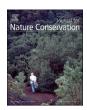
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Current threats faced by amphibian populations in the southern cone of South America

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ARTICLE INFO

ABSTRACT

Keywords: Amphibian conservation Argentina Chile In this work, we update and increase knowledge on the severity and extent of threats affecting 57 populations of 46 amphibian species from Chile and Argentina in southern South America. We analyzed the intrinsic conservation problems that directly impact these populations. We shared a questionnaire among specialists on threats affecting target amphibian populations with information on i) range, ii) historical occurrence and abundance, iii)

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https://doi.org/10.1016/j.jnc.2022.126254

Received 9 December 2021; Received in revised form 23 June 2022; Accepted 30 July 2022 Available online 5 August 2022

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Declining populations Threats to biodiversity population trends, iv) local extinctions, v) threats, and vi) ongoing and necessary conservation/research. We assessed association patterns between reported threats and population trends using multiple correspondence analysis. Since 2010, 25 of 57 populations have declined, while 16 experienced local extinctions. These populations were affected by 81% of the threat categories analyzed, with those related to agricultural activities and/or habitat modifications being the most frequently reported. Invasive species, emerging diseases, and activities related to grazing, ranching, or farming were the threats most associated with population declines. Low connectivity was the most frequent intrinsic conservation problem affecting 68% of the target populations, followed by low population numbers, affecting 60%. Ongoing monitoring activity was conducted in 32 (56%) populations and was the most frequent research activity. Threat mitigation was reported in 27 (47%) populations and was the most frequent ongoing management activity. We found that habitat management is ongoing in 5 (9%) populations. At least 44% of the amphibian populations surveyed in Chile and Argentina are declining. More information related to the effect of management actions to restore habitats, recover populations, and eliminate threats such as invasive species is urgently needed to reverse the conservation crisis facing amphibians in this Neotropical region.

1. Introduction

Amphibians are declining worldwide (McCallum, 2007; Pimm et al., 2014). They are the most threatened vertebrates worldwide, with more than 33 % of the 7217 assessed species categorized as threatened and 37 extinct (IUCN Red List, 2021). Considering that nearly half of the Datadeficient species are newly described or rare species with very restricted distribution ranges, some authors suggested that threatened amphibian species could reach ~50 % (González-del-Pliego et al., 2019). The decline of amphibian populations has been monitored since the 1970 s when herpetologists reported the first cases of extinction and decimation of local amphibian populations (Blaustein & Wake, 1990; Wake & Morowitz, 1991, Houlahan et al., 2000). Since then, many efforts have been made to better understand the drivers associated with these declines. Proposed factors include habitat loss, pollution, exotic invasive species, infectious diseases, climate change, and overexploitation related to the pet trade and food industry (Beebee & Griffiths, 2005; Blaustein et al., 2011; Bishop, Angulo, & Lewis, 2012). Studies on the threats that affect amphibian populations have increased in recent years. However, a considerable part of the tropics and the southern hemisphere still lacks sound background knowledge on this topic.

More than 45 % of the worlds' amphibian diversity is concentrated in the Neotropics, making it the most diverse region, with more than 3,500 species (Vences & Kohler, 2008; Frost, 2021). Forty-two percent of the 3,463 amphibian species assessed in the Neotropics are experiencing population decline, and a similar number of species (41 %) are globally threatened (IUCN, 2021). The southernmost area of the Neotropics, also known as the southern cone of South America, includes three countries: Argentina, Chile, and Uruguay. Argentina and Chile sustain many endemic and threatened amphibian species. Argentinean amphibian biodiversity is \sim 177 species, of which 44 are considered endemic, 36 threatened, two Possibly Extinct (Telmatobius ceiorum and Telmatobius laticeps), and 56 are declining and undergoing local extinctions (e.g., Pleurodema somuncurense, Atelognathus patagonicus, Ceratophrys ornata, among others) (Vaira, Pereyra, Akmentins, & Bielby, 2017). The amphibian biodiversity of Chile comprises ~ 60 amphibian species, of which 37 are endemic (Correa, 2019). The IUCN Red List (2021) refers to 62 species native to Chile, of which 34 are under a threatened category, two (Rhinoderma rufum and Telmatobius pefauri) are Possibly Extinct (although updated information on the latter species indicated there are extant populations, Fibla et al., 2017) and 35 are declining and experiencing local extinctions (e.g., Rhinoderma darwinii, Telmatobius dankoi, and Eupsophus insularis, among others). At the national level, the "Reglamento de Clasificación de Especies Silvestres" (RCE), which applies criteria very similar to those of the IUCN, considers that 44 of the 62 Chilean amphibian species evaluated to be threatened (Correa, 2019).

Species conservation assessments are a valuable tool for understanding the conservation status of species throughout their entire distribution. However, they fail to consider conservation management

units that usually consist of smaller populations below the species level (Mee et al., 2015). In this context, detailed information on the status of these populations and lower-level units (e.g., local populations; see below) is needed to lead management actions (Akcakaya, Mills & Doncaster, 2007; Weckworth et al., 2018). In 2018, a team of Argentinean and Chilean specialists working on the research and conservation of amphibians was formed to address conservation efforts in the southern cone of South America. One of the first goals of this team was to update knowledge about the threats affecting southern Neotropical amphibian populations and lower-level management units. In this study, we assess the current status, trend and threats affecting amphibian populations (sensu lato) in the Southern Cone. We also reported new information on the severity and extent of threats affecting 57 populations of 46 amphibian species in the southernmost Neotropical countries. Finally, we investigated the underlying associations between current threats and population trends and identified current conservation actions and priorities. This information is critically important and timely to inform management actions for the long-term conservation of amphibian populations in Argentina and Chile.

2. Materials and methods

2.1. Target populations and sites

We focused on populations and local populations rather than species considering that 1) threats vary considerably among populations of the same species, 2) populations are not only evolutionary units but also conservation units, and 3) the population-level conservation approach is less affected by changes in organismic taxonomy (Lindenmayer & Burgman, 2005). However, in some critically endangered and rangerestricted distribution amphibians, the target populations represent the entire species (e.g., Pleurodema somuncurense and Telmatobius dankoi). We consider a population as a group of individuals with a high mating probability with each other compared to their probability of mating with a member of different populations (Pianka 1994). In addition, we defined a local population as a group of individuals from a population that occupy a single habitat patch and are linked to other local populations with which they share metapopulation dynamics (Hansky, 1999). In the case of Rhinoderma species, for which a large amount of information is available, populations were grouped for operational purposes based on common threats. For Rhinoderma darwinii, 92 populations (among extant and extinct) were grouped into northern, central, and southern groups composed of 19, 23, and 50 populations, respectively (Table A1, Appendix A). Similarly, 18 recently extinct populations of Rhinoderma rufum were grouped together. Each of these four groups (three Rhinoderma darwinii and one Rhinoderma rufum) is hereinafter referred to as a population. We used the local population level to identify local extinction processes. Appendix A (Table A1) shows details of locality, country, and biological species identity for the 57 amphibian populations studied. To facilitate the identification of specific populations in each analysis, we assigned a number to each of the populations studied (see Tables A1, A5, and A6, Appendix A). As shown in Tables A2 and A5 (Appendix A), we investigated more than one population per amphibian species in nine cases (e.g., two populations of *Boana pulchella*, three of *Rhinella arenarum*, and three of

Rhinoderma darwinii). The locations of the 57 populations analyzed in this study are presented in Fig. 1.

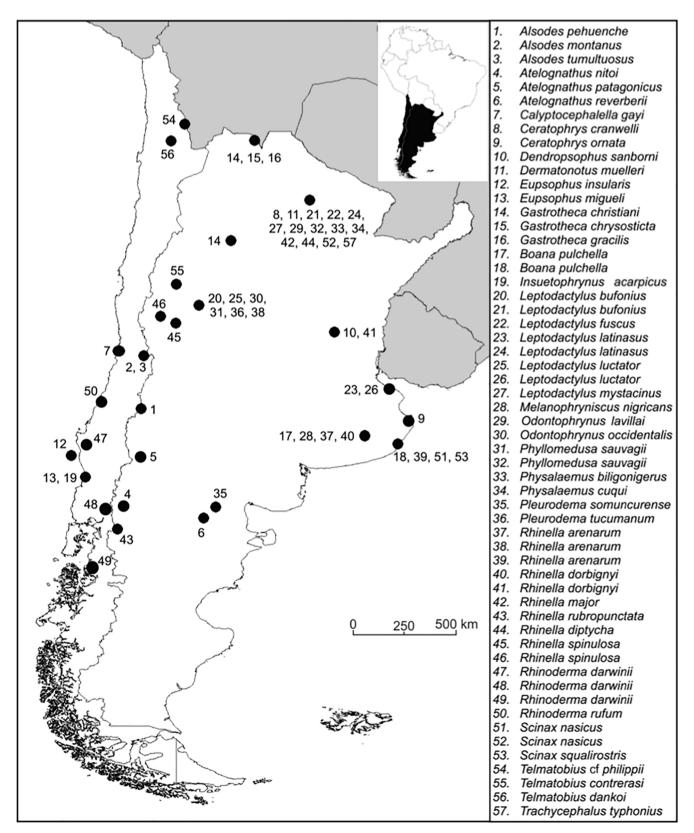


Fig. 1. Location of the 57 amphibian populations from Argentina and Chile included in the present study.

2.2. Data collection

A questionnaire focused on threats affecting target amphibian populations was shared among co-authors. To participate in this work, we considered contributors, researchers, and practitioners with in-deep knowledge of the amphibian species they were reporting and a minimum of three consecutive years of field monitoring for one (or more) specific populations. Data collected for each of the 57 amphibian populations included: 1) distributional range; 2) historical occurrence and abundance in three time periods (before 1970, between 1970 and 2010, and since 2010) as unknown, absent, vagrant, occasional, present in isolated populations, and widespread; 4) population trends (from 2010 to present) as unknown, increasing, stable, or declining and particularly declining populations, were categorized into four categories: minor decline (less than 30 %), moderate decline (30-49 %), high decline (50-79 %), extreme decline (more than 80 %). We used wide distribution ranges (from 20 to 30 %) to determine categories of decline and long monitoring periods to avoid confounding population declines with natural year-to-year fluctuations in individual numbers. 5) Local extinction (at population and/or local population levels); 6) past and present threats affecting target populations, and 7) existing and needed conservation and research activities. The raw data are shown in Table A1 of Appendix A. Data provided by contributors come from various sources: peer-reviewed articles, reports, thesis, monographs, species action plans, and some unpublished communications. To further facilitate comparisons between our study and previous work, we also provided the IUCN Red List population trend (Table A2, Appendix A).

We compiled the threats affecting each population and the existing and necessary conservation and research activities following the standardized categories of the IUCN Hierarchical Unified Classification of Direct Threats and the Conservation Measures Partnership (CMP) (hereinafter IUCN-CMP categories; IUCN and CMP, 2012; Table A1). The IUCN and CMP classify the threats into hierarchical levels (1, 2, and 3; Table A3, Appendix A). We used the IUCN-CMP Level 3 threat categories in all statistical analyses, except in a few cases where only Level 2 categories were available (Table A3, Appendix A; IUCN and CMP, 2012). We used the IUCN-CMP Tier 1 threat categories (main threat categories hereafter) to improve visualization and clarity in assessing population trends. For each threat category identified, and following IUCN recommendations (IUCN, 2013), we asked contributors to indicate several ordinal categories showing the timing, extent (i.e., the proportion of the population affected), and severity (i.e., overall decline) of the threats faced by each population (Table A1, Appendix A).

For threat timing, we defined five categories: a) only in the past and unlikely to return, b) only in the past, now suspended, but could come back in the long term, c) ongoing, d) only in the future (could occur in 10 years or three generations of the species assessed), and e) uncertain or unknown (Table A1, Appendix A). To indicate the extent of the threat, we recognized four categories: a) minor, affecting a negligible population proportion, b) less than 50 %, affecting the minority of the population, c) 50-100 %, affecting the majority of the population, and d) unknown (Table A1, Appendix A). As shown in Table A1, Appendix A, we defined the severity categories as follows: a) none (no decline or likely to cause negligible declines), b) fluctuating (causing or likely to cause fluctuations), c) slow decline (causing or likely to cause relatively slow but significant declines, i.e., less than 20 % in 10 years or three generations), d) rapid decline (causing or likely to cause rapid declines, i.e., 20-30 % in 10 years or three generations), e) very rapid decline (causing or likely to cause substantial declines, i.e., greater than 30 % in 10 years or three generations), and f) unknown.

Endangered species are often pressured by intrinsic population features that can be natural (a range-restricted species with a low natural density) or the result of stressors pushing the population below its minimum viable number. These features can lead to a long-term viability problem in a target population, even when threats are alleviated, and can also threaten genetic diversity (Nonic & Sijacic-Nikolic,

2019). For this reason, we decided to record this information in the surveys. We identified five intrinsic population features for each population assessed: 1. Low population number, 2. Low number of adult males, 3. Low number of adult females, 4. Low connectivity among local populations, 5. Inbreeding. We also identified the perceived categorical impact of these intrinsic factors on target populations as low, moderate, or high.

Existing and necessary research and conservation activities and their expected impact on the populations studied are provided in Table A1 of Appendix A. The reported activities included: research (monitoring, search for new populations, basic and applied studies), population management (activities directly aimed at increasing survival and the number of individuals, alleviating threats, recovering wild populations, etc.), habitat management (restoration and creation of new habitats), exsitu management (for education, rescue and/or reintroduction), translocation of individuals, awareness campaigns, sustainable alternatives for local communities, capacity building/laws/policies, and direct area protection (creation of reserves and/or sanctuaries) (Table A1, Appendix A).

2.3. Data analysis

To assess the patterns of association between reported threats and population trends, we developed a multiple correspondence analysis (MCA) using the ca package in the R statistical environment (Nenadic & Greenacre, 2007, R Development Core Team, 2016). We included 25 categorical variables (i.e., the reported population trend and the 24 specific threat categories considered in this study; see Tables A4 and A5). For the MCA, the variable "population trend" had two-character states: "Not declining", meaning stable or increasing, and "Declining". The values used for the remaining 24 threat variables corresponded to the extent of the current threat (i.e., threats whose timing value was 2). Threats were grouped into two-state characters: 0 for extent values indicating that they affect a negligible or the minority of the target population; and 1 for extent values affecting the majority of the population (Table A1, Appendix A). The analysis outcome is a set of eight coordinates showing the association between the different variables and their character state (population trends and threat extent). We then plotted the results in the lowest-dimensional Euclidean space (2d) to assess association patterns between categories, meaning that lower distances have more association (Fig. 5). We selected a multiple correspondence analysis based on a simple Correspondence Analysis (Benzécri, 1973) of the indicator matrix (setting lambda = "indicator"). We visualized the results using symmetric maps with the row and column coordinates of the two dimensions with the largest eigenvalues (Fig. 5).

In some analyses, we used major threat categories (e.g., see Fig. 5) where the same population could contribute with more than one case to each main category, as the categories are composed of several specific threat categories (e.g., the Energy Production & Mining main category comprises two distinct categories: Oil & Gas Drilling and Mining & Quarrying; thus, an assessed population could contribute up to two cases to the main category).

3. Results

3.1. Current population trend

Our study showed that 25 (44 %) of the 57 amphibian populations have declined since 2010 (Fig. 5 and Table A5). Five populations (9 %), two of them from Argentina (*Gastrotheca christiani* from the Yunga rainforest and *Atelognathus patagonicus* from the Patagonian plateau of Neuquén Province) and three from Chile (*Rhinoderma darwinii* from northern populations, i.e., the Bio-Bio region, *Rhinoderma rufum* from central Chile, and *Telmatobius dankoi* from Calama) are experiencing a drastic decline (Figs. 2 and 5). Eight other populations (14 %) are also

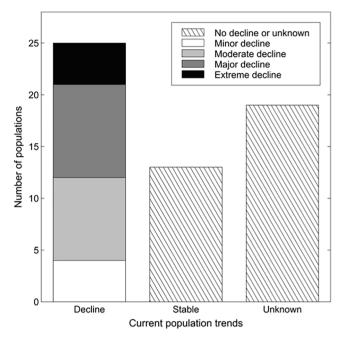


Fig. 2. Current population trends for the 57 amphibian populations studied across the southern cone of South America. Different levels of population decline are highlighted with different shades.

experiencing significant declines, including populations of Alsodes pehuenche, Eupsophus insularis, Eupsophus migueli, Gastrotheca chrysosticta, Leptodactylus luctator, Rhinella spinulosa, R. darwinii, and Telmatobius cf. philippii (Figs. 1 and 2). Four populations are experiencing a moderate decline, including the IUCN Critically Endangered Pleurodema somuncurense, the Endangered Rhinoderma darwinii, and a population of the Near Threatened Ceratophrys ornata. Eight populations (14 %) showed a minor decline, including the threatened Melanophryniscus nigricans and a population of R. darwinii (Fig. 2). Finally, 13 populations (23 %) were considered stable, and 19 populations (33 %) have an unknown trend (Figs. 2 and 5, See Tables A1, A4, and A5 for more details).

We reported extinctions of 16 local populations. Populations of Atelognathus patagonicus, A. reverberii, Gastrotheca christiani, Boana pulchella, Leptodactylus bufonius, Leptodactylus latinasus, Rhinella arenarum,

and *Rhinella dorbignyi* have experienced at least one local extinction to date. In the case of *Insuetophrynus acarpicus*, a local extinction at the Queule locality seems likely, but further monitoring is needed to confirm this information. At least two local extinctions have been documented for the Critically Endangered *Pleurodema somuncurense*, and a third potential one is still being assessed (Kacoliris, pers. obs.). Evaluated populations of *Rhinoderma darwinii* (southern populations), *Telmatobius* cf. *philippii*, and the recently described *Melanophryniscus nigricans* have experienced three local extinctions to date. Concerning *Rhinoderma darwinii* Chilean populations, at least seven local extinctions were documented in the population of the Bio-bío region and 17 in the population of the Araucanía region. *Rhinoderma rufum* from Chile had the highest records of local extinctions, accounting for all known 18 populations (Tables A1 and A5, Appendix A; Fig. 5).

3.2. Current threats

The amphibian populations assessed were affected by 30 (81 %) of the total specific threat categories identified in this study (See Fig. 3 for the 11 threat categories). On average, 3 ± 4 threats affected the populations (N = 57). The main threats affecting wild amphibian populations in southern South America are related to human activities such as Agriculture & Aquaculture. This category was recognized as the most frequently affecting amphibian populations, followed by Residential & Commercial Development, Natural System Modifications (i.e., disruption of natural processes), Climate Change & Severe Weather, and Invasive and Other Problematic Species/Genes & Diseases (Fig. 5, Tables A1 and A3, Appendix A). Tables A1 and A3 of Appendix A provide detailed supporting information on specific threat categories affecting the assessed populations (see Fig. 5).

The MCA showed a large dispersion of coordinates in space among the different threats. However, we generally observed that stable or increasing amphibian population trends corresponded mainly to the absence of many threats (negative values in dimension 2). Conversely, declining population trends seem to be associated with many threats (positive values in dimension 2; based on specific threat categories listed in IUCN-CMP; Table A1; Fig. 4; Table A3, Appendix A). The presence of invasive non-native/alien species and diseases was the specific threat category most closely associated with population declines (MCA; number 1 in Fig. 4; rank 1 in Table A1). This threat category negatively affected 38 of the 57 (66 %) populations assessed. Smallholder grazing/ranching/farming was the second specific threat associated with

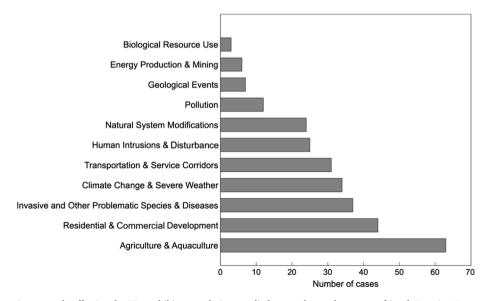


Fig. 3. Major threat categories currently affecting the 57 amphibian populations studied across the southern cone of South America. Data were classified according to the IUCN-CMP Level 1 threat categories. See column "timing," value "2" in Table A1 of Appendix A for raw data.

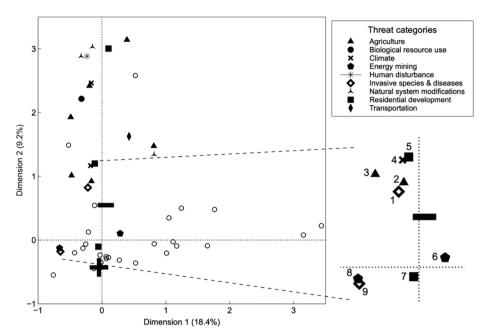


Fig. 4. Multiple correspondence analysis (MCA) on 25 categorical variables (population trend and 24 specific threat categories). The first two dimensions explained 30% of the data distribution. The figure includes the two-character states of all 25 variables (black "+" for stable/increasing population trend, and black "—" for decreasing population trend; small open circles: 24 threats with character state "absence," small black symbols: 24 threats with character state "present"). The 24 specific threat categories were grouped into nine major groups based on the IUCN-CMP Level 1 threat categories. The box in the right panel details the major threat categories for each symbol. In contrast, the right down expansion of the figure shows the most important specific threat categories related to the declining population trend (Table A3, Appendix A): 1. Invasive non-native/alien species diseases, 2. Small-holder grazing, ranching, or farmer, 3. Agroindustry plantation, 4. Droughts/desertification, 5. Urban areas, 6. Oil & gas drilling, 7. Commercial and industrial areas, 8. Mining & quarrying, 9. Problematic native species/diseases.

population declines, affecting 41 (72 %) of the populations (Table A3, Appendix A; Fig. 4). This threat currently affects most populations suffering extreme declines, such as *Rhinoderma darwinii*, *Rhinoderma rufum*, and *Gastrotheca christiani*. It is also recognized to have affected populations of the Critically Endangered *Atelognathus patagonicus* in the past (but not at present). The agro-industrial plantation was the third

specific threat related to population declines (Table A3, Appendix A; Fig. 4), although it affected only 9 (16 %) of the populations assessed. Among these populations, *Rhinoderma darwinii* and *Rhinoderma rufum* showed an extreme decline, *Eupsophus migueli* a major decline, and *Ceratophrys ornata* a moderate decline (Table A5, Appendix A).

The specific threats identified in this study showed variation in

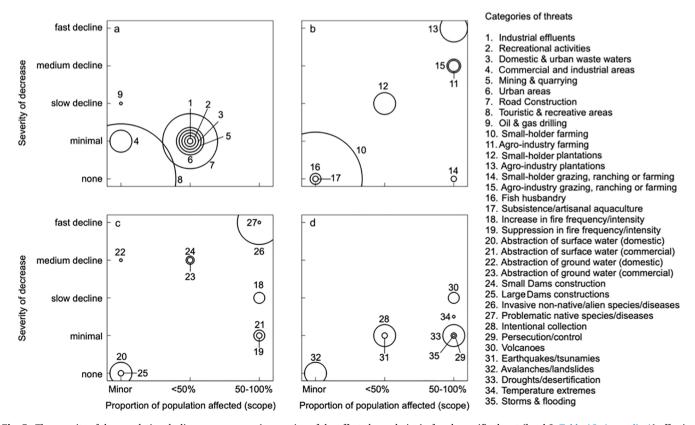


Fig. 5. The severity of the population declines versus scope (proportion of the affected population) of each specific threat (level 2, Table A2, Appendix A) affecting the 57 amphibian populations from the southern cone of South America. The threat categories are based on the hierarchical Unified Classification of Direct Threats from the IUCN-CMP. The data are presented in four figures. The number of populations for each case is proportional to the size of the circles (i.e., small circles: fewer populations; large circles: more populations). For data on timing, scope, and severity of threats and the identity of the populations affected, see Table A1, Appendix A.

extent and severity among the amphibian populations assessed (Table A1). Agro-industrial plantation; Agro-industrial farming; Agro-industrial grazing, ranching, or farming; Invasive non-native/alien species/diseases, and Problematic native species/diseases were identified as threats combining high severity and large extent (Fig. 5). The following threats showed a low severity and extent: Touristic & recreative areas; Smallholder farming; Fish husbandry; Subsistence/artisanal aquaculture; Abstraction of surface water (domestic) and Avalanches/landslides. However, the latter three threats currently affect many amphibian populations (Table A1, Appendix A). Other threats affected < 25 % of amphibian populations with low severity (Fig. 5; Tables A1 and A6).

3.3. Intrinsic population features

This study reported intrinsic population features for 49 of the 57 amphibian populations studied. The most frequently features listed were low connectivity and low population numbers with 39 (68 % of the studied populations) and 34 reports (60 %), respectively. However, low population numbers were most frequently listed as having a high impact on target populations in 16 cases (28 %), followed by connectivity, which was reported to have a high impact in 13 cases (21 % of the populations). We found a low number of adult males and females in 21 (37 %) and 20 (35 %) populations studied, respectively. Still, this problem had a high impact (14 %) in only eight populations per case (males and females). Potential inbreeding depression affected 16 populations but had a high impact in only four cases (7 %).

3.4. Research and management

Population research was recorded in 37 of the 57 amphibian populations studied (Table A1). The most frequent ongoing activity was population monitoring, reported for 32 (56 %) of the populations studied. Searching for new populations and basic research are ongoing in 24 (42 %) populations, while applied research was the least common, reported for only 12 (21 %) populations. Species management was reported for 27 (47 %) populations, with threat management being the most frequent ongoing activity (16 % of the populations studied). Habitat management was an ongoing activity in only five (9 %) populations. Still, habitat management was reported as planned (needed) for the future in nine populations (16 %). Ex-situ management is ongoing for only four species, Rhinella arenarum, Pleurodema somuncurense, Telmatobius dankoi, and Rhinoderma darwinii. The former species were managed for educational purposes, while the last three species had rescue and reintroduction purposes in the ex-situ programs. An ex-situ program for Telmatobius dankoi was recently established at the National Zoo of Chile. Ex-situ management is planned for another 11 (19 %) populations studied. Translocations are ongoing management practices in five populations, while they are planned for nine (16 %) populations in the future. Species already accounted for in-situ to in-situ translocations are Telmatobius dankoi, Ceratophrys ornata, Gastrotheca christiani, Gastrotheca gracilis, and Melanophryniscus nigricans. In the case of Pleurodema somuncurense, ex-situ to in-situ translocations have already been conducted (Martínez-Aguirre, Calvo, Velasco, Arellano, & Kacoliris, 2019). Among other ongoing management practices, we identified raising awareness campaigns and capacity building in 24 (42 %) studied populations. In five (9 %) populations, we recorded sustainable alternatives for local communities and laws and policies reinforcements in eight (14%). Area protection was reported as ongoing management in 17 populations and listed as planned for the future in another nine (16 %) populations (Table A1, Appendix A).

4. Discussion

Of the 217 amphibian species assessed by the IUCN Red List in Chile and Argentina, 79 (37 %) are declining, while another 48 (22 %) have

unknown trends. Invasive non-native/alien species diseases and smallholder grazing/ranching/farmer are the main threats associated with these declining species. The reports provided in the IUCN Red List agree with our results where both threats were associated with population declines. Other threats reported in the IUCN Red List that affect amphibians' species are dams, pollution from agricultural and forestry effluents, and logging. In our study, the latter three threats were not often documented for most declining populations, indicating that they are not strongly associated with declines or that their effects on target populations have yet to be observed or recorded. However, in the particular case of Pleurodema somuncurense, a combination of threats, including the creation of a small dam with high livestock pressure, has led to local extinction in recent times (Velasco et al. 2016). Although we observed that water pollution is affecting Alsodes pehuenche, Alsodes tumultuosus, Calyptocephalella gayi, Gastrotheca gracilis, and Leptodactylus latinasus populations, its effect is yet unknown, so further studies are required at a local scale.

Our MCA showed that the invasive species/diseases threat category was strongly associated with population declines and was among those most frequently associated with rapid population declines. In amphibians, this threat includes two different threats: invasive species and emerging infectious diseases, both of which are widely known to affect amphibians worldwide. Salmonids are one of the most harmful invasive species affecting amphibian populations in the Southern Cone (Martín-Torrijos et al., 2016; Lobos et al., 2020; Miloch, Bonino, Leynaud, & Lescano, 2020). Previous studies have documented the negative effect of invasive salmonids on several amphibian populations analyzed in this study. For example, the invasive rainbow trout, Oncorhynchus mykiss, severely affects the occupancy of native Pleurodema somuncurense and Rhinella arenarum in Patagonia (Velasco et al., 2018). Rainbow trouts are also predators of the Critically Endangered frog Alsodes pehuenche (Zarco, Corbalán & Debandi 2020), the Vulnerable aquatic frog Telmatobius oxycephalus (Brunetti, 2008) and severely affects the distribution patterns of endemic amphibians in central Argentina (Miloch et al., 2020). The main local population of Atelognathus patagonicus was entirely extirpated from its large habitat due to the introduction of nonnative fish (mainly Percichthys trucha and other salmonids; Fox et al., 2005; Cuello, Perotti & Iglesias, 2009; Sanguinetti et al., 2014).

Other invasive species besides salmonids affect amphibians in the Southern Cone. The invasion of the African clawed frog Xenopus laevis correlates with the disappearance of the endemic frog Calyptocephalella from many sites in central Chile (Azat, pers. obs.). The chameleon cichlid (Australoheros facetus) is predator of several native amphibians (Calyptocephalella gayi, Alsodes nodosus, Pleurodema thaul, and Rhinella arunco) in the Chilean Mediterranean region (Alzamora & Lobos, 2021). The tetra fish Psalidodon eigenmanniorum, which has been translocated outside its native range, predates on tadpoles of Leptodactylus luctator native populations in San Juan, Argentina (Rodriguez, Martínez & Acosta, 2014). The widely distributed rat Rattus rattus also predates on native amphibians, as has been documented for populations of Eupsophus insularis (Lobos pers. obs.). Habitat disturbance due to the replacement of native forests by the invasive tree Pinus radiata has also played an essential role in the disappearance of Rhinoderma rufum (Soto-Azat et al., 2013a).

The second sub-threat widely affecting Neotropical amphibians is related to emerging diseases such as the chytrid fungus *Batrachochytrium dendrobatidis* (*Bd*) and *Ranavirus* (Stuart et al., 2008). *Ranavirus* has not been widely documented for amphibians in Chile and Argentina, but morbidity and mortality events have already been reported for the Critically Endangered frog *Atelognathus patagonicus* (Fox et al., 2006). Also, *Xenops laevis* has been identified as a *Ranavirus* reservoir in Chile, and mortality events have been reported in the native amphibian *Calyptocephalella gayi* (Soto-Azat et al., 2016). In the case of *Bd*, it has been found to affect most of the species assessed in the present study (Herrera, Steciow & Natale, 2005; Arellano et al., 2009; Ghirardi et al., 2009; 2012; 2014; Alvarado-Rybak et al., 2021b). In Chile, *Bd* has been

associated with the decline of Rhinoderma darwinii and the potential extinction of Rhinoderma rufum (Soto-Azat et al., 2013b; Valenzuela-Sánchez et al., 2017). In addition, Alvarado-Rybak et al. (2021a) have reported a severe mortality event in a captive breeding program of Calyptocephalella gayi in Chile due to a chytridiomycosis outbreak. In Argentina, the presence of Bd in some amphibian populations was not directly associated with declines, as observed in Atelognathus reverberii (Arellano et al., 2015), Alsodes pehuenche (Ghirardi et al., 2014), and Pleurodema somuncurense (Arellano et al., 2017). However, Bd-related mortality events were reported for Atelognathus patagonicus, Telmatobis atacamensis and Telmatobius pisanoi (Fox et al., 2006; Barrionuevo & Mangione, 2006). Also, this chytrid was identified as the potential cause of a severe mortality event in a captive breeding program of Pleurodema somuncurense (Kacoliris pers. obs.). Since Bd alone or in synergy with other threats is prone to cause amphibian decline and mortality, it should be monitored over time.

Our MCA showed that small-holder grazing, ranching, or farming was the second most common threat associated with declines. This threat category affects several amphibian populations that cover small ranges and/or occur in remote locations. Of the 57 populations assessed, 25 (44 %) have distribution ranges of less than 10 km²; 25 have ranges of less than 500 km², while only 7 (12 %) have ranges greater than 500 km². Alsodes montanus, Atelognathus nitoi, Atelognathus patagonicus, Ceratophrys ornata, Eupsophus insularis, Eupsophus migueli, Melanophryniscus nigricans, Odontophrynus lavillai, Pleurodema somuncurense, Rhinella rubropunctata, Rhinoderma darwinii, and Rhinoderma rufum were among the endangered amphibians with small ranges affected by this threat category. The scenario for Rhinoderma rufum is the worst among the populations assessed in this study since it has been considered Possibly Extinct since 1981 (Soto-Azat et al., 2013a). Although the assessed population of Ceratophrys ornata, which covers less than 10 % of the species' range in Argentina, was moderately affected by this threat, it was mainly affected by other threats such as urban and tourism activities, road construction, and agriculture. It is important to note that, throughout its range, habitat loss due to agriculture could be one of the main threats to Ceratophrys ornata (Vaira et al., 2012; Deutsch, Bilenca & Agostini, 2017).

The methodology applied in this study analyzed the relationship between the observed declines and the main threats that affect amphibian populations in a broad framework (i.e., considering all the assessed populations). However, in particular cases, a threat that did not show a strong relationship with population decline was identified as having a high impact on some target populations. For example, climate change was identified as a major threat to *Alsodes pehuenche*, in synergy with small-holder cattle ranching. The decrease in winter snowfall caused a reduction in water flow and the drying up of several streams occupied by this species. This change in water availability affected this frog due to habitat reduction and promoted a shift in the local economy. The lack of quality grasslands pushed farmers to switch from goat to cattle farming, leading to further impact on the habitat due to trampling and increased water demand. Consequently, frogs that survived the drought now face the impact caused by cattle.

In addition, some studies analyzed the impact of climate change on *Rhinoderma darwinii*. Using species distribution models and considering dispersal limitations, Uribe-Rivera et al. (2017) estimated a 23–40 % reduction in suitable habitats for this species between 1970 and 2010 due to climate change alone. Estimation of future impacts of climate change on suitable habitats for *Rhinoderma darwinii* predicted a loss of up to 56 % of its potential range by 2080 (Azat et al., 2021).

Mining was the main threat to the Critically Endangered frog *Telmatobius dankoi* (Lobos and Azat, pers. obs.). This species is found in a single locality near the city of Calama in northern Chile. In June 2019, the only habitat occupied by this species dried up completely, probably due to water abstraction for mining activities. Currently, one pond sustains the last surviving wild population of *Telmatobius dankoi*, the most threatened Chilean amphibian.

Even if the main threats are alleviated, 45 % of the assessed populations (79 %) still have other intrinsic conservation problems that affect their long-term survival and genetic diversity. Intrinsic conservation problems are related to biological, population, and ecological traits and not necessarily to external factors such as human impacts. However, it is worth mentioning that intrinsic conservation problems and external threats often act together (e.g., small natural range coupled with human-mediated habitat loss and fragmentation). The most frequent intrinsic conservation problem reported in this study was related to natural connectivity. This situation is expected to affect amphibians with low population densities and restricted to small areas or habitats. Low population numbers, a frequently natural condition in several highly threatened and/or endemic amphibians, were associated with high impact among assessed populations of Atelognathus nitoi, Gastrotheca christiani, Gastrotheca chrysostica, Gastrotheca gracilis, Melanophryniscus nigricans, Phyllomedusa sauvagii, Pleurodema somuncurense, Rhinoderma darwinii, and Rhinoderma rufum. Historical records show that these species have naturally small population sizes (except for the Chilean populations of Rhinoderma, which were abundant before the 1970 s), a condition that likely worsened after the emergence and increase of human-related threats. The current density of these populations has reached a critical point, making their recovery more challenging. These low densities and the consequent loss of genetic diversity also impact the ability of populations to adapt to other threats, including disease and climate change. Demographic management and threat alleviation are necessary to ensure the continued viability of these populations, as established in the action plans for Rhinoderma darwinii, Atelognathus patagonicus, and Pleurodema somuncurense (IUCN, 2018; Kacoliris et al., 2018; 2019; Azat et al., 2021).

Research and management are underway to improve the conservation status of the amphibian populations assessed. Monitoring was the most reported ongoing research activity, while threat management was the most reported conservation activity. Worryingly, there are only a few reports of ongoing management to remove invasive species affecting the amphibian populations assessed. Invasive species removal is a major concern since our study recognized this threat as one of the threats most associated with population decline. Currently, incipient management of this type is being conducted for *Pleurodema somuncurense* (Kacoliris pers. obs.). Moreover, since 2005, comprehensive management for Atelognathus patagonicus conservation has been carried out in Laguna Blanca National Park, where perch and trout are being removed from the primary habitat once occupied by this amphibian (Sanguinetti et al., 2014). Invasive fish removal has been demonstrated to be highly effective in restoring amphibian populations (Knapp et al., 2007; Miró et al., 2020). Therefore, sound actions to remove invasive species and demographic management of highly threatened amphibians are needed to save relict populations of South American amphibians.

Our study suggests that 44 % of the populations studied in Chile and Argentina are declining. This value is slightly higher than that reported in the IUCN Red List species-level assessments. This worrisome scenario is associated with several threats, among which invasive species, emerging diseases, and small-holder cattle ranching were most commonly related to population decline. However, ongoing management actions to mitigate these threats are still insufficient. As mentioned in Sutherland et al. (2004), more information is urgently needed regarding the effect of management actions on habitat restoration, population recovery, and removal of threats such as invasive species. This information might help mitigate the conservation crisis facing amphibians in the Southern Cone.

5. Conclusions

Nearly half of the populations assessed in this study are declining, and one-third are experiencing local extinctions. The main threats associated with declines and local extinctions in our study were related to invasive predators, emerging diseases, and habitat perturbation

caused by cattle ranching. Invasive species and habitat perturbation must receive special attention from policymakers, practitioners, and resource managers to alleviate the erosion of genetic diversity among amphibian species. Our results are of great importance concerning risks related to species-level losses and conservation of genetic diversity (i.e., population and local population levels) by policy makers and practitioners. The large number of amphibian populations experiencing declines and local extinctions, increasing threats, and an overall lack of sound management plans lead to a perfect storm that threatens the long-term viability of South American amphibian species and populations. Alleviating the primary threats identified in this study (with particular emphasis on invasive species and habitat loss), undertaking activities to restore declining populations, and continuing monitoring and research are crucial to mitigating the plight facing most amphibian populations in the Southern Cone.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Kacoliris F, Arellano M, Di Pietro D, Kass N, Martinez-Aguirre T, Velasco M and Williams J want to thanks to Conservation Leadership Programme, Conservation Follow-up Award, Mohamed Bin Zayed Species Conservation Fund, People Trust in Endangered Species, Rufford Booster Grant, Amphibian Ark, National Geographic Society, EDGE of Existence, Fondo de Investigación Científica y Tecnológica (FONCYT, PICT 2018-00891), Consejo Nacional de Investigaciones Científicas y Técnicas, Proyectos de Investigación Plurianuales (CONICET, PIP 2021-2023). G. Agostini and C. Deutsch want to thanks to Neotropical Grassland Conservancy, Rufford Foundation and National Geographic Society for financial support. In loving memory of Dr. Phil Bishop.

Funding

This work was partially funded by Conservation Leadership Programme, Conservation Follow-up Award, Mohamed Bin Zayed Species Conservation Fund, People Trust in Endangered Species, Rufford Foundation, Amphibian Ark, National Geographic Society, EDGE of Existence, Fondation Ensemble, Fondo de Investigación Científica y Tecnológica (FONCYT, PICT 2018-00891), Proyectos de Investigación Plurianuales CONICET (CONICET, PIP 2021-2023), Proyecto de Investigación Orientada CONICET (PIO CONICET 094), Proyecto de Unidad Ejecutora CONICET (PUE INECOA 22920170100027CO) Fondo Nacional de Desarrollo Científico y Tecnológico (Fondecyt 1211587), Neotropical Grassland Conservancy, Amphibien-Fonds Stiftung Artenschutz, Idea Wild.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jnc.2022.126254.

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