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Original Contribution

Niche Contraction of an Endangered Frog Driven by the Amphibian Chytrid Fungus

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Abstract: Introduced pathogens can alter the geographic distribution of susceptible host species. For example, *Batrachochytrium dendrobatidis* (Bd) is a fungal pathogen that has been linked to the global decline and extinction of numerous amphibian species during the last four decades. A growing number of studies have described the distribution of Bd and susceptible hosts across the globe; however, knowledge on how Bd may shape the climatic niche of susceptible species is still missing. We estimated the effect of Bd on the geographic distribution and niche dynamics of the critically endangered lowland robber frog (*Craugastor ranoides*) in Costa Rica. We found a reduction of 98% in the geographic range of this species by 1995, following the epizootic outbreaks of Bd that affected Costa Rica in the 1980 and early 1990s. We also quantified niche contraction and found that the species is currently restricted to dry and warm environments that have been considered unsuitable for Bd. Our results contribute to the understanding of how emerging pathogens shape the climatic niches and geographic distribution of susceptible species.

Keywords: Amphibian declines, *Batrachochytrium dendrobatidis*, Extinction, Host–pathogen dynamic, Niche-based modeling, Niche dynamic

INTRODUCTION

Global biodiversity is facing a mass extinction as human activities have contributed to population declines and pushed numerous species toward extinction (Wake and Vredenburg 2008; Barnosky et al. 2011). One major threat to many species globally is the introduction of pathogens (Butchart et al. 2010). Diseases caused by pathogens may severely impact the geographic distribution of susceptible host species (Minchella and Scott 1991; Daszak et al. 2000). Furthermore, interactions of introduced pathogens with other major drivers of extinction like climate change and land-use change might exacerbate the global extinction crisis (Hof et al. 2011). Currently, more studies are needed to understand the mechanisms by which pathogens shape

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the distribution and niche of susceptible host species (Soberón and Nakamura 2009; Ricklefs 2010; Wisz et al. 2013). Conducting studies of host–pathogen interactions in the context of geographic range and niche dynamics can help identify changes in the host species range, allowing researchers to propose more effective management for population recovery (Purvis et al. 2000; Scheele et al. 2017).

Recently, the concept of niche contraction has been considered to identify the mechanisms that cause a reduction in species' distribution (Soberón 2007; Holt 2009). The niche reduction hypothesis proposes mechanisms to explain how environmental conditions can regulate the distribution and impact of threats, causing the contraction of a species' realized niche to a subset of the environmental conditions occurring in its historical niche (Scheele et al. 2017). Although innovative, the niche reduction hypothesis does not consider all potential threats, for example, the role that interspecific competition plays in niche dynamics (Doherty and Driscoll 2018). Thus, new studies that quantify the impact of threats on niche contraction across heterogeneous environments are a crucial tool to apply and evaluate conservation strategies on susceptible species (McDonald et al. 2018).

Amphibians are an ideal system to study how pathogens shape a susceptible host's distribution and realized niche (Daszak et al. 2003; Bielby et al. 2008). At least 45% of all amphibian species have declined in population size or gone extinct during the last four decades (Monastersky 2014). Many of these declines have been linked to chytridiomycosis (Voyles et al. 2009), a deadly skin disease for some amphibian species caused by the fungal pathogen *Batrachochytrium dendrobatidis* (hereafter Bd; Longcore et al. 1999). Outbreaks of chytridiomycosis have caused mass mortalities of amphibians globally (Collins 2010; Catenazzi 2015) and represent one of the greatest documented loss of biodiversity attributable to a pathogen (Scheele et al. 2019a). Nevertheless, a host species' capacity to tolerate Bd may vary across a heterogeneous environment (Puschendorf et al. 2011; Zumbado-Ulate et al. 2019a), potentially resulting in niche contraction in regions where conditions are ideal for Bd growth (Puschendorf et al. 2011). Therefore, identifying niche contraction is key for understanding Bd-driven declines across the range of declined amphibian species and to be able to propose specific management strategies for amphibian populations (Scheele et al. 2019b).

In Central America, epizootic outbreaks of Bd during the 1980s and early 1990s caused numerous declines and local extinctions of amphibians (Puschendorf et al. 2006; Bolaños 2009; Zumbado-Ulate et al. 2019b). These Bd-driven epizootic declines mostly affected species that inhabited middle elevation environments (1000–2500 m) where moisture and temperature matched the optimal conditions for the occurrence of chytridiomycosis (Pounds et al. 2006). Recent rediscoveries of susceptible host species outside suitable environments for chytridiomycosis (i.e., refugia from disease) (Puschendorf et al. 2009; Chaves et al. 2014) suggest that these species suffered changes in their distribution and realized niches in response to chytridiomycosis outbreaks. Conducting retrospective studies that examine changes in the geographic distribution of susceptible species after deadly outbreaks (e.g., Zumbado-Ulate et al. 2019a) can illuminate how Bd shaped current geographic ranges and affected niche dynamics of susceptible host species (Hitchman et al. 2018; Miller et al. 2018).

In this work, we used available climatic information, robust datasets, and rigorous modeling techniques to quantify the effects of chytridiomycosis on the geographic distribution and climatic niche of a highly susceptible host species, the lowland robber frog (*Craugastor ranoides*). Because habitat suitability for Bd varies across a host's distribution, we predicted that the geographic range of the susceptible lowland robber frog would be restricted to unsuitable regions for the development of chytridiomycosis after the pathogen's introduction (Puschendorf et al. 2011). We also predicted that the host's climatic niche would contract, causing the centroid to move toward the environments less suitable for Bd infection (Scheele et al. 2017). This study sheds light on how Bd shapes realized niches and geographic distribution of host species (Scheele et al. 2019b). Our framework can be used by policy-makers to evaluate the risk of environmental threats and prioritize regions for conservation purposes (Mendelson et al. 2019; Scheele et al. 2019b).

METHODS

Study Species

The lowland robber frog (*C. ranoides*, Fig. 1) belongs to the *C. punctariolus* species series (Campbell and Savage 2000; Hedges et al. 2008), a clade that includes 34 stream-dwelling species distributed from Mexico to Panama (Savage 2002). Most species within this clade have catastrophically declined since the mid-1980s (Ryan et al. 2008).

Figure 1. Female individual of the lowland robber frog (*Craugastor ranoides*) in Santa Elena Peninsula, Guanacaste, Costa Rica. Photographed by Katherine González.

For example, the lowland robber frog had a wide distribution in lowlands and midlands of eastern Nicaragua, Costa Rica, and western Panama (Savage 2002) before epizootic outbreaks of Bd occurred across its distribution during the 1980s and 1990s. Currently, the lowland robber frog is only known to occur in the tropical dry forest on the Santa Elena Peninsula, in the Northwest Pacific of Costa Rica (Fig. 2) (Puschendorf et al. 2009; Zumbado-Ulate et al. 2011).

Occurrence Data

We gathered occurrence data for the lowland robber frog from three sources: (1) the herpetological database of the Museo de Zoología at Universidad de Costa Rica (UCR, http://museo.biologia.ucr.ac.cr/), (2) the Global Biodiversity Information Facility (GBIF, www.gbif.org) (Flemons et al. 2007), and 3) published literature (Puschendorf et al. 2009; Zumbado-Ulate et al. 2007). We constrained occurrences to the distribution polygon proposed for this species by the International Union of Conservation of Nature (IUCN) (IUCN 2019) to identify and remove geographical outliers to ensure the accuracy of the occurrence dataset (Rondinini

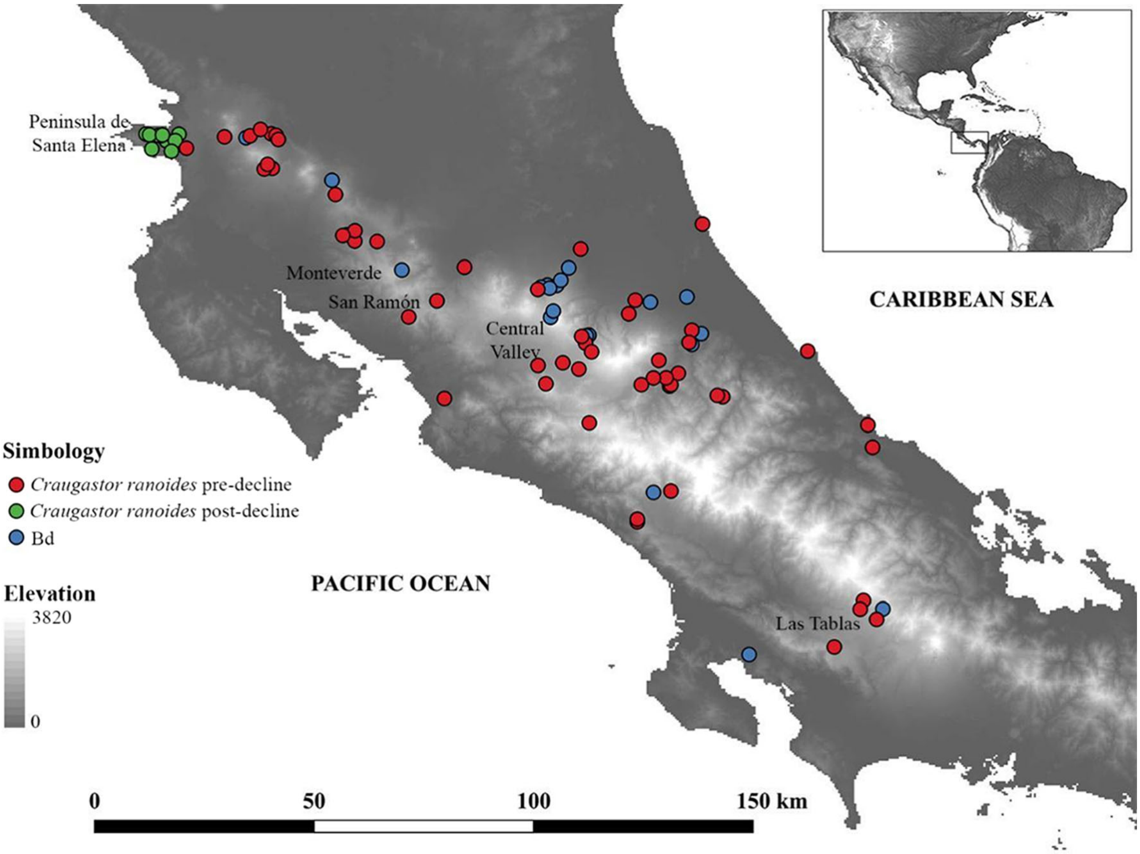

Figure 2. Historical and contemporary distribution of the lowland robber frog (*Craugastor ranoides*) and histology-confirmed cases of chytridiomycosis in Costa Rica. Records of *C. ranoides* and chytridiomycosis are color-coded. The map shows the name of localities where amphibian declines have been linked to chytridiomycosis.

et al. 2006). Occurrence records of the lowland robber frog were classified into (1) pre-decline (collected before 1995, hereafter "pre-decline") and (2) post-decline periods (collected from 1995 to date, hereafter "post-decline"). We set this chronologic boundary according to the wave-like dispersal hypothesis proposed for Bd across Central America (Lips et al. 2008). This hypothesis suggests that Bd was introduced in Costa Rica in the middle 1980s and moved southward, reaching Panama around 1995. Due to the rapid rate of spread that the pathogen exhibited in Central America, it is likely that Bd expanded its range across most of Costa Rica by 1995 (Whitfield et al. 2016).

For Bd, we used the histology-only dataset (Puschendorf et al. 2009) which comprises the localities where Bd was diagnosed through histological detection in Costa Rica during pre-decline times (which confirms chytridiomycosis, "hereafter epizootic Bd"). This dataset was used to produce the first suitability map for Bd in Costa Rica (Puschendorf et al. 2009) and includes all the histology-detection data available for the country. We did not consider other datasets where detection of Bd has been conducted with PCR techniques (e.g., Zumbado-Ulate et al. 2019a) because we limited our detection to localities where chytridiomycosis was diagnosed and the severity of damage on amphibian skin assessed.

To control for spatial autocorrelation, we considered points to be independent occurrences if the occurrence points were at a minimum distance of 1 km apart, which is the resolution of the climatic layers. Filtering was done using the R package "Ecospat" (Di Cola et al. 2017). We focused our study in Costa Rica because there is limited evidence that *C. ranoides* occurs elsewhere (Puschendorf et al. 2019).

Climatic Predictors

We downloaded all 19 bioclimatic variables of WorldClim (version 1.4; http://www.worldclim.org/bioclim) at a spatial resolution of 30 arc-s (Hijmans et al. 2005). Multicollinearity among variables is a common problem in multivariate analyses that can cause undesired effects, such as coefficient shifts, selection of insignificant variables, model overfitting and incorrect response curves (De Marco and Nóbrega 2018; Dormann et al. 2007; Sillero and Barbosa 2020). To avoid multicollinearity and reduce redundancy among variables, we retained only eight variables (Table S1). We used the function "*vifcor*" from the R package "usdm" (Naimi et al. 2014), to find the pairs of variables with a correlation coefficient greater than 0.8 and excluded the ones with the highest variance inflation factor (VIF). For data extraction and model construction, we calibrated all models to the extent of Costa Rica by cropping the bioclimatic layers with a defined bounding box (N 7.750–11.500, W 82.150–86.250).

Because the lowland robber frog is a stream breeding species, utilizing only climatic variables may overestimate the suitable area for this species because predictions do not adjust to fast-flowing streams. However, we decided to keep our predictions to all the study area because most of the geographic distribution of this species includes numerous fast-flowing rocky streams due to the extensive hydrographic network of Costa Rica (Fig. S2). Furthermore, robber frogs have been reported moving throughout the forests (Zumbado-Ulate et al. 2011). By limiting the predictions to streams, we risk excluding a relevant part of the habitat used by the species.

Species Distribution Models (SDMs)

We built SDMs for the lowland robber frog in two time-periods: pre-decline and post-decline. We also generated a SDM to predict the habitat suitability for epizootic Bd in Costa Rica. We calibrated the SDM using the maximum entropy algorithm (MaxEnt) (Phillips et al. 2006; Elith and Leathwick 2009). Our tuned SDMs were developed with "ENMeval" (Muscarella et al. 2014), a package that facilitates the construction and evaluation of MaxEnt-generated SDMs with tuned settings, therefore avoiding the selection of overfitted models. We generated 27 candidate models for each dataset using a combination of linear, quadratic, and hinge feature classes (L, Q, H), and regularization multipliers ranging from 1 to 5 (with increases of 0.5) (Fig. S1).

To account for small sample sizes, which can be a limitation for model building (Shcheglovitova and Anderson 2013), we used two methods for data partitioning according to the number of occurrences: "block" and n-1 "jackknife." The block method was used to model the pre-decline and the epizootic Bd dataset, whereas the "n-1 jackknife" for the post-decline dataset. The "Jackknife" method was used for the post-decline dataset because it can assess the predictive ability of SDMs using as few as five occurrences (Pearson et al. 2007). To select the most robust model, we used two metrics: (1) the average area under the receiver operation characteristic curve (AUCTEST) to evaluate environmental discrimination and (2) minimum training present omission rate (ORMTP) to evaluate overfitting (Muscarella et al. 2014).

The final (best) models were used for accessing species suitability across the landscape. We transformed all predictions into binary maps to estimate the reduction in the geographic area occupied by the lowland robber frog across Costa Rica. Binary maps were produced using a 10th percentile presence threshold (Radosavljevic and Anderson 2014). (Detailed methods are provided in supporting information.)

Niche Dynamics

We were interested in comparing the overlap in climatic niche space between (1) pre- and post-decline populations of the lowland robber frog and (2) the distribution of epizootic Bd with both pre-decline and post-decline populations of the lowland robber frog. We made these comparisons using ordination (PCA-env sensu Broennimann et al. 2012) and smoothed kernel density following to Broennimann et al. (2007, 2012) and Petitpierre et al. (2012).

We estimated niche overlaps between climatic niche spaces using the Schoener's *D* metric (Schoener 1968), assuming the smoothed density of occurrences as probability distributions defined over the multivariate climatic space (Broennimann et al. 2012). To determine whether climatic niches of one species (or population) changed relative to the other, we used the niche similarity test (Warren et al. 2008). Niche similarity assesses whether the climatic niche of one species (or population) is more (or less) similar than expected based on the environmental conditions present on the background of the other species (or population). We further explored niche dynamics of the lowland robber frog using three different metrics: unfilling, expansion, and stability. Unfilling represents the climatic space of the pre-decline population that was not occupied by the post-decline population. Stability describes the proportion of climatic niche shared by pre-decline and post-decline populations. Expansion indicates the climatic space of the post-decline populations that were not occupied by pre-decline populations. Niche analyses were performed in the "ecospat" package (Di Cola et al. 2017) in R. (Detailed methods are provided in supporting information.)

RESULTS

SDMs

Our SDM for the pre-decline distribution of the lowland robber frog (Fig. 3a) predicted a total area of 19,554.4 km^2 as suitable habitat for this species, corresponding to 37.53% of continental Costa Rica. The highest suitability values were predicted at intermediate elevations (500–1500 m), including the pre-montane and tropical forest of the Central Valley, Caribbean slope, and Southern Pacific. High suitability was also predicted in the lowlands ($<$ 500 m) in the Southern Pacific and the North Pacific coast. The SDM for the post-decline distribution predicted a suitable area of 441.3 km^2 (0.85% of continental Costa Rica), with populations restricted to the dry forest lowlands of the Pacific Northwest of Costa Rica (0–500 m; Fig. 3b). The area predicted as suitable for epizootic Bd in Costa Rica (Fig. 3c) closely matches the area predicted as suitable for the pre-decline population of the lowland robber frog. Conversely, the predicted suitability for epizootic Bd was low in the dry forest lowlands where remnant (post-decline) populations of the lowland robber frog occur (Fig. 3a, c).

Niche Dynamics

We found little overlap (*D* = 0.01) between the climatic conditions of the pre- and post-decline populations of the lowland robber frog, and this overlap was not different than what was expected by chance based on the niche similarity test (Table 1). A large proportion of the climatic space occupied by the pre-decline population of the lowland robber frog is no longer occupied by the post-decline distribution (unfilling = 0.99, Table 1). This contraction was followed by a change in the shape and position of the centroid in the environmental envelope of the lowland robber frog toward drier and warmer conditions (Fig. 4). Our results also show a potential expansion of the post-decline populations of the frog to new climates (expansion = 0.62, Table 1, Fig. 4).

We found a moderate overlap (*D* = 0.41) between the pre-decline climatic niches of the lowland robber frog and that of epizootic Bd (Fig. 5). The climatic niche of the epizootic Bd was highly similar to that of the pre-decline frog population based on the environmental conditions on background of pre-decline frog population (*p* = 0.04). However, the test performed in the opposite direction

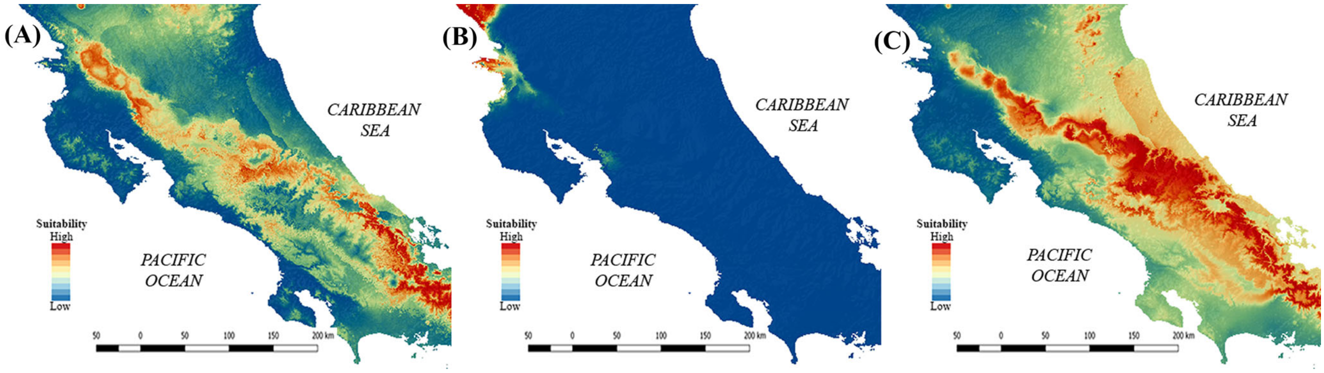

Figure 3. Species distribution models. **a** Predicted distribution (before 1995) and **b** Predicted post-decline distribution (1995 to date) of the lowland robber frog (*Craugastor ranoides*); **c** Predicted distribution of epizootic Bd based on histology-confirmed cases.

Table 1. Niche Dynamics of the Lowland Robber Frog *Craugastor ranoides* in Costa Rica During the Pre-decline and Post-decline Times (Before and After 1995) and Epizootic *Batrachochytrium dendrobatidis* (Bd).

Comparison	*D*	Unfilling	Stability	Expansion
Pre-decline *versus* post-decline	0.004 (0.83)	0.99	0.38	0.62
Post-decline *versus* pre-decline	0.004 (0.42)			
Pre-decline versus epizootic Bd	0.41 (0.04)	0.24	0.93	0.07
Epizootic Bd *versus* pre-decline	0.41 (0.08)			
Post-decline *versus* epizootic Bd	0 (1)	1	0	1
Epizootic Bd *versus* post-decline	0 (1)			

Niche similarity test (D) and three niche indexes are presented. Values between parentheses represent p-value of statistical tests.

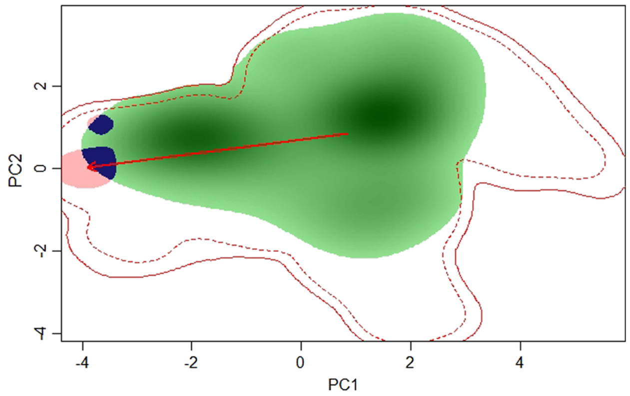

Figure 4. Climatic niche occupied by the lowland robber frog (*Craugastor ranoides*). Colored areas represent pre-decline distribution (before 1995, green); post-decline distribution (after 1995, pink); and overlapping space (blue). Arrows indicate the direction of the niche contraction. Continuous and dotted lines represent 100 and 50% of the total climatic conditions available in the region, respectively. The density of occurrences is shown by darker colors. Overlapping space is represented in blue (Color figure online).

delivered nonsignificant results (Table 1). Finally, we found no overlap ($D = 0$) between the post-decline climatic niches of the lowland robber frog and that of epizootic Bd. Together, these results suggest that during the time of epizootics, Bd occurred in an area containing climatic conditions only suitable for pre-decline populations.

Discussion

Our study shows that the geographic distribution of the lowland robber frog changed from 37.53 to 0.85% of continental Costa Rica from pre-decline to post-decline times, with remnants populations restricted to the dry forest lowlands of the Pacific Northwest. Our study suggests that the introduction of Bd may have driven a strong reduction (98%) in the geographical distribution of this species, resulting in a subsequent contraction of its original climatic niche (Figs. 3 and 4). This niche contraction was characterized by a change in shape and orientation of the niche centroid toward drier and warmer climate condi-

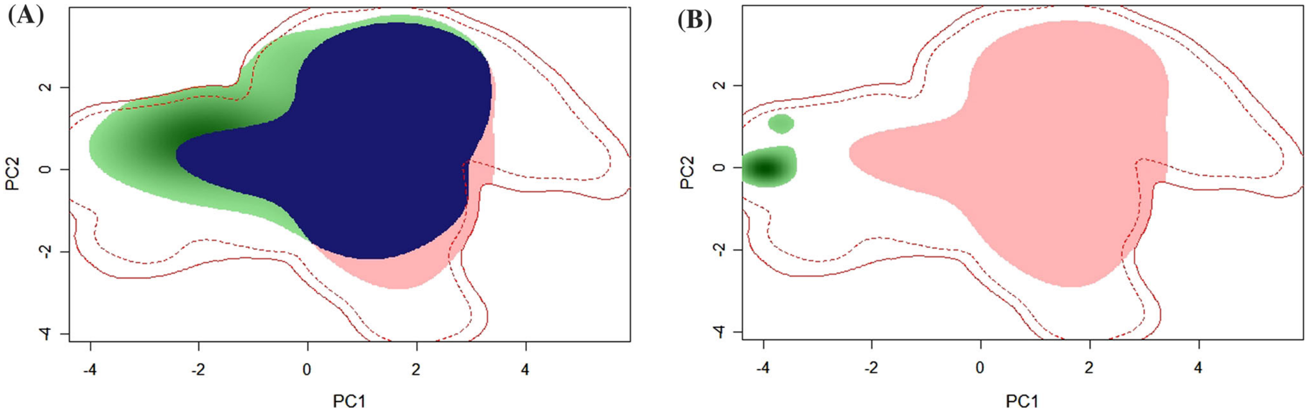

Figure 5. Climatic niches occupied by the lowland robber frog *Craugastor ranoides* (green) and epizootic Bd (pink) in Costa Rica, with overlap indicated in blue. **a** Pre-decline period (before 1995). **b** Post-decline period (1995 to date). Continuous and dotted lines represent 100 and 50% of the total climatic conditions available in the region, respectively. The density of occurrences is shown by darker colors. Overlapping space is represented in blue (Color figure online).

tions. Our findings suggest that the niche contraction experienced by the lowland robber frog spatially and temporally match the epizootic outbreaks of Bd that occurred in Costa Rica during the 1980s and 1990s (Pounds and Crump 1994; Lips et al. 2003; Bolaños 2009). To our knowledge, this is the first study that quantifies a niche contraction caused by Bd (but see Becerra-López et al. 2017).

Although our results suggest strong niche contraction, we also identified a signal that the post-decline population of the lowland robber frog experienced niche expansion, occupying climatic conditions that were previously not occupied by the pre-decline population. This may occur if, for example, individuals from neighboring Cordillera Volcánica de Guanacaste had migrated to Santa Elena Peninsula in response to epizootic outbreaks of Bd. However, considering the short period time for this migration (around 15 years) this expansion in unlikely. The occurrence of at least one pre-decline record of the lowland robber frog in the proximity of Santa Elena peninsula (Sasa and Solórzano 1995) suggests that this species may have already occurred in the Santa Elena Peninsula, but in low densities, which may indicate an area of low suitability or sink populations. Thus, our observed expansion may instead reflect scarce survey efforts in the Peninsula during the pre-decline period.

The niche contraction of the lowland robber frog pushed this species to the extremely dry and warm conditions of the tropical dry forest at the Santa Elena Peninsula (Janzen 1998). Although it has been suggested that the lowland robber frog is highly susceptible to Bd (Puschendorf et al. 2009), it is likely that the local environmental conditions in the tropical dry forest (average temperatures above 27 °C and mean annual precipitation below 1500 mm) may constrain Bd infection, allowing persistence of the remnant populations that inhabit the Santa Elena Peninsula (Zumbado-Ulate et al. 2011, 2014; Whitfield et al. 2017). The high habitat suitability we found for epizootic Bd in most of Costa Rica, which is congruent with previous studies (Pounds et al. 2006; Puschendorf et al. 2009), may explain the large niche contraction of the lowland robber frog in most of its distribution.

According to metapopulation models (Marsh and Trenham 2001; Griffiths et al. 2010; Heard et al. 2015), extinction risk becomes severe if remnant populations of the lowland robber frog consist of sink populations occurring at the marginal areas of the species' range, where conditions for existence are suboptimal compared to the ones at the historical core of a species' range (Lawton 1993; Vucetich and Waite 2003). Species experiencing range contractions have been found to exhibit reduced tolerance to other threats and loss of fitness and genetic diversity (Holt 2009; Burke 2012; Martínez-Freiría et al. 2016). However, remnant peripheral populations of the lowland robber frog may also represent sites of future speciation events (Puschendorf et al. 2019). Potential future speciation is supported by Savage (2002), who suggested that populations of the lowland robber frog in the tropical dry forest are potential subspecies or perhaps a new species within the *C. punctariolus* species series. Therefore, the conservation of peripheral populations supports the persistence of endangered species and may also protect evolutionary distinct subspecies and populations (Lesica and Allendorf 1995; Channell and Lomolino 2000).

CONCLUSION

Our study contributes to the growing knowledge of host–pathogen niche dynamics. By integrating ordination techniques and ecological niche modeling, we identified a contraction in both niche space and geographical distribution of an endangered species in response to epizootic outbreaks of Bd. Additional studies are necessary to track relict species (García-Rodríguez et al. 2012) and elucidate the mechanisms by which Bd shapes the niche and geographic distribution of susceptible amphibian species (Scheele et al. 2019a). However, this study indicates that pathogens can rapidly affect species distribution and push hosts species into "refuges from decline." Certainly, the niche contraction documented in our study could be a consequence of rapid adaptation to outbreaks of a deadly pathogen (Christie and Searle 2018), so we recommend evaluating the genetic diversity and population structure of these remnant populations (Thompson 1998; Altizer et al. 2003). Our approaches can be applied to other species in the *C. punctariolus* clade that seem to be restricted to small distributions in dry ecosystems such as *C. taurus* in Costa Rica or *C. azueroensis* in Panama (Köhler et al. 2012; Chaves et al. 2014). They will also be useful if applied to other taxa affected by pathogens such as bats affected by White-nose syndrome (Frick et al. 2010), birds affected by West Nile Virus (Komar et al. 2003), and snakes affected by the fungus *Ophidiomyces ophiodiicola* (Allender et al. 2015; Franklinos et al. 2017).

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DECLARATIONS

CONFLICT OF INTEREST The authors declare that they have no conflict of interest.

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