

Mapping the risk of North American arboreal amphibians to the fungal pathogen *Batrachochytrium dendrobatidis*

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ABSTRACT

Amphibian populations have been significantly impacted by the disease chytridiomycosis (chytrid), caused by the fungus *Batrachochytrium dendrobatidis* (*Bd*). The fungus undergoes an aquatic zoospore stage and therefore can be transmitted through water and is known to predominantly affect stream-dwelling species. But the fungus is spreading to arboreal habitats, and a growing number of species are impacted by chytrid. I compiled a list of arboreal and non-arboreal amphibian species in North America and recorded each species' history of *Bd* infection or known susceptibility. A habitat suitability model for *Bd* in North America predicts the potential distribution of the chytrid fungus. I provide an assessment of which species occupy the suitable areas presented by the model. I used the *Bd* suitability model to assess the difference between the risk of arboreal amphibians to contacting *Bd* compared to species that are not arboreal. I calculated the proportion of each species' range that overlaps with regions modeled as highly suitable for *Bd*, and compared the proportion overlap calculations of arboreal and non-arboreal species. I found no significant difference between the mean percentage overlap of arboreal species ranges with *Bd* and non-arboreal species range overlap with *Bd*, suggesting that species of both habits are at risk of contacting the fungus. I then analyzed whether this percentage of overlap is correlated with the species' known history of risk, and found no significant relationship, possibly due to limitations of data availability and lack of research. This study highlights the need for broader inquiry and into the effects chytridiomycosis will have to exposed amphibian species.

KEYWORDS

GIS, chytridiomycosis, spatial analysis, disease, suitability model, traits

INTRODUCTION

The disease chytridiomycosis has been linked to the decline or extinction of over 200 amphibian species on every continent where amphibians exist, leading to a significant loss of biodiversity worldwide (Skerratt et al. 2007, Fisher et al. 2009). Amphibians are of further concern because the high permeability of their skin makes them particularly sensitive to environmental toxins, making amphibian species indicators of pollution levels (Alford and Richards 1999). Individuals infected by the epidermal fungal colonies of chytridiomycosis, often die by cardiac arrest (Longcore et al. 1999, Voyles et al. 2009). This fungal cutaneous disease is caused by the fungus *Batrachochytrium dendrobatidis* (*Bd*) (Lips et al. 2003). However, susceptibility to death by the chytrid fungus is species-specific; although some species experience rapid die-offs, others are asymptomatic and can thus act as carriers (Gaertner et al. 2009, Searle et al. 2011).

The fungal pathogen *Bd* undergoes an aquatic zoospore stage and is thus transmitted through water (Johnson and Speare 2003). Although terrestrial and stream-dwelling species are commonly infected, arboreal species have also tested positive for the fungus (Rothermel et al. 2008). Some arboreal species breed in water, presenting a potential means of infection (Greenberg et al. 2017). However, species that do not rely on or live in close proximity to streams, like many arboreal species, may still be susceptible. *Bd*'s aquatic zoospores can survive in and be transmitted through rainfall, and *Bd* zoospores have been found in bromeliad water sources in Panama, a common microhabitat for arboreal amphibians (Cossel and Lindquist 2009, Kolby et al. 2015).

Although *Bd* has had the most significant impact on anuran populations, salamanders are also susceptible to the fungus (Gaertner et al. 2009, Cheng et al. 2011). Some salamanders, such as those in the *Plethodon* genus, have a skin microbiome that provides a defense against *Bd* (Muletz Wolz et al. 2017). Despite this apparent defense, species in this genus are nevertheless susceptible to death resulting from chytridiomycosis when exposed to *Bd* (Cheng et al. 2011). Further, a study testing 36 anuran species and 7 salamander species for chytridiomycosis found that 2 salamander species and 10 anuran species tested positive for the disease, and all species tested positive were in North America (Ouellet et al. 2005).

A habitat suitability model for *Bd* in Canada, Mexico, and the continental United States uses *Bd*'s known localities coupled with environmental tolerances and the presence of a host to predict the potential distribution of the chytrid fungus (Yap et al. 2018). The model particularly highlights the mountain ranges in the western half of the United States, and a majority of the eastern United States and Mexico as providing suitable habitat for *Bd*. However, there has not yet been an assessment of which species occupy the suitable areas presented by the model.

This study uses the *Bd* suitability model to assess the difference between the risk of arboreal amphibians to *Bd* compared to species that are not arboreal. To evaluate spatial risk, I determine the overlap of range maps of threatened frogs, toads, and salamanders with areas suitable for *Bd* in North America. I assess risk in terms of percentage overlap of the amphibian's range with *Bd*-suitable areas, and compare the average overlap of arboreal and non-arboreal species. I also weigh the known susceptibilities of each species. I analyzed the relationship between the records of the chytrid fungus for threatened amphibian species in North America and the proportion of the species' range that overlaps with areas suitable for *Bd*. This analysis of species ranges with respect to *Bd* distribution is necessary to assess potential risk of exposure to *Bd*.

METHODS

Species information collection

To compile a list of arboreal amphibians, I used different search terms to query the AmphibiaWeb database (AmphibiaWeb 2017). In AmphibiaWeb's "Search the Database" tab, I entered "arboreal" into the "Account Text" search bar to search through the database's species descriptions, then "tree frog" into the "Vernacular name" search bar to search for the arboreal anurans that are considered tree frogs. I collected each species' binomial, IUCN Red List code, the continent on which the species exists, and the species known history or risk of susceptibility to *Bd*. I searched the literature for each species' history of *Bd* infection and whether susceptibility is known.

To cross-reference my data, I searched "arboreal" in the search bar on AmphibiaWeb's left hand side, which ran a Google Custom Search of the database, and added any species that were

missing from my original searches that also exhibit arboreality. To further ensure completion, I searched AmphibiaWeb for North American species using the “Search the Database” tab’s “Countries” option. I selected Canada, United States, and Mexico, left all other fields blank, and searched through all 644 resulting species accounts for evidence of arboreality. I added species that were missing from my original searches. All other species are considered to be non-arboreal for the purpose of this analysis.

Species range map collection

I used the range maps from AmphibiaWeb and IUCN Red List (AmphibiaWeb, The IUCN Red List of Threatened Species). I created separate shapefiles for arboreal and non-arboreal species based on the species information I collected. I then queried each of these two shapefiles to only include the species categorized as “Vulnerable,” “Endangered,” or “Critically Endangered” by IUCN standards and exported shapefiles for threatened arboreal species and threatened non-arboreal species (The IUCN Red List of Threatened Species). I used ArcMap’s “Dissolve (Data Management)” tool for all layers to ensure that each species range was regarded as a single polygon. I projected each layer using AcrMap’s “Project (Data Management)” tool with Albers Equal Area Conic projection as the output coordinate system.

Quantifying overlap

I added the *Bd* suitability model to the ArcMap document (Yap et al. 2018). The Maxent model is a 32-bit floating point raster and does not have an attribute table. To obtain a shapefile of areas deemed highly suitable for *Bd*, I used ArcGIS’s “Reclassify (Spatial Analyst)” tool using the classifications used by Yap et al (2018) to obtain a raster with three classes of *Bd* suitability. I used the “Raster to Polygon (Conversion)” tool to convert this raster to a shapefile for analysis. I extracted from this shapefile the polygons of areas highly suitable for *Bd*. I projected this layer using AcrMap’s “Project (Data Management)” tool with Albers Equal Area Conic projection as the output coordinate system. I used the “Tabulate Intersection (Analysis)” tool to quantify the overlap between amphibian species ranges and *Bd*-

suitable areas and obtain a .dbf table that includes the area of intersection and percentage of intersection.

Comparing overlap of arboreal and non-arboreal species

I imported this .dbf file as a .csv into R and ran a Welch's two-sample t-test to compare the mean percentage overlap calculations between arboreal and non-arboreal species (R Development Core Team 2014).

Relationship between percentage overlap and chytrid history

From the information I collected about each species' known history with or susceptibility to *Bd*, I ranked each species on a scale of 1-5 with the following key: 1= No information about chytrid or *Bd* history or susceptibility, 2= the species was tested negative for *Bd*, 3= the species is suspected to be susceptible to die-offs, 4= the species has been tested positive for *Bd*, 5= the species is known to have experienced *Bd*-related die-offs. I considered each species with a ranking of 3, 4, or 5 to be *Bd* positive, and species with ranks 1 or 2 to be *Bd* negative for the purposes of this analysis. I performed a logistic regression in R to analyze the relationship between whether the species is *Bd* positive or negative and the percentage of its range that intersects with *Bd*-suitable areas.

RESULTS

Species Information and Ranges

North America has 331 salamander and anuran species. Two hundred and eighteen of North America's amphibians are not arboreal. One hundred and thirteen arboreal amphibians are present in North America: 30 salamanders and 83 anurans. Forty-three arboreal species are categorized as Critically Endangered or Endangered according to IUCN Red List Categories (International Union for the Conservation of Nature and Natural Resources, 2000).

Comparisons of known chytrid susceptibility from literature searches showed relatively few differences between arboreal and non-arboreal species. When normalized by the number of

species in each group, there is a higher rate of non-arboreal species that have little information available about their history with the chytrid fungus as compared to arboreal species. A higher proportion of arboreal species have been tested negative for *Bd* than non-arboreal species. Roughly equal amounts of arboreal and non-arboreal species have experienced *Bd*-related die-offs (Table 1). Appendix A summarizes the chytrid rank for each species.

Table 1. Rates of *Bd* History Among Threatened Amphibians. The known history or susceptibility to the chytrid fungus for arboreal and non-arboreal species normalized by the number of species in each category of arboreal or non-arboreal. “Total Species” includes only threatened species with some portion of their range intersecting with regions suitable for *Bd*. The rates for each category are calculated by dividing the number of species in each chytrid rank (see Appendix 1) by the “Total Species.”

	No information about Chytrid	Tested Negative	Suspected Susceptibility	Tested positive for <i>Bd</i> or Suspected to be Susceptible	Experienced <i>Bd</i> -related Die-offs	Total Species
Non-Arboreal	0.60	0.06	0.14	0.15	0.040	174
Arboreal	0.39	0.25	0.20	0.12	0.045	44

Quantifying Overlap

Based on the range maps for these species, threatened non-arboreal amphibian ranges are in the eastern and western regions of North America (Figure 1a). All arboreal species with these classifications are located in Mexico, with a concentration in the country’s southern and eastern regions (Figure 1b). The mean range size of species with greater than 95% range overlap with *Bd*-suitable regions is approximately 337 km², while the mean range size of species with less than 5% range overlap is 21,611 km², and the mean range size of all amphibians in this study is 10,631 km².

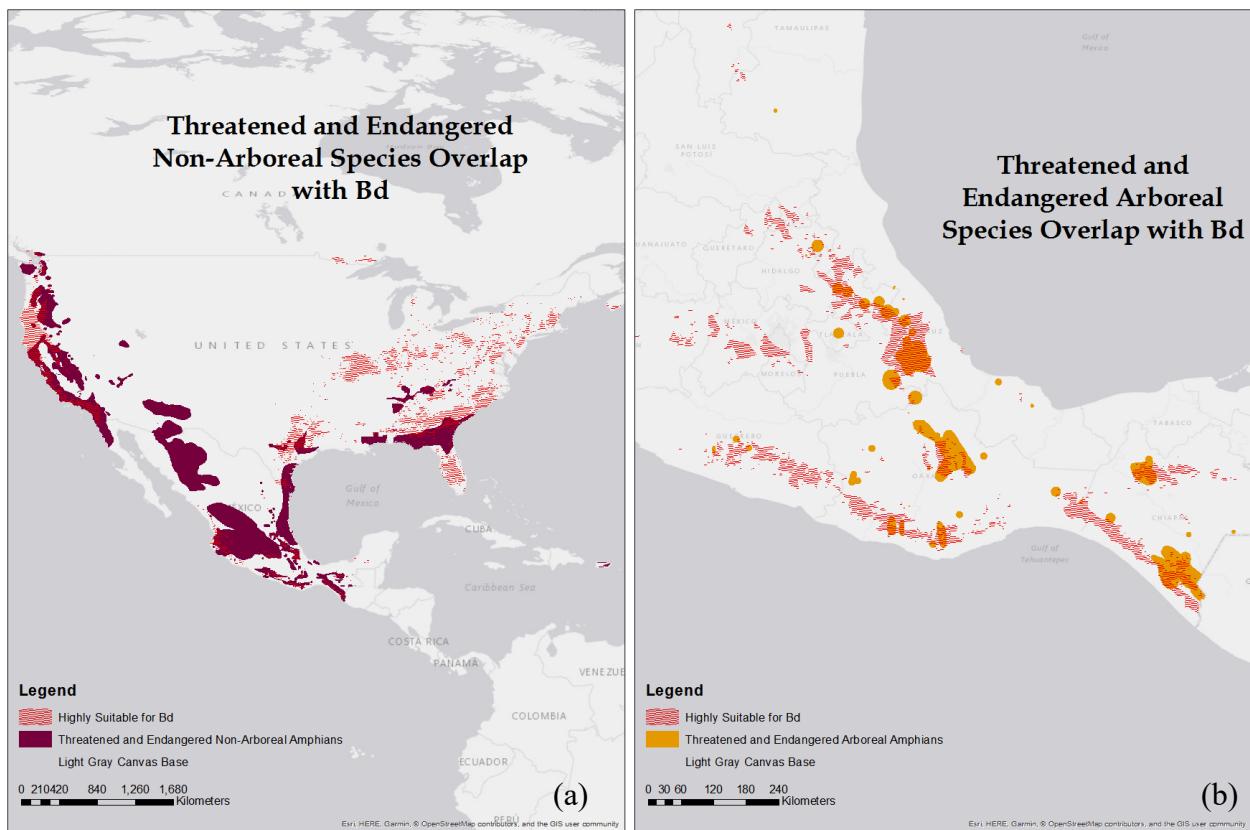


Figure 1. Ranges of Threatened Species and *Bd*-Suitable Regions. Each map displays the spatial relationship between species ranges and *Bd*-suitable regions in North America. (a) is the ranges of threatened non-arboreal species, and (b) is the ranges of threatened arboreal species.

Of these threatened North American amphibians, 218 species have some part of their range that intersects with *Bd*-suitable areas. Ninety-four of these species have over half of their ranges in regions suitable for the chytrid fungus. A summary of percentage overlap calculations for each species is available in Appendix B.

By contrast, non-arboreal amphibians with IUCN codes VU, EN, CR, while still present in the southern half of Mexico, also have species ranges in the northeastern region of Mexico, Southeastern Texas, and throughout California (Figure 1).

Comparing Overlap of Arboreal and Non-Arboreal Species

There is no significant difference between the mean percentage overlap of arboreal species ranges with *Bd*-suitable regions and the overlap of species that are not arboreal (Figure 2). The mean percentage overlap of arboreal species is 55.90%, and the mean percentage overlap

of non-arboreal species and *Bd* is 47.87%. The difference of these means is not statistically significant, so the null hypothesis that the mean percentage overlap calculations for arboreal and non-arboreal species is equal cannot be rejected ($p=0.1133$).

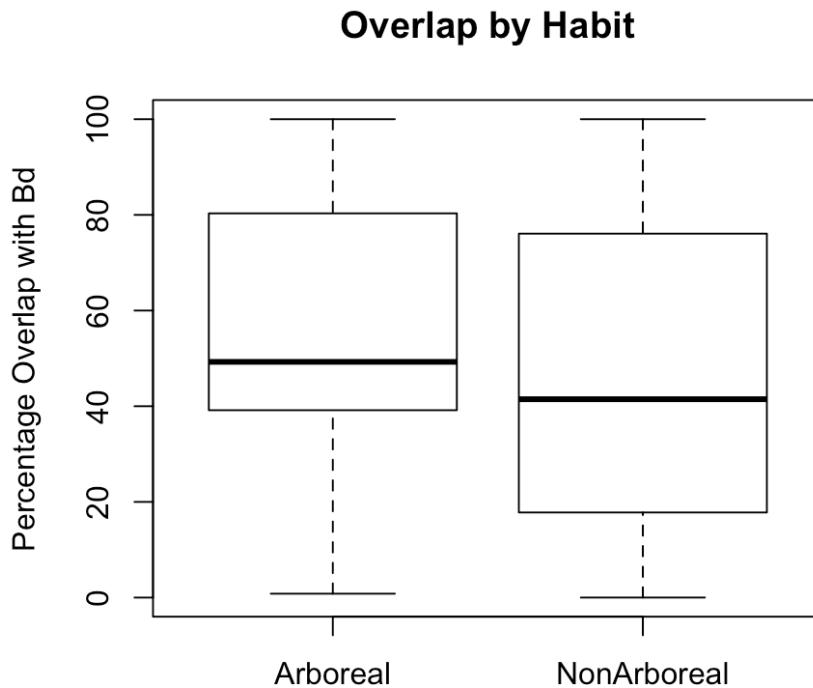


Figure 2. Mean Percentage Range Overlap with *Bd*. No significant difference can be assumed between the average percentage overlap with *Bd* for arboreal species compared to that of non-arboreal species.

Relationship Between Percentage Overlap and Chytrid History

The logistic regression to analyze the relationship between percentage overlap calculations and species' known history of chytrid was not statistically significant ($p=0.91$).

DISCUSSION

Knowing the amphibian species presence in regions where chytrid may occur is essential to understand the fungus's impact and spread and to prioritize management practices accordingly. No significant differences exist between arboreal and non-arboreal species in either

the known history of *Bd* susceptibility or in overlap of species range maps with areas modeled as highly-suitable for the chytrid fungus. The results of this study therefore emphasize that arboreal and non-arboreal species are both at risk for *Bd*.

History of Risk and Quantifying Overlap

Arboreal and non-arboreal North American species are both known to be significantly affected by the chytrid fungus. Among the species included in this study, arboreal and non-arboreal species have about equal rates of *Bd*-related die-offs. There is also no significant difference between the average percentage of overlap with regions highly suitable for *Bd* for arboreal and non-arboreal species, indicating a need to include species of each habitat in research and management priorities. Although using range maps as descriptors for species does not account for population densities within the range or microhabitat use (Hurlbert and White 2005), the potential presence of *Bd* in the species' ranges is an important indicator of the species' potential to contact the fungus. Species ranges are useful in visualizing and generalizing overlap with *Bd*.

The average size of species ranges with a high percentage overlap with *Bd* is smaller than the average range size of North American species overall, and the average size of species ranges with a low percentage overlap with *Bd* is larger than the average range size of North American species overall. Species with smaller ranges are more likely to have a larger portion of their extent of occurrence threatened. This risk based on range size is of concern because smaller ranged species are most at risk of decline when a portion of their extent is infected with the fungus (Primm et al. 2014).

Relationship Between Percentage Overlap and Chytrid History

Although there was no significant correlation between chytrid ranking and percentage overlap calculations, contacting *Bd* is a known means of contracting chytrid (Berger et al. 1998). This discrepancy in my findings could be due to lack of evidence in the literature regarding the species susceptibilities. For instance, there is no information about species history or susceptibility to chytrid for 20 of the 36 species with more than 95% of their range within

regions suitable for *Bd*. These species need more research to understand how they may be impacted by this intersection. The high number of species with no information about chytrid history indicates that more research and data is needed to more comprehensively analyze this spatial correlation. This result is therefore indicative of significant gaps in knowledge regarding species susceptibility and history. Furthermore, the *Bd* suitability model represents regions where the fungus can exist and not necessarily where it does exist. Not all regions modeled as highly-suitable actually house the fungus. Rather, this intersection analysis presents the potential risk to species if the fungus were to occupy its fundamental niche in its continual spread.

Further, a way to study amphibian die-off risk more comprehensively is to conduct a cumulative risk assessment analyzing the various extrinsic and intrinsic factors that could threaten each species (US EPA n.d.). This would include additional threats to amphibians, such as climate change and habitat loss, as well as consideration of intrinsic biological characteristics that could affect susceptibility to death by chytrid. Some species can carry the fungus but remain asymptomatic, which can imply that others are hypersensitive to contracting chytrid upon contact with the fungus (Davidson et al. 2003, Stockwell et al. 2010). Life history traits such as an aquatic juvenile state or stream-breeding habits could also be taken into account in a cumulative risk assessment (Bielby et al. 2008, Woodhams et al. 2011). These differences in susceptibility are an essential factor in understanding the impacts and spread of the chytrid fungus. Species such as *Plectrohyla siopela*, *Craugastor guerreroensis*, *Plectrohyla psarosema* would be appropriate candidates for a cumulative risk assessment, as each has a small range size (approximately 18 km², 7 km², and 12 km² respectively), 100% range overlap with regions highly suitable for *Bd*, and have a known history of chytrid. They are thus at risk of serious decline within their range because of *Bd* and should be monitored accordingly.

Limitations and Future Directions

A more thorough approach to map *Bd* risk to species would use maps showing population density gradients within occupied areas or niche comparison tools such as ENMTools to compare the suitability models of *Bd* and amphibian species (Warren et al. 2010). Because the porosity of range maps leads to an overestimation of the species' extent of occurrence (Hurlbert and White 2005), for species with a proportion range overlap with *Bd*, actual contact would

depend on microhabitat use within its range. It is unclear how species would be impacted when some portion of their range maps intersect with *Bd*- suitable regions while other portions are clear from the fungus. Such species, with approximately half of their range maps in *Bd*-suitable areas, would be of interest for a niche comparison study.

Broader Implications

Chytrid is spreading worldwide, and a growing number of species are being impacted by chytridiomycosis (Francis Skerratt et al. 2007). Research efforts for chytrid should not be limited to species exhibiting characteristics traditionally thought to impact susceptibility, such as an aquatic life stage or breeding habit, and should also acknowledge the fungus's potential to spread to species of other habits (Bielby et al. 2008, Woodhams et al. 2011). The presence of *Bd* in arboreal water sources and the more recent discovery of the fungus's dispersal through rainwater support my claim that further research and conservation efforts should include species beyond those with characteristics or habits considered risk factors, such as aquatic, terrestrial species, or otherwise water-associated species (Cossel and Lindquist 2009, Cheng et al. 2011, Kolby et al. 2015). This study of overlap highlights the need for conservation research and management plans to broaden their scope beyond species that have traits traditionally correlated to susceptibility. Chytrid should be viewed as a threat that is expanding and spreading across amphibian species. Research and conservation plans have the opportunity to frame work to reflect this need and to reach a wider range of species in their efforts.

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APPENDIX A

Appendix A1. Chytrid Threat to Threatened Arboreal Amphibian Species. Each arboreal species with an IUCN Red List code of Vulnerable, Endangered, or Critically Endangered is ranked based on their history or known susceptibility to the chytrid fungus. Key: 1= No information about chytrid or Bd history or susceptibility, 2= tested negative for Bd, 3=suspected susceptibility to die-offs, 4=tested positive for Bd, 5= die-offs

Chytrid threat ranking	Species
1	<i>Bolitoglossa chinanteca</i> , <i>Charadrahyla chaneque</i> , <i>Charadrahyla trux</i> , <i>Craugastor alfredi</i> , <i>Craugastor decorates</i> , <i>Cryptotriton adelos</i> , <i>Dendrotriton megarhinus</i> , <i>Hyla walkeri</i> , <i>Incilius cristatus</i> , <i>Megastomatohyla mixomaculata</i> , <i>Megastomatohyla nubicola</i> , <i>Plectrohyla charadricola</i> , <i>Pseudoeurycea saltator</i> , <i>Thorius adelos</i> , <i>Thorius arboreus</i> , <i>Thorius magnipes</i> , <i>Tlalocohyla godmani</i>
2	<i>Bolitoglossa engelhardti</i> ⁱ , <i>Bolitoglossa flavimembris</i> ² , <i>Bolitoglossa franklini</i> ⁱⁱ , <i>Charadrahyla taeniopus</i> ⁱⁱⁱ , <i>Chiroppterotriton chiropterus</i> ^{iv} , <i>Chiroppterotriton lavae</i> ⁵ , <i>Dendrotriton xolocalcae</i> ^v , <i>Megastomatohyla pellita</i> ^{vi} , <i>Parvimolge townsendi</i> ^{vii} , <i>Pseudoeurycea nigromaculata</i> ⁵ , <i>Pseudoeurycea unguidentis</i> ²
3	<i>Charadrahyla altipotens</i> ^{viii} , <i>Charadrahyla nephila</i> ^{ix} , <i>Plectrohyla avia</i> ^x , <i>Plectrohyla calthula</i> ^{xi} , <i>Plectrohyla celata</i> ^{xii} , <i>Plectrohyla hartwegi</i> ^{xiii} , <i>Plectrohyla hazelae</i> ^{xiv} , <i>Plectrohyla ixil</i> ^{xv} , <i>Plectrohyla thorectes</i> ^{xvi}
4	<i>Agalychnis moreletii</i> ^{xvii} , <i>Duellmanohyla ignicolor</i> ^{xviii} , <i>Plectrohyla arborescens</i> ^{xix} , <i>Plectrohyla cyclada</i> ¹⁵ , <i>Plectrohyla guatemalensis</i> ¹⁵
5	<i>Bromeliohyla dendroscarta</i> ^{xx} , <i>Craugastor polymniae</i> ^{xxi}

Appendix A2. Chytrid Threat to Threatened Non-Arboreal Amphibian Species. Each non-arboreal species with an IUCN Red List code of Vulnerable, Endangered, or Critically Endangered is ranked based on their history or known susceptibility to the chytrid fungus. Key: 1= No information about chytrid or Bd history or susceptibility, 2= tested negative for Bd, 3=suspected susceptibility to die-offs, 4=tested positive for Bd, 5= die-offs

Chytrid threat ranking	Species
1	<i>Ambystoma cingulatum</i> , <i>Ambystoma leorae</i> , <i>Ambystoma ordinarium</i> , <i>Batrachoseps regius</i> , <i>Batrachoseps stebbinsi</i> , <i>Batrachoseps wrighti</i> , <i>Bolitoglossa flaviventris</i> , <i>Bolitoglossa rostrata</i> , <i>Bolitoglossa veracrucis</i> , <i>Bolitoglossa zapoteca</i> , <i>Chiropterotriton chondrostega</i> , <i>Chiropterotriton dimidiatus</i> , <i>Chiropterotriton magnipes</i> , <i>Chiropterotriton multidentatus</i> , <i>Chiropterotriton orculus</i> , <i>Chiropterotriton terrestris</i> , <i>Craugastor hobartsmithi</i> , <i>Craugastor matudai</i> , <i>Craugastor montanus</i> , <i>Craugastor silvicola</i> , <i>Craugastor spatulatus</i> , <i>Craugastor uno</i> , <i>Craugastor vulcani</i> , <i>Cryptotriton alvarezdeltoroi</i> , <i>Ecnomiohyla valancifer</i> , <i>Eleutherodactylus angustidigitorum</i> , <i>Eleutherodactylus dixoni</i> , <i>Eleutherodactylus grandis</i> , <i>Eleutherodactylus leprus</i> , <i>Eleutherodactylus modestus</i> , <i>Eleutherodactylus nivicolimae</i> , <i>Eleutherodactylus rubrimaculatus</i> , <i>Eleutherodactylus saxatilis</i> , <i>Eleutherodactylus syristes</i> , <i>Eleutherodactylus verricipes</i> , <i>Eurycea chisholmensis</i> , <i>Eurycea junaluska</i> , <i>Eurycea latitans</i> , <i>Eurycea naufragia</i> , <i>Eurycea tridentifera</i> , <i>Eurycea waterlooensis</i> , <i>Exerodonta chimalapa</i> , <i>Gyrinophilus gulolineatus</i> , <i>Gyrinophilus palleucus</i> , <i>Hydromantes brunus</i> , <i>Hydromantes shastae</i> , <i>Incilius macrocristatus</i> , <i>Incilius spiculatus</i> , <i>Incilius takanensis</i> , <i>Lithobates dunnii</i> , <i>Lithobates johni</i> , <i>Lithobates okaloosae</i> , <i>Megastomatohyla mixe</i> , <i>Notophthalmus meridionalis</i> , <i>Phaeognathus hubrichti</i> , <i>Plectrohyla calvicollina</i> , <i>Plethodon amplus</i> , <i>Plethodon asupak</i> , <i>Plethodon cheoah</i> , <i>Plethodon meridianus</i> , <i>Plethodon sherando</i> , <i>Plethodon stormi</i> , <i>Pseudoeurycea ahuitzotl</i> , <i>Pseudoeurycea altamontana</i> , <i>Pseudoeurycea aquatica</i> , <i>Pseudoeurycea aurantia</i> , <i>Pseudoeurycea boneti</i> , <i>Pseudoeurycea brunnata</i> , <i>Pseudoeurycea cafetalera</i> , <i>Pseudoeurycea cochranae</i> , <i>Pseudoeurycea conanti</i> , <i>Pseudoeurycea gadovii</i> , <i>Pseudoeurycea gigantea</i> , <i>Pseudoeurycea goebeli</i> , <i>Pseudoeurycea juarezi</i> , <i>Pseudoeurycea lineola</i> , <i>Pseudoeurycea melanomolga</i> , <i>Pseudoeurycea naucampatepetl</i> , <i>Pseudoeurycea orchileucus</i> , <i>Pseudoeurycea orchimelas</i> , <i>Pseudoeurycea parva</i> , <i>Pseudoeurycea praecellens</i> , <i>Pseudoeurycea smithi</i> , <i>Pseudoeurycea tenchalli</i> , <i>Pseudoeurycea teotepec</i> , <i>Pseudoeurycea tlahcuiloh</i> , <i>Pseudoeurycea werleri</i> , <i>Rhyacotriton olympicus</i> , <i>Thorius aureus</i> , <i>Thorius boreas</i> , <i>Thorius dubitus</i> , <i>Thorius grandis</i> , <i>Thorius infernalis</i> , <i>Thorius lunaris</i> , <i>Thorius macdougallii</i> , <i>Thorius maxillabrochus</i> , <i>Thorius minutissimus</i> , <i>Thorius minydemus</i> , <i>Thorius munificus</i> , <i>Thorius narisovalis</i> , <i>Thorius omiltemi</i> , <i>Thorius papaloae</i> , <i>Thorius pulmonaris</i> , <i>Thorius schmidti</i> , <i>Thorius spilogaster</i>
2	<i>Craugastor pygmaeus</i> ³ , <i>Eurycea rathbuni</i> ²² , <i>Eurycea wallacei</i> ²³ , <i>Gyrinophilus subterraneus</i> ²⁴ , <i>Incilius perplexus</i> ²⁵ , <i>Plethodon petraeus</i> ²⁶ , <i>Plethodon welleri</i> ²⁷ , <i>Pseudoeurycea lynchii</i> ⁴ , <i>Pseudoeurycea rex</i> ² , <i>Pseudoeurycea robertsi</i> ⁴ , <i>Thorius troglodytes</i> ⁴
3	<i>Ambystoma bishopi</i> ²⁸ , <i>Anaxyrus canorus</i> ²⁹ , <i>Craugastor greggi</i> ³⁰ , <i>Duellmanohyla chamulae</i> ³¹ , <i>Duellmanohyla schmidtorum</i> ³² , <i>Ecnomiohyla echinata</i> ³³ , <i>Eleutherodactylus longipes</i> ³⁴ , <i>Exerodonta pinorum</i> ³⁵ , <i>Hypopachus barberi</i> ¹³ , <i>Incilius cycladen</i> ³⁶ , <i>Incilius tutelarius</i> ³⁷ , <i>Lithobates omiltemanus</i> ³⁸ , <i>Plectrohyla acanthodes</i> ³⁹ , <i>Plectrohyla crassa</i> ⁴⁰ , <i>Plectrohyla cyanomma</i> ⁴¹ , <i>Plectrohyla lacertosa</i> ⁴² , <i>Plectrohyla matudai</i> ⁴³ , <i>Plectrohyla mykter</i> ⁴⁴ , <i>Plectrohyla pentheter</i> ¹⁷ , <i>Plectrohyla psarosema</i> ⁴⁵ , <i>Plectrohyla pycnochila</i> ⁴⁶ , <i>Plectrohyla robertsorum</i> ⁴⁷ , <i>Plectrohyla siopela</i> ⁴⁸ , <i>Plethodon shermani</i> ⁴⁹ , <i>Thorius pennatulus</i> ^{2,7}

4	<i>Ambystoma altamirani</i> ⁱ⁷ , <i>Ambystoma californiense</i> ⁵⁰ , <i>Ambystoma mexicanum</i> ¹⁷ , <i>Anaxyrus californicus</i> ⁵¹ , <i>Anaxyrus houstonensis</i> ⁵² , <i>Craugastor rhodopis</i> ² , <i>Eurycea nana</i> ²² , <i>Eurycea neotenes</i> ²² , <i>Eurycea sosorum</i> ²² , <i>Eurycea tonkawae</i> ⁵³ , <i>Exerodonta melanomma</i> ¹⁷ , <i>Lithobates megapoda</i> ¹⁷ , <i>Lithobates sevostus</i> ⁵⁴ , <i>Lithobates sierramadrensis</i> ⁵⁵ , <i>Necturus alabamensis</i> ⁵⁶ , <i>Plectrohyla sabrina</i> ¹⁸ , <i>Plectrohyla sagorum</i> ¹⁸ , <i>Pseudoeurycea bellii</i> ⁴ , <i>Pseudoeurycea firscheini</i> ⁴ , <i>Pseudoeurycea leprosa</i> ⁴ , <i>Pseudoeurycea longicauda</i> ⁴ , <i>Ptychohyla erythromma</i> ¹⁸ , <i>Ptychohyla leonhardschultzei</i> ⁱ⁸ , <i>Rana draytonii</i> ⁵⁰ , <i>Rana pretiosa</i> ⁵⁷ , <i>Rana sierrae</i> ⁵⁸
5	<i>Craugastor guerreroensis</i> ¹⁸ , <i>Craugastor lineatus</i> ⁵⁹ , <i>Exerodonta juanitae</i> ^{56, 60} , <i>Lithobates subaquavocalis</i> ⁶¹ , <i>Rana chiricahuensis</i> ⁶¹ , <i>Rana muscosa</i> ^{62, 63} , <i>Rana tarahumarae</i> ⁶³

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APPENDIX B

Appendix B. Percentage Overlap of Amphibian Species Ranges with Bd-Suitable Areas and Total Range Size

Binomial	Habitat	Percentage overlap	Total area (km²)
<i>Craugastor matudai</i>	NonArboreal	100	10.1478492
<i>Plethodon asupak</i>	NonArboreal	100	385.337692
<i>Plectrohyla siopela</i>	NonArboreal	100	18.1427917
<i>Eleutherodactylus niviclimiae</i>	NonArboreal	100	11.6050295
<i>Megastomatohyla nubicola</i>	Arboreal	100	154.483735
<i>Eurycea tonkawae</i>	NonArboreal	100	1102.74691
<i>Thorius aureus</i>	NonArboreal	100	17.2403775
<i>Pseudoeurycea parva</i>	NonArboreal	100	13.9442246
<i>Plectrohyla pycnochila</i>	NonArboreal	100	32.2179674
<i>Eurycea nana</i>	NonArboreal	100	66.7090699
<i>Craugastor guerreroensis</i>	NonArboreal	100	7.34890276
<i>Thorius spilogaster</i>	NonArboreal	100	33.4993785
<i>Plethodon stormi</i>	NonArboreal	100	2648.4816
<i>Eurycea rathbuni</i>	NonArboreal	100	75.301046
<i>Hydromantes shastae</i>	NonArboreal	100	4111.38972
<i>Craugastor montanus</i>	NonArboreal	99.99999999	154.959089
<i>Eurycea chisholmensis</i>	NonArboreal	99.99999996	81.1048026
<i>Eurycea waterlooensis</i>	NonArboreal	99.99999993	7.23574785
<i>Chirotteriton chiropterus</i>	Arboreal	99.9999999	100.220638
<i>Eurycea sosorum</i>	NonArboreal	99.99999989	34.6835828
<i>Dendrotriton xolocalcae</i>	Arboreal	99.99999989	8.13846087
<i>Pseudoeurycea robertsi</i>	NonArboreal	99.99999984	16.8206668
<i>Gyrinophilus subterraneus</i>	NonArboreal	99.99999983	4.90791821
<i>Plectrohyla psarosema</i>	NonArboreal	99.99999976	11.8722501
<i>Eurycea tridentifera</i>	NonArboreal	99.99999974	323.600588
<i>Eurycea neotenes</i>	NonArboreal	99.99999972	49.9807137
<i>Eurycea naufragia</i>	NonArboreal	99.99999942	69.6270734
<i>Parvimolge townsendi</i>	Arboreal	99.93695332	770.712633
<i>Thorius munificus</i>	NonArboreal	99.80472661	43.07146
<i>Pseudoeurycea lineola</i>	NonArboreal	99.67977335	564.399229
<i>Thorius pennatus</i>	NonArboreal	99.50477062	811.160816
<i>Ambystoma leorae</i>	NonArboreal	99.26634229	39.5907708
<i>Plectrohyla calvicollina</i>	NonArboreal	98.93669359	57.0318833
<i>Pseudoeurycea saltator</i>	Arboreal	98.89275084	6.48644032

<i>Plectrohyla cyanomma</i>	NonArboreal	97.19057851	67.34804
<i>Thorius lunaris</i>	NonArboreal	96.49595499	211.21275
<i>Inciilus spiculatus</i>	NonArboreal	94.02998849	56.0258203
<i>Pseudoeurycea juarezi</i>	NonArboreal	93.83990169	149.535224
<i>Pseudoeurycea unguidentis</i>	Arboreal	93.66267129	45.3989028
<i>Plectrohyla celata</i>	Arboreal	92.24910551	222.577651
<i>Dendrotriton megarhinus</i>	Arboreal	92.00051137	44.3822162
<i>Pseudoeurycea melanomolga</i>	NonArboreal	90.44079562	43.7372749
<i>Pseudoeurycea cafetalera</i>	NonArboreal	90.35213959	3274.86149
<i>Pseudoeurycea naucampatepetl</i>	NonArboreal	89.71291347	66.3740351
<i>Bromeliohyla dendroscarta</i>	Arboreal	89.70354012	2043.22451
<i>Thorius minydemus</i>	NonArboreal	89.61543897	145.456655
<i>Thorius macdougalli</i>	NonArboreal	88.89497342	554.926415
<i>Thorius boreas</i>	NonArboreal	87.78543444	154.246428
<i>Megastomatohyla mixomaculata</i>	Arboreal	86.33754613	1090.4309
<i>Pseudoeurycea altamontana</i>	NonArboreal	85.51439906	531.387687
<i>Pseudoeurycea smithi</i>	NonArboreal	81.96192367	265.043746
<i>Thorius arboreus</i>	Arboreal	81.73207692	26.2873856
<i>Megastomatohyla pellita</i>	Arboreal	78.89454563	1177.76761
<i>Plethodon shermani</i>	NonArboreal	78.35178012	1492.38195
<i>Pseudoeurycea praecellens</i>	NonArboreal	76.66672533	25.5589344
<i>Eurycea latitans</i>	NonArboreal	76.07209948	10295.9165
<i>Thorius omiltemi</i>	NonArboreal	75.83747371	40.1606685
<i>Plectrohyla thorectes</i>	Arboreal	73.31511013	369.733929
<i>Plectrohyla acanthodes</i>	NonArboreal	72.62268359	977.982475
<i>Chirotterotriton dimidiatus</i>	NonArboreal	71.28081575	255.558522
<i>Chirotterotriton lavae</i>	Arboreal	71.27844065	80.5926335
<i>Phaeognathus hubrichti</i>	NonArboreal	70.64058699	1326.78955
<i>Chirotterotriton magnipes</i>	NonArboreal	70.39702606	402.506786
<i>Eleutherodactylus syristes</i>	NonArboreal	69.51482306	391.940137
<i>Agalychnis moreletii</i>	Arboreal	68.69552895	4741.48054
<i>Pseudoeurycea conanti</i>	NonArboreal	68.69427378	50.8924729
<i>Ptychohyla leonhardschultzei</i>	NonArboreal	67.71906664	1219.56646
<i>Charadrahyla taeniopus</i>	Arboreal	67.6061549	8500.7302
<i>Plectrohyla ixil</i>	Arboreal	67.02628033	163.21385
<i>Exerodonta melanomma</i>	NonArboreal	67.01666256	1446.18558
<i>Thorius narisovalis</i>	NonArboreal	65.76614893	84.1529109
<i>Plectrohyla robertsorum</i>	NonArboreal	65.62999669	167.400794
<i>Plethodon sherando</i>	NonArboreal	65.08048255	58.2816775

<i>Plectrohyla matudai</i>	NonArboreal	64.67378256	1850.2088
<i>Craugastor spatulatus</i>	NonArboreal	64.39013089	95.2606387
<i>Plectrohyla avia</i>	Arboreal	62.08845866	1416.51372
<i>Bolitoglossa engelhardti</i>	Arboreal	60.78891749	139.830261
<i>Anaxyrus houstonensis</i>	NonArboreal	60.66637911	31369.6924
<i>Duellmanohyla chamulae</i>	NonArboreal	58.76170495	518.65801
<i>Plectrohyla lacertosa</i>	NonArboreal	58.23367579	329.027691
<i>Rana draytonii</i>	NonArboreal	56.98170945	212636.365
<i>Pseudoeurycea lynchii</i>	NonArboreal	56.96818731	152.116705
<i>Plectrohyla sagorum</i>	NonArboreal	56.46321221	1943.97907
<i>Eleutherodactylus dixoni</i>	NonArboreal	56.3808598	155.804385
<i>Incilius tutelarius</i>	NonArboreal	56.16116595	1823.84821
<i>Pseudoeurycea firscheini</i>	NonArboreal	55.4759337	165.143164
<i>Pseudoeurycea gadovii</i>	NonArboreal	54.14050729	1168.19528
<i>Thorius troglodytes</i>	NonArboreal	53.4234211	172.237104
<i>Plectrohyla mykter</i>	NonArboreal	52.50571519	1168.28984
<i>Hydromantes brunus</i>	NonArboreal	52.07631616	719.135626
<i>Plectrohyla arborescens</i>	Arboreal	51.92126916	3680.76854
<i>Lithobates subaquavocalis</i>	NonArboreal	50.63610693	304.26678
<i>Thorius grandis</i>	NonArboreal	50.29365637	40.3114416
<i>Pseudoeurycea nigromaculata</i>	Arboreal	50.0902018	84.9462372
<i>Plectrohyla hazelae</i>	Arboreal	49.92918388	545.540378
<i>Ptychohyla erythromma</i>	NonArboreal	49.35446799	2509.10729
<i>Bolitoglossa franklini</i>	Arboreal	48.61532897	2401.20766
<i>Gyrinophilus gulolineatus</i>	NonArboreal	48.3420115	5344.70979
<i>Duellmanohyla ignicolor</i>	Arboreal	48.1159644	202.049775
<i>Craugastor rhodopis</i>	NonArboreal	48.02679861	18612.3538
<i>Craugastor decoratus</i>	Arboreal	47.97490548	6045.86901
<i>Pseudoeurycea gigantea</i>	NonArboreal	47.9646109	5169.61935
<i>Plectrohyla charadricola</i>	Arboreal	47.04011516	1506.22189
<i>Craugastor uno</i>	NonArboreal	46.31427489	350.830826
<i>Plectrohyla hartwegi</i>	Arboreal	45.99935622	2061.59171
<i>Craugastor pygmaeus</i>	NonArboreal	45.8195831	11094.3893
<i>Craugastor hobartsmithi</i>	NonArboreal	45.17398442	6530.19438
<i>Duellmanohyla schmidtorum</i>	NonArboreal	45.12143047	14207.1822
<i>Pseudoeurycea tlahcuiloh</i>	NonArboreal	44.88780382	50.3368444
<i>Pseudoeurycea teoteppec</i>	NonArboreal	44.64689534	107.231145
<i>Thorius pulmonaris</i>	NonArboreal	44.35132639	50.2964208
<i>Charadrahyla altipotens</i>	Arboreal	44.25789439	11.7751038

<i>Craugastor silvicola</i>	NonArboreal	43.85946566	122.315073
<i>Cryptotriton adelos</i>	Arboreal	43.76192787	67.3500463
<i>Chiroppterotriton orculus</i>	NonArboreal	42.9429103	10051.9017
<i>Tlalocohyla godmani</i>	Arboreal	42.8201782	9579.26056
<i>Charadrahyla trux</i>	Arboreal	42.13599612	87.8000083
<i>Anaxyrus californicus</i>	NonArboreal	41.53302074	121157.855
<i>Exerodonta pinorum</i>	NonArboreal	41.39832786	1190.1489
<i>Ambystoma altamirani</i>	NonArboreal	41.39284579	1613.92246
<i>Pseudoeurycea leprosa</i>	NonArboreal	41.01958362	13472.947
<i>Charadrahyla nephila</i>	Arboreal	40.9330662	1858.04436
<i>Thorius dubitus</i>	NonArboreal	39.83622362	92.3198659
<i>Plethodon amplus</i>	NonArboreal	39.75274544	619.675356
<i>Exerodonta chimalapa</i>	NonArboreal	39.61914487	273.589607
<i>Incilius cycladen</i>	NonArboreal	39.59884772	7586.66754
<i>Plectrohyla cyclada</i>	Arboreal	39.37800366	3362.86961
<i>Incilius cristatus</i>	Arboreal	38.95375629	112.909795
<i>Bolitoglossa flaviventris</i>	NonArboreal	38.67609152	701.690932
<i>Ambystoma mexicanum</i>	NonArboreal	38.61199528	114.968494
<i>Thorius adelos</i>	Arboreal	37.97233283	626.833346
<i>Plectrohyla guatemalensis</i>	Arboreal	37.49760558	2835.64746
<i>Cryptotriton alvarezdeltoro</i>	NonArboreal	37.43200334	49.5436498
<i>Hypopachus barberi</i>	NonArboreal	37.20848477	8309.47677
<i>Exerodonta juanitae</i>	NonArboreal	37.06737446	2916.683
<i>Ambystoma californiense</i>	NonArboreal	36.94950347	27500.7603
<i>Eleutherodactylus rubrimaculatus</i>	NonArboreal	36.84507026	3853.27221
<i>Craugastor greggi</i>	NonArboreal	36.17270182	22.1493154
<i>Pseudoeurycea tenchalli</i>	NonArboreal	35.45577977	99.4014142
<i>Pseudoeurycea ahuitzotl</i>	NonArboreal	34.75482113	52.9748097
<i>Eleutherodactylus verrucipes</i>	NonArboreal	33.95314409	3720.66983
<i>Rana pretiosa</i>	NonArboreal	33.69977985	160607.679
<i>Plectrohyla crassa</i>	NonArboreal	33.40026003	86.2004152
<i>Pseudoeurycea aurantia</i>	NonArboreal	32.78614332	37.2171989
<i>Chiroppterotriton terrestris</i>	NonArboreal	32.36455416	34.5861394
<i>Bolitoglossa flavimembris</i>	Arboreal	31.7840195	492.318557
<i>Rana muscosa</i>	NonArboreal	30.9928473	77562.0569
<i>Charadrahyla chaneque</i>	Arboreal	30.54552301	336.346646
<i>Eurycea junaluska</i>	NonArboreal	30.40924428	10390.2821
<i>Ecnomiohyla echinata</i>	NonArboreal	30.35360471	35.2741237
<i>Ambystoma cingulatum</i>	NonArboreal	30.17844379	126106.325

<i>Chiropterotriton chondrostega</i>	NonArboreal	29.9282593	778.678601
<i>Pseudoeurycea aquatica</i>	NonArboreal	29.54195234	133.773768
<i>Megastomatohyla mixe</i>	NonArboreal	29.04584532	35.8405639
<i>Eurycea wallacei</i>	NonArboreal	28.71759855	125.220562
<i>Thorius papaloae</i>	NonArboreal	28.66645574	136.699809
<i>Pseudoeurycea goebeli</i>	NonArboreal	28.58697522	344.929159
<i>Craugastor lineatus</i>	NonArboreal	27.08346562	12569.0442
<i>Lithobates omiltemanus</i>	NonArboreal	26.99013971	1189.2747
<i>Batrachoseps wrighti</i>	NonArboreal	26.91046362	26306.7739
<i>Lithobates sierramadrensis</i>	NonArboreal	26.8963375	12759.5245
<i>Rana sierrae</i>	NonArboreal	25.42996584	47804.2585
<i>Thorius schmidti</i>	NonArboreal	23.90878034	216.190579
<i>Bolitoglossa chinanteca</i>	Arboreal	23.56820699	2391.67065
<i>Thorius minutissimus</i>	NonArboreal	23.35362609	54.9114076
<i>Chiropterotriton multidentatus</i>	NonArboreal	20.46282458	5133.62834
<i>Ambystoma bishopi</i>	NonArboreal	20.42043638	38346.1454
<i>Pseudoeurycea boneti</i>	NonArboreal	20.10661082	4478.51533
<i>Lithobates megapoda</i>	NonArboreal	18.55580555	82298.5943
<i>Gyrinophilus palleucus</i>	NonArboreal	17.7927024	25245.4124
<i>Bolitoglossa zapoteca</i>	NonArboreal	16.64923114	83.6043023
<i>Anaxyrus canorus</i>	NonArboreal	15.48475811	22764.0684
<i>Bolitoglossa rostrata</i>	NonArboreal	14.76882808	76.9742884
<i>Ambystoma ordinarium</i>	NonArboreal	14.68932751	4928.40133
<i>Thorius infernalis</i>	NonArboreal	14.58099935	34.9648022
<i>Incilius tacanensis</i>	NonArboreal	13.6706872	26.8586714
<i>Thorius magnipes</i>	Arboreal	13.22708195	46.1390168
<i>Eleutherodactylus modestus</i>	NonArboreal	12.48907905	5646.6227
<i>Pseudoeurycea bellii</i>	NonArboreal	11.69498443	199503.685
<i>Craugastor polymniae</i>	Arboreal	11.2763415	331.19486
<i>Pseudoeurycea orchileucus</i>	NonArboreal	10.9556802	101.852883
<i>Eleutherodactylus longipes</i>	NonArboreal	10.87927339	7093.02539
<i>Incilius macrocristatus</i>	NonArboreal	10.74538192	5346.08344
<i>Eleutherodactylus leprus</i>	NonArboreal	10.57474869	1212.60888
<i>Lithobates sevostus</i>	NonArboreal	10.55160687	28805.7891
<i>Plectrohyla pentheter</i>	NonArboreal	10.42957562	2517.56125
<i>Pseudoeurycea longicauda</i>	NonArboreal	9.600371107	319.573472
<i>Notophthalmus meridionalis</i>	NonArboreal	8.549506018	109749.867
<i>Eleutherodactylus angustidigitorum</i>	NonArboreal	8.318489332	11083.1445
<i>Plethodon cheoah</i>	NonArboreal	8.216715463	234.610322

<i>Incilius perplexus</i>	NonArboreal	7.378749916	5458.16478
<i>Plethodon meridianus</i>	NonArboreal	7.087369713	1336.57195
<i>Thorius maxillabrochus</i>	NonArboreal	6.130089215	886.950741
<i>Rana tarahumarae</i>	NonArboreal	6.049762818	174171.622
<i>Pseudoeurycea brunnata</i>	NonArboreal	5.607889452	17.8221008
<i>Necturus alabamensis</i>	NonArboreal	5.557478411	11355.8868
<i>Batrachoseps regius</i>	NonArboreal	5.357258568	3553.32786
<i>Plethodon welleri</i>	NonArboreal	5.066680285	5444.09548
<i>Lithobates johni</i>	NonArboreal	4.961635354	2152.00404
<i>Pseudoeurycea cochranae</i>	NonArboreal	4.817775687	1803.02296
<i>Plectrohyla sabrina</i>	NonArboreal	4.545460003	28.4061926
<i>Eleutherodactylus saxatilis</i>	NonArboreal	4.09277435	328.416498
<i>Eleutherodactylus grandis</i>	NonArboreal	3.857458788	50.8822503
<i>Craugastor alfredi</i>	Arboreal	3.832984134	36815.5274
<i>Pseudoeurycea werleri</i>	NonArboreal	3.420066288	206.45876
<i>Plectrohyla calthula</i>	Arboreal	2.934439821	18.4462894
<i>Lithobates dunni</i>	NonArboreal	2.432860286	1570.78504
<i>Plethodon petraeus</i>	NonArboreal	1.583895273	489.955669
<i>Batrachoseps stebbinsi</i>	NonArboreal	1.469705224	993.35218
<i>Rhyacotriton olympicus</i>	NonArboreal	1.203899389	23701.6336
<i>Ecnomiohyla valancifer</i>	NonArboreal	1.191659719	1378.56792
<i>Lithobates okaloosae</i>	NonArboreal	1.07378864	919.432713
<i>Hyla walkeri</i>	Arboreal	0.812699569	1573.29929
<i>Rana chiricahuensis</i>	NonArboreal	0.702513065	386345.905
<i>Craugastor vulcani</i>	NonArboreal	0.154997966	1728.24439
<i>Pseudoeurycea orchimelas</i>	NonArboreal	0.111749034	1389.88078
<i>Pseudoeurycea rex</i>	NonArboreal	0.055694606	123.361976
<i>Bolitoglossa veracrucis</i>	NonArboreal	0.006895605	4821.63886