

Geographical context of forgotten amphibians: Colombian "Data Deficient species" *sensu* IUCN

Cristian Román-Palacios^{1,*} & Alejandro Valencia-Zuleta^{2,*}

- Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A.; cromanpa94@email.arizona.edu
- Programa de Pós-Graduação em Ecologia e Evolução, Departamento de Ecologia, Universidade Federal de Goiás, ICB V, 74690-900 Goiânia, GO, BRAZIL; alejandrovalencia08@gmail.com
 * Equal contribution

Received 19-II-2018. Corrected 24-V-2018. Accepted 22-VI-2018.

Abstract: Whereas more than 10 % of global amphibian richness is known to occur in Colombia, almost 16 % of these species are currently classified as Data Deficient according to the IUCN. These estimates suggest that the available data for a large portion of amphibians occurring in Colombia is insufficient to assess extinction risk. Here we aim to (1) review the available information on the distribution of the Colombian Data Deficient (DD hereafter) amphibians, (2) analyze their geographic distribution, and (3) evaluate the relationship between anthropogenic impact and their current conservation status. For this, we first compiled geographical records for the DD amphibian species using primary sources. Geographical records were obtained mainly from taxonomic descriptions and non-systematic surveys. We then estimated the geographical range and inferred the potential distribution for each species using letsR and MaxEnt, respectively. We quantified the human footprint for each species and tested the relationship between spatial distribution and anthropogenic change across populations. Analyses are here based on 128 of the 129 DD amphibian species that occur in Colombia. We found that most of these species were recently described and have small geographic ranges. A large proportion of these DD amphibians inhabit the Colombian Andes, and their populations have been strongly affected by human activities. Overall, the spatial clustering suggests that many of these species have faced similar environmental and anthropogenic pressures that have contributed to their rareness. We also suggest that the conservation status for several of the analyzed DD amphibians should be changed to account for the threats they face. Rev. Biol. Trop. 66(3): 1272-1281. Epub 2018 September 01.

Key words: Andes; Anura; Caudata; conservation; human footprint; MaxEnt.

Given that biodiversity is currently threatened by human-mediated processes, multiple initiatives have been proposed to assess the conservation status of the different taxonomic groups across the globe (Thomas et al., 2004; International Union for Conservation of Nature [IUCN], 2016). Even though more than 86 313 mammal, bird, reptile, amphibian, fish, insect, mollusk, and plant species are now classified under a given threatened category by the IUCN, about 16 % of these are still indicated as Data Deficient (hereafter DD; 13 713 species). The currently unavailable information on population size, range area, and rate of population decline for these species classifies them under a category that does not diagnose their conservation status (Rodrigues, Pilgrim, Lamoreux, Hoffmann, & Brooks, 2006; IUCN, 2016; Collen et al., 2016). This trend is also more notorious in the Neotropical region, where the number and extent conservation plans of local governments significantly contrast with its outstanding diversity.

Recent efforts to classify the conservation status of amphibian species have been triggered by the rapid decline in populations' sizes. Yet, a large amount of the extant diversity is still unassessed (Kiesecker, Blaustein, & Belden, 2001; Blaustein & Kiesecker, 2002; Stuart et al., 2004; Meredith, Van Buren, & Antwis, 2016). For instance, among the assessed amphibian species, 41 % are currently classified under a threatened category, and *ca.* 20 % are indicated as Data Deficient (Parsons, 2016). Given these circumstances, efforts made in describing the natural history, ecology, and spatial context of DD species represent a priority for increasing efficiency of the ongoing and future conservation plans (Vie et al., 2008; Morais et al., 2013; Parsons, 2016).

Here we analyze amphibian species that are currently classified as DD and occur in Colombia (IUCN, 2016). Colombia is a 'megadiverse' country that harbors nearly 10 % of the global amphibian richness (*ca.* 813 species) (Acosta-Galvis & Cuentas, 2017). A lack of protective measures to minimize the impact of human-mediated process on the natural populations has led to ~32 % of the amphibian species being classified as under threat (i.e., 256 species). Furthermore, 16 % of total amphibian species in the country are, for now, classified under a DD category (129 species) (UICN, 2016).

To address a lack of information available for DD category, we compiled the largest dataset of geographical occurrences for the DD amphibian species distributed in Colombia. Based on this dataset, the realized and potential geographic distribution for 99 % of the Colombian DD amphibians were analyzed. Realized distribution (or range size) was analyzed using the R package letsR (Vilela & Villalobos, 2015) and potential distribution was inferred using MaxEnt (Phillips, Dudík, & Schapire, 2006). Based on the inferred geographical distribution for each species, we analyzed the estimated anthropogenic impact on the DD populations.

The primary aim of this study is to characterize the geographical context of the DD species occurring in Colombia. This involves the description of their geographical ranges and the quantification of the anthropogenic pressures that each species experiences throughout

(0) (0)

its distribution. We specifically used this information to address whether the DD category describes accurately the current conservation status of the same amphibian taxa. We demonstrate that, in general, this category hides the potential threats that are experienced by most of these amphibian species.

MATERIALS AND METHODS

Data collection: Our analyses are based on the geographical records for 128 amphibian species present in Colombia and listed as DD by the IUCN. We searched for DD amphibian species in Colombia using the IUCN database (by June 2017). Next, we used scientific articles, books, and museum databases to compile an occurrence database for every DD species in Colombia. Each of the analyzed occurrences, supported by at least a single reference, is provided in Table S1. We did not include Leptodactylus hallowelli since the taxonomic limits are problematic and can cause the inclusion of erroneous registries into the database (de Sá et al., 2014). When coordinates were not available from the authors, we used the exact locality name retrieved from the publication to obtain longitude and latitude estimates (i.e., geocoding). The latter analyses were performed using the ggmap v.2.6.1 R package (Kahle & Wickham, 2013; Table S2). Furthermore, even when this approach was used for most records from the 20th century, we visually evaluated the accuracy of these estimates (Table S1).

Species distribution: For every analyzed species, geographical distribution was described using two approaches. We first estimated the extension of the 80 % higher average probability of occurrence using MaxEnt (hereafter referred as 80 % HPO) (Phillips et al., 2006). This estimate is based on the set of cells having a presence probability larger than the 80 % of the maximum presence probability for a given species. Importantly, species with less than three geographical occurrences were excluded from analyses (Hernández, Graham, Master, & Albert, 2006; Elith et al., 2011;

Rinnhofer et al., 2012; Wisz et al., 2008). We also highlight that recent analyses have shown that for non-widespread species (as most DD species; Table S1 and Table S2), three observations are enough for yielding reliable results (van Proosdij, Sosef, Wieringa, & Raes, 2016).

For MaxEnt analyses we first constructed in R a projected spatial points object using all the geographical records per species. Then, all 19 BIOCLIM raster layers (1 km resolution) (Booth, Nix, Busby, & Hutchinson, 2014) were cropped to an extent corresponding to the species' geographical maximums plus 5° in each direction (i.e. North, South, West, and East). We removed collinearity between predictors using remove Collinearity function implemented in the Virtualspecies package version 1.1 (Leroy, Meynard, Bellard, & Courchamp, 2016). We ran MaxEnt from R using dismo package version 1.1-1 (Hijmans, Phillips, Leathwick, & Elith, 2011). The following parameters were used for the same analyses: 'randomtestpoints = 30', 'betamultiplier = 1', 'linear = true', 'quadratic = true', 'product = true', 'threshold = true', 'hinge = true', 'threads = 2', 'responsecurves = true', 'jackknife = true'. For species having less than five registries, we did not include the 'randomtestpoints' parameter. By last, Raster files construction for the MaxEnt output was made using predict function in R, over the subset of cropped climatic raster layers.

We also estimated the geographical range using the R package lestR (Vilela & Villalobos, 2015). These estimations are based on a presence/absence that is constructed through the *rangesize* function implemented in the same package. Grid cell resolution was set to 0.5° (~100 Km²) for both analyses.

Human footprint: We quantified the human footprint for each DD species using The Global Human Footprint Dataset Version 2 (Wildlife Conservation Society [WCS] & the Columbia University Center for International Earth Science Information Network [CIESIN], 2005). Importantly, this dataset is a proxy for human-mediated disturbance of natural systems, and therefore, is expected to be positively correlated to the anthropogenic effects on amphibian populations (Sanderson et al., 2002). Human footprint ranges from 0 % to 100 %, with higher values indicating stronger anthropogenic disturbances. This dataset is based on nine global layers that summarizes anthropogenic pressures within the following major categories: (1) population density, (2) built-up areas, (3) nighttime lights, (4) land use/land cover, and (5) human access (coastlines, roads, railroads, navigable rivers). Here we specifically analyzed the average human footprint for each species based on the estimated values across populations.

We then used linear regressions to test the relationship between human footprint, description year and the between-species distance for the DD amphibian species. We first asked whether species described a long time ago have the smallest geographic ranges. Secondly, we tested the relationship between the age of species description and average human footprint across species. We were mostly interested in testing whether recently described species were less affected by anthropogenic activities. Then, we addressed if non-widespread species were more affected by human-mediated processes (i.e., higher human footprint). Lastly, we tested for local patterns in the geographic distribution of the three variables that were evaluated (geographic range, description year and human footprint) using spatial autocorrelation analyses (Moran's Index).

RESULTS

We compiled a total of 478 occurrences for 128 of the 129 DD species of amphibians distributed in Colombia, with most records corresponding to only three species: *Pristimantis lynchi* (5 %), *Bolitoglossa lozanoi* (3 %), and *Vitreorana ritae* (3 %) (Table S1, Table S2 and Table S3).

Distribution of the DD amphibians: Colombian DD amphibian species are also known from Costa Rica, Ecuador, Panamá, Perú, and Venezuela. Within Colombia, 60 % of the locality data were documented from Antioquia (77 records), Boyacá (38 records), Caquetá (38 records), Cauca (25 records), Magdalena (25 records), and Valle del Cauca (24 records). Sucre and Quindío departments had the lowest number of occurrences (one record each). Slopes of the Colombian Andes contained most of the occurrences for DD amphibians (Fig. 1). Other areas with a high number of DD species were the inter-Andean valleys, the Sierra Nevada de Santa Marta



Fig. 1. Distribution of the Colombian Deficient Data (DD) amphibian species. Cell size was set to $0.5^{\circ} \times 0.5^{\circ}$. (made by CRP)



Fig. 2. Summary of mean description year for the Colombian Deficient Data (DD) amphibian species. Cell size was set to $0.5^{\circ} \times 0.5^{\circ}$. (made by CRP)

•

and the Amazonian lowlands (Fig. 1). We also found that most recently described (year as a continuous variable) are primarily distributed in the highland Andes (Fig. 2).

Species distribution and geographic ranges: The 80 % HPO (MaxEnt) was estimated for 58 species that had at least three occurrences. MaxEnt results revealed that 14 species have 80 % HPO ranges smaller than 50 km² (Pristimantis carmelitae, P. cristinae, Caecilia occidentalis, Colostethus imbricolus, Rhinella ruizi, P. scopaeus, Allobates cepedai, Anomaloglossus lacrimosus, Centrolene medemi, P. corniger, P. epacrus, P. apiculatus, P. leucopus, and P. laticlavius; Table S3. However, species as Bolitoglossa phalarosoma, Epicrionops colombianus, Hyloxalus chocoensis, Rhaebo colomai, and Callimedusa perinesos showed estimated range sizes larger than 20000 km². The average range size using letsR was 6000 km² (Fig. 3). We found an exponential relationship between both measurements of range size (MaxEnt vs. letsR; log (80 % HPO) \sim range size: $r^2 = 0.9616$, P < 0.0001), but no general geographic pattern in the distribution of range size was found by none of the two approaches (MaxEnt or letsR).

Human footprint: The estimated values of mean human footprint across populations of



Fig. 3. Estimated average range size (degrees) of the Colombian Deficient Data (DD) amphibian species. Cell size was set to $0.5^{\circ} \times 0.5^{\circ}$. (made by CRP)



Fig. 4. Estimated average footprint percentage on the Colombian Deficient Data (DD) amphibian species. Cell size was set to $0.5^{\circ} \times 0.5^{\circ}$. (made by CRP)

the same species ranged from 6.5 % for *Caecilia bokermanni* to 71 % for *Pristimantis apiculatus* and *Pristimantis ocellatus*. The average human footprint across all the analyzed species was 37 %. As expected, the human footprint on DD species showed greater values near the major cities (e.g., Colombian Andes; Fig. 4).

We did not find a significant relationship between the 80 % HPO area and the number of observations ($r^2 = 0.0449$, P = 0.1133). However, we found a negative relationship between the geographical range size and description year (*slope* = -11.6133; r^2 = 0.2132, P = 0.0044). The latter suggest that recently described DD species have usually smaller geographical ranges. Human footprint did not show any significant relationship with description year ($r^2 = 0.0321$, P = 0.074). We also found that both range size and human footprint explained almost 15 % of the variance in description year ($r^2 = 0.1419$, P = 0.0002).

Lastly, we found a high spatial autocorrelation for all descriptors that were analyzed (description year, range size and human footprint; Fig. 5). A significant positive autocorrelation with distance was found in description year (P = 0.0482, *Distance* = 77.8284 cells; Fig. 5A) and range size (P = 0.0001, *Distance* = 77.8243 cells). This suggest that species occurring more closely in space are expected to have been described in similar years and have similar range sizes. The local pattern in range size is stable up to 120 cells (P = 0.0069, *Distance* = 120.7643 cells; Fig. 5B). Human footprint is significantly similar in closely distributed species within 74 cells (P < 0.05), but this tendency is inverted at distances greater than 174 cells (P = 0.0011, *Distance* = 174.7679 cells; Fig. 5C).

DISCUSSION

Here, we compiled the largest dataset for DD amphibians and explored the relationship between range size, description year, and human footprint. Given that about 16 % of the amphibians in Colombia are currently categorized as DD (128 out of ~813 species) (Acosta-Galvis & Cuentas, 2017), studies that describe the conservation status of DD amphibian species in the country are particularly important. To date, only a few studies have focused on this aspect. First, the red book of amphibians from Colombia reclassifies three DD species as vulnerable to extinction (Bolitoglossa lozanoi, Oophaga occultator and Pristimantis carranguerorum) (Rueda-Almonacid, Lynch, & Amézquita, 2004). Secondly, the regional assessment for Valle del Cauca department suggested reclassifying two DD species to critically endangered and vulnerable categories (Anomaloglossus atopoglossus and A. lacrimosus, respectively) (Castro & Bolívar, 2010). In general, this panorama suggests two things. First, DD amphibians are also easily classified under a different category after further information is analyzed. Second, the conservation status of about 96 % of the Colombian DD amphibians remains to be analyzed.

Our results suggest that most DD species occur in the Andes slopes, with these species also being the most recently described, experiencing the highest human impact, and having the smallest geographical ranges. The approach used here does not weight the human footprint across species based on geographical range sizes. Instead, the estimated values of



Fig. 5. Standardized Moran's I spatial correlograms for the Data Deficient species of Amphibians distributed in Colombia. Moran's I range from +1 (perfect positive spatial correlation) to - 1 (perfect negative spatial correlation); where 0 indicates no spatial correlation. A. Year. B. Range. C. Human footprint.

()

anthropogenic impact are based on the mean footprint across populations of the same species (Vilela & Villalobos, 2015). A widespread species can occur in multiple cells with low human impact, and conversely, a very geographically restricted taxon can be only present in highly-impacted areas.

Several explanations can be given about why species are classified under a DD category. We highlight that most of the records compiled here for DD species fall within the Colombian political limits (80 % of the analyzed species are only found in Colombia; 102 species). Importantly, the lack of information for most of these DD species prevents the reclassification into extinction risk categories. For instance, multiple DD species have not been registered since its description year, their biology is largely unknown, and are classified in groups with remarkable taxonomic problems. Specifically, most DD species were described between 1950 and 2000, with no additional observations made since the same year (Table S1 and Table S3). In other cases, DD species as Ctenophryne minor and Strabomantis cadenai, were described based on a few individuals from a single locality. We also point out that most of the remaining DD species belong to cryptic species complexes (e.g., Pristimantis, Colostethus, Hyloxalus, caecilians) that usually require some advanced degree of expertise to yield accurate identifications (Butchart & Bird, 2010). Misidentifications of DD species as other taxa can therefore contribute to the apparent rareness of the DD species.

We found that the distribution of DD amphibian richness in Colombia follows also the general distribution of amphibian richness in the country. We suggest that the high frequency of DD species in the Andes probably responds to the elevated frog endemism in the same area. The role of endemism in driving the number of DD species is still to be addressed (Isik, 2011), but is very likely to be strong in the same region. Along the same lines, previous studies have also suggested that most DD species are found within highly diverse regions (Brito, 2010), and this is something that is worth exploring in more depths.

The Colombian Andes are settled on a highly-transformed area where more than 60 % of the natural coverage has been already lost, and where exploitation of natural resources (e.g., copper, gold, nickel, natural gas, petroleum) still threatens the temporal and spatial continuity of the different natural populations (Armenteras, Rodríguez, Retana, & Morales, 2011). Given that amphibians account for 95 % of the endemic species in Colombia, and that the same species are accurate proxies of the impact of human activities on natural populations (Duellman, 1999), we estimated the anthropogenic impact on their populations using the human footprint database. Our results indicated the highest human footprint in populations from the Andean region (mean = 37 %; range = 6.5-71 %). This suggest that human-mediated processes are one of the major the drivers of their rareness in the Andes. However, we do not discard that species' rareness is actually being driven by other ecological and evolutionary processes that are not evaluated here but explored elsewhere (e.g. niche conservatism).

In summary, most DD amphibian studied here are only known to occur in very restricted localities from the Colombian Andes. The same places were found to have experienced high levels of anthropogenic impact. Based on our results, we highlight that urgent conservation actions must be taken for species that occur in a few localities with elevated environmental degradation. The establishment of wildlife refuges (or "Refugios de Vida Silvestre"), or specific local conservation strategies, might be an optimal solution to minimize the human footprint on these very restricted species. However, we are not aware of specific plans for the ex-situ conservation of any of these species, but we think this is something that is worth considering.

Examples of endangered DD species are Ameerega andina, Centrolene scirtites, Niceroforina colombiana, Pristimantis xestus, and P. susagae. The conservation category for another species such as *Cochranella litoralis*, *Nymphargus chami*, *Pristimantis ocellatus*, *P. tubernasus*, and *P. apiculatus*, is also worth reconsidering. Furthermore, species that are restricted to the Sierra Nevada de Santa Marta (*Pristimantis carmelitae* and *P. cristinae*) and Chocoan lowlands (*Anomaloglossus lacrimosus*) are currently classified as DD but might also be classified as endangered. In addition to these species, 14 other DD species were inferred to have very restricted geographical ranges (< 50 km²) (Table S3).

Most of the analyzed Colombian DD species can be considered to be critically endangered based on the criteria listed by the IUCN (2012) and Vie et al. (2008). Again, we highlight that DD species can be easily reclassified under a threat category after a short examination. These conclusions have been reached before by other studies, which have also suggested the DD category masks the real threatened status of many species (Howards & Bickford, 2014; Parsons, 2016). Studies like ours have previously been conducted in other countries to study the conservation status of DD species (e.g., Brazil) (Brito, 2010; Morais et al., 2013; Parsons, 2016). However, we highlight that the problems identified by these kind of studies (i.e., focused on a single country or political region) can be specifically targeted and approached in short periods of time. These studies are also expected to elevate interest and focus the attention of the local communities, governments, and scientists, on these largely "forgotten" species. We encourage researchers, not only from Colombia but from anywhere, to conduct similar or complementary analyses on the DD fauna.

ACKNOWLEDGMENTS

We thank Aldemar Acevedo (Pontificia Universidad Católica de Chile, Chile), Cesar Augusto Medina (University of Arizona, USA), and four additional reviewers for comments and suggestion on the manuscript. We also thank the University of Arizona for financial support for CRP, and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for support to AVZ.

RESUMEN

Contexto geográfico de los anfibios olvidados: especies colombianas con "Datos Insuficientes" según la UICN. A pesar de que más del 10 % de la riqueza global de anfibios se encuentra en Colombia, cerca del 16 % de estas especies es actualmente clasificada con Datos Deficientes según la IUCN. Estas estimaciones sugieren que los datos disponibles para esta gran porción de anfibios que habitan en Colombia, son insuficientes para evaluar su riesgo de extinción. En este documento nosotros (1) revisamos la información disponible sobre la distribución de los anfibios colombianos con Datos Deficientes (ó DD), (2) analizamos su distribución geográfica, e (3) hipotetizamos sobre la relación entre el impacto antropogénico y su estado de conservación. Para esto, compilamos los registros geográficos para las especies de anfibios DD usando referencias primarias. Los registros geográficos fueron obtenidos principalmente a partir de descripciones taxonómicas y búsquedas no sistemáticas. Para estimar la distribución geográfica e inferir la distribución potencial de cada especie usamos letsR y MaxEnt, respectivamente. Cuantificamos la huella humana para cada especie y evaluamos la relación entre la distribución espacial y el cambio antropogénico entre poblaciones. Los análisis fueron basados en 128 de las 129 especies de anfibios que se encuentran en Colombia y actualmente son clasificadas como DD. Encontramos que la mayoría de estas especies fueron descritas recientemente, y presentan una distribución geográfica reducida. Una gran proporción de estas especies de anfibios DD habitan los Andes colombianos, y sus poblaciones han sido fuertemente afectadas por las actividades humanas. Este agrupamiento geográfico sugiere que muchas de estas especies enfrentan similares presiones ambientales y antropogénicas que contribuyen a su rareza. Sugerimos además que el estado de conservación para muchas de las especies de anfibios DD aquí analizados podría ser reevaluado para considerar las amenazas que enfrentan.

Palabras clave: Andes; Anura; Caudata; Conservación; Huella Humana; MaxEnt.

REFERENCES

- Acosta-Galvis, A. R. & Cuentas, D. (2017). Lista de los Anfibios de Colombia: Referencia en linea V.05., 2015.0. Retrieved from http://www.batrachia.com
- Armenteras, D., Rodríguez, N., Retana, J., & Morales, M. (2011). Understanding deforestation in montane and lowland forests of the Colombian Andes. *Regional Environmental Change*, 11, 693-705.

- Blaustein, A. R., & Kiesecker, J. M. (2002). Complexity in conservation: Lessons from the global decline of amphibian populations. *Ecology Letters*, 5, 597-608.
- Booth, T. H., Nix, H. A., Busby, J. R., & Hutchinson, M. F. (2014). Bioclim: the first species distribution modelling package, its early applications and relevance to most current MaxEnt studies. *Diversity and Distributions*, 20, 1-9.
- Brito, D. (2010). Overcoming the Linnean shortfall: Data deficiency and biological survey priorities. *Basic and Applied Ecology, 11*, 709-713.
- Butchart, S. H. M., & Bird, J. P. (2010). Data Deficient birds on the IUCN Red List: What don't we know and why does it matter? *Biological Conservation*, 143, 239-247.
- Castro, F. & Bolívar, W. (2010). Libro rojo de los anfibios del Valle del Cauca. Corporación Autónoma Regional del Valle del Cauca, CVC. Santiago de Cali: Feriva impresores SA.
- Collen, B., Dulvy, N. K., Gaston, K. J., Gärdenfors, U., Keith, D. A., Punt, A. E., ... Akçakaya, H. R. (2016). Clarifying misconceptions of extinction risk assessment with the IUCN Red List. *Biological Letters*, 12, 1424-1442.
- de Sá, R. O., Grant, T., Camargo, A., Heyer, W. R., Ponssa, M. L., & Stanley, E. L. (2014). Systematics of the Neotropical genus *Leptodactylus* Fitzinger, 1826 (Anura: Leptodactylidae): Phylogeny, the relevance of non-molecular evidence, and species accounts. *South American Journal of Herpetology*, 9, 1-128.
- Duellman, W. E. (1999). Distribution Patterns of Amphibians in South America. In W. E. Duellman (Ed.), *Patterns of distribution of amphibians: a global perspective* (pp. 212-255). Maryland, USA: Johns Hopkins University Press.
- Elith, J., Phillips, S. J., Hastie, T., Dudík, M., Chee, Y. E., & Yates, C. J. (2011). A statistical explanation of MaxEnt for ecologists. *Diversity and Distribution*, 17, 43-57.
- Hernández, P. A., Graham, C. H., Master, L. L., & Albert, D. L. (2006). The effect of sample size and species characteristics on performance of different species distribution modeling methods. *Ecography*, 29, 773-785.
- Hijmans, R. J., Phillips, S., Leathwick, J., & Elith, J. (2011). Package 'dismo'. Retrieved from http:// cran.r-project.org/web/packages/dismo/index.html
- Howard, S. D., & Bickford, D. P. (2014). Amphibians over the edge: silent extinction risk of Data Deficient species. *Diversity and Distribution*, 20, 837-846.
- International Union for Conservation of Nature (IUCN). (2012). Red List Categories and Criteria: Version

3.1. (I. S. S. Commission, Ed.), International Union for Conservation of Nature (Second). Gland, Switzerland and Cambridge, UK.

- International Union for Conservation of Nature (IUCN). (2016). The IUCN Red List of Threatened Species. Version 2016-3. Retrieved from http://www.iucnredlist.org
- Isik, K. (2011). Rare and endemic species: why are they prone to extinction? *Turkish Journal of Botany*, 35, 411-417.
- Kahle, D., & Wickham, H. (2013). ggmap: Spatial Visualization with. *R Journal*, *5*, 144-161.
- Kiesecker, J. M., Blaustein, A. R., & Belden, L. K. (2001). Complex causes of amphibian population declines. *Nature*, 410, 681-684.
- Leroy, B., Meynard, C. N, Bellard, C., & Courchamp, F. (2016). Virtualspecies, an R package to generate virtual species distributions. *Ecography*, 39, 599-607.
- Meredith, H. M. R., Van Buren, C., & Antwis, R. E. (2016). Making amphibian conservation more effective. *Conservation Evidence*, 13, 1-6.
- Morais, A. R., Siqueira, M. N., Lemes, P., Maciel, N. M., De Marco, P., & Brito, D. (2013). Unraveling the conservation status of data deficient species. *Biological Conservation*, 166, 98-102.
- Parsons, E. C. M. (2016). Why IUCN Should Replace "Data Deficient" Conservation Status with a Precautionary "Assume Threatened" Status - A Cetacean Case Study. *Frontiers in Marine Science*, 3, 193.
- Phillips, S. J., Dudík, M., & Schapire, R. E. (2006). Maximum entropy modeling of species geographic distributions. *Ecological Modelling*, 190, 231-259.
- Rinnhofer, L. J., Roura-Pascual, N., Arthofer, W., Dejaco, T., Thaler-Knoflach, B., Wachter, G. A., ... Schlick-Steiner, B. C. (2012). Iterative species distribution modelling and ground validation in endemism research: An Alpine jumping bristletail example. *Biodiversity and Conservation, 21*, 2845-2863.
- Rodrigues, A. S. L., Pilgrim, J. D., Lamoreux, J. F., Hoffmann, M., & Brooks, T. M. (2006). The value of the IUCN Red List for conservation. *Trends in Ecology* & *Evolution*, 21, 71-76.
- Rueda-Almonacid, J. V., Lynch, J. D., & Amézquita, A. (2004). Libro rojo de los anfibios de Colombia. J. V. Rueda-Almonacid, J. D. Lynch, & A. Amézquita (Eds.) (Primera). Bogotá: Conservación Internacional Colombiana, Universidad Nacional, Instituto de Ciencias Naturales, Ministerio del Medio Ambiente.
- Sanderson, E. W., Jaiteh, M., Levy, M. A., Redford, K. H., Wannebo, A. V., & Woolmer, G. (2002). The Human

Footprint and the Last of the Wild. *Bioscience*, 52, 891-904.

- Stuart, S. N., Chanson, J. S., Cox, N. A., Young, B. E., Rodrigues, A. S. L., Fischman, D. L., & Waller, R. W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science*, 306, 1783-1786.
- Thomas, C. D., Cameron, A., Green, R. E., Bakkenes, M., Beaumont, L. J., Collingham, Y. C., ... Williams, S. E. (2004). Extinction risk from climate change. *Nature*, 427, 145-148.
- van Proosdij, A. S. J, Sosef, M. S. M., Wieringa, J. J., & Raes, N. (2016). Minimum required number of specimen records to develop accurate species distribution models. *Ecography*, 39, 542-552.
- Vié, J. C., Hilton-Taylor, C., Pollock, C., Ragle, J., Smart, J., Stuart, S. N., & Tong, R. (2008). The IUCN Red List: a key conservation tool. In J. C. Vié, C. Hilton-Taylor,

& S. N. Stuart (Eds.), *Wildlife in a changing world-An analysis of the 2008 IUCN Red List of Threatened Species* (pp. 1-14). Gland, Switzerland: IUCN.

- Vilela, B., & Villalobos, F. (2015). LetsR: a new R package for data handling and analysis in macroecology. *Methods in Ecology and Evolution*, 6, 1229-1234.
- Wildlife Conservation Society (WCS) & the Columbia University Center for International Earth Science Information Network (CIESIN). (2005). Last of the Wild Project, Version 2, 2005 (LWP-2): Global Human Footprint Dataset (Geographic). NASA Socioeconomic Data and Applications Center (SEDAC), Palisades, NY.
- Wisz, M. S., Hijmans, R. J., Li, J., Peterson, A. T., Graham, C. H., Guisan, A., & NCEAS Predicting Species Distributions Working Group. (2008). Effects of sample size on the performance of species distribution models. *Diversity and Distribution*, 14, 763-773.

