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Biogeography of Chilean Herpetofauna: Biodiversity Hotspot and Extinction Risk

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1. Introduction

The distribution of living organisms on our planet is not random: evidence accumulated since the eighteenth and nineteenth centuries by the pioneering work of European explorers and naturalists documented the existence of large differences in the number and types of species living in different places on the planet (Brown & Lomolino, 1998, Meynard et al., 2004). The importance and impacts of a geographical approach to the study of biodiversity are evident today, after more than two centuries, as the observations of these early naturalists are still under active investigation. In this biogeographical context, the study of the most biodiverse areas, and understanding of the mechanisms that operate to maintain diversity are fundamental to the development of conservation strategies. However, conservation strategies must be built on a solid understanding the biota, as well as clear identification of the life history, dispersal, and biogeographic and environmental factors that affect a region's biodiversity (Meynard et al., 2004).

Few prior studies are available to develop a dynamic synthesis of the variables influencing herpetofaunal biogeography in Chile. The lack of basic information about the herpetofauna and its biology, and the dispersed nature of existing information have impeded studies in this area of knowledge (Vidal, 2008). Biogeographical studies often are been based on understanding relationships between phylogeny and geographic distribution (e.g., Brooks & van Veller, 2001), but such studies have not been possible on the Chilean herpetofauna primarily because the phylogenetic relationships among many groups have not yet been resolved. A robust biogeographical analysis is needed to enhance opportunities for further evolutionary research and to frame conservation strategies.

2. Biogeography

Biogeography is the science of spatial pattern of biodiversity, both present and past, and how such patterns arise. The development of this branch of ecology addresses many questions (Vidal, 2008), including: Why are species or taxonomic groups (e.g., genera, families, orders) confined to current distributional ranges (García-Barros et al., 2002); what factors restrict a species to a particular place, and what prevents colonization of other areas (Teneb et al., 2004); how and to what extent do climate, topography and interactions with other organisms limit the distribution of species (Losos & Glor, 2003); and how do environmental events and processes (e.g., continental drift, Pleistocene glaciation, climate change) shape the current distribution of species (Brown & Lomolino, 1998; Hughes et al., 2002)?

In essence, biogeography investigates the relationships between patterns (non-random distribution and repetitive organization) and processes (pattern causality) that determine the geographical distributions of organisms. Although biogeographers attempt to summarize these patterns and processes from different perspectives of study (e.g., descriptive biogeography, ecological, historical, paleoecological), the emphasis of each is under constant discussion (Vidal, 2008). Historical biogeography has been particularly controversial. According to Nelson (1969), "the problem of historical biogeography" was the lack of methodology to uncover patterns of association between organisms and their geographical distribution, and the absence of a general explanation for these patterns. He concluded that the key elements that could solve the "problem" are the combination of information from phylogenetic systematics and Earth history. Nearly 50 years later, historical biogeography has been divided into at least two lines of research, fundamentally differing in their concepts and analytical techniques on distribution (Brooks & McLennan, 2002). These two approaches involve inductive/verification and hypothetic-deductive/falsacionist (Brooks et al., 2001). The former, commonly known as vicariance biogeography or cladistic biogeography (e.g., Nelson & Rosen, 1980), is based on the assumption that vicariant speciation is the most recurrent and link phylogeny to historical geology. The second approach on the other hand, originated from the proposal of Wiley (1981) using phylogenetic relationships between species and their geographic distributions to explore the contribution of different modes of speciation.

The ultimate objective of biogeography is an evolutionary perspective (e.g., Morrone, 2007) to understand the past, present, and future of the biota, and from the perspective of conservation biogeography to promote strategies appropriate for species stewardship (Myers, 1988; Álvarez & Morrone, 2004). In recent years biogeography has begun to play an important role in biodiversity conservation issues (Tognelli et al., 2008) since, as discussed below, these studies identify areas of high diversity or endemism that may be a high priority for conservation programs.

2.1 Biogeography of the Chilean herpetofauna

One of the main questions in historical biogeography is how to delimit the areas of greater richness or endemism within continents (Nelson & Platnick, 1981; Humphries & Parenti, 1986; Cardoso da Silva & Oren 1996). This question is usually analyzed by means of overlapping distribution maps of taxa, which can be used to detect areas with a high concentration of overlapping species ranges (Haffer, 1978; Cracraft, 1985). However, methodological difficulties have been reported when analyzing a large number of species (Morrone, 1994). It also is somewhat subjective, since there are no defined criteria for analyzing the inconsistencies (Linder, 2001). Such studies have been conducted in both plants and animals (e.g., Heyer, 1988; Benkendorff & Davis; 2002, García-Barros et al., 2002; Teneb et al., 2004), allowing the visualization of distribution patterns of many species, which are then contrasted with the geomorphological and bioclimatic history of the study area (Brown & Lomolino, 1998).

The inventory of Chilean herpetofauna has been in a state of flux due to taxonomic instability, especially among the reptiles (Donoso-Barros, 1966; Veloso & Navarro 1988; Núñez & Jaksic, 1992; Pincheira-Donoso & Núñez, 2005). However, the geographical distribution of many species recently has been clarified, improving information on taxa known only from type localities (Formas, 1995) and the fauna of undersampled areas (Mendez et al. 2005), as well as information from Chilean herpetological collections (e.g., Nuñez, 1992; e.g., Sepúlveda et al., 2006; Correa et al., 2007).

In Chile we now recognize 191 species of herpetozoans, including species of sea turtles and the island species, but excluding introduced species. Of this, 59 are amphibians, assigned to 14 genera among four families (Table 1).

Family	Genus	Richness
Bufonidae	*Rhinella*	4
	Nannophryne	1
Cycloramphidae	*Rhinoderma*	2
	Alsodes	16
	Eupsophus	9
	Hylorina	1
	Insuetophrynus	1
Ceratophryidae	*Atelognathus*	2
	Batrachyla	4
	Chaltenobatrachus	1
	Telmatobius	10
Calyptocephalellidae	*Calyptocephalella*	1
	Telmatobufo	4
	Pleurodema	3
Total: 4 familes	14 genera	59 species

Table 1. Families, genera, species number of amphibians found in Chile.

Reptiles include for 131 species, assigned to 17 genera among nine families (Table 2). Although the herpetofauna of Chile is low compared to other Neotropical countries, many authors have recognized Chile's high level of endemism. Formas (1979), Ortiz & Díaz-Páez (2006) and Vidal (2008) reported that 67%, 61% and 55% (respectively) of amphibians are endemic to Chile, while Veloso et al (1995) and Vidal (2008) indicate that 50% and 48%, respectively of reptiles are endemic. These authors considered different criteria to determine the endemism of particular species, illustrating the need for clear definition of the concept. High levels of endemism have been interpreted as the result of endogenic diversification (Figure 1) due to the existence of the natural barriers of the cold Pacific Ocean, the Andes, the Atacama Desert to the north, and extreme weather conditions in the south (Torres-Mura, 1994; Schulte et al., 2000; Díaz-Páez et al., (2002).

Although these natural isolating barriers have encouraged endemism, present-day herpetofaunal biogeography is the result of Pleistocene and earlier Cenozoic epochs, including the long and complex forest history of Patagonia. Glaciers were recently more extensive in Patagonia, covering most of southern continent. During episodes of glacial

Family	Genus	Richness
Dermochelyidae	*Dermochelys*	1
Cheloniidae	*Chelonia*	1
	Caretta	1
	Lepidochelys	1
Colubridae	*Tachymenis*	2
	Philodryas	4
Elapidae	*Pelamis*	1
Teiidae	*Callopistes*	1
Scincidae	*Cryptoblepharus*	1
Leiosauridae	*Diplolaemus*	4
	Pristidactylus	4
Tropiduridae	*Liolaemus*	94
	Phymaturus	6
	Microlophus	6
Gekkonidae	*Homonota*	2
	Lepidodactylus	1
	Phyllodactylus	1
Total: 9 families	17 genera	131 species

Table 2. Families, genera, species number of Chilean reptiles.

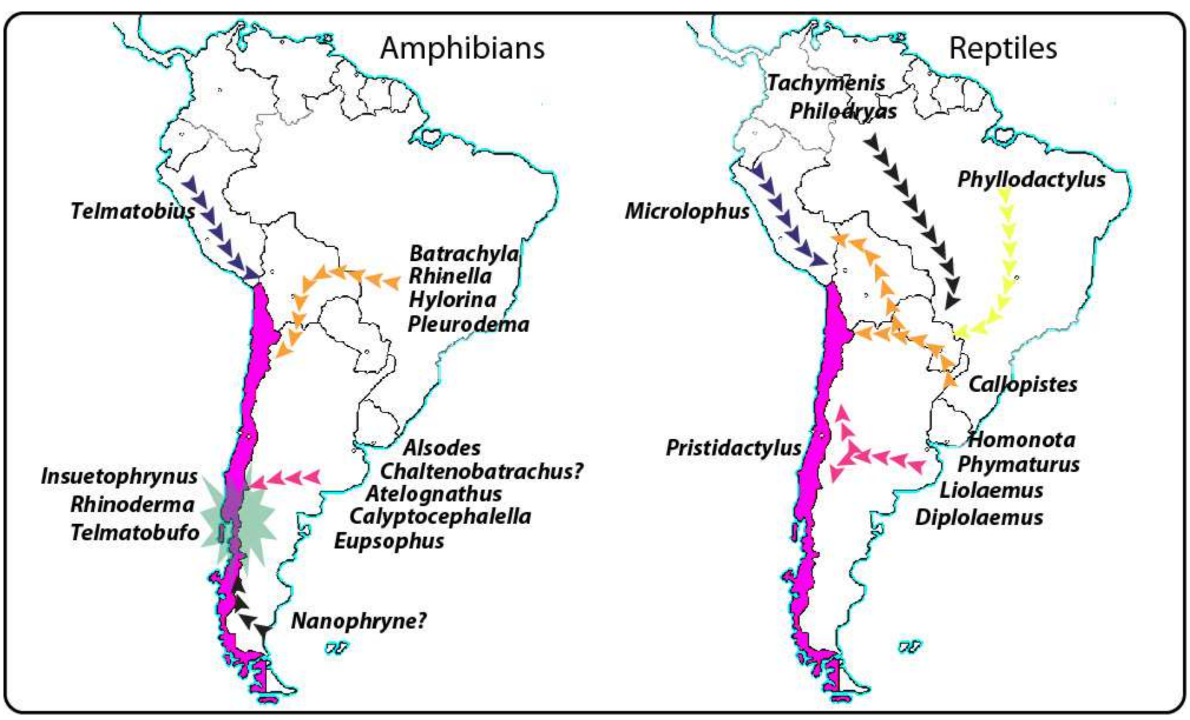

Fig. 1. Scheme representing the different origins of the genera of extant Chilean amphibians and reptiles, based on Vuilleumier (1968), Lynch (1978), Duellman (1979), and Cei (2000) and Basso et al (2011).

maximum herpetofaunal species associated with *Nothofagus* forests may have disappeared or, alternatively, may have been isolated in one or more refugia in southern South America, later expanding their ranges northward after the retreat of the glaciers (Vuilleumier, 1968; Lynch, 1978; Duellman 1979). However, according to Cei (2000), older parents of the fauna can be placed chronologically at the Cretaceous-Paleocene boundary, i.e. in the initial phase of the Andean uplift, which lead to the current configuration and topography of South America. Overall, some herpetofaunal species and genera have colonized the Andean biogeographic province from different parts of South America, while many taxa diversified *in situ* during late Cenozoic time (Figure 1).

The geographic distribution of both amphibians and reptiles shows the opposite distribution along to north-south axis in Chile. As shown in Figure 2, amphibians are found mainly in the central-southern Chile, while reptiles occupy the center-north. The genus *Telmatobius* is the only genus represented exclusively in the northern Chile, with species distributed mainly in elevation. Among the amphibians, *Rhinella* and *Pleurodema* have wide geographic ranges from 18 º S to 49 º S, but include few species. A few genera have restricted distributions, such as both *Atelognathus* (which has a few species) and *Insuetophrynus* (a monospecific genus). In contrast, other genera have wide geographic distributions, including *Hylorina* or *Calyptocephalella*, both of which are monospecific genera. Probably, the wide range of current distribution is due to the origin of these latter genera within the region (Duellman, 1979). Recently, Basso et al. (2011) reported a new genus in the family Ceratophryidae: *Chaltenobatrachus*, which has been described as monotypic genus (*C. grandisonae* = *A. grandisonae*) related to *Atelognathus*. The existence of *Chaltenobatrachus* in the region may be similar to the evolutionary history of *Atelognathus*, *Batrachyla* and *Hylorina*; however, given the recent description, it is difficult for us to explain its origin in the Argentinian-Chilean Patagonia.

Among the reptiles (Fig. 2), the genus *Liolaemus* has the largest range, while other genera, except *Microlophus*, *Phymaturus* and *Phyllodactylus* have intermediate sized distributions. Interestingly, when comparing the diversity of both groups, reptiles have a lower richness of genera than do amphibians. Moreover, within the reptiles no more than eight genera overlap in distribution, while among amphibians, up to 10 genera have overlapping ranges. This suggests that, at least for the reptiles, a few genera (e.g., *Liolaemus*, *Tachymenis*) have been able to adapt to a greater variety of environments, achieving greater diversification and breadth of geographic range (Vidal, 2008). On this point the geographic range of the genus *Liolaemus* may be related to the large number of species in Chile (Vidal et al., 2009). In contrast, the two *Tachymenis* colubrid species occur across a broad range, implying that it may be much more plastic than other reptile taxa.

3. Biodiversity hotspot

A biogeographic "hotspot" is a term was originally coined by Myers (1988, 1990) to refer to areas with elevated levels of species richness and endemism, and hotspots also often are areas that coincide with other human alterations. The term hot-spot was used by Prendergast et al. (1993) and Gaston & Williams (1996) to refer to areas of extreme taxonomic richness. While the initial definition contained restrictions, today this concept has been expanded and more overtly conceptualized, and from which, to contribute to new conservation strategies (Myers et al., 2000). For species richness and endemism, potential causal factors in the distribution patterns have been described, and which are associated with historical processes (Gaston, 2000; Allen et al., 2002).

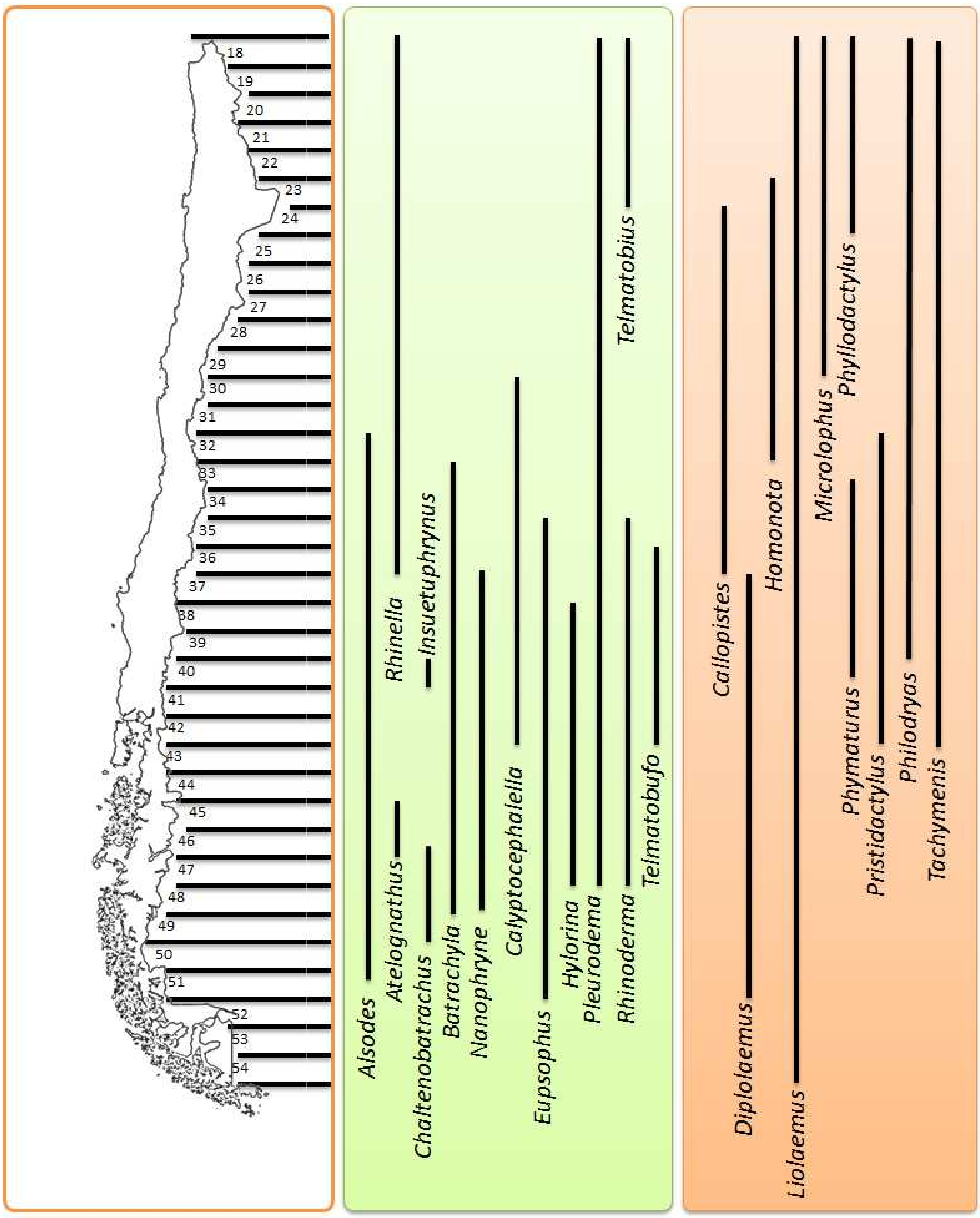

Fig. 2. Map of Chile showing diversity of amphibian and reptiles genera per degree of latitude.

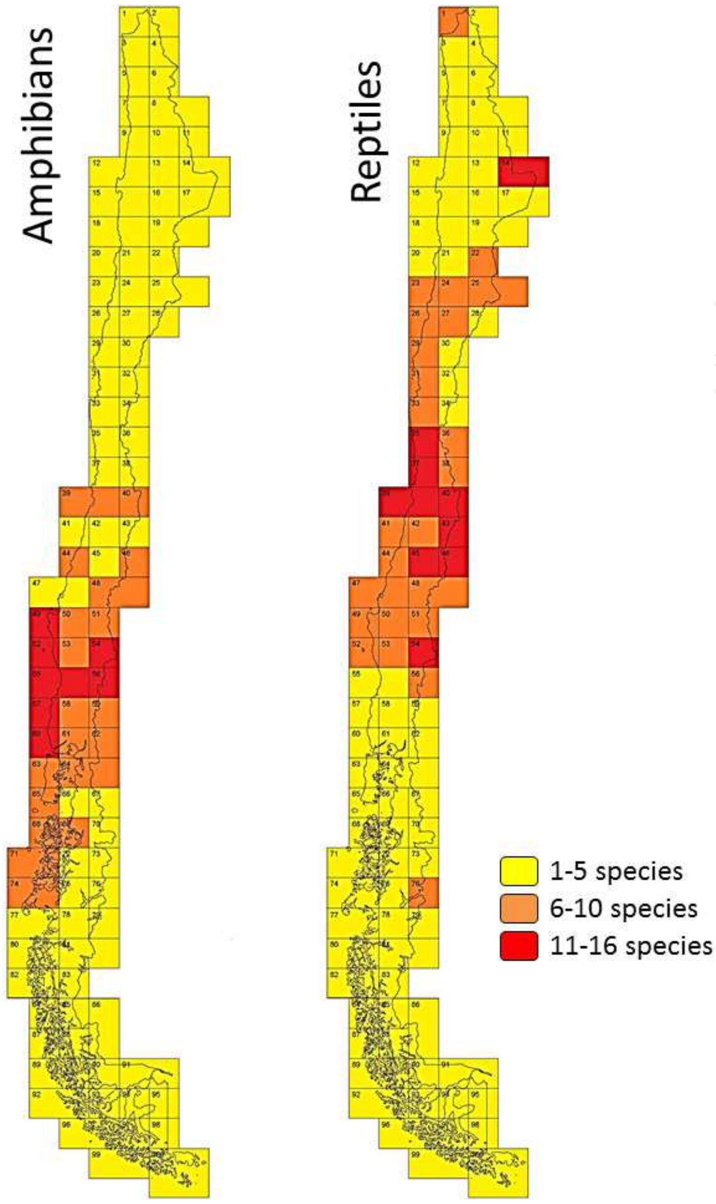

Fig. 3. Chilean amphibian and reptile species richness in 1° latitude by 1° longitude landscape quadrats (after Vidal, 2008). Quadrants in red show the highest species richness, with differences between amphibians (on the left) and reptiles (on the right).

In this context, many taxa are likely apomorphic species (apospecies; Moreno et al., 2006), which have not had sufficient time to move into other areas (e.g., *Eupsophus nahuelbutensis*, *Pristidactylus volcanensdis*), or correspond to ancestral forms (palaeospecies; Kirejtshuk, 2003;) that formerly occupied large areas (e.g., *Calyptocephalella gayi*, *Callopistes maculatus*) but now are restricted to small areas (Brown & Lomolino, 1998; Tribsch & Schönswetter, 2003; Cei, 2000). Thus, an area that concentrates many species (a hot-spot) may be an "evolutionary novelty", a site from which many new genera and species to emerge (Tribsch, 2004), whether remain endemic or not. Several potential hot spots have been reported in Chile, including the coastal range (Méndez et al., 2005; Smith-Ramírez, 2004; and in the Antofagasta region (Veloso & Núñez, 1998). In an analysis of endemism hotspots, Vidal (2008) considered the number of endemic species per degree latitude, finding hotspot located in north and central Chile (Fig. 3).

Interestingly, the distribution of herpetofauna are in direct relationship with its environment dependence, which would explain the presence of these proposed herpetofaunal hotspots coinciding with areas of higher winter rainfall in the Chilean-Valdivian forests (Chile Central), the hotspot proposed by Myers et al. (2000), and other in northern Chile. Both areas have the highest herpetofaunal species richness, but also more human intervention and fewer national parks that protect these species (Vidal et al., 2009).

4. Correlation between biological variables

Analysis of the conservation status of taxa in an area or country allows to link extinction risk with morphological, ecological and/or environmental variables. Studies focused on vertebrates have reported that several variables (e.g., body size) are positively associated with risk of extinction, ecological traits, phylogenetic and genetic features, and habitat degradation (Murray & Hose, 2005; Anderson et al., 2011). The loss of biodiversity of amphibians and reptiles has become an important global trend (Gibbons et al., 2000; IUCN, 2010). In this context, Corey & Waite (2008) suggest that threats to amphibians are concentrated in South and Central America, the Caribbean, and Australia. In addition, it has been suggested that some herpetozoan clades are especially prone to extinction by virtue of shared evolutionary histories (Lips et al., 2003; Case et al., 1998).

Body size among animals is directly related to physiological, morphological, ecological and evolutionary characteristics, as well as extinction risk. The relationship between body size and extinction risk recently has been a topic of interest to researchers because both variables are related to direct human influences (Fig. 4). As the body size of mammals increases so does the risk of extinction. However, similar studies of herpetozoa have not been conducted (Cardillo, 2003), nor have links between distribution, habitat conditions, and biological characteristics, such as body size. From our results, central Chile has a marked species concentration (Fig. 3). Biodiversity hotspots are biogeographic regions that are significant reservoirs of biodiversity and are threatened with destruction. Therefore, Chilean herpetozoa in this area are likely at increased extinction risk (Tribsch, 2004). Although the validity of this trend has been previously supported for herpetozoa, it has not yet been associated with other variables, such as body size, conservation status and extinction risk, as seen below.

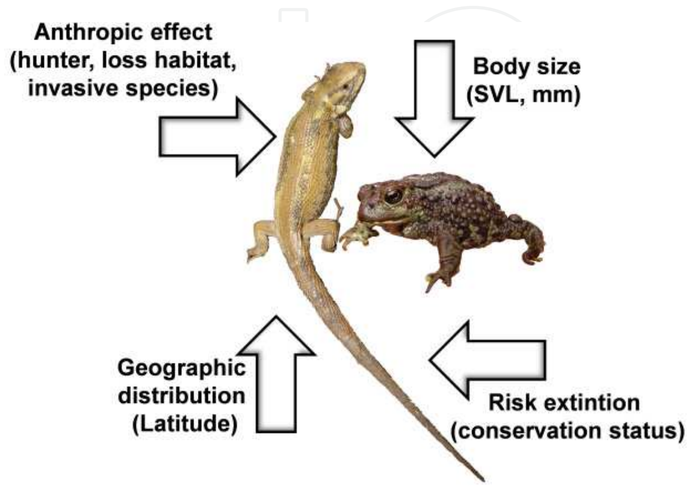

Fig. 4. Synergic effect of some variables involved in extinction risk among the amphibians and reptiles of Chile.

To evaluate extinction risk it is necessary to relate a species conservation status to variables realted to extinction. While Chilean herpetozoa are categorized at the species level as to conservation status, many taxa are categorized as Data Deficient (DD; IUCN, 2010). Here we consider species at risk of extinction, those species categorized as Critically Endangered (CE), Endangered (E) and Vulnerable (V), following categorizations for amphibians and reptiles as proposed by IUCN (2010), and Nuñez et al. (1997), respectively. In accordance to this are considered at risk only those species found within the categories mentioned above (EC, E, and V). By grouping them and observe their latitudinal distribution in which we can detect that Central Chile is an area with numerous species with elevated extinction risk. Of particular concern are reptiles in the north-central area from 25 ° to 44 ° S latitude, and amphibians in the south from 34 ° to 44 ° S latitude. This concentration of threatened and endangered species coincides with proposed biodiversity hotspot for herpetofauna in Chile (Fig. 3).

The scarcity of information on Chilean amphibians and reptiles prevents analysis of associative patterns: however, body size appears to be related of extinction risk for both classes (Meiri, 2008). In reptiles the risk of extinction increases with its frequency in quadrants, while in the case of amphibians restricted distribution is related to extinction risk (Fig. 5). These patterns appear related to human impacts on both classes because reptiles are

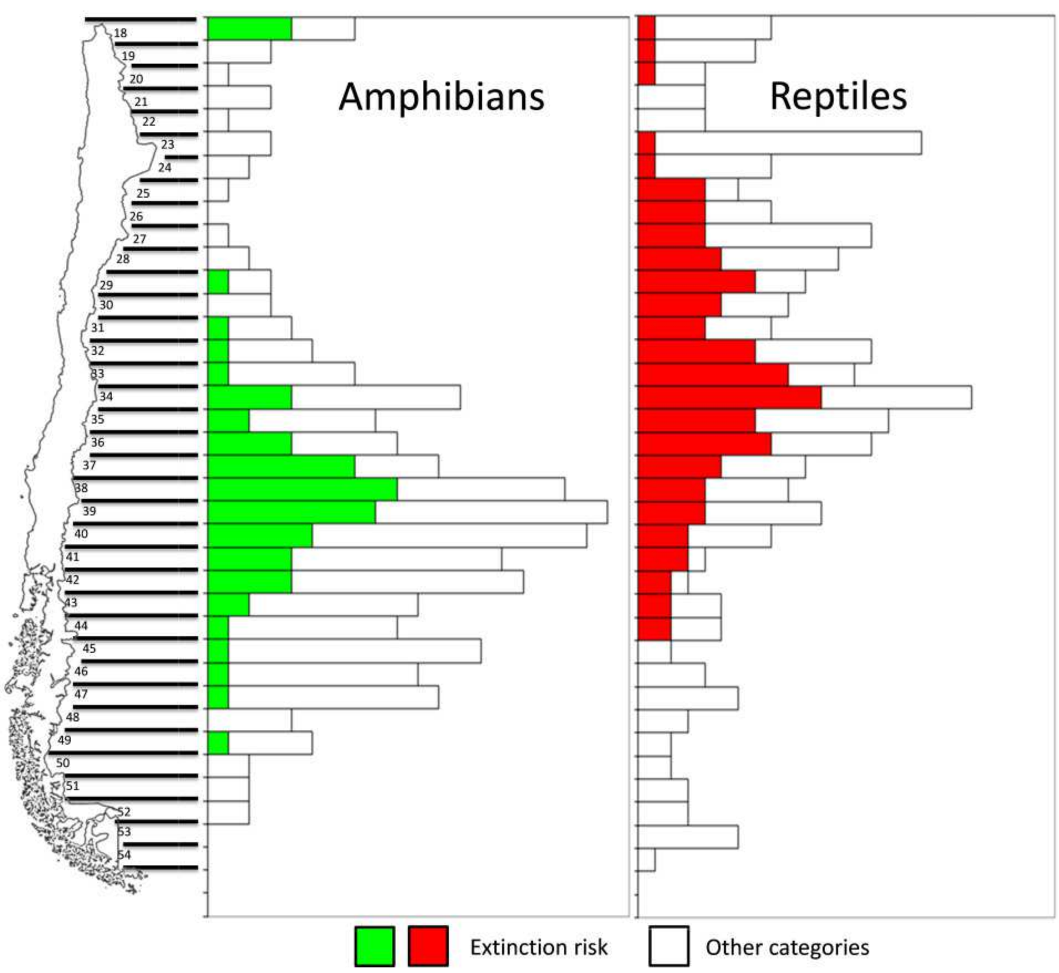

Fig. 5. Map of Chile showing herpetozoa taxa in relation to their extinction risk for each degree of latitude.

generally easier to observe and enjoy have greater interest on the part of man, whether due to aversive fear and beliefs, beauty (by virtue of colour, morphology, or as pets.) Furthermore, among amphibians the risk increases as frequency decreases, relating biological patterns and habitat dependence. It is intuitively obvious that the risk of extinction is greater for populations consisting of a few individuals than for those having many, but it also may be greater for populations undergoing greater flux than those with low temporal variability (Pimm et al., 1988).

Recent studies indicate that modern extinctions and declines of species have been phylogenetically selective (Cardillo, 2003). Thus, the habitat loss together the intrinsic traits some species make them particularly extinction-prone (Figure 4). Also, smaller-bodied species seem to be less vulnerable to decline and extinction than larger species (Gaston & Blackburn, 1995; Cardillo & Bromham, 2001). Furthermore, there may be tradeoffs between different traits; for example, smaller species may have an advantage in higher reproductive output and higher population densities, but larger species may have an advantage in greater mobility and energetic efficiency (Bielby, 2008; Sodhi et al., 2008). Nonetheless, larger vertebrates have a higher risk of extinction, and the explanation appears to be an inverse relationship between population size versus body size (Cardillo & Bromhman, 2001). In addition, the bigger the species the more vulnerable it may be to human persecution and hunting, while smaller species are generally more vulnerable to habitat loss due to anthropic activity (Cardillo, 2003; Sodhi et al., 2008). Similarly it has been established that smaller size confers greater protection.

We tested these extinction risk concepts using our Chilean herpetofaunal data. Among Chilean amphibians, the most important factor in risk is distribution (Figure 6, r Spearman = -0.52; $P<0.001$). For this class, size does not affect risk as much as habitat dependence; therefore, it appears that species with more limited ranges have the greatest risk of extinction. In contrast, body size among reptiles exacerbate extinction risk (Figure 6, r Spearman = 0.29; $P<0.05$), with many explanatory reasons. Thus, it is possible that body size directly determines a species' vulnerability: smaller species may, for instance, be less likely targets for human hunters, or less common prey items for invasive predators (Cardillo & Bromham, 2001). For example, *Calyptocephalella gayi* (Chilean Big frog) is the largest amphibian species in the country and is consumed due to their body size and good flavor of the meat. The species is broadly used for human consumption and an increase in the level of wild harvest has occurred since approximately 2000. The United States has been a significant commercial importer of wild-caught specimens of this species. From 2003 to 2007, 10,861 wild specimens were exported to the United States and were all traded for commercial purposes (Defenders of Wildlife, 2008). In the case of reptiles, *Callopistes maculatus* (Iguana Chilena) is the largest terrestrial reptile species and is negatively affected by traffic and trade (Auliya, 2003). According to Fitzgerald & Ortiz (1994), *C. maculatus* is "in danger" throughout its range due to habitat destruction, and in recent years by increasing harvest to meet international demand. During the years 1981-1991 this species sustained significant population loss from harvest, with the export of at least 2,400 live specimens (JNCC, 1993), which were sold as pets or used for the removal of skin (Díaz-Páez et al., 2008). Both of these large bodied species remain vulnerable to extinction due to harvest pressure.

Body size also may be correlated with other life-history or ecological traits that influence vulnerability, such as reproductive output, mobility, energy requirements or population density. Cardillo (2003) considered the additive impacts of environmental change on extinction risk. For example, the collapse of Pleistocene megafauna was exacerbated by environmental change, including deforestation (Sodhi et al., 2008).

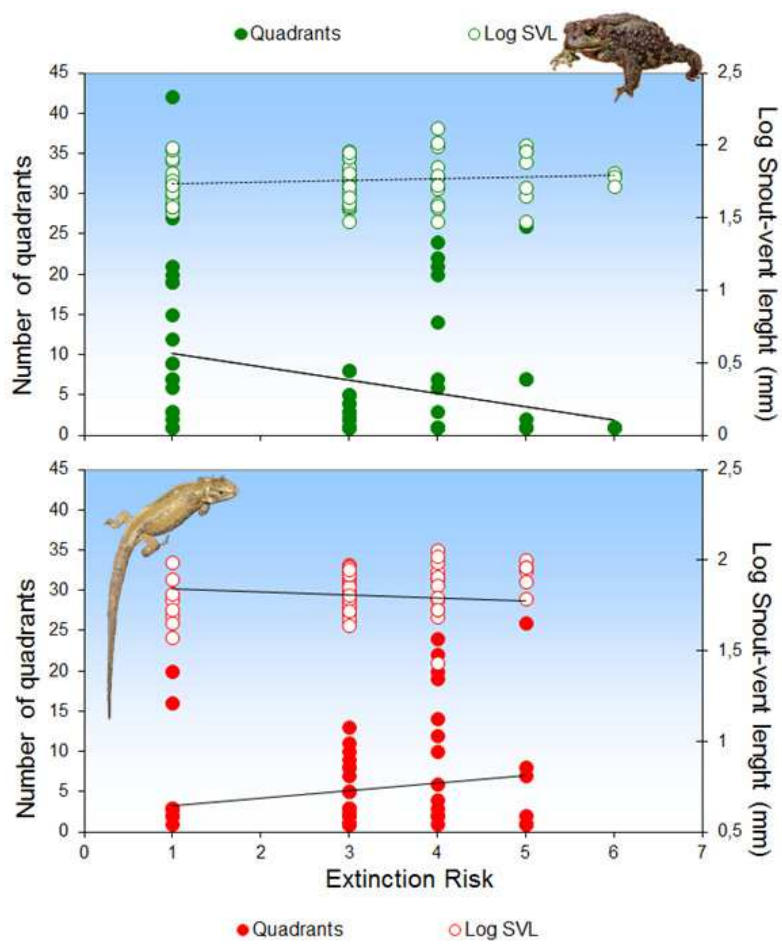

Fig. 6. Relationship between number of quadrants, snout-vent length (SVL) and extinction risk for Amphibians and Reptiles from Chile.

Behavioural, morphological, and physiological characteristics appear to make some species more susceptible than others to extinction. In general, large-sized species with restricted distributions and habitat specialization tend to be at greater risk of anthropogenic extinction than are others within their respective taxa (Sodhi et al., 2009). Our data support the findings of Cardillo (2003), who found that body size, distribution and ecological specialization increase the risk of anthropogenic extinction, especially in situations with rapid habitat loss.

5. Critical body size for conservation

Many studies suggest that larger bodied species are more susceptible to extinction than are smaller species (Cardillo & Bromham, 2001), while Murray & Hose (2005) reported no relationship. Our results show weak effect of body size on extinction risk in herpetozoans, although we note that snout–vent length was a predictor in the extinction risk (Figs. 5 and 6) based on IUCN status. There appear to be critical body size ranges in both classes: amphibians with small body sizes have a higher threat status, while increased body size in reptiles increases extinction risk. Similar analyses of Regional patterns from Australia and Central America corroborate our findings (Hero et al., 2005; Lips et al., 2003).

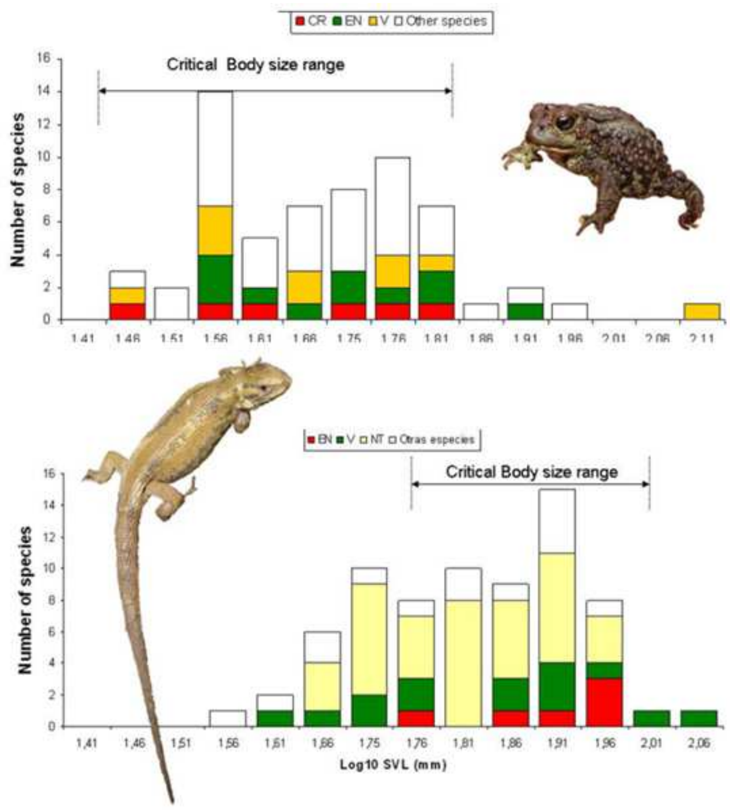

Fig. 7. Body sizes frequency distribution of Chilean herpetofauna, with status conservation according to IUCN (2010) for amphibians and Nuñez et al. (1997) for reptiles.

We used a combination of morphological and distribution data to elucidate extinction risk in Chile, finding that body size influenced extinction risk in opposite ways for the two classes (Fig. 7). Differences between our results and those of other analogous studies likely reflect different biogeographic realms (e.g., Australia Hero et al. 2005, Murray & Hose 2005, Williams & Hero 1998; or Central America Lips et al., 2003). Additionally, the biological traits underlying increased extinction risk/decline can and often do vary according to the particular threat involved, the environment of the location of study, and the species involved (Owens & Bennett, 2000). Our analyses explore the generalities that exist despite these differences, but will miss some of the specific regional correlates.

6. Conclusions

We present the first dynamic synthesis of the biogeographic variables affecting Chilean herpetozoa. Inadequate basic information has impeded or delayed studies in the Andean realm. Biogeographical knowledge plays a fundamental role in conservation because the relationship between geographic distribution and extinction risk can reveal new conservation issues and strategies. The herpetofauna of Chile has a lower richness relative to tropical and subtropical South America (Duellman, 1979) due to its prolonged geographical isolation (Armesto et al., 1995). This history of isolation has contributed to the uniqueness of Chilean herpetofaunal assemblage, with many endemic taxa (Arroyo et al., 1999; (Veloso et al., 1995). In Chile, amphibians and reptiles have the highest level of endemism of any vertebrate class, and endemism is focused in the hotspot in central Chile.

Different evolutionary processes are involved in anthropogenic extinction risk among the Chilean herpetofauna. Smaller species may have lower energy requirements and larger population sizes, making them more resilient to human disturbances. The higher reproductive potential of smaller species may reduce population recovery time following disturbance (Gaston & Blackburn, 1995). In contrast, larger species have lower reproductive rates and higher net energetic demands, requiring larger home ranges. We report a positive association between body size and extinction risk among reptiles. Larger species are affected more by harvest (Cardillo & Bromhan, 2001) and by habitat alteration, including the introduction of non-native species, as is happening in Chile today. Overall, we conclude that life-history traits influence extinction risk, with smaller-bodied amphibians affected by environmental changes, and larger bodied reptiles affected by harvest and habitat loss.

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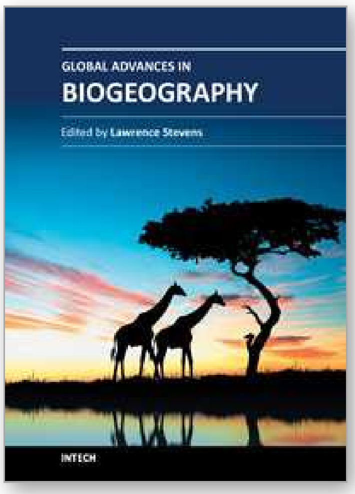

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