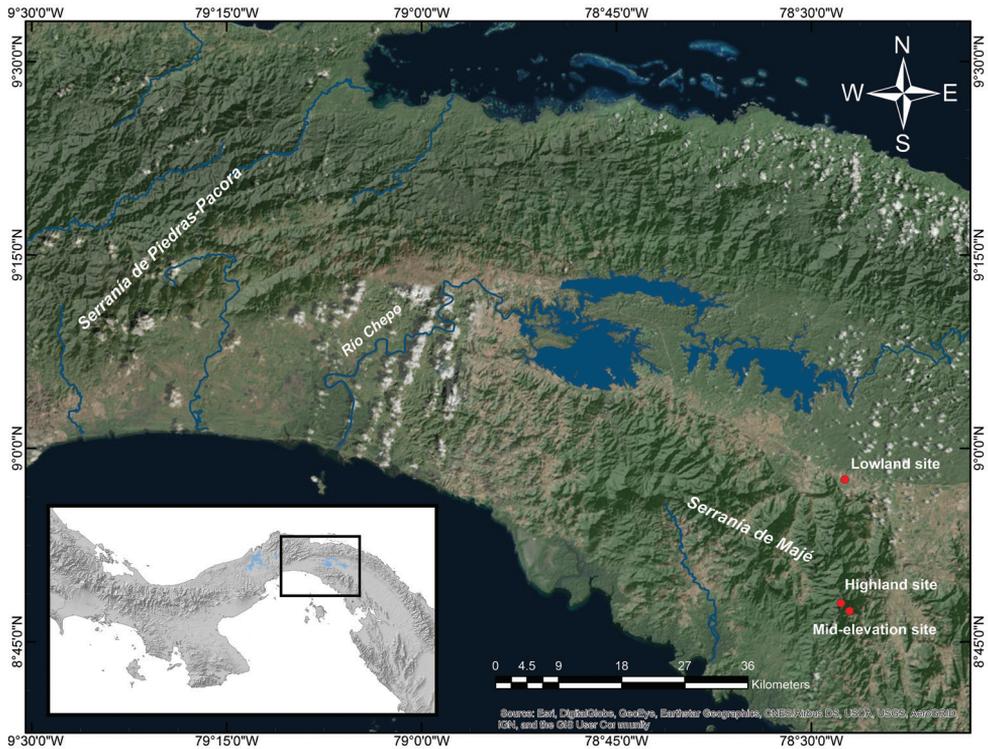


Figure 1. Map showing the location of the study sites in the Serranía de Majé and the Serranía de Piedras-Pacora across the valley of the Chepo River.

lated Mao Tau (Colwell et al. 2004) and plotted sample-based rarefaction curves with 95% confidence intervals.

To determine β diversity for assessing the variation in species composition across sites, we also used all post-metamorphic amphibians captured at each site, and conducted a cluster analysis based on Jaccard dissimilarity measures estimated with the R function `vegdist` from the *vegan* package (Oksanen et al. 2017). In order to identify clusters, we built a dendrogram using the unweighted pair-group method based on arithmetic averages (UPGMA), using function `hclust` from the default R package *stats*. This analysis was completed in the R version 3.3.3 (R Core Team, 2017).

Results

Our team conducted 280 person-hours of surveys (lowland site: 125; mid-elevation site: 96; highland site: 59) and identified 38 amphibian species from all three amphibian orders, ten families, and 22 genera (Table 1). The total number of species for the surveyed area within the Serranía de Majé was estimated as 44 species based on the upper 95% confidence interval of the Mao Tau function (Table 2).

Table 1. List of species and number of post-metamorphic individuals found at the three surveyed sites across the elevational gradient in the Serranía de Majé. The letter ‘L’ refers to a species that was recorded by its larvae and ‘V’ by its vocalizations. The IUCN conservation status is based on the IUCN (2018). ‘E’ represents a species that is endemic to Central America (CA) based on Johnson et al. (2015).

Order	Family	Genus	Species	Lowland	Mid-elevation	Highland	IUCN status	Endemic to CA
Anura	Aromobatidae	<i>Allobates</i>	<i>talamancae</i>	2	1		LC	
	Bufonidae	<i>Rhaebo</i>	<i>haematiticus</i>		9	11	LC	
		<i>Rhinella</i>	<i>alata</i>	13	1	1	LC	
		<i>Rhinella</i>	<i>horribilis</i>	2	1		LC	
	Centrolenidae	<i>Espadarana</i>	<i>prosolepon</i>	L	8	V	LC	
		<i>Cochranella</i>	<i>euknemos</i>		3		LC	
		<i>Hyalinobatrachium</i>	<i>colymbiphyllum</i>	1			LC	
		<i>Hyalinobatrachium</i>	<i>fleischmanni</i>	3			LC	
	Craugastoridae	<i>Hyalinobatrachium</i>	<i>vireovittatum</i>		1		DD	E
		<i>Craugastor</i>	<i>crassidigitus</i>	1	9	1	LC	
		<i>Craugastor</i>	<i>fitzingeri</i>	5	3		LC	
		<i>Craugastor</i>	<i>naniformis</i>	15	3		LC	
		<i>Pristimantis</i>	aff. <i>latidiscus</i>			4	–	–
		<i>Pristimantis</i>	<i>caryophyllaceus</i>			57	NT	E
		<i>Pristimantis</i>	<i>cruentus</i>		1	71	LC	
		<i>Pristimantis</i>	<i>gaigei</i>	1			LC	
		<i>Pristimantis</i>	<i>moro</i>			10	LC	
		<i>Pristimantis</i>	<i>pardalis</i>			1	NT	E
	Dendrobatidae	<i>Pristimantis</i>	<i>ridens</i>		1		LC	
		<i>Pristimantis</i>	<i>taeniatus</i>			V	LC	
		<i>Strabomantis</i>	<i>bufoniformis</i>	2			LC	
	Dendrobatidae	<i>Colostethus</i>	aff. <i>pratti</i>	11	9	4	–	–
		<i>Dendrobates</i>	<i>auratus</i>	8	19		LC	
		<i>Silverstoneia</i>	aff. <i>nubicola</i>	3	12	4	–	–
	Eleutherodactylidae	<i>Diasporus</i>	aff. <i>diastema</i> *	21			–	–
		<i>Diasporus</i>	<i>majeensis</i> **			1	–	E
	Hyllidae	<i>Agalychnis</i>	<i>callidryas</i>	L	4		LC	
		<i>Dendropsophus</i>	<i>microcephalus</i>	10			LC	
		<i>Boana</i>	<i>rosenbergi</i>	4			LC	
		<i>Scinax</i>	<i>rostratus</i>	2			LC	
<i>Scinax</i>		<i>ruber</i>	3			LC		
<i>Smilisca</i>		<i>phaeota</i>	6			LC		
<i>Smilisca</i>		<i>sila</i>		12		LC		
Leptodactylidae	<i>Engystomops</i>	<i>pustulosus</i>	13	1		LC		
	<i>Leptodactylus</i>	<i>fragilis</i>	3			LC		
	<i>Leptodactylus</i>	<i>savagei</i>	1	V		LC		
Caudata	Plethodontidae	<i>Oedipina</i>	<i>complex</i>			1	LC	
Gymnophiona	Caeciliidae	<i>Caecilia</i>	<i>isthmica</i>		1		DD	E
3	10	22	38	130	99	166		

* This species refers to the *Diasporus* aff. *diastema* from the Serranía de Majé as suggested by Batista et al. (2016).

** Described by Batista et al. (2016), only known from Panamá; therefore, considered endemic to CA.

Table 2. Total number of post-metamorphic individuals and species per site, and the site-level estimated richness as a function of the 95% confidence intervals (CI) calculated by the function Mao Tao.

Site	Number of Individuals	Number of species observed (Sobs)	Expected 95% CI upper limit
Lowland	130	22	24.64
Mid-elevation	99	19	25.58
Highland	166	12	16.57
All sites	395	37	44.08

The greatest number of species was found at the lowland site (24 spp., Table 2; individuals catch per unit of search effort: 1.04), where the search effort was the highest, and where multiple aquatic habitats were available (i.e. ponds and forest streams). The most abundant species at this site were *Diasporus* aff. *diastema* (sensu Batista et al. 2016), *Craugastor raniformis* and *Engystomops pustulosus* (Table 1). *Espadarana prosoblepon* and *Agalychnis callidryas* were detected at this site with larval surveys. The mid-elevation site had fewer species than the lowland site (22 spp., Table 2; individuals catch per unit of search effort: 1.03); however, despite lower search effort at this site, the upper 95% confidence intervals of the Mao Tau function estimated very similar species number (i.e., 25 spp. at the lowland site and 26 spp. at the mid-elevation site). The most abundant species at the mid-elevation site were *Dendrobates auratus*, *Silverstoneia* aff. *nubicola* and *Smilisca sila* (Table 1). In addition, at this site two species were detected only by their vocalizations: *Pristimantis taeniatus* and *Leptodactylus savagei*. The lowest richness was observed at the highland site (13 spp., Table 2; frog catch per unit of search effort: 2.81), because of limited searching effort, fewer habitats, and the lower diversity of the upland area. The estimated number of species for this site based on the upper 95% confidence intervals of the Mao Tau function was 17 spp., and the most abundant species at this site were *Rhaebo haematiticus*, *Pristimantis caryophyllaceus*, *P. cruentus*, and *P. moro* (Table 1). Moreover, the glassfrog, *Espadarana prosoblepon*, was detected at this site only by its vocalization.

The individual-based rarefaction curves for the total area surveyed (Figure 2A) and at the site level (Figure 2B) showed a substantial decrease in the slope as the number of individuals increased with search effort. Thus, while the upper 95% confidence interval of the Mao Tau function suggests that not all species present in the area were observed, the amphibian community determined in these surveys might be representative of the extant community in Serranía de Majé.

Based on the Jaccard dissimilarity coefficients calculated, the community composition was more similar between the low and mid-elevation sites relative to the high elevation site (Table 3, Figure 3). As expected, the sites that most differed were the low versus high elevation sites. However, six species were consistently present across all three elevation sites: *Rhinella alata*, *Espadarana prosoblepon*, *Craugastor crassidigitus*, *Colostethus* aff. *pratti*, and *Silverstoneia* aff. *nubicola*.

Table 3. Number of species shared between pairs of sites along an elevational transect of the Serranía de Majé (below the diagonal); total number of species per site including the species registered by post-metamorphic stages, vocalization, or larval stage (**diagonal**); and Jaccard similarity coefficients (1 - dissimilarity estimate) for each pair of sites (*above the diagonal*).

	Lowland	Mid-elevation	Highland
Lowland	24	0.32	0.13
Mid-elevation	13	22	0.24
Highland	5	7	13

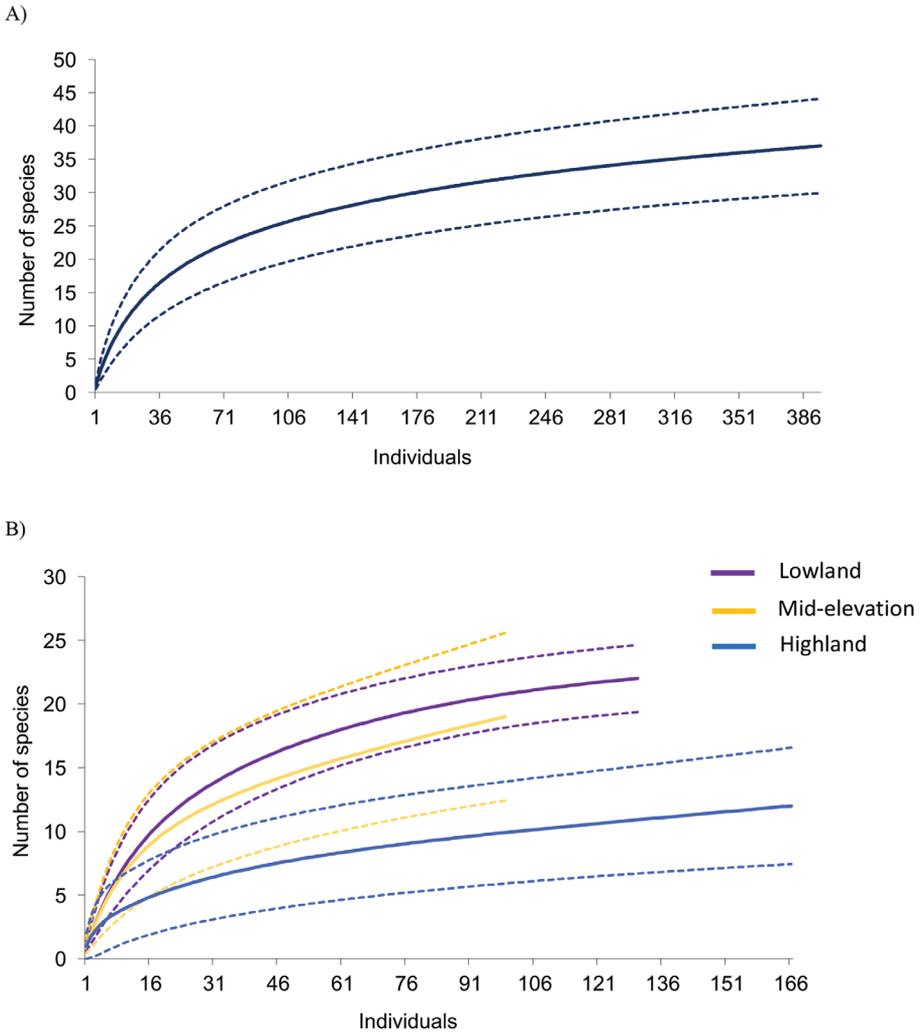


Figure 2. Individual-based rarefaction curves showing the estimated richness as a function of the upper 95% confidence interval (CI) calculated by the function Mao Tao. **A** Rarefaction curve combining all data obtained for the Serranía de Majé transect **B** rarefaction curves for low (120 – 150 m), intermediate (797 m), and high elevation (1,240–1,365 m) survey sites.

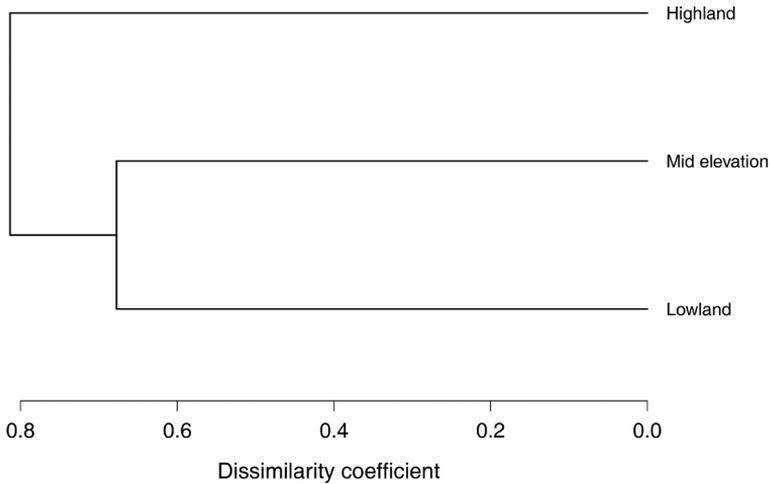


Figure 3. Site-level dendrogram based on Jaccard dissimilarities and built with the unweighted pair-group method based on arithmetic averages (UPGMA). This analysis was based on all post-metamorphic amphibians captured at each site.

Discussion

The present study represents the first attempt to characterize the composition and altitudinal diversity pattern of the amphibian community from the isolated Serranía de Majé of eastern Panamá. We determined that the composition of the species community across the altitudinal gradient was comprised by species from both Mesoamerican and South American groups, and that taxonomic genera from South America dominated the composition of the community (South American genera: 82%; Mesoamerican genera: 18%). In addition, the observed proportion in the composition of genera is consistent with the diversity pattern determined by Savage (2002) for eastern Panamá, where genera from South American groups represented over 50% of the genera comprising the amphibian assemblage.

The species found during this study represent 17% of the native amphibian species of Panamá (AmphibiaWeb 2018). However, the estimated total number of species based on the rarefaction analysis suggests that the richness of the study area is slightly higher than what we observed. In addition, the recent discovery of two new amphibian species from the Serranía de Majé, *Bolitoglossa chucantiensis* and *Diasporus majeensis* (see Batista et al. 2014b, 2016), suggest that this region might be high in endemism, as previously suggested for eastern Panamá (Crawford et al. 2010a).

Amphibians, occurring in Central America, have their highest species richness at intermediate elevations (Savage 2002, Wiens et al. 2006, Whitfield et al. 2016). This general altitudinal diversity pattern might also apply to the Serranía de Majé considering that, despite the relatively lower search effort and lower number of individuals encountered at the mid-elevation site, we observed and estimated a species richness simi-

lar to that of the lowland site (i.e., site with the highest observed richness). In addition, we determined similar estimates of individuals catch per unit of search effort (lowland site: 1.04 vs. mid-elevation site:1.03) between the lowland and mid-elevation sites. Hence, these results suggest that an increase in sampling effort at the mid-elevation site will potentially increase the number of species detected. Lastly, the observed altitudinal pattern of species richness could have been influenced by the variation across sites in the area covered during the surveys and the habitat types present at the sampling sites. In particular, the number of observed species at the highland site was potentially affected by the absence of streams and ponds, and the reduced patch size of the cloud forest.

In terms of β diversity, the higher similarity in the community composition between the mid-elevation and highland sites compared to that between the lowland and highland sites, suggests that the composition at intermediate elevations in Serranía de Majé might result, in part, by an overlap in the altitudinal distribution of the species associated with higher and lower altitudes; a pattern previously observed for the anuran communities from the Panamá Canal watershed (Ibáñez et al. 2002). In addition, despite the mid-elevation and highland sites being closer to each other (i.e., ~2 km apart) than to the lowland site, the community composition between the mid-elevation and highland sites was less similar than the composition between the mid-elevation and lowland sites. The higher similarity in the community composition between the mid-elevation and lowland sites compared to that with the highland site suggests that the highland site might be comprised by species with restricted altitudinal distributions. For instance, the dissimilarity associated with the highland site in our study was potentially influenced by the observation of species with restricted altitudinal ranges, such as: *Pristimantis* aff. *latidiscus*, *P. caryophyllaceus*, *P. moro*, *P. pardalis* and *Diasporus majeensis*.

The Serranía de Majé is isolated from the other mountain ranges in the region by the valleys of the Chepo and Chucunaque Rivers (Figure 1), which could have represented physical barriers leading to genetic isolation of populations that could have resulted in allopatric speciation (Cadena et al. 2011). Preliminary results from a comparison between the amphibian communities from the Serranía de Majé and Serranía de Piedras-Pacora (Ibáñez et al. 1994, Sosa and Guerrel 2013), located across the valley of the Chepo River (Figure 1), showed a lower species diversity at the Serranía de Majé and a decrease in the similarity of species composition as elevation increases (Figure 4). In addition, the highest elevations studied at these two mountain ranges are about 106 km apart (airline distance), and their dissimilarity is largely due to the disproportionate number of species that are present in Serranía de Piedras-Pacora but potentially absent in Serranía de Majé. Hence, thus far, seems that dispersal limitation has potentially played a major role in shaping the amphibian community at Serranía de Majé; nonetheless, more studies would be necessary to address this. Lastly, the decrease in similarity in species composition as elevation increases is consistent with the general pattern of amphibians endemism observed in Central America, that shows that a substantial portion of endemic species in the region are associated with upland regions (Whitfield et al. 2016).

Central America, while being a hotspot for amphibian diversity, is a region with a high proportion of threatened amphibian species. For instance, 41% of the regional

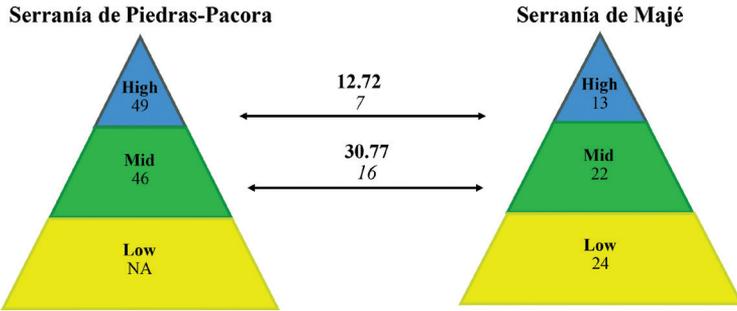


Figure 4. Diagram showing a decrease with elevation in the similarities of amphibian species assemblages associated with sites from the Serranía de Piedras-Pacora mountain range and the isolated Serranía de Majé mountain range. The numbers represent the shared species between sites (N), Jaccard similarity coefficients (N) and total number of species at the site level (N). Each color represents an elevation category, where the lowlands (< 400 m) are represented in yellow, mid-elevation sites (400–800 m) in green, and highlands (> 800 m) in blue. NA = no data available.

pool of species that have been assessed by the IUCN (International Union for Conservation of Nature) are under one of the following categories of the Red List of Threatened Species: critically endangered, endangered or vulnerable (reviewed in Whitfield et al. 2016). Within this context, the amphibian community of the Serranía de Majé does not seem, at first, to be comprised of species of high conservation concern given that 76% of the species registered in this study are under the category ‘least concern’ of the IUCN Red List of Threatened Species (IUCN 2018). However, the Serranía de Majé harbors amphibian species that could be regarded as threatened species, as well as poorly known species lacking an evaluation of their conservation status. For example, based on the IUCN criteria, two of the recorded species are considered near threatened (i.e., *Pristimantis caryophyllaceus* and *P. pardalis*), and two others are data deficient (i.e., *Caecilia isthmica*, and *Hyalinobatrachium vireovittatum*). Importantly, these two species that are considered near threatened and the two data deficient ones are endemic to Central America (Johnson et al. 2015). Notably, in this study we also found four species, which include one species from the genus *Pristimantis* (*P. aff. latidiscus*), two dendrobatids (*Colostethus aff. pratti* and *Silerstoneia aff. nubicola*) and one species from the *Diasporus diastema* species group (i.e., *Diasporus aff. diastema* suggested by Batista et al. 2016), that are potential new species and, together with the recently described *Diasporus majeensis*, lack an assessment by the IUCN.

Our survey provides baseline information for exploration and conservation efforts by identifying species in the area requiring immediate assessment and conservation action (Table 1). Importantly, this study might also inform the delimitation of protected areas based on species with restricted distribution ranges. This is particularly relevant given the absence of biological reserves within this mountain range that are recognized by the national system of protected areas (Jaramillo et al. 2010), and the increasing deforestation pressure in the region (Parker et al. 2004). Lastly, considering the arrival of *Bd* to the Serranía de Majé some years after this study (Küng et al. 2014), the

baseline information provided by this inventory could potentially serve to determine *Bd*-induced changes in the amphibian community. In particular, at mid and high elevations, where disease-induced losses of amphibian diversity have been substantial in Central America, including Panamá (Lips 2016).

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References

- AmphibiaWeb (2018) AmphibiaWeb. University of California, Berkeley. <http://amphibiaweb.org> [Accessed 17 September 2018]
- Angher GR, Christian DG (2000) Distributional records from the highlands of the Serranía de Majé, an isolated mountain range in eastern Panamá. *Bulletin-British Ornithologists Club* 120: 173–178.
- Batista A, Hertz A, Mebert K, Köhler G, Lotzkat S, Ponce M, Vesely M (2014a) Two new fringe-limbed frogs of the genus *Ecnomiophyla* (Anura: Hylidae) from Panamá. *Zootaxa* 3826: 449–25. <https://doi.org/10.11646/zootaxa.3826.3.2>
- Batista A, Köhler G, Mebert K, Vesely M (2014b) A new species of *Bolitoglossa* (Amphibia: Plethodontidae) from eastern Panamá, with comments on other species of the *adspersa* species group from eastern Panamá. *Mesoamerican Herpetology* 1: 97–121. <https://doi.org/10.11646/zootaxa.4039.1.2>
- Batista A, Köhler G, Mebert K, Hertz A, Vesely M (2016) An integrative approach to reveal speciation and species richness in the genus *Diasporus* (Amphibia: Anura: Eleutherodactylidae) in eastern Panamá. *Zoological Journal of the Linnean Society* 178: 267–311. <https://doi.org/10.1111/zoj.12411>
- Cadena CD, Kozak KH, Gomez JP, Parra JL, McCain CM, Bowie RCK, Carnaval AC, Moritz C, Rahbek C, Roberts TE, Sanders NJ, Schneider ChJ, VanDerWal J, Zamudio KR, Graham CH (2011) Latitude, elevational climatic zonation and speciation in New World vertebrates. *Proceedings of the Royal Society B: Biological Sciences* 279: 194–201. <https://doi.org/10.1098/rspb.2011.0720>

- Colwell RK, Mao CX, Chang J (2004) Interpolating, extrapolating, and comparing incidence-based species accumulation curves. *Ecology* 85(10): 2717–2727. <https://doi.org/10.1890/03-0557>
- Colwell RK (2006) EstimateS: Statistical Estimation of Species Richness and Shared Species from Samples (Software and User's Guide), Version 8.0. <http://viceroy.eeb.uconn.edu/estimates>
- Crawford AJ, Ryan MJ, Jaramillo CA (2010a) A new species of *Pristimantis* (Anura: Strabomantidae) from the Pacific Coast of the Darien Province, Panamá, with a molecular analysis of its phylogenetic position. *Herpetologica* 66: 192–206. <https://doi.org/10.1655/09-018R1.1>
- Crawford AJ, Lips KR, Bermingham E (2010b) Epidemic disease decimates amphibian abundance, species diversity, and evolutionary history in the highlands of Central Panamá. *Proceedings of the National Academy of Sciences USA* 107: 13777–13782. <https://doi.org/10.1073/pnas.0914115107>
- Duque-Caro H (1990) The Choco Block in the northwestern corner of South America: structural, tectonostratigraphic, and paleogeographic implications. *Journal of South American Earth Sciences* 3: 71–84. [https://doi.org/10.1016/0895-9811\(90\)90019-W](https://doi.org/10.1016/0895-9811(90)90019-W)
- Holdridge LR (1967) Life Zone Ecology. Tropical Science Center, San Jose, 206 pp.
- Hortal J, Borges PAV, Gaspar C (2006) Evaluating the performance of species richness estimators: sensitivity to simple grain size. *Journal of Animal Ecology* 75: 274–287. <https://doi.org/10.1111/j.1365-2656.2006.01048.x>
- Ibáñez R, Arosemena FA, Solís FA, Jaramillo CA (1994) Anfibios y reptiles de la Serranía Piedras-Pacora, Parque Nacional Chagres. *Scientia* 9: 17–31.
- Ibáñez R, Rand AS, Jaramillo CA (1999a) Los Anfibios del Monumento Natural Barro Colorado, Parque Nacional Soberanía y Areas Adyacentes / The Amphibians of Barro Colorado Nature Monument, Soberanía National Park and Adjacent Areas. Editorial Mizrachi & Pujol, Panamá, 187 pp. [https://doi.org/10.1643/0045-8511\(2000\)000\[0628:br\]2.0.co;2](https://doi.org/10.1643/0045-8511(2000)000[0628:br]2.0.co;2)
- Ibáñez R, Rand AS, Ryan MJ, Jaramillo CA (1999b) Vocalizaciones de Ranas y Sapos del Monumento Natural Barro Colorado, Parque Nacional Soberanía y Areas Aledañas / Vocalizations of Frogs and Toads from Barro Colorado Nature Monument, Soberanía National Park and Adjacent Areas. Compact Disc. Sony Music Entertainment, Costa Rica. [https://doi.org/10.1643/0045-8511\(2000\)000\[0628:br\]2.0.co;2](https://doi.org/10.1643/0045-8511(2000)000[0628:br]2.0.co;2)
- Ibáñez R, Condit R, Angehr G, Aguilar S, García T, Martínez R, Sanjur A, Stallard R, Wright SJ, Rand AS, Heckadon S (2002) An ecosystem report on the Panama Canal: monitoring the status of the forest communities and the watershed. *Environmental Monitoring and Assessment* 80: 65–95. <https://doi.org/10.1023/a:1020378926399>
- Ibáñez R, Crawford AJ (2004) A new species of *Eleutherodactylus* (Anura: Leptodactylidae) from the Darién Province, Panamá. *Journal of Herpetology* 38: 240–243. <https://doi.org/10.1670/12-03A>
- IGNTG (Instituto Geográfico Nacional “Tommy Guardia”) (2007) Atlas Nacional de la República de Panamá. Novo Art, Panamá, 290 pp.
- James TY, Toledo LF, Rödder D, Leite DS, Belasen AM, Betancourt-Román CM, Jenkinson TS, Lambertini C, Longo AV, Ruggeri J, Collins JP, Burrowes PA, Lips KR, Zamudio KR, Longcore JE (2015) Disentangling host, pathogen, and environmental determinants of a recently emerged wildlife disease: lessons from the first 15 years of amphibian chytridiomycosis research. *Ecology and Evolution* 5: 4079–4097. <https://doi.org/10.1002/ece3.1672>

- Jaramillo CA, Wilson LD, Ibáñez R, Jaramillo F (2010) The herpetofauna of Panamá: Distribution and conservation status. In: Wilson LD, Twonson JH, Johnson JD (Eds) Conservation of Mesoeamerican Amphibians and Reptiles. Eagle Mountain Press, Eagle Mountain, Utah, 604–671.
- Johnson JD, Mata-Silva V, Wilson LD (2015) A conservation reassessment of the Central American based on the EVS measure. *Amphibian & Reptile Conservation* 9: 1–94.
- Kilburn VL, Ibáñez R, Sanjur O, Bermingham E, Suraci JP, Green DM (2011) Ubiquity of the pathogenic chytrid fungus, *Batrachochytrium dendrobatidis*, in anuran communities in Panamá. *EcoHealth* 7: 537–548. <https://doi.org/10.1007/s10393-010-0634-1>
- Kozak KH, Wiens JJ (2010) Niche conservatism drives elevational diversity patterns in Appalachian salamanders. *The American Naturalist* 176: 40–54. <https://doi.org/10.1086/653031>
- Küng D, Bigler L, Davis LR, Gratwicke B, Griffith E, Woodhams DC (2014) Stability of microbiota facilitated by host immune regulation: informing probiotic strategies to manage amphibian disease. *PLoS One* 9(1): e87101–11. <https://doi.org/10.1371/journal.pone.0087101>
- Lips KR (1999) Mass mortality and population declines of anurans at an upland site in western Panamá. *Conservation Biology* 13: 117–125. <https://doi.org/10.1046/j.1523-1739.1999.97185.x>
- Lips KR, Brem F, Brenes R, Reeve JD, Alford RA, Voyles J, Carey C, Livo L, Pessier AP, Collins JP (2006) Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proceedings of the National Academy of Sciences* 103: 3165–3170. <https://doi.org/10.1046/j.1523-1739.1999.97185.x>
- Lips KR (2016) Overview of chytrid emergence and impacts on amphibians. *Philosophical Transactions of the Royal Society B* 317: 20150465. <https://doi.org/10.1098/rstb.2015.0465>
- Mittermeier RA, Myers N, Gil PR, Mittermeier CG (1999) Hotspots. CEMEX, Mexico City.
- Myers CW (1969) The ecological geography of cloud forest in Panamá. *American Museum Novitates* 2396: 1–52.
- Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2017) vegan: Community Ecology Package. R package version 2.4–3. <https://CRAN.R-project.org/package=vegan>
- Parker T, Carrion J, Samudio R (2004) Environment, biodiversity, water, and tropical forest conservation, protection, and management in Panamá: assessment and recommendations (biodiversity and tropical forestry assessment of the USAID/PANAMÁ Program). Washington, PA: Chemonics International Inc. Task Order# 824, BIOFOR IQC No. I-00-99-00014-00.
- Pinto-Sánchez NR, Ibáñez R, Madrián S, Sanjur OI, Bermingham E, Crawford AJ (2012) The Great American Biotic Interchange in frogs: multiple and early colonization of Central America by the South American genus *Pristimantis* (Anura: Craugastoridae). *Molecular Phylogenetics and Evolution* 62: 954–972. <https://doi.org/10.1016/j.ympev.2011.11.022>
- R Core Team (2017) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <https://www.R-project.org/>
- Rebollar EA, Hughey MC, Harris RN, Domangue RJ, Medina D, Ibáñez R, Belden LK (2014) The lethal fungus *Batrachochytrium dendrobatidis* is present in lowland tropical forests of far eastern Panamá. *PLoS ONE* 9: e95484–8. <https://doi.org/10.1371/journal.pone.0095484>
- Rodríguez-Brenes S, Rodríguez D, Ibáñez R, Ryan MJ (2016) Spread of amphibian chytrid fungus across lowland populations of Túngara frogs in Panamá. *PLoS ONE* 11: e0155745–8. <https://doi.org/10.1371/journal.pone.0155745>

- Rueda JV, Castro F, Cortez C (2006) Técnicas para el inventario y muestreo de anfibios: Una compilación. In: Angulo A, Rueda-Almonacid JV, Rodríguez-Mahecha JV, La Marca E (Eds) Técnicas de Inventario y Monitoreo para los Anfibios de la Región Tropical Andina. Conservación Internacional. Serie Manuales de Campo N°2. Panamericana Formas e Impresos SA, Bogotá, 135–171. <https://doi.org/10.5479/10088/31959>
- Savage JM (2002) The Amphibians and Reptiles of Costa Rica: a Herpetofauna between Two Continents, between Two Seas. University of Chicago Press, Chicago, 934 pp. <https://doi.org/10.1080/10635150490424619>
- Seutin G, White WN, Boag PT (1991) Preservation of avian blood and tissue samples for DNA analyses. *Canadian Journal of Zoology* 69: 82–90. <https://doi.org/10.1139/z91-013>
- Sosa A, Guerrel J (2013) Riqueza, diversidad, y abundancia de anfibios en el bosque nuboso de Cerro Azul, sector Alto Chagres, Parque Nacional Chagres, Panamá. *Tecnociencia* 15: 57–75.
- The IUCN Red List of Threatened Species (2018) Version 2018-1. www.iucnredlist.org [Downloaded on 23 September 2018]
- Vanzolini PE, Heyer WR (1985) The american herpetofauna and the interchange. In: Stehli FG, Webb SD (Eds) The Great American Biotic Interchange. Plenum Press, New York, 475–487. https://doi.org/10.1007/978-1-4684-9181-4_18
- Webb DS (2006) The Great American Biotic Interchange: patterns and processes. *Annals of the Missouri Botanical Garden* 93: 245–257. [https://doi.org/10.3417/00266493\(2006\)93\[245:tgabip\]2.0.co;2](https://doi.org/10.3417/00266493(2006)93[245:tgabip]2.0.co;2)
- Whitfield SM, Lips KR, Donnelly MA (2016) Amphibian decline and conservation in Central America. *Copeia* 104: 351–379. <https://doi.org/10.1643/CH-15-300>
- Wiens JJ, Graham CH, Moen DS, Smith SA, Reeder TW (2006) Evolutionary and ecological causes of the latitudinal diversity gradient in hylid frogs: treefrog trees unearth the roots of high tropical diversity. *The American Naturalist* 168: 579–596. <https://doi.org/10.2307/3873455>

Supplementary material I

Table S1. List of voucher specimens collected at the three surveyed sites along the altitudinal gradient in the Serranía de Majé

Authors: Daniel Medina, Roberto Ibáñez, Karen R. Lips, Andrew J. Crawford

Data type: specimen list.

Explanation note: The list includes taxonomy of voucher specimens and collection number, date and locality data. CH = Collection of Herpetology, AJC = Andrew J. Crawford field tag, and MVUP = Museo de Vertebrados de la Universidad de Panamá.

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