

Ecological functions of neotropical amphibians and reptiles: a review

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Abstract

Amphibians and reptiles (herps) are the most abundant and diverse vertebrate taxa in tropical ecosystems. Nevertheless, little is known about their role in maintaining and regulating ecosystem functions and, by extension, their potential value for supporting ecosystem services. Here, we review research on the ecological functions of Neotropical herps, in different sources (the bibliographic databases, book chapters, etc.). A total of 167 Neotropical herpetology studies published over the last four decades (1970 to 2014) were reviewed, providing information on more than 100 species that contribute to at least five categories of ecological functions: i) nutrient cycling; ii) bioturbation; iii) pollination; iv) seed dispersal, and; v) energy flow through ecosystems. We emphasize the need to expand the knowledge about ecological functions in Neotropical ecosystems and the mechanisms behind these, through the study of functional traits and analysis of ecological processes. Many of these functions provide key ecosystem services, such as biological pest control, seed dispersal and water quality. By knowing and understanding the functions that perform the herps in ecosystems, management plans for cultural landscapes, restoration or recovery projects of landscapes that involve aquatic and terrestrial systems, development of comprehensive plans and detailed conservation of species and ecosystems may be structured in a more appropriate way. Besides information gaps identified in this review, this contribution explores these issues in terms of better understanding of key questions in the study of ecosystem services and biodiversity and, also, of how these services are generated.

Keywords: ecological functions; Neotropical region; ecosystems; reptiles; amphibians

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Introduction

Amphibians and reptiles (herps) are an abundant and diverse component of many terrestrial and freshwater ecosystems (Pough et al. 2004, Wells 2007, Collins & Crump 2009), contributing to a diverse range of ecological functions (Young et al. 2004, Pough et al. 2004, Tyler et al. 2007, Wells 2007, Collins & Crump 2009). However, they are much less studied than mammals (Kunz et al. 2011) and birds (Sekercioglu 2006, Whelan et al. 2008), and scientific knowledge of their role in ecosystem functioning is inconsistent and incomplete (Urbina-Cardona 2008, Valencia-Aguilar et al. 2013).

The generally low level of understanding regarding the roles that amphibians and reptiles play in ecosystems is well illustrated by recent global studies (Bickford et



al. 2010, Hocking & Babbitt 2014). In response to evidence of rapid population declines of amphibians and reptiles worldwide (Rueda-Almonacid 1999, Gibbons et al. 2000, Lips et al. 2006, Reading et al. 2010), the International Union for the Conservation of Nature (IUCN) carried out a global evaluation and established criteria for determining the degree of threat to species of amphibians (Stuart et al. 2004), and a similar approach has been recently applied to reptiles (Böhm et al. 2012). Both studies identified considerable data shortfalls, and these were particularly apparent in the Neotropics - this region contains the largest number of amphibian species (49.2%) and has suffered the highest rates of population decline (63.1%) (Stuart et al. 2004).

The rapid and ongoing reduction of herp species richness worldwide has added urgency to efforts to understand the ecological roles that they play within ecosystems (Stuart et al. 2004, Lips et al. 2006, Connelly et al. 2011). The present work contributes to this goal by providing a heuristic framework for categorizing the functions of amphibians and reptiles in Neotropical ecosystems. Previously we explored the benefits to human society provided by elements of the neo-tropical herpetofauna (Valencia-Aguilar et al. 2013), here we explore their ecological roles; acknowledging these are not mutually exclusive. It is essential to understand the functional processes behind the ecosystem services, this new contributions seek to contribute to these gaps in knowledge. We describe the research trends of the past 20 years, identifying information gaps with respect to specific ecosystem functions and defining future investigation topics. As such, we aim to provide a robust database platform for future studies on how herps affect ecosystem functioning in the Neotropics, and how they are responding to the ongoing environmental changes within these ecosystems.

Materials and methods

This study was based on a review of the literature about the ecological functions of amphibians and reptiles in Neotropical ecosystems. Here, the term “function” denotes the relation between the parts (taxa) and the system, understood as the functions or roles that organisms perform within a system (Jax 2005).

Sources of information: Information was compiled from the following sources: a) the bibliographic databases ISI WEB OF KNOWLEDGE, JSTOR, EBSCO, Science Direct, SCOPUS, and Google Scholar; b) Book chapters containing information on Neotropical herps, and; c) Information provided by researchers. The search for information was restricted with keywords and boolean connectors (AND, OR). The following search words or terms were used: ecosystem function, ecological function, amphibian, reptile, tadpole, frog, toad, caecilian, salamander, lizard, snake, caiman, turtle, tortoise, role, bioturbation, decomposition, primary/secondary production, sediment, consumption, nutrient cycling, nutrient flow, excretion, biological control, mosquito control, diet, predation, food habit, seed dispersal, seed ingestion, dispersers, frugivore, saurocory, pollination, foraging, and flower.

Compilation of information: Studies published over the last four decades (1970 to 2014) and conducted in the 32 countries were compiled into a data matrix and analyzed by geographic region, year of publication, taxon (the study follows the current nomenclature for amphibians [Frost 2011] and reptiles [Uetz 2012]), type of experiment (field or laboratory), year of the study and ecological function.

Results and discussion

The total number of studies compiled resulted in 167, corresponding to: 67 % on amphibians and 33 % on reptiles. Most studies (76 %) were based in South America, followed by Central America (14 %) and the Caribbean (10 %) (**Figure 1**). The vast majority (95%) of the sources were from electronic databases, 4.35% from libraries and less than 1% was provided by researchers.

Several studies of ecological functions of amphibians and reptiles were grouped into the following five categories: nutrient cycling, energy flow through trophic chains (as predator and prey), bioturbation, seed dispersal, and pollination (**Table 1**), showing that the numbers of publications on these themes have increased considerably in recent years (**Figure 2**). Moreover, in the focus of the research, distinct historical trends were observed: in the 1970s, there was an emphasis on

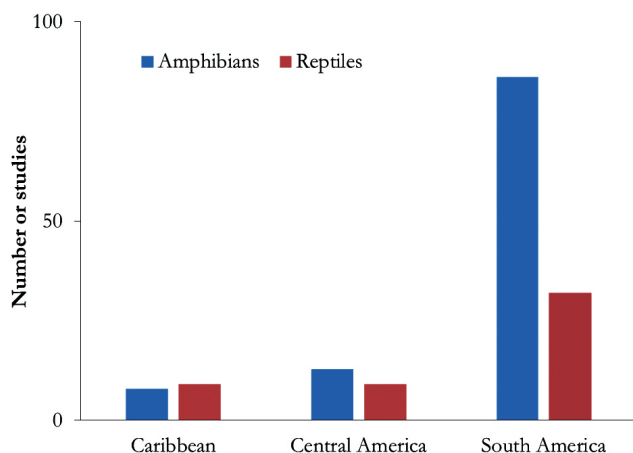


Fig. 1. Geographical origin of studies on Neotropical amphibians and reptiles.

nutrient cycling and energy flow through trophic chains. Studies performed in the 1980s began to discuss the role of herps in seed dispersal and by the 1990s, bioturbation arose as a distinct research topic. Finally, in the 2000s there was an increase in the number of studies focused on energy flow and seed dispersal. In this last decade some researchers also began discussing the role of reptiles (turtles and

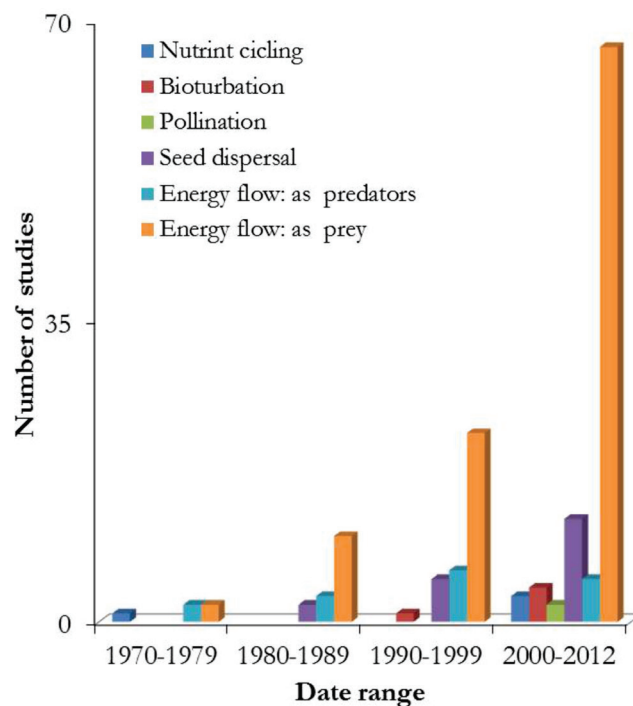


Fig. 2. Number of studies from the last four decades on the ecological functions of amphibians and reptiles in the Neotropics.

lizards mainly) in the pollination of plants (mainly in insular ecosystems).

Table 1. Number of studies evaluating the ecological functions of amphibians and reptiles in Neotropical ecosystems.

| Ecological function | Number of studies | | Species number | | References | |
|------------------------------------|-------------------|----------|----------------|----------|--|---|
| | Amphibians | Reptiles | Amphibians | Reptiles | | |
| Nutrient cycling | 3 | 1 | 2 | 1 | Fitkau (1970), Beard et al. (2002, 2003), Connelly et al. (2011) | |
| Bioturbation | 5 | 0 | 4 | 0 | Flecker et al. (1999), Arias et al. (2002), Ranvestel et al. (2004), Connelly et al. (2008), Colon-Gaud et al. (2010) | |
| Pollination | 0 | 2 | 0 | 1 | Sazima & Sazima (2005), Sazima et al. (2009) | |
| Seed dispersal | 2 | 17 | 1 | 18 | Da Silva et al. (1989), Da Silva & Britto-Pereira (2006), Iverson (1985), Fialho (1990), Traveset (1990), Cortes-Figueira et al. (1994), Moll & Jansen (1995), Willson et al. (1996), Varela & Bucher (2002), Castro & Galetii (2004), Celedón-Neghme et al. (2005, 2008), Strong & Fragoso (2006), Guzmán & Stevenson (2008), Jerozolimski et al. (2009), Rivera (2010), Sadeghayobi et al. (2011), Blake et al. (2012) | |
| Energy flow through trophic chains | as predators | 20 | 7 | 17 | 4 | Spielman & Sullivan (1974), Heyer et al. (1975), Henderson et al. (1987), Pérez-Higareda et al. (1989), Michaud & Dixon (1989), Spiller & Shoener (1990, 1997), Dial & Roughgarden (1995), Marques & Sazima (1997), Da Costa et al. (1998), Duarte et al. (1999), Rodríguez & González (2000), Bernarde et al. (2000), Wild (2001), Peltzer & Lajmanovich (2003), Verdade et al. (2000), Vaz-Silva et al. (2003), Zuffi (2004), Peltzer et al. (2005), Attademo et al. (2005, 2007a, b), De Souza et al. (2009) |
| | as prey | 78 | 23 | 74 | 19 | Suppl.1 |

Eighty-two percent of the studies evaluated the role of amphibians and reptiles in energy flow through trophic chains, 12 % documented the importance of reptiles (mostly lizards and tortoises) for seed dispersal and the viability of the seeds after being excreted. Only 1 % of the studies investigated the role of herps in the pollination of plants, and all of these studies focused on reptiles. Three from five functions were reported through all of the studies for both amphibians and reptiles (Table 1).

Seventy-three percent of the papers reviewed were anecdotal field observations, half of which were carried out on reptiles. Only 27 % of the studies were experimental (field and laboratory research), including 13 % performed on amphibians and 14 % on reptiles. Both experimental and observational studies were conducted at different spatial and temporal scales, with a minimum duration of a day or a month (for the observational and experimental studies, respectively) and a maximum of two years (in the case of one experimental study).

In the observational studies only qualitative variables were used to describe the data (mostly regarding predation). In contrast, both qualitative and quantitative data were collected in the experimental studies to describe feeding habits and behaviors, to characterize assemblages, to evaluate and measure the effects of the presence and absence of certain species of amphibians and reptiles on other animal populations (e.g., control over population densities of herbivore arthropods) and plant populations as in the case of seed dispersal). As well as to compare dynamics, to estimate population movements, and to study mutualism (e.g., pollination and the seed dispersal).

The roles of 142 species of amphibians and reptiles were documented for the five ecological functions identified (Table 1). Of these species, 93 were amphibians belonging to three orders and 17 families. Hylidae and Bufonidae exhibited the greatest number of functions documented, with four and three, respectively. Whereas for Centrolenidae, Eleutherodactylidae, Leiuperidae, Leptodactylidae, and Ranidae, only two functions were documented. For reptiles, 49 species were reported, belonging to three orders (two sub-orders) and 17 families. Alligatoridae, Iguanidae, Scincidae, Teiidae, Tropiduridae, and Testudinidae were the families with the greatest number of functions documented, with two each one.

Ecological Functions

Nutrient cycling: Animals are important in nutrient cycling through their effect on nutrient flow and consequently in the availability, inputs, recycling, and loss of these nutrients in the ecosystem (Vilá 1998, Milton & Kaspari 2007). Animals can provide nutrients through excretion (e.g., nitrogen and phosphorus) at rates comparable with mineralization and biological fixation (Hickerson et al. 2012). For example, some fishes excrete nutrients in organic (urea) or inorganic forms (ammonia and phosphate) at rates potentially important for primary producers and heterotrophic microbes, supporting a substantial part of their demands for nutrients (Vanni 2002, Contosta et al. 2011). Given the high population densities ($\sim 20,000$ individuals ha^{-1}) of species such as *Eleutherodactylus coqui* (Stewart & Woolbright 1996) in tropical forests, herps clearly have the potential to significantly affect the concentrations and flow of nutrients (Sin et al. 2008). *E. coqui* and other similar abundant species, increase nutrient availability through their residues (feces, urine, and carcasses) and population movements increasing the rate of recycling in the ecosystems where they are present.

The coqui frog (*E. coqui*) has been observed to produce approximately 8.9 Kg of feces per hectare per year, which contain 34.2 % C and 5.7 % N. In addition, the urine contains 4.5 % DOC, 3.3 % Ca, 3.1 % K, and more NH_4^+ than NO_3^- , elements and nutrients that are used by plants for their growth, development, and productivity (Beard et al. 2002, 2003). This increase in the rate of cycling is possible because, in spite of their size, *E. coqui* returns energy to the system in more assimilable forms (NH_4^+) as a result of the large quantity of the nutrients they ingest through their prey. Similarly, this frog can reduce by 28 % the number of aerial invertebrates, reduce herbivory (by approximately 80 % on a small scale), and increase the production of new foliage in plants and the rate of succession in forests after a perturbation, when the densities of plants in early succession and the density of the frogs are high. Conversely, the absence of *E. coqui* may reduce the quantity of K (between 5.7-6.6 Kg/ha) and P (between 3.1-3.7 Kg/ha) available for the decomposition of the litter, with serious consequences for the rates of nutrient cycling, since these elements are essential for microbial activity and plant growth (Beard et al. 2002, 2003).

Tadpoles of *Espadarana prosoblepon*, *Sachatamia albomaculata*, *Hyalinobatrachium colymbiophyllum*, and *Centrolene* sp. have also been observed to play an important role in the cycling of nutrients in the aquatic systems they inhabit in Panama. These tadpoles feed by scraping the surface of decomposing leaves thereby stimulating fungal activity in the litter (Connelly et al. 2011). This increase in fungal biomass may be due to the high rates of excretion of nutrients by the tadpoles during the dry season, when their densities are high, tadpoles can excrete between 0.15 and 3.6 $\mu\text{g/hr}$ of ammonia, which represents approximately 7 % of the volume of absorption in these systems (Whiles et al. 2006).

The rate of nutrient cycling in ecosystems can also be affected by the relocation of nutrients caused by the behavior of the consuming organisms (Kitchell et al. 1979). For example, during the 1970s fish populations in some central Amazonian lakes were observed to be declining, a trend that was linked to the loss of caimans from these habitats (Fittkau 1970, 1973). Given that the waters in these lakes are quite poor in essential electrolytes, primary production is almost impossible, and the food chain is based on organic material that enters the water from the surrounding forests. Fishes originating from other tributaries migrate to these lakes to reproduce, serving as food for the caimans and other organisms, such as predatory fishes, turtles, and aquatic mammals. These and other allochthonous foods are rapidly transformed into nutrients and expelled by the caimans, and other predators, through their feces into the system, serving as a base for limited primary production that is then consumed by a new generation of fishes, thus maintaining the trophic network. This pattern probably explains why the disappearance of the caimans apparently affected the biological communities of the lake, especially of the fishes.

Further research is especially needed on the impact of the presence (or absence) of tadpoles, juveniles, and adults on the concentration and availability of nutrients, population density (of the species present at various trophic levels), plant biomass, and primary productivity at different temporal and spatial scales. Specifically, researchers need to quantify the degree to which activities such as feeding, excretion (feces and urine), the construction or use of burrows, and

population movements may be affecting the energy and nutrient flow in aquatic and terrestrial systems.

Bioturbation: Bioturbation refers to the influence of organisms on the physical structure of the benthic habitat. According to Moore (2006), the bioturbators, are a type of ecosystem engineering in streams, and are defined as organisms that directly or indirectly control the availability of resources to other organisms through the “physical modification, maintenance, or creation of habitats” (Jones et al. 1994). For example, some freshwater vertebrates and invertebrates can significantly influence the deposition of sediments, sediment levels in the substrates, and the oxygen content in the substrate through their behavior and by the ingestion of fine particulate matter (Connelly et al. 2008, Creep et al. 2010). Tadpoles can be important bioturbators, directly or indirectly modifying the distribution of sediments and directly influencing the trophic dynamics and the energy flow in the system (Flecker et al. 1999, Ranvestel et al. 2004).

Tadpoles of *Pseudis paradoxa* and *Lithobates palmipes*, which actively consume periphyton and sediments rich in organic matter, provide a clear example of amphibian induced bioturbation. These tadpoles modify the structure of the habitat during their foraging activities by reducing the accumulation of sediments. This, in turn, benefits other consumers that do not process the sediments as efficiently as benthic insectivorous fishes (*Characidium*), which must filter their food through sediment because they are not morphologically equipped to obtain nutrients from detritus (Flecker et al. 1999, Arias et al. 2002, Solomon et al. 2004).

Direct consumption of organic sediments by tadpoles is a mechanism for the resuspension of the sediments in rivers. Thus, tadpoles can represent a connection between deposited particles and those that are entrained (Whiles et al. 2006). In some aquatic systems in Panama, tadpoles of *Atelopus zeteki*, *Lithobates warszewitschii*, and *Hyla* sp. consume periphyton, organic and inorganic sediments. This reduces the total quantity of these resources in the ecosystem and influences the biomass, diversity, and dynamics for periphyton and sediments. Furthermore, these grazers can facilitate primary production in tropical streams by removing sediments. Similarly, the physical perturbation associated with the feeding

activities of tadpoles also influences the dynamics of the sediments (Ranvestel et al. 2004, Whiles et al. 2006). The absence of these tadpoles would cause an increase in benthic sedimentation and the biovolume of algae, potentially affecting basic resources and the functional structure of the trophic assemblage (Ranvestel et al. 2004, Connelly et al. 2008, Colon-Gaud et al. 2010a). Nevertheless, the impact of tadpoles on the structure and function of an aquatic system varies, and the removal of one or more species may not have significant effects due to ecological redundancy (Colon-Gaud et al. 2009, 2010b).

Pollination: Pollination can be directly affected by biological interactions between animals and plants, potentially benefiting both groups of organisms (Godínez-Álvarez 2004). Although the role of reptiles in pollination has rarely been considered, there is evidence that lizards can play an important role in plant reproduction, with this process apparently being more important on islands than on continents (Godínez-Álvarez 2004). In Brazil, during the dry season, the lizard *Trachylepis atlantica* visits the flowers of the tree *Erythrina velutina*, attracted by secretions of diluted nectar which the lizard uses as a source of water and energy. During the day, the lizard forages in the inflorescences, introducing its head into the flowers to lick up the nectar that accumulates at the base. As the lizard moves among the inflorescences, grains of pollen adhere to the scales of its head, shoulders, abdomen, and extremities. *T. atlantica* may thus be acting as a pollinating agent for the flowers of *E. velutina*, because foraging and bodily contact with the anthers and stigmas of the inflorescences would favor the cross-pollination of these trees (Sazima et al. 2005, 2009).

Seed dispersal: Most tropical plants produce fleshy fruits that are consumed principally by frugivores, which act as dispersers of numerous seeds. Differences in behavior among dispersers may influence the patterns of distribution of the seeds and thus the structure of the forest (Clark et al. 2001). Amphibians and reptiles are mainly considered to be carnivores. However, some herbivorous lizards, tortoises and turtles may play an essential role in the reproduction of some plants through their role in seed dispersion (Valido & Olesen 2007, Galindo-Urbe & Hoyos-Hoyos 2007). Few studies have evaluated the role

of amphibians as potential disseminators of seeds. Nevertheless, there is evidence that this process can occur: Da Silva et al. (1989), Fialho (1990), and Da Silva & Britto-Pereira (2006) observed that *Xenohyla truncata* intentionally consumed fruits of *Anthurium harrisii* and *Erythroxyllum ovalifolium* in a sand-dune ecosystem in Brazil. When *A. harrisii* fruit was given to *X. truncata* frogs, they consumed the fruit and excreted the seeds, which successfully germinated under laboratory conditions. Furthermore, it was noticed that fruits of these plants are commonly ingested by this frog in the dunes over the course of a few months. Based on these observations, the authors suggest that *X. truncata* consumes the fruit of both plants as part of its diet, and frequently defecates the seeds onto the axils of the bromeliad *Neoregelia cruenta*, increasing the possibility of germination in relation to those that fall onto the sandy ground.

Various lizard species have been recorded to consume fruits and seeds (Table 2), demonstrating their potential role in the reproduction of some plants (Godínez-Álvarez 2004). For example, the lizard *Cyclura* disperses the seeds of *Eugenia uniflora*, *Genipa americana*, *Cereus peruvianus* and *Solanum viarum*, distributing them in places favorable for germination and establishment (Castro & Galetti 2004). Likewise, *Tropidurus torquatus* actively consumes fruits of *Erythroxyllum ovalifolium* during the dry season, defecating the seeds in open areas and sandy soils where they are usually preyed upon by insects and do not germinate (Fialho 1990). Even though *T. torquatus* is not an efficient disperser of *E. ovalifolium*, it is more effective dispersing the seeds of *Melocactus violaceus* (seeds founded in the excreta of the lizards germinate more rapidly than those that are not consumed). Moreover, *Melocactus* sp. exhibits a number of specific adaptations (size and bright color of the fruit and its diurnal pattern of release), that make the fruits more likely to be dispersed by *T. torquatus* (Cortes-Figueira et al. 1994).

Many Neotropical lizards consume fruits that are very different in type, size and color, affecting seed germination (Godínez-Álvarez 2004). Consuming fruits can influence the dormancy and germination of the seed, the probability of survival, and the rate of growth of the seedling (Valido & Olesen 2007) (Table 2). For example, seeds of *Coccoloba uvifera* and *Casasia clusiiifolia* germinated rapidly after passing

Table 2. Plants frequently consumed and dispersed by nine species of lizards in five countries in the Neotropics. * Common germination rates for seeds consumed by lizards and for those seeds that were not consumed. + Higher germination rate for seeds consumed by lizards than for seeds not consumed. – No information.

| Country | Consuming species | Species consumed | % Seeds in feces | % Viability of seeds | % Seeds germinated | Days of retention | References |
|------------|-------------------------------|------------------------------|------------------|----------------------|--------------------|-------------------|-------------------------------|
| Argentina | <i>Teiús teyón</i> | <i>Ziziphus mistol</i> | 59 | 99 | * | – | Varela & Bucher (2002) |
| Bahamas | <i>Cyclura rileyi</i> | <i>Casasia clusiaefolia</i> | | | 71 | | Iverson (1985) |
| | | <i>Coccoloba wifera</i> | – | – | 38,3 | 4 | |
| | <i>Cyclura carinata</i> | <i>Eugenia foetida</i> | | | 4,5 | | |
| | <i>Tropidurus torquatus</i> | <i>Melocactus violaceus</i> | 80 | viables | + | – | Cortés-Figueira et al. (1994) |
| Brasil | <i>Tropidurus torquatus</i> | <i>Eugenia uniflora</i> | | | 79 | | Castro & Galetti (2004) |
| | | <i>Genipa americana</i> | | | 95 | | |
| | | <i>Cereus peruvianus</i> | – | – | * | 1-2 | |
| | | <i>Solanum viarum</i> | | | 42 | | |
| Chile | <i>Liolaemus pictus</i> | <i>Nertera granadensis</i> | 62 | – | 50 + | 5-7 | Willson et al. (1996) |
| | | <i>Rebunium hypocarpium</i> | 28 | – | * | | |
| | <i>Phymaturus flagellifer</i> | <i>Calandrinia</i> sp. | 13 | 14 | + | | Celedón-Neghme et al. (2005) |
| | | <i>Rumex acetosella</i> | 10 | 7 | 73 | – | |
| | <i>Liolaemus bellii</i> | <i>Berberis empetrifolia</i> | 6,9 | 75 | * | | Celedón-Neghme et al. (2008) |
| Costa Rica | <i>Ctenosaura similis</i> | <i>Acacia farnesiana</i> | – | 100 | – | – | Traveset (1990) |

through the tract of *Cyclura* sp., which expelled the seeds in its feces four days after consumption. Trials of germination and tests of viability conducted with seeds of *Berberis empetrifolia*, *Rumex acetosella* and *Calandrinia* sp. consumed by the lizard *Phymaturus palluma* indicated that pass through the digestive tract has various effects: although the viability of the seeds of *B. empetrifolia* consumed by the lizard was greater than the viability of those that were not consumed, there were no differences in the percentage of germination. In contrast, the viability of the seeds of *R. acetosella* and *Calandrinia* sp. consumed by the lizard was lower than those obtained from fruits. However, the percentage germination of consumed seeds of *R. acetosella* was greater than those not consumed (Celedón-Neghme et al. 2005). Similarly, seeds of *Berberis empetrifolia* consumed by *Liolaemus bellii* showed a higher rate of germination after passing through the digestive tract. This improvement is most likely due to the modification of the seed coat within the digestive

tract, consumed seeds showed a greater deterioration than seeds extracted from fruits (Celedón-Neghme et al. 2008). Accordance to this information, *P. palluma* may be influencing the structure and diversity of the flora present in its habitat, and *L. bellii* may be acting as an effective disperser of *B. empetrifolia* because it improves the germination of seeds and deposits them in favorable sites for plant's development (Celedón-Neghme et al. 2005, 2008).

Some Neotropical tortoises (*Chelonoidis carbonaria*, *C. chilensis*, *C. denticulata*, *Rhinoclemmys funerea* and *R. annulata*) play an important role in the dispersion and germination of numerous plant species in forests in Argentina, Brazil, Costa Rica, Ecuador, and Peru. Seeds of plants from different species and a wide variety of families (Table 3) have been found in the feces of these tortoises. Most (91 %) of these seeds showed no signs of external damage and were viable, almost all germinated after being consumed and excreted

Table 3. Plants frequently consumed and dispersed by four species of tortoises in five countries in the Neotropics.* Common germination rates for seeds consumed by tortoise and for those seeds that were not consumed. + Higher germination rate for seeds consumed by tortoise than for seeds not consumed. – No information.

| Country | Consuming species | Species consumed | % Seeds in feces | % Viability of seeds | % Seeds germinated | Days of retention | References |
|-------------------------------|--------------------------------|-------------------------------|------------------|----------------------|--------------------|-------------------|---|
| Argentina | <i>Chelonoidis chilensis</i> | <i>Ziziphus mistol</i> | 50 | 91 | * | 6-9 | Varela & Bucher (2002) |
| | | <i>Prosopis nigra</i> | 29 | 91 | – | 7-8 | |
| | | <i>Celtis pallida</i> | 21 | 91 | + | 4-6 | |
| Brasil | <i>Chelonoidis carbonaria</i> | <i>Ficus</i> sp. | 62 | 100 | – | 3-17 | Strong & Fragoso (2006), Jerozolimski et al. (2009) |
| | | <i>Aechmea</i> sp. | 14 | 93 | – | | |
| | | <i>Genipa americana</i> | 9 | 91 | – | | |
| | <i>Chelonoidis denticulata</i> | <i>Jacaratia spinosa</i> | 49 | 95 | – | | |
| | | <i>Clarisia ilicifolia</i> | 5 | 94 | – | | |
| | | <i>Brosimum lactescens</i> | 4 | 96 | – | | |
| | | <i>Porouma guianensis</i> | 3 | 100 | – | | |
| | | <i>Tetragastris altissima</i> | 1 | 96 | – | | |
| | | <i>Spondias mombin</i> | 1 | 100 | – | | |
| | | <i>Celtis</i> sp. | 0,40 | 100 | – | | |
| <i>Attalea maripa</i> | 0,19 | 100 | – | | | | |
| Ecuador | <i>Chelonoidis nigra</i> | <i>Hippomane mancinella</i> | 2,37 | – | – | 6-28 | Blake et al. (2012) |
| | | <i>Opuntia echios</i> | 33,62 | – | – | | |
| | | <i>Psidium galapageium</i> | 41,81 | – | * | | |
| | | <i>Psidium guajava</i> | 38,15 | – | – | | |
| | | <i>Passiflora edulis</i> | 0,25 | – | – | | |
| Perú | <i>Chelonoidis denticulata</i> | <i>Rollinia</i> sp. | 2,81 | – | – | 21 | Guzmán & Stevenson (2008) |
| | | <i>Ficus cf. insipida</i> | 7 | – | – | | |
| | | <i>Ficus cf. maxima</i> | 2,33 | – | + | | |
| | | <i>Ficus</i> sp. | 46,67 | – | – | | |
| | | <i>Rauvolfia micrantha</i> | 1,14 | – | 59 | | |
| | | <i>Jacaratia digitata</i> | 0,63 | – | – | | |
| | | <i>Cecropia membranacea</i> | 3,82 | – | – | | |
| | | <i>Cecropia sciadophylla</i> | 4,91 | – | – | | |
| | | <i>Loreya strigosa</i> | 18,67 | – | – | | |
| | | <i>Miconia</i> sp. | 1,23 | – | – | | |
| <i>Helicostylis tomentosa</i> | 1,08 | – | – | | | | |

by the tortoises (Varela & Bucher 2002, Jerozolimski et al. 2009). A high percentage of seeds that were recovered from feces germinated more rapidly than those extracted directly from the fruits, possibly due to increases of the permeability of the seed endocarp (Varela & Bucher 2002, Jerozolimski et al. 2009).

The high abundance and diversity of viable seeds found in tortoise feces is partly a consequence of the inability of tortoises to chew and their limited capacity

to process what they ingest. Tortoises also exhibit a high mobility while they retain the seeds in their digestive tracts (Guzmán & Stevenson 2008, Jerozolimski et al. 2009). These characteristics make tortoises important seed dispersers, contributing to the colonization of new habitats and promoting genetic flow between sub-populations of plants. Tortoise-assisted dispersal also increases seedling survival by reducing predation, herbivory and infestation by pathogens (Moll & Jansen 1995, Strong & Fragoso 2006).

Energy flow through trophic chains: predators and prey:

Herps as predators. Herps can regulate populations of certain organisms through biotic interactions such as predation and competition. These processes, in the case of arthropods eaters, can reduce the number of adult individuals or larvae (Schmitz & Sokol-Hessner 2002, Maerz et al. 2005, Schmitz 2008, Homyack et al. 2010, Mooney et al. 2010, Best & Welsh 2014). For example, in the Bahamas, leaves of the tree *Coccoloba uvifera*, or seagrape, are often affected by Homoptera (Cicadellidae and Aphididae), Hemiptera (Pentatomidae), Coleoptera (Scarabaeidae), and larvae of Lepidoptera (Tortricidae, Noctuidae) and Hymenoptera (Formicidae). These cause necrosis in parts of the plant tissue or create holes, resulting in loss of leaf area. Lizards, such as *Anolis sagrei*, are often the major predators of these herbivorous arthropods, significantly reducing both types of leaf damage through direct consumption of the arthropods (Spiller & Schoener 1990, 1997). Similarly, in Puerto Rico, there was an increase of 46 % in the damage to rainforest canopy leaves, caused by arthropods (Blattaria and Orthoptera) in the absence of *Anolis*, whereas when the lizards were present, herbivory was reduced by up to 20 % (Dial & Roughgarden 1995).

Given that competition for food among predators depends on prey availability (Blaustein & Chase 2007), evaluating predator-prey interactions may help to understand the role of a “natural enemy” in an ecosystem, either because it alters the food resources of other species or because it acts as a direct predator (Bellows 2001).

Tadpoles from many species are predators of insect larvae such as mosquitoes and dragonflies that use the same microhabitats. For example, tadpoles of *Osteopilus septentrionalis* predate the mosquito *Culex quinquefasciatus* in the Bahamas and Cuba, with individual tadpoles consuming between 13 and 21 larvae per day, a number that varies as a function of the density of the larvae (Spielman & Sullivan 1974, Rodríguez & González 2000). *Culex* sp. is never abundant when tadpoles were present and introduction of tadpoles to sites with *Culex* sp. larvae is often sufficient to make the mosquitoes disappear. The tadpoles clearly help to regulate the abundance of these mosquitoes during the rainy season in which the reproduction of

O. septentrionalis coincides with the period of maximum abundance of *C. quinquefasciatus* (Spielman & Sullivan 1974, Rodríguez & González 2000).

In the Neotropical region, reptiles (snakes, lizards, turtles and alligators) feed on a variety of invertebrates and vertebrates (Myers et al. 1978; Heymann 1987; Michaud & Dixon 1989; Kluge 1981; Ortiz et al. 1997; Zamprogno & Zamprogno 1998; Grismer 2000; Prado 2003; Laverty & Dobson 2013). For example, the diet of the species of Crocodylia shows a marked difference during ontogeny. While neonates and juveniles are predominantly insectivore, adults can feed on mollusks, crustaceans, fish, iguanas, snakes, turtles, birds and mammals (Pérez-Higareda et al. 1989; Ortiz et al. 1997; Rivas et al. 1999; Morales-Betancourt 2013). Likewise, snakes, lizards and turtles feed on amphibians, other species of reptiles and mammals (Heymann 1987; Silva & Hillesheim 2004).

Herps as prey. The availability of nutrients and energy is an important driver of community dynamics (Bouchard & Bjorndal 2000). In this sense, food chains constitute an important part of the flow of energy in ecosystems through a network of nutritional relationships (Govenar 2012). Amphibians and reptiles may be responsible for a considerable part of the energy flow in aquatic and terrestrial ecosystems since they can represent an abundant source of protein, mainly for animals at higher trophic levels, and because they often achieve high population densities and are efficient at converting ingested energy into biomass (Boyd & Goodyear 1971, Wells 2007). Furthermore, because amphibians lack hard tissues such as feathers, beaks, hair, or chitin that are difficult to digest, they are a high-quality source of nutrition for other animals (Burton & Likens 1975, Bouchard & Bjorndal 2000, Wells 2007, Collins & Crump 2009).

The eggs, embryos, and tadpoles of frogs also offer a potential source of energy for other organisms due to their high protein content. In this sense, larval anurans are often key elements in the trophic networks of ponds and streams, where they can achieve high densities and biomass (Schiesari et al. 2009). Among the organisms that predate frogs are invertebrates, such as molluscs, crustaceans, arachnids, coleopterans, hymenopterans, orthopterans, hemipterans, and dipterans (Kluge 1981, Villa et al. 1982, Hayes 1983,

Villa & Townsend 1983, Pramuk & Alamillo 2002, Menin & Giaretta 2003, Peltzer & Lajmanovich 2003, Jara & Perotti 2004, Vockenhuber et al. 2008, Ortega-Andrade 2008, Valencia et al. 2011). There are also many vertebrate predators, including caecilians, other anurans, snakes, and tortoises (Heyer et al. 1975, Heyer & Muedeking 1976, Vaira & Coria 1994, Mendes 1996, Verdade et al. 2000, Feltrim & Zaninicechin 2000, Solé & Kwet 2003, Cassimiro & Bertoluci 2003, Cuello et al. 2005, Mendes 2001, Verdade et al. 2000, Puente-Rolón 2001, Ortega-Andrade 2008) (Suppl. 1).

Although predation of adult amphibians by invertebrates is less common than egg and larvae predation, it may also have an important effect on population dynamics (Toledo 2005). Adult amphibians are especially vulnerable to predation when they gather at sites of reproduction (Wells 2007). Various invertebrate taxa have been observed to prey on juvenile and adult amphibians, including insects (Bastos et al. 1994, Buitenhoff 1995, Haddad & Bastos 1997, Pineda 2003, Brasileiro et al. 2003a, Toledo 2003, Figueiredo de Andrade et al. 2010, Costa-Pereira et al. 2010, Santos-Silva & Ferrari 2012), crabs (Caldart et al. 2011), and arachnids (Formanowicz et al. 1981, Hayes 1983, Bastos et al. 1994, Del Grande & Moura 1997, Bernarde et al. 1999, Gray et al. 1999, Summers 1999, Villanueva-Rivera et al. 2000, Aucone & Card 2002, Boistel 2002, Prado & Borgo 2003, Menin et al. 2005, Ortega-Andrade 2008, Manzanilla et al. 2008, Barbo et al. 2009, Santana et al. 2009, Costa-Pereira et al. 2010, Maffei et al. 2010, Caldart et al. 2011).

Amphibians and reptiles are a component of the diet of various species of fishes, birds, mammals, and even other amphibians and reptiles, playing an important role in population dynamics of predators (Duellman & Trueb 1994, Toledo 2005, Wells 2007, Caldart et al. 2011). More than 100 species of Neotropical amphibians (15 families) and reptiles (21 families) have been reported to be prey of numerous groups of vertebrates, such as fishes, amphibians, reptiles, birds and mammals (Suppl. 2).

Despite the large number of reports regarding amphibians and reptiles as prey and predators (Suppl. 2), consumption of dead animals (necrophagy) has frequently been underestimated or minimized (DeVault & Krochmal 2002). In Brazil, Sazima & Strüssmann

(1990) observed individuals of *Helicops modestus*, *Hydrodynastes gigas* and *Liophis miliaris* consuming carcasses of anurans *Rhinella schneideri* and *Hypsiboas albomarginatus*. In Costa Rica, Mora (1999) observed an individual of *Leptodeira annulata* consuming carcasses of *Lithobates vaillanti* in an advanced state of decomposition.

Some species of Neotropical insects, snakes, birds, and mammals have preferences for the consumption of various species of amphibians and reptiles. Although the majority of these reports are anecdotal, this information indicates these groups play a major role of in the diet of certain predators. For example, among the food items most frequently consumed by the snakes *Uromacer catesbyi*, *U. frenatus* and *U. oxyrhynchus* are the frog *Osteopilus dominicensis*, the lizards *Anolis olsoni*, *A. semilineatus* and *Ameiva chrysolaela* (Henderson et al. 1987). The falcon *Leucopternis princeps* frequently hunts individuals of the caecilian *Caecilia orientalis* (48.1 % of its diet) and the snake *Atractus occipitoalbus* (34.6 % of its diet) to feed its young (Greeney et al. 2008). Predation on the anurans *Engystomops pustulosus* and *Hyalinobatrachium fleischmanni* by the bat *Trachops cirrhosus* seems to have influenced the evolution of the various types of signals involved in the reproduction of these frogs species (Ryan et al. 1982, Delia et al. 2010).

Given that predator-prey relations between species can directly or indirectly affect a particular population (animal or plant), it would also be valuable to investigate associations that may occur between amphibians, reptiles, and communities of herbivorous arthropods. In particular, researchers should measure and quantify the effects of these interactions on the growth, predation, and productivity of plants. In this context, comparing the rate of folivory in the presence and absence of predatory species of certain herbivorous arthropods would help to demonstrate the importance of these predators in pest regulation and the possible positive effects for economically important plant species.

Conclusion

The loss of amphibians and reptiles highlights the need to improve the knowledge about this group, given that studies conducted over the last four decades demonstrate the importance of more than 100 herps species in several ecological functions. For example, the role of salamanders and turtles in matter and energy

transfer between aquatic and terrestrial system have been widely studied in temperate regions, nevertheless in the Neotropics this information is limited. The existing herpetological literature, is incomplete and scattered, therefore is necessary to generate basic information about ecophysiology, reproductive biology, ethology, feeding ecology and population dynamics, especially with regard to structure (age, sex, size, and weight of individuals), population density, use of habitat (basic requirements for food and shelter), and population movements (dispersion of individuals of a species). These species traits can be studied via functional ecology, for the understanding of the relationships between these traits, their variability and effects on the ecosystems. Such characteristics shapes some of the ecosystem services provided by amphibians and reptiles, for example biological pest control, seed dispersal and water quality, through functions like energy flow through trophic chain (like predators), consuming of fruits, seeds, nutrient cycling and bioturbation, respectively.

We show how amphibians and reptiles contribute to different ecological functions, also highlighting the need to develop studies aimed to the understanding of the mechanisms that occur behind these general ecological functions, through the study of functional traits and ecological processes. We also emphasize the need for research involving more study time (at least one year), quantitative data collection and experimental models in field. The knowledge and understanding of the functions that the herps (organisms abundance and diversity) perform in the ecosystems, formulated in a more appropriate way, will aid to develop management plans for transformed landscapes, restoration or recovery projects of landscapes (involving aquatic and terrestrial systems), and the development of complete conservation strategies for species and ecosystems. Improving the understanding of how ecosystem services offered are generated for biodiversity, is undoubtedly the first step towards formal recognition of human benefits derived from the operation of those services. Keeping in mind this is one of the central topics from the perspective of ecosystem services.

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Conflicts of interest

There are no conflicts of interest with funding sources or institutions.

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Funciones ecológicas de los anfibios y reptiles neotropicales: una revisión

Resumen. Los anfibios y reptiles (herpetos) son dos de los grupos de vertebrados más abundantes y diversos en los ecosistemas Neotropicales. Sin embargo, poco se conoce sobre su papel en el mantenimiento y la regulación de las funciones del ecosistema y, por extensión, de su potencial aporte en el suministro de servicios ecosistémicos. En este estudio se realizó una revisión sobre las funciones ecológicas de los herpetos Neotropicales, usando diferentes recursos (búsqueda en bases de datos, capítulos de libros, etc.). Se revisó un total de 167 estudios de herpetología Neotropical, publicados en las últimas cuatro décadas (1970-2014). Estos estudios proporcionaron información sobre más de 100 especies que contribuyen al menos con cinco categorías de funciones ecológicas: i) ciclaje de nutrientes; ii) bioturbación; iii) polinización; iv) dispersión de semillas, y; v) flujo de energía a través de los ecosistemas. Muchas de estas funciones proveen servicios ecosistémicos claves para el bienestar humano, como el control biológico de especies plaga, dispersión de semillas y calidad del agua. Al conocer y entender las funciones que ejercen los herpetos en los ecosistemas se podrán estructurar de una forma más adecuada planes de manejo en paisajes transformados, proyectos de restauración o recuperación de paisajes que involucren sistemas acuáticos y terrestres, y planes completos y detallados de conservación de especies y ecosistemas. Además de los vacíos de información detectados en la presente revisión, esta contribución profundiza en la comprensión de algunas preguntas claves en el estudio de los servicios ecosistémicos y la biodiversidad y, además, de cómo se generan estos servicios.

Palabras clave: funciones ecológicas; región Neotropical; ecosistemas; reptiles; anfibios; revisión

Funções ecológicas de anfibios e répteis neotropicais: uma revisão

Resumo. Os anfibios e répteis são dois dos grupos de vertebrados mais abundantes e diversos nos ecossistemas neotropicais. No entanto, pouco se sabe sobre o seu papel na manutenção e regulação das funções dos ecossistemas e sua potencial contribuição para o fornecimento de serviços ecosistêmicos. Neste estudo, foi realizada uma avaliação sobre as funções ecológicas dos anfibios e répteis neotropicais, utilizando diferentes recursos (busca em bases de dados, capítulos de livros, etc.). Um total de 167 estudos publicados nas últimas quatro décadas (1970-2014) foram encontrados sobre as funções ecológicas dos anfibios e répteis neotropicais os quais forneceram informações sobre mais de 100 espécies que contribuem no: i) ciclo de nutrientes; ii) bioturbação; iii) polinização; iv) dispersão de sementes, e; v) fluxo de energia através dos ecossistemas. Enfatizamos a necessidade de desenvolver estudos para ampliar o conhecimento das funções ecológicas dos ecossistemas neotropicais e os mecanismos por detrás destes, através do estudo das características funcionais e análise dos processos ecológicos. Muitas destas funções estão relacionadas com os principais serviços ecosistêmicos para o bem estar humano como o controle biológico de espécies de pragas, dispersão de sementes e qualidade da água. Ao conhecer e compreender as funções que desempenham os répteis nos ecossistemas, podem ser estruturados planos de gestão nas paisagens culturais, projetos de restauração ou recuperação de paisagens que envolvem sistemas aquáticos e terrestres, e desenvolver planos abrangentes e detalhados de conservação de espécies e ecossistemas. Além das lacunas de informação identificadas nesta avaliação, esta contribuição explora essas questões em termos de uma melhor compreensão das questões-chave no estudo dos serviços dos ecossistemas e da biodiversidade além de como esses serviços são gerados.

Palavras-chave: funções ecológicas; região Neotropical; ecosistemas; répteis; anfibios; revisão