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Effects of amphibian species loss on freshwater ecosystem structure and functioning: current knowledge and research gaps

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ABSTRACT

Effects of amphibian species loss on freshwater ecosystem structure and functioning: current knowledge and research gaps.

Amphibians are one of the most endangered groups of vertebrates, and they have key ecological roles in freshwater ecosystems and linking the aquatic and terrestrial environments. Still, studies on how amphibian species loss can alter freshwater ecosystem structure and functioning are scarce. This review summarizes the results of 129 studies exploring the effects of amphibians on freshwater communities (algae, zooplankton and macroinvertebrates) and food webs, as well as key ecosystem processes (leaf litter decomposition, phytoplankton and periphyton accrual, nutrient cycling, and ecosystem metabolism). Most studies (71%) focused on anuran species and less so on urodeles (21%) or both groups (8%). While we found some general patterns, species-specific characteristics often induced different outcomes. The high variety of results suggests that amphibians should be prioritized in future experimental studies if we are to understand the ecological consequences of species loss in this vulnerable group.

KEY WORDS: freshwater ecosystems, amphibians, Anura, Caudata, periphyton, decomposition, communities.

RESUMEN

Efectos de la pérdida de especies de anfibios en el funcionamiento y la estructura de ecosistemas de agua dulce: conocimiento actual y necesidades de investigación.

Los anfibios son uno de los grupos de vertebrados más amenazados y tienen un papel clave en el funcionamiento de los ecosistemas de agua dulce y como nexo entre ecosistemas dulceacuícolas y terrestres. Sin embargo, los estudios sobre cómo afecta la pérdida de anfibios a la estructura y funcionamiento de ecosistemas de agua dulce son escasos. Esta revisión resume los resultados de 129 estudios que han investigado los efectos de los anfibios en comunidades de agua dulce (algas, zooplancton y macroinvertebrados) y en redes tróficas, así como en procesos ecosistémicos (descomposición de hojarasca, acumulación de fitoplancton y perifiton, ciclos de nutrientes, y metabolismo de ecosistemas). La mayoría de los estudios (71%) se enfocaban en especies de anuros y había menos investigando urodelos (21%) o ambos grupos (8%). Aunque se encontraron algunos patrones generales, normalmente las características específicas de cada especie inducían diferentes efectos. La gran variedad de resultados sugiere que se deberían priorizar los anfibios en futuros

estudios experimentales para entender las consecuencias ecológicas de la pérdida de especies de este grupo vulnerable.

PALABRAS CLAVE: *ecosistemas de agua dulce, anfibios, Anura, Caudata, perifiton, descomposición, comunidades.*

INTRODUCTION

Biodiversity is currently declining at rates that are comparable to those reported for past mass extinctions, where more than three quarters of Earth's species were lost in geologically short intervals (Barnosky et al., 2011, Ceballos et al., 2017). Unlike those events, which were caused by extreme natural phenomena, species losses at present are being mostly originated by anthropogenic impacts such as habitat loss and fragmentation (Haddad et al., 2015), pollution (Sigmund et al., 2023), climate change (Thomas et al., 2004), or the expansion of invasive species (Bellard et al., 2016) and emergent diseases (Daszak et al., 2000). Importantly, while species extinctions are worrying by themselves due to the intrinsic value of biodiversity (Ghilarov, 2000, IPCC, 2014), they can also bring important consequences for ecosystem functioning that need to be investigated (Boyero et al., 2021, Cardinale et al., 2011, Cardinale et al., 2006, Hooper et al., 2012).

Freshwater ecosystems are especially important for Earth's biodiversity, since they harbour around 6% of all described species despite the fact that they only occupy the 0.8% of the global surface (Dudgeon et al., 2006). However, these ecosystems are suffering extinction rates considerably higher than those of marine or terrestrial ecosystems (Reid et al., 2019, Sala et al., 2000). Remarkably, freshwater ecosystems are not only affected by the loss of freshwater species, but also by extinctions in their surrounding terrestrial ecosystems. This occurs because of the strong land-water interactions existing in riparian areas, with terrestrial plants providing fundamental resources for aquatic consumers, and animals such as insects and amphibians having both aquatic and terrestrial life stages (Kominoski et al., 2013). Freshwater ecosystem functioning and structure are known to be affected by biodiversity loss at different trophic levels, both through bottom-up and top-down effects, in both brown and green food webs (Cardinale et al., 2011). Brown food webs are sets of trophic relationships whose flux of energy proceeds from the processing of dead organic matter (Odum, 1969). Bottom-up effects have been more or less well documented for them, with higher diversity in a leaf litter mixture often inducing faster decomposition than would be expected based on the species present in the mixture (López-Rojo et al., 2018), although the effects of plant diversity on decomposition are variable and highly dependent on species identities (Cardinale et al., 2011, Swan, 2021). In green food webs, those whose flux of energy proceeds from primary producers such as plants or algae (Odum, 1969), the reported effects of algal diversity on ecosystems are stronger and more consistent, if not universal, with higher diversity leading to higher rates of primary production or algal biomass accrual (Cardinale et al., 2011). While top-down effects have been less studied, a higher diversity of consumers generally leads to higher consumption rates. Thus, higher detritivore diversity can accelerate decomposition through facilitation and resource partitioning (Gessner et al., 2010), with particularly strong effects when species differ in traits such as body size or mouthparts (Swan, 2021, Tonin et al., 2018), and higher grazer diversity can more efficiently reduce periphyton biomass accrual (Hillebrand & Shurin, 2005).

Amphibians are one of the most endangered groups of vertebrates, with nearly 40% of species threatened of extinction, having suffered important species losses in the three orders in the class Amphibia: Anura (frogs and toads), Caudata (salamanders and newts) and Gymnophiona (caecilians; Bolochio et al., 2020, Collins, 2010, Wake & Vredenburg, 2008). Amphibian population declines are driven by several factors that interact among them. Climate change decreases amphibian survival through reductions in the time that temporary waters are available for amphibian larval development, isolation of their popula-

tions due to amphibians having to move to higher locations to maintain in their temperature range, and increase in their exposure to UV radiation due to lower water depth (Blaustein et al., 2003, Blaustein et al., 2010, Li et al., 2013, Lundsgaard et al., 2020). Habitat loss and fragmentation is highly linked to agriculture due to wetland, forest and grassland destruction to create new crop fields, infrastructure to connect them, or dams for water supply. These have effects on amphibian populations, mainly causing direct deaths and displacing them to less suitable habitats and isolating them, which imply a reduction in genetic diversity and an increase of their vulnerability to stochastic events (Cushman, 2006). Pollution effects can be caused by several contaminants, such as pesticides, fertilizers, heavy metals or microplastics, and despite the different consequences depending on each pollutant, in general they cause reduced survival and growth, impaired development, and morphological and behavioural abnormalities (Blaustein et al., 2003, López-Rojo et al., 2024, Wesner et al., 2020). Invasive species also have severe effects on amphibian conservation, as many taxa, mainly fishes, other amphibians, reptiles, mammals and crayfish can predate on native amphibians. Some invaders, mainly plants, are ecosystem engineers that severely modify terrestrial and aquatic habitats. Invasive amphibians can also compete with native ones for resources, hybridize with them, producing sterile hybrids that reduce the reproductive success or fertile hybrids that can outcompete their parental population, and spread diseases (Falaschi et al., 2020, Nunes et al., 2019). Recently, emergent infectious diseases have been the most devastating factor causing amphibian extinctions (Fisher & Garner, 2020). In the last decades, global commerce has made possible that fungal pathogens increase their distribution area and their virulence through recombination and hybridization with previously allopatric related lineages (Fisher et al., 2012), a phenomenon that has been aggravated by climate change (Thumsová et al., 2025). Thus, invasive fungal pathogens have spread worldwide, infecting native plants and animals and leading to the decline and extinction of more sensitive taxa, which represents an enormous threat for host species (Almeida et al., 2019, Fisher et al., 2020, Fisher et al., 2012, Harvell et al., 2002, Thumsová et al., 2023). Most affected amphibians have been reduced or extinct due to infection by *Batrachochytrium dendrobatidis* Longcore, Pessier & D.K. Nichols and *Ranavirus* (Berger et al., 1998, Fisher & Garner, 2020, Lips, 2016, Rosa et al., 2017), with European urodeles also threatened by *B. salamandrivorans* Martel A., Blooi M., Bossuyt F., Pasmans F. (Martel et al., 2014, Stegen et al., 2017).

Amphibians are important consumers in many freshwater ecosystems, where they can influence ecosystem functioning through top-down effects in different ways depending on their trophic level, which can vary from primary consumers to top predators (Davic & Welsh Jr, 2004, Hocking & Babbitt, 2014). Many anuran larvae are periphyton grazers, often more efficient than invertebrates, and they are known to control periphyton biomass accrual and algal communities through direct consumption (Barnum et al., 2022, Connelly et al., 2008, Kupferberg, 1997b, Mallory & Richardson, 2005, Ranvestel et al., 2004, Rowland et al., 2017, Whiles et al., 2013). Anuran larvae can also influence ecosystem processes through nutrient release due to bioturbation ¬– that is, the removal of sediment and upper periphyton layers– and excretion, which can stimulate primary production and decomposition and control nutrient cycling (Connelly et al., 2008, Iwai & Kagaya, 2007, Iwai et al., 2009, Kupferberg, 1997b, Rugenski et al., 2012, Schmidt et al., 2019, Whiles et al., 2013). In addition, they can influence invertebrate communities in different ways, since they can either compete with them for resources or facilitate their access to underlying food (Barnum et al., 2022, Colón-Gaud et al., 2009, Colón-Gaud et al., 2010, Kupferberg, 1997b, Ranvestel et al., 2004).

On the other hand, urodele larvae and adults are predators that feed on zooplankton, macroinvertebrates or other amphibian larvae, depending on their size. Thus, their activity can alter the abundance and community structure of their prey (Arribas et al., 2014, Blaustein et al., 1996, Holomuzki et al., 1994, Urban, 2013). Besides, their predatory activity not only affects their prey, but can also control lower trophic levels through top-down effects and trophic cascades. On the one

hand, predators can induce direct effects, with prey consumption leading to reduced prey abundance, which in turn leads to lower consumption of basal resources by this prey (Blaustein et al., 1996, Holomuzki et al., 1994). On the other hand, predators can also have indirect effects through nutrient release due to bioturbation and excretion (Munshaw et al., 2013); or due to changes in prey foraging activity in the presence of predators (Alonso et al., 2024b).

MATERIALS AND METHODS

This review attempts to summarize the knowledge on how amphibian biodiversity loss affects freshwater ecosystem structure and functioning. Specifically, it examines how depletion or diversity reduction of anurans and urodeles influence leaf litter decomposition, periphyton photosynthesis and accrual and structure of algal and invertebrate communities, food webs, nutrient cycling, and ecosystem metabolism. With that aim, a literature search was conducted in the Web of *Science*, using the terms TS=(amphibian* OR anuran* OR frog* OR toad* OR tadpole* OR urodele* OR salamander* OR newt*) and TS=(decomposition* OR photosynthesis* OR periphyton* OR biofilm* OR alga* OR web* OR top-down* OR consumptive*) and TS=(pond* OR stream* OR freshwater* OR aquatic*) not TS=(newtonian OR newton OR ecotoxic*).

The search was done on the 13th of June of 2025, with no lower time range indicated (i.e., all studies published up to the searching date were included). Initially, 931 records were identified. Then, a selection of articles of interest was done, based on the available information in the title and abstract, followed by a thorough content check that resulted in 129 publications that fulfilled our searching criteria. We decided to retain the papers examining effects of amphibian presence or diversity on ecosystem structure and functioning (phytoplankton biomass, periphyton accrual and community, macrophyte and metaphyton biomass, zooplankton abundance and community, macroinvertebrate abundance, growth and community, food web structure, leaf litter decomposition, nutrient cycling and ecosystem metabolism). The selected records included 113 empirical studies, 15 review papers and a paper proposing a mathematical model.

RESULTS

From the three orders in the class Amphibia – Anura (frogs and toads), Caudata (salamanders and newts) and Gymnophiona (caecilians)–, all studies focused on the first two ones, since caecilians are scarce and they present terrestrial larvae, so they do not affect directly freshwater ecosystems. In contrast, most anurans and urodeles have aquatic larvae and terrestrial adults, or even have entirely aquatic adults (Pough et al., 2018). Considering the 113 empirical studies, 81 papers focused on anurans, 23 focused on urodeles, and 9 studied both groups.

Effects of anuran loss on freshwater ecosystems

Out of the 90 studies that addressed the effects of anuran loss on freshwater ecosystems, 12 considered total depletion of complex communities, whereas the rest addressed the loss of specific species. All papers studying total depletion were field studies conducted in streams of Panama, except for one performed in USA, where they compared ecosystem functioning and structure before and after amphibian depletion due to *Batrachochytrium dendrobatidis*. Taking into account the 67 experimental studies included in this review that addressed the effects of the absence of single anuran species, a total of 56 species of 14 different families was analysed.

Anuran loss effects on phytoplankton varied depending on the species, but with contrasting results even within the same species. Considering the 20 studies that have examined phytoplankton responses to anuran loss, 6 of them found reductions in phytoplankton biomass, 8 did not detect any effect, 5 observed increases, and one found one species loss having no effect whereas the loss of the other reduced phytoplankton biomass (Table 1, Table S1 (supplementary information, available at https://www.limnetica.com/en/limnetica)). Anuran loss effects on periphyton were more consistent, with 33 of the 55 studies which analyse this variable showing an increase in periphyton, as well as 3 more observing an increase after the

Table 1. Effects of the different anuran species loss on phytoplankton, periphyton, macrophyte y metaphyton, zooplankton, macroinvertebrates, leaf litter decomposition and ecosystem metabolism. *Efectos de la desaparición de las distintas especies de anuros en fitoplancton, perifiton, macrófitos y metafiton, zooplancton, macroinvertebrados, descomposición de hojarasca y metabolismo del ecosistema.*

Specie lost	Location	Phytoplankton	Periphyton	Macrophytes and metaphyton	Zooplankton	Macroinvertebrates	Leaf litter decomposition	Ecosystem respiration	Ecosystem primary production
Agallychnis callidryas	Panama, Central America	-[1], -[2], +[3]	+[1], +[2]		+[1], +[2], +[3]				
Alytes obstetricans	Spain, Europe		+[4], -[5]			-[4]			
Anaxyrus americanus	USA, North America	+[6]	0[6], 0[7], 0[8], +[9], +[10], +[11], +[12]		0[6]	+[9], -[12]			0[9]
Anaxyrus boreas	USA, North America	+[15]	+[15], ≠[16], +[17]		+[15]				
Anaxyrus woodhousii	USA, North America	0[18], 0[19]	0[18], 0[19], 0[20]		0[18]				
Aquarana catesbeiana	USA and Canada, North America		0[21]	+[22]					
Aquarana catesbeiana	USA, North America*	0[23]	+[24]	+[24]	0[23]	+[23], 0[25]			
Ascaphus truei	Canada and USA, North America		+[26], 0[27], +[28], +[29], 0[30]		0[30]	≠[21], +[23], +[28], 0[30]	0[26]	-[26]	
Batrachyla taeniata	Argentina, South America					-[31]	0[31]		
Bombina variegata	Italy, Europe					+[32]			
Boophis quasiboehmei	Madagascar, Africa						-[33]		

Cont.

Table 1, Cont.

Specie lost	Location	Phytoplankton	Periphyton	Macrophytes and metaphyton	Zooplankton	Macroinvertebrates	Leaf litter decomposition	Ecosystem respiration	Ecosystem primary production
Bufo bankorensis	Taiwan, Asia		+[34]						
Bufo bufo	UK and Italy, Europe		+[35], +[36]			+[32]			
Bufo japonicus	Japan, Asia					-[37]			
Bufotes viridis	Israel, Asia					+[38]			
Crinia signifera	Australia, Oceania					+[39]			
Dendropsophus ebraccatus	Panama, Central America	-[1], 0[2]	+[1], +[2]		0[1], +[2]				
Dendropsophus minutus	Brazil, South America		+[40]						
Discoglossus galganoi	Spain, Europe	-[41]		-[41]	+[41]				
Epidalea calamita	Spain, Europe	-[41]	+[41]	-[41]	+[41]				
Hyla andersonii	USA, North America	0[19]	0[19]						
Hyla chrysoscelis	USA, North America	+[42]	+[42]		0[42]				
Hyla meridionalis	Spain, Europe	-[41]		-[41]	+[41]				
Hyla versicolor	USA, North America	+[43], 0[44]	+[11], +[12], +[43], +[44]		+[43], 0[44]	-[12]	0[45]	0[45]	
Limnodynastes tasmaniensis	Australia, Oceania	-[46]		+[46]	+[46]	+[46]			-[46]
Limnodynastes peronii	Australia, Oceania					+[39]			
Lithobates blairi	USA, North America		+[47]						+[47]

Cont.

Table 1, Cont.

Specie lost	Location	Phytoplankton	Periphyton	Macrophytes and metaphyton	Zooplankton	Macroinvertebrates	Leaf litter decomposition	Ecosystem respiration	Ecosystem primary production
Lithobates clamitans	Canada, North America		$+^{48}$, $+^{49}$	$+^{22}$			$-^{50}$		
Lithobates palmipes	Venezuela, South America		0^{51}, $\neq^{52}$						
Lithobates pipiens	USA, North America	$+^{6}$	0^{6}, 0^{8}		0^{6}				
Lithobates sphenocephalus	USA, North America	0^{53}, $-^{54}$	0^{53}, $+^{54}$, $+^{55}$		0^{53}, 0^{54}	$+^{54}$			
Lithobates sylvaticus	USA, North America	0^{56}	0^{56}, $+^{57}$, 0^{58}, $+^{59}$, $+^{60}$		0^{56}, $+^{58}$, $+^{59}$, 0^{60}	$\neq^{58}$, $+^{59}$, $+^{60}$		0^{56}	0^{56}
Lithobates warszewitschii	Panama, Central America		$+^{61}$			0^{61}			
Litoria ewingii	New Zealand, Oceania*	$-^{62}$	$+^{62}$	$+^{62}$		$+^{62}$	0^{62}		
Litoria genimaculata	Australia, Oceania						0^{63}		
Litoria serrata	Australia, Oceania		0^{64}				$-^{64}$		
Mantidactylus melanopleura	Madagascar, Africa						$-^{33}$		
Myxophies coggeri	Australia, Oceania		$+^{64}$				0^{64}		
Pelobates cultripes	Spain, Europe	$-^{41}$		$+^{41}$, $+^{63}$	$+^{41}$				
Pelophylax perezi	Spain, Europe	$-^{41}$		$-^{41}$	$+^{41}$				
Pseudacris crucifer	USA, North America	0^{19}, 0^{53}	0^{19}, $+^{53}$, 0^{57}		0^{53}				
Pseudacris regilla	USA, North America	0^{66}	$+^{20}$, $-^{66}$, 0^{67}	$+^{66}$	0^{66}, 0^{67}				0^{67}

Cont.

Table 1, Cont.

Specie lost	Location	Phytoplankton	Periphyton	Macrophytes and metaphyton	Zooplankton	Macroinvertebrates	Leaf litter de-composition	Ecosystem respiration	Ecosystem primary production
Pseudacris triseriata	USA, North America	0^{18}	0^{18}		0^{18}				
Ptychadena anchietae	Non stated, Africa					$+^{68}$			
Rana boylii	USA, North America		$+^{23}$, $-^{67}$		$+^{67}$				$-^{67}$
Rana cascadae	USA, North America	0^{69}	$+^{69}$		$+^{69}$				
Rana japonica	Japan, Asia					$-^{37}$			
Rana ornativentris	Japan, Asia					$-^{37}$			
Rana temporaria	UK and Italy, Europe		$+^{36}$, $+^{70}$			$+^{33}$, $+^{70}$			
Ranoidea alboguttata	Australia, Oceania	$-^{71}$	0^{71}			0^{71}	0^{71}		
Rhacophorus arboreus	Japan, Asia					$-^{37}$			
Scinax fuscovarius	Panama, Central America		$-^{72}$						
Smilisca sila	Panama, Central America		$+^{73}$				0^{73}	$-^{73}$	
Total depletion	Panama, Central America		$+^{74}$, $+^{75}$, $+^{76}$, $+^{77}$, $+^{78}$, $+^{79}$, $+^{80}$, $+^{81}$			$\neq^{74}$, $+^{75}$, $\neq^{76}$, 0^{77}, $-^{79}$, $-^{80}$, 0^{81}, $\neq^{82}$, 0^{83}	0^{83}	$-^{78}$, $-^{79}$, $-^{81}$, 0^{83}	$+^{78}$, 0^{79}, $+^{81}$
Total depletion	USA, North America					$\neq^{84}$			

[1]Costa & Vonesh (2013a), [2]Costa & Vonesh (2013b), [3]Hite et al. (2018), [4]Alonso et al. (2022), [5]Alonso et al. (2024a), [6]Distel & Boone (2010), [7]Distel & Boone (2009), [8]Distel & Boone (2011), [9]Holomuzki & Hemphill (1996), [10]Holomuzki (1997), [11]Smith & Burgett (2012), [12]Smith et al. (2012), [13]Rettig et al. (2021), [14]G. R. Smith et al. (2016), [15]Harjoe et al. (2022), [16]Bennett et al. (2015), [17]Wood & Richardson (2010), [18]Harris (1995), [19]Morin (1995), [20]Morin et al. (1990), [21]Smith et al. (2006), [22]France & Welbourn (1992), [23]Preston et al. (2012), [24]Kupferberg (1997a), [25]Lawler et al. (1999), [26]Atwood et al. (2014), [27]Kiffney & Richardson (2001), [28]Lamberti et al. (1992), [29]Mallory & Richardson (2005), [30]Rosenfeld (1997), [31]Jara & Pueta (2023), [32]Manenti et al. (2017), [33]Ramamonjisoa & Natuhara (2018), [34]Wang & Kam (2019), [35]Bardsley & Beebee (2000), [36]Bardsley & Beebee (2001), [37]Iwai & Kagaya (2007), [38]Blaustein & Margalit (1994), [39]Mokany & Shine (2003), [40]de Lima Mamede & Nomura (2021), [41]Arribas et al. (2014), [42]Dvorsky et al. (2023), [43]Van Meter et al. (2011), [44]Van Meter & Swan (2014), [45]Van Meter et al. (2012), [46]Mokany (2007), [47]Ward et al. (2023), [48]Graham & Vinebrooke (1998), [49]Holomuzki (1998), [50]Stoler et al. (2016), [51]Knoll et al. (2009), [52]Solomon et al. (2004), [53]Mills & Semlitsch (2004), [54]Rowland et al. (2017), [55]Hernandez & Chalcraft (2012), [56]Rubbo et al. (2012), [57]Morin & Johnson (1988), [58]Parlato & Mott (2023), [59]Parlato & Mott (2025), [60]Rohr & Crumrine (2005), [61]Barnum et al. (2013), [62]Earl et al. (2023), [63]Iwai et al. (2009), [64]Schmidt et al. (2019), [65]Pinero-Rodríguez et al. (2021), [66]Anderson & Kneitel (2015), [67]Kupferberg (1997b), [68]McLachlan (1981), [69]Buck et al. (2015), [70]Brönmark et al. (1991), [71]Iwai et al. (2012), [72]Cochak et al. (2024), [73]Rugenski et al. (2012), [74]Barnum et al. (2022), [75]Colón-Gaud et al. (2009), [76]Colón-Gaud et al. (2010), [77]Connelly et al. (2008), [78]Connelly et al. (2014), [79]Rantala et al. (2015), [80]Ranvestel et al. (2004), [81]Whiles et al. (2013), [82]Colón-Gaud et al. (2010), [83]Connelly et al. (2011), [84]T. C. Smith et al. (2016).

loss of one species, but no effect for the loss of another, and another 3 ones finding only changes in algal community composition. However, there were also 2 studies that found amphibian loss inducing a decrease in periphyton, 13 that found no effect, and another one that found reduction for one species and no effect for the other. Besides, 3 of the 5 studies considering sediment mass found increases after amphibian loss, with other one showing increases for one species and no effect for the other, and the remaining one founding decreased sediment mass after tadpole loss (Table 1, Table S2 (supplementary information, available at https://www.limnetica.com/en/limnetica)). When taking into account amphibian depletion, all of the 8 studies in Panamanian streams found increases in periphyton accrual after amphibian loss (Table 1, Table S2). Only 4 studies analysed the effects of anurans loss on macrophytes, and they increased in all of them (Table 1, Table S3 (supplementary information, available at https://www.limnetica.com/en/limnetica)). A similar pattern was observed for metaphyton, which showed an increase after anuran loss in the 3 studies that analysed it (Table 1, Table S3).

Anuran loss induced two main different responses on zooplankton, with 11 out of the 21 studies detecting no changes in zooplankton abundance or communities, 9 of them finding an increase in zooplankton after anuran loss and one study which found either increase or no effect, depending on the species (Table 1, Table S4 (supplementary information, available at https://www.limnetica.com/en/limnetica)). Anuran loss can influence macroinvertebrate abundance and community structure, but effects are again highly variable. Most studies showed that amphibian loss increased macroinvertebrate abundance, survival or size, with 12 of the 25 studies showing that pattern, 2 showing increases for one species and no effect for another, and another finding increases or decreases depending on macroinvertebrate development stage. However, other 4 found reduced abundance, survival or size after amphibian loss, and 6 studies showed no effects on size, survival or abundance, although 2 of them observed changes in community composition (Table 1, Table S5 (supplementary information, available at https://www.limnetica.com/en/limnetica)). In streams which have suffered amphibian depletion, the pattern is similarly unclear, with one study observing increased macroinvertebrate abundance, two observing reductions, three finding changes in community and four observing no significant effects (Table 1, Table S5). The effects of anuran depletion on food webs are unclear and require more research (Table S6, supplementary information, available at https://www.limnetica.com/en/limnetica): in Panamanian stream with amphibian depletion, one study found that food webs were similar, whereas the other found a reduction in organic matter transfer from producers to all consumers (Table S6). Despite the fact that the loss of specific anuran species altered food webs in the four studies that analysed it, the changes were different in each of them (Table S6).

Regarding leaf litter decomposition, most studies have found no effects of anuran loss, with 7 out of 10 studies showing this pattern, although another study found either no effect or reductions of leaf litter decomposition depending on the species, and other 2 observed reduced decomposition (Table 1, Table S7 (supplementary information, available at https://www.limnetica.com/en/limnetica)). Related with leaf litter, the two studies that analysed leaf litter nutrients found that anuran loss reduced them, and another study found a reduction in FPOM after amphibian loss (Table S7). In streams with total depletion, only one study observed leaf litter decomposition, and found that it was not significantly affected, as well as bacterial and fungal biomass, with other four studies observing alterations in particulate organic matter after amphibian depletion (Table S7).

Only one study examined nutrient cycling, finding that it was slowed down after amphibian loss. However, other studies have measured changes in nutrient concentrations and the results are divided between studied that observed anuran loss reducing nutrient concentration, with 4 of the 8 studies, and absence of significant effects in the other 4 (Table S8, supplementary information, available at https://www.limnetica.com/en/limnetica). Both studies analysing nutrient cycling after amphibian depletion in streams found that it was slowed down (Table S8). Regarding ecosystem respiration, most studies have found reduced ecosystem respiration after amphibian loss

in both single species loss (2 of the 3 studies) and amphibian depletion (3 of 4 studies), with the remaining ones finding no significant effect (Table 1, Table S8). In primary production, results are more varied, with one study showing increases after anuran loss, 2 without significant effects, another with a reduction of primary production, and the last one with no effect or reduction depending on the species (Table 1, Table S8), and when taking into account full ecosystems which have suffered amphibian depletion, 2 studies found an increase in primary production and another one did not find significant effects (Table 1, Table S8).

Effects of urodele loss on freshwater ecosystems

Considering the 53 experimental studies included in this review that addressed the effects of the absence of specific species, a total of 17 species of urodeles were studied, belonging to 4 of the 9 families of urodeles.

The response of phytoplankton to urodele presence and density is ambiguous, with 5 of the 10 studies that addressed it showing phytoplankton reductions after urodele loss and the other 5 studies showing no effects (Table 2, Table S1). In periphyton, urodele loss did not significantly affect it in most studies (8 out of 13), although there are 4 studies that observed periphyton accrual reduction after urodele loss and one that found and increase periphyton accrual (Table 2, Table S2). Only one study observed the effects of urodele loss on macrophyte biomass and found reductions in plant biomass, however, urodele loss was simultaneous to that of several anurans, and thus its effect could not be differentiated (Table 2, Table S3).

Zooplankton abundance was generally enhanced after urodele loss, with 6 of the 12 studies showing that result, but one study showed a reduction in zooplankton abundance and the other 5 had no effect on abundance, although 2 of them showed changes in community structure (Table 2, Table S4). Similar effects were found for macroinvertebrates, where most studies (8 out of 15) observed an increase in macroinvertebrate abundance after urodele loss, with another one observing either an increase in abundance or no effect depending on the species lost, another showing changes in community structure and 5 studies finding no significant differences (Table 2, Table S5). Only two studies have observed the effects of urodele density on food webs, finding that changes in density altered food webs. However, as these studies implied the loss of the whole community, including anurans and urodeles, it is unclear whether effects were mediated by urodeles (Table S6).

Only two studies have analysed the effects of urodeles on leaf litter decomposition, and they have observed contrasting results, with one of them observing an increase in decomposition after urodele loss, and the other one showing a reduction in leaf litter decomposition after urodele loss, without effects on aquatic hyphomycete communities (Table 2, Table S7). Only one study analysed the effect of urodeles on nutrient cycling, and found that urodele loss slowed down nutrient recycling. And in the two studies considering nutrient concentration in water, one of them observed increased PO_4- concentration after urodele loss, and another one found no effects, but there could be complex interactions among species, since their loss was coupled with those of several anurans (Table S8). Only two studies have examined the effects of urodele loss on ecosystem metabolism and showed contrasting results, with one of them observing no effect, and the other ones finding increased respiration and primary production after urodele loss (Table 2, Table S8).

DISCUSSION

Effects of anuran loss on freshwater ecosystems

The effects of anuran loss on phytoplankton were mainly related to tadpole feeding behaviour. The positive effects of anuran larvae loss are mainly due to the disappearance of more generalist species that can feed efficiently both in periphyton and phytoplankton and actively reduced its biomass through foraging and consumptive effects (Dvorsky et al., 2023), whereas the loss of other species that feed preferentially on periphyton and have lower efficiency filtering phytoplankton, generally showed no significant effect (Buck et al., 2015, Preston et al., 2012, Rubbo et al., 2012). Although the effects of nonconsumptive effects

Table 2. Effects of the different urodele species loss on phytoplankton, periphyton, macrophyte y metaphyton, zooplankton, macroinvertebrates, leaf litter decomposition and ecosystem metabolism. *Efectos de la desaparición de las distintas especies de urodelos en fitoplancton, perifiton, macrófitos y metafiton, zooplancton, macroinvertebrados, descomposición de hojarasca y metabolismo del ecosistema.*

Specie lost	Location	Phytoplankton	Periphyton	Macrophytes and metaphyton	Zooplankton	Macroinvertebrates	Leaf litter decomposition	Ecosystem respiration	Ecosystem primary production
Ambystoma maculatum (larvae)	USA, North America	0^{1}, 0^{2}, 0^{3}	0^{1}, 0^{2}, 0^{3}		$+^{1}$, $+^{2}$, 0^{3}	0^{2}, $+^{4}$		0^{3}	0^{3}
Ambystoma opacum (larvae)	USA, North America	$-^{5}$	0^{5}		$+^{6}$				
Ambystoma tigrinum (adult)	Canada, North America	$-^{7}$			0^{7}	$+^{7}$, $\neq^{8}$			
Ambystoma tigrinum (larvae)	Canada, North America	$-^{7}$, $-^{9}$			0^{7}, $\neq^{9}$	$+^{7}$, $\neq^{8}$			
Ambystoma talpoideum (larvae)	USA, North America	$-^{10}$	$+^{10}$		$\neq^{10}$, 0^{11}	$\neq^{10}$	$+^{10}$	$+^{10}$	$+^{10}$
Cynops pyrrhogaster (adult)	Japan, Asia		$-^{12}$						
Desmognathus quadramaculatus (larvae)	USA, North America					0^{13}			
Dicamptodon tenebrosus (larvae)	USA, North America		0^{14}			0^{14}			
Eurycea bislineata (larvae)	USA, North America		0^{15}			0^{16}			

Cont.

Table 2, Cont.

Specie lost	Location	Phytoplankton	Periphyton	Macrophytes and metaphyton	Zooplankton	Macroinvertebrates	Leaf litter decomposition	Ecosystem respiration	Ecosystem primary production
Eurycea wilderae (larvae)	USA, North America					0[13]			
Gyrinophylus porphyriticus (larvae)	USA, North America		0[15]			+[16]			
Gyrinophylus porphyriticus (adult)	USA, North America		0[15]						
Hynobius retardatus (larvae)	Japan, Asia					+[17]			
Notophthalmus viridescens (adult)	USA, North America	-[5], 0[18], 0[19]	0[5], 0[18]		≠[19]				
Salamandra infraimmaculata (larvae)	Israel, Asia		-[20]		+[20], +[21]	+[20]			
Salamandra salamandra (larvae)	Spain, Italy, Germany and Sweden, Europe		-[22]			0[22], +[23], +[24], +[25], 0[26]	-[22]		
Triturus marmoratus (larvae)	Spain, Europe		-[27]						
Triturus pygmaeus (larvae)	Spain, Europe	-[28]		-[28]	+[28], -[29]				

[1]Harris (1995), [2]Rowland et al. (2017), [3]Rubbo et al. (2012), [4]Burgett & Chase (2015), [5]Morin (1995), [6]Urban (2013), [7]Benoy (2008), [8]Wissinger et al. (1999), [9]Holomuzki et al. (1994), [10]Rudolf & Van Allen (2017), [11]Rudolf & Van Allen (2017), [12]Ramamonjisoa & Mori (2019), [13]Keitzer & Goforth (2013), [14]Atlas et al. (2013), [15]Bayer et al. (2021), [16]Bayer & Lowe (2021), [17]Takatsu (2022), [18]Relyea et al. (2005), [19]Mills & Semlitsch (2004), [20]Blaustein et al. (1996), [21]Blaustein (1997), [22]Alonso et al. (2024b), [23]Manenti et al. (2020), [24]Nery & Schmera (2016), [25]Ptatscheck et al. (2025), [26]Reinhardt et al. (2017), [27]Alonso et al. (2024a), [28]Arribas et al. (2014), [29]Cabrera-Guzmán et al. (2017).

are also important, since they can induce that the loss of both generalist species and benthic grazer have no effect or even reduced phytoplankton biomass, likely due to the absence of tadpole nutrient release through excretion and the control of macrophytes and periphyton by tadpole grazing, which compete with phytoplankton for nutrient and light (Anderson & Kneitel, 2015, Costa & Vonesh, 2013a, Earl et al., 2023, Iwai et al., 2012, Mokany, 2007, Rowland et al., 2017). The different outcomes with the loss of the same species showed the importance of specific conditions, since ecosystem limitations determinate the effects of species loss (Costa & Vonesh, 2013a, 2013b, Hite et al., 2018, Van Meter & Swan, 2014, Van Meter et al., 2011). For example, light was more limiting than nutrient concentration, and thus, controlled effects of anuran loss, as the lack of nutrient release due to anuran excretion reduced phytoplankton abundance in light conditions, but had no effect on shadow conditions (Earl et al., 2023).

Periphyton showed a more consistent response to anuran loss, with the loss of tadpoles inducing an increase in periphyton accrual due to anuran larvae being highly efficient grazers, whose effect cannot be substituted by other grazers as macroinvertebrates (Alonso et al., 2022, Atwood et al., 2014, Barnum et al., 2013, Barnum et al., 2022, Brönmark et al., 1991, Colón-Gaud et al., 2009, Rowland et al., 2017, Rugenski et al., 2012, Whiles et al., 2013). However, it is important to consider that the magnitude of the effect depends on the species, because tadpoles of different species can be more or less efficient grazers than others (Costa & Vonesh, 2013a, 2013b, Kupferberg, 1997a, Morin & Johnson, 1988, Schmidt et al., 2019, G. R. Smith et al., 2016). Not only tadpole species influenced their effects, but also the size of the individuals, since the absence of big individuals induced greater increases in periphyton accrual than the loss of smaller ones (Parlato & Mott, 2025). These effects of anuran loss on periphyton do not affect evenly to all algal taxa. The main increases after tadpole loss were filamentous green algae and diatoms, specially big-sized, stalked and loosely attached ones, in detriment of small and firmly attach algae, since the former ones are more easily removed by bioturbation and are less prone to intact passage through tadpole gut and subsequent recolonization (Alonso et al., 2022, Barnum et al., 2013, Barnum et al., 2022, Connelly et al., 2008, Graham & Vinebrooke, 1998, Lamberti et al., 1992, Ranvestel et al., 2004, Solomon et al., 2004, Wang & Kam, 2019). These differential effects on the different algal taxa can even induce periphyton accrual reduction after amphibian loss, as observed with *Cladophora*, which increased the net growth of periphyton due to being avoided by tadpoles, which at the same time reduced its competitive pressure due to their consumption of diatoms (Kupferberg, 1997b). Despite being usually weaker than consumptive effects, indirect effects are also important and can lead to absence of effects of anuran loss on periphyton or even a decrease due to tadpole nutrient release in the water column and macrophyte cover reduction (Anderson & Kneitel, 2015, Iwai et al., 2012, Parlato & Mott, 2023). Other mechanisms could also reduce periphyton accrual and algal richness after anuran loss on periphyton in tropical areas, where anuran larvae and adults favour algal propagation when they stick to frog skin or are eaten by tadpoles and colonize new areas after intact passage through the guts (Cochak et al., 2024). Besides, it is also important to consider other components of freshwater communities when assessing the effects of amphibian diversity on periphyton accrual, since the combination of anurans with invertebrates grazers as mayflies and snails leads to facilitation mechanisms that can induce greater increases in periphyton accrual after their loss than were expected based on their individual effects (Bennett et al., 2015, Holomuzki & Hemphill, 1996, Rosenfeld, 1997). Interactions among different anuran species are also important, as the loss of the only anuran species of one ecosystem can induce an increase in periphyton accrual, but in presence of other anuran species, it could reduce periphyton accrual if this species outcompeted other more active species, displacing them from the best foraging sites, but after their loss those other species can increase grazing pressure on periphyton (Alonso et al., 2024a, Alonso et al., 2022). The inorganic components that attach to periphytic algae are also important for ecosystem functioning as they influence algal composition and hinder the access

to periphyton to small grazers (Ranvestel et al., 2004), and it have been observed to increase after anuran loss, due to tadpole removing sediment mass while feeding more efficiently than invertebrates (Connelly et al., 2008, Flecker et al., 1999, Ranvestel et al., 2004, Schmidt et al., 2019, Solomon et al., 2004, Wood & Richardson, 2010).

Macrophytes and metaphyton also showed an increase after anuran loss. That increase in macrophyte biomass was caused by tadpole scrapping leading to considerable damage in macrophytes (Anderson & Kneitel, 2015, Earl et al., 2023, Pinero-Rodríguez et al., 2021), with differences depending on anuran traits, with greater effects with the loss of bigger and more active tadpoles (Arribas et al., 2014). Plant identity is also important, as tadpoles prefer feeding on plants depending on their traits, and even if in the presence of only one species, they are going to feed on it and reduce its biomass, in the presence of several plants, they could mainly feed on the preferred species, inducing shifts in the community after their loss, due to the recovering of the one suffering the highest grazing pressure (Earl et al., 2023). The increase in metaphyton biomass after anuran loss was due to similar mechanisms, since tadpoles reduced their biomass by grazing them, especially when plants are smaller and softer (France & Welbourn, 1992, Kupferberg, 1997a, Mokany, 2007).

These different effects observed for anuran loss in zooplankton could be again dependent on the species, with some studies showing no effects and others finding an increase in zooplankton abundance and altered communities after tadpole loss. The effect of those species on zooplankton is mainly caused by tadpole competing with them over resources, as phytoplankton or other floating organic particles, since, in absence of predators, zooplankton are mainly limited by resource availability, and tadpoles can reduce it even if they are not as efficient in their foraging (Buck et al., 2015, Costa & Vonesh, 2013a, Harjoe et al., 2022, Hite et al., 2018). Still, differences could also be due related to other factors, since the same species was shown to either reduce zooplankton abundance or have no effect, depending on the specific conditions (Costa & Vonesh, 2013a, 2013b, Parlato & Mott, 2023, 2025, Rohr & Crumrine, 2005, Van Meter & Swan, 2014, Van Meter et al., 2011). It could be due to the different initial zooplankton communities, since tadpoles outcompete some zooplankton taxa, as copepod nauplii and rotifers, but had no effect on others, such as cladocerans and ostracods (Van Meter et al., 2011). Tadpole size can also influence zooplankton communities, with greater tadpoles having more influence than smaller ones, even if they are of the same species, given their greater potential to induce trophic cascades (Parlato & Mott, 2025).

Anuran loss can influence macroinvertebrate community structure, but effects are again highly variable, with some studies showing changes in species composition, others finding reductions or increases in overall abundance or macroinvertebrate size, and still others showing no effects. The increase in macroinvertebrate abundance and size or the alterations in community after tadpole loss can be due to different pathways. Small macroinvertebrates with fast cycles and flying adults, as Culididae and Chironomidae, can be benefitted by amphibian loss since tadpoles can reduce their abundance through predation and dislodging of their cases while grazing, and adult insect avoid laying eggs on ponds with tadpoles (Blaustein & Margalit, 1994, Earl et al., 2023, Holomuzki & Hemphill, 1996, Kiffney & Richardson, 2001, Mokany, 2007, Mokany & Shine, 2003, Rohr & Crumrine, 2005, Rowland et al., 2017). In the case of greater or strict macroinvertebrate grazers, as snails, similar results are found due to competitive pressure, due to anuran larvae being more efficient grazers than most invertebrates (Atwood et al., 2014, Brönmark et al., 1991, Kiffney & Richardson, 2001, Lamberti et al., 1992, Preston et al., 2012, Rohr & Crumrine, 2005). Negative effects on macroinvertebrate abundance and size after tadpole loss have been shown mainly for more generalist macroinvertebrates as caddisflies and isopods, due to tadpoles releasing particulate organic matter that invertebrates can feed on, allowing their access to previously unavailable resources though bioturbation and altering leaf litter conditioning and traits (Alonso et al., 2022, Iwai & Kagaya, 2007, Jara & Pueta, 2023). Although negative effects of anuran loss have also been found for strict grazers, as snails, which reduced their abundance after tadpole loss, due to tadpoles

feeding on phytoplankton inducing resource relocation from the floating column to the benthos by ingestion and egestion or nutrient cycling (Smith et al., 2012). Anuran loss not only affect their competitors, but can also affect their predators depending on the species lost, as observed with the increase of dragonfly larvae after the loss of non-palatable tadpoles, whereas loss of tadpoles without noxious substances had no effect (Manenti et al., 2017). The ecological context is highly important in determining which of these effects is more dominant. Regarding anuran larvae, it is important to consider the species lost, the other amphibians in the community and their development stage and size (Kupferberg, 1997b, Parlato & Mott, 2023, 2025). But macroinvertebrate community is also a key determinant of those effects, noy only because the different invertebrates species are affected differently depending on their characteristics, as explained before, but also due to the interactions among species that modulate anuran loss effects. For example, tadpole loss increased chironomid abundance but only in communities with presence of mayflies, since only in the presence of both species, bioturbation was strong enough to affect chironomid larvae (Rosenfeld, 1997). Complex interactions can also be found due to different life forms of metamorphosing insects, as chironomid larval abundance and size reduced by tadpole loss, since their activity produce particulate organic matter that larval chironomids can feed on, but ultimately tadpole loss had a positive effect on adult chironomid abundance, since tadpoles eat their pupae (McLachlan, 1981). Changes in communities after depletion of complex amphibian communities were related to the different ecosystem responses to anuran loss, as increases in sediment accrual and algal biomass, homogenization of algal biofilm, reductions in the amount of available CPOM and its palatability, with a great importance of the macroinvertebrate community composition (Barnum et al., 2022, Colón-Gaud et al., 2009, Colón-Gaud et al., 2010, Rantala et al., 2015).

The wide range of interactions among anurans and macroinvertebrate described in the previous paragraph favour the understanding of the contrasting effects of anuran loss on food webs that have been observed. The food web structure can be maintain after amphibian loss due to generalist and plastic behaviour of invertebrates (Barnum et al., 2015). Oppositely, a decrease in organic matter transfer can be induced by an increase in periphyton due to the lack of tadpoles that act as the main grazers, what also changed the food web structure from one mainly based on periphyton to another where the main transfer started on particulate organic matter (Whiles et al., 2013). The loss of anuran species altered food webs due to changes in trophic positions of the other species, as other anuran changed their feeding to take advantage of empty niches left by the lost species (Arribas et al., 2015, Belouard et al., 2024), fish and macroinvertebrates altered their diet due to the absence of residues produced by tadpole excretion, bioturbation and carcasses (Barnum et al., 2013, Gobel et al., 2023), and macroinvertebrates increased their niches after competitive and predatory release due to tadpole loss (Gobel et al., 2023).

The absence of effects of amphibian loss on leaf litter decomposition found in most studies is likely due to tadpoles preferring to feed on other substrates, mainly periphyton, making their consumptive effects scarce (Connelly et al., 2011, Earl et al., 2023, Iwai et al., 2012). However, interactions among species are also important in this variable, as loss of some anuran species showed no effect by themselves, but it reduced the effect of shredder macroinvertebrates on leaf litter decomposition, since tadpoles release nutrients that increase leaf litter palatability, produce FPOM that invertebrates can feed on, favouring a bigger invertebrate size, facilitate invertebrate feeding on leaves by removing biofilm and sediment, and increase nutrient content of leaves by increasing the concentration of dissolved nutrients available to immobilization in leaves by microbial decomposers (Iwai & Kagaya, 2007, Iwai et al., 2012, Iwai et al., 2009, Rugenski et al., 2012). Although there are some tadpoles whose loss directly decrease leaf litter decomposition, through similar pathways to those that benefitted macroinvertebrate activity, as well as direct consumption of leaves (Ramamonjisoa & Natuhara, 2018, Schmidt et al., 2019, Stoler et al., 2016). Tadpole loss can also affect to other related processes as particulate organic matter production,

but the effects on each size portion of particulate organic matter is highly dependent on amphibian characteristics and environmental conditions, as they can be decreased after tadpole loss due to tadpole increasing it through faecal materials and releasing small fragments of periphyton and leaves while grazing, or increase after their loss due to tadpole consuming it (Colón-Gaud et al., 2009, Colón-Gaud et al., 2010, Rantala et al., 2015, Rugenski et al., 2012). Besides, amphibian depletion did not induce any change in fungal or bacterial communities, which may be due to tadpoles feeding on microbes while grazing, but also stimulating their growth through nutrient release, with both processes disappearing after tadpole loss (Connelly et al., 2011). All of this shows the importance of species-specific characteristics of different anurans in their effects on leaf litter decomposition, since traits such as size, feeding mode and activity can determine whether their presence affects leaf litter decomposition and the extent of these effects.

The slowing down of nutrient cycling and reductions in nutrient concentrations usually found after tadpole loss are likely due to tadpole consumption of periphyton, phytoplankton, or more rarely invertebrates, and release of the nutrients stored there through excretion (Iwai et al., 2012, Knoll et al., 2009, Mokany, 2007, Ramamonjisoa & Natuhara, 2018, Rantala et al., 2015, Wang & Kam, 2019, Whiles et al., 2013). Although nutrient release is also related to their stoichiometry and different species would induce greater increases of some nutrients or others, what could be the cause of the absence of effects after the loss of other anuran larvae (Holomuzki, 1998, Iwai et al., 2012, Iwai et al., 2009, Knoll et al., 2009, Kupferberg, 1997b, Preston et al., 2012).

The different results for ecosystem metabolism observed after tadpole loss in different studies and species could be explained by the environmental differences. Streams with a greater importance of primary production are more likely to be influenced by amphibian loss that those mainly heterotrophic, since their main effect is over periphytic algae, what could explain the decrease in respiration after anuran loss in Canadian and Panamanian streams (Atwood et al., 2014, Connelly et al., 2008, Rantala et al., 2015, Whiles et al., 2013) and the absence of effects in US ponds (Rubbo et al., 2012). The variety of consequences of amphibian loss among studies measuring respiration associated with leaf litter decomposition is likely due to water characteristics, since effects of amphibian loss on respiration depends on indirect effect through nutrient release, and the different in ecosystem chemistry could determine if amphibian loss cause reduction of respiration or no effect (Connelly et al., 2011, Rugenski et al., 2012, Van Meter et al., 2012). Effects of amphibians on primary production also rendered different results in the different species, with two counteractive processes that leaded to different outcomes depending on the strength of each one. Amphibian loss could reduce primary production due to the increase of nutrient concentration caused by tadpole activity (Connelly et al., 2008, Kupferberg, 1997b, Mokany, 2007), but it could also increase it due to anuran intense consumptive effects on periphyton that limited the potential primary production of the ecosystems due to the scarcity of producers (Connelly et al., 2008, Ward et al., 2023, Whiles et al., 2013). These different effects are likely induced by the different algal communities, since depending on if tadpole grazing induce a stronger reduction in algae with higher or lower primary production efficiency, their loss can cause contrasting effects.

Effects of urodele loss on freshwater ecosystems

The response of phytoplankton to urodele loss is ambiguous and may depend on the amphibian species, since the different predatory effects on herbivorous organisms leads to different phytoplankton responses. Thus, both adult and larvae salamander loss reduced phytoplankton chlorophyll through trophic cascades on phytoplankton consumers such as zooplankton, macroinvertebrates and anurans, as well as by stimulating algal growth by releasing nutrients through excretion (Arribas et al., 2014, Benoy, 2008, Holomuzki et al., 1994, Morin, 1995). The presence or absence of these effects varied depending on species, but the developmental stage could also be influencing the variety of patterns; for example, the loss of early stages, which feed mainly on zooplankton, reduced phytoplankton biomass, but this was not

the case for later stages, which feed on macroinvertebrates and anuran larvae and thus did not induce a trophic cascade affecting phytoplankton (Rudolf & Van Allen, 2017). However, these differences were also found for salamanders of the same species and development stage, what could be due to the complexity of trophic cascades, since they can lead to different outcomes depending on the identity and traits of all the components of the ecosystem, as the different interactions among species can significantly alter those processes (Mills & Semlitsch, 2004, Morin, 1995, Relyea et al., 2005).

Most studies on urodele effects on periphyton have shown no effects, as observed for several North American salamanders, both adults and larvae, due to the absence of top-down effects that reached the basal resources since the consumer communities compensated those effects or the abundance of armoured predator-resistant invertebrates precluded any change in their communities (Atlas et al., 2013, Bayer & Lowe, 2021, Harris, 1995, Morin, 1995, Rowland et al., 2017, Rubbo et al., 2012). However, developmental stage was also an important factor, as salamander loss induced an increase in periphyton biomass when salamander larvae were at early and intermediate stages but not at later stages (Rudolf & Van Allen, 2017). A different trend was found for urodeles in Europe and Asia, whose loss reduced periphyton density through trophic cascades, since their predatory pressure on grazing zooplankton, macroinvertebrates and anuran tadpoles was strong enough to trophic cascades that reduced grazing pressure on algae. It was caused by both, direct consumption and reduction of consumer abundance, and indirect effects with changes in macroinvertebrate behaviour leading to feed on other resource which leaves them less exposed to swimming predators as leaf litter (Alonso et al., 2024a, Alonso et al., 2024b, Blaustein et al., 1996, Ramamonjisoa & Mori, 2019). Still, when comparing their effects with those of the loss of anuran larvae, urodele effects were weaker, and they were overridden by the presence of anurans. These lower effects than anurans observed for urodeles are likely due to anurans directly reducing periphyton accrual through direct consumption, whereas urodeles induce trophic cascades that increase periphyton accrual through consumption of the grazers. However, both groups can also affect periphyton through other indirect effects, such as nutrient release on the water column or sediment removal, which favour algal growth, and thus, affecting negatively periphyton accrual after their loss (Alonso et al., 2024a, Rowland et al., 2017).

Effects of urodeles on zooplankton communities were complex and likely dependent on the characteristics of both amphibian and zooplankton communities. The increases in zooplankton abundance or biomass after urodele loss observed for larvae of different urodeles could be expected given that several salamander species feed on zooplankton, although it could also be due to zooplankton releasing diapause eggs in salamander presence, delaying their clutching after salamander reaches low densities (Blaustein, 1997, Blaustein et al., 1996, Harris, 1995, Rowland et al., 2017, Urban, 2013). But, since not all zooplankton taxa are equally affected by predation, zooplankton abundance can be maintained even if community is altered since the most sensitive taxa will increase their abundance in detriment of the more resistant ones, which were dominant in salamander presence (Benoy, 2008, Cabrera-Guzmán et al., 2017, Mills & Semlitsch, 2004). The abundance of those taxa more resistant to predation or a preferential feeding of salamanders on other preys as macroinvertebrates could lead to absence of effects of their loss (Benoy, 2008, Roe et al., 2006, Rubbo et al., 2012). These differences among species could be due to salamander size or development stage, since large salamanders preferentially feeds on macroinvertebrates and only some zooplankton taxa, leading to lower effects on zooplankton than smaller urodeles (Benoy, 2008), and similarly, salamander loss altered zooplankton communities in their first and intermediate stages, but not at later stages, when their diet shift towards larger preys (Rudolf & Van Allen, 2017).

Effects of urodeles on macroinvertebrate communities were complex and depended on several factors. Most studies found an increase in macroinvertebrate abundance and changes in community structure after urodele loss due to the predatory pressure that adult and larvae urodeles

induce on invertebrates (Benoy, 2008, Blaustein et al., 1996, Takatsu, 2022). However, others found no effect, which could be due to the different urodele species (Bayer & Lowe, 2021), but also to macroinvertebrate community, since armoured invertebrates are less affected by urodele activity (Atlas et al., 2013). The fact that some species loss render either increases of invertebrate abundance or no effects, suggest that consequences of urodele loss on macroinvertebrates depend not only on the species, but also on their habitat, developmental stage and their interactions with the rest of the community (Alonso et al., 2024b, Burgett & Chase, 2015, Manenti et al., 2020, Nery & Schmera, 2016, Ptatscheck et al., 2025, Reinhardt et al., 2017, Rowland et al., 2017). Developmental stage influenced the effects of salamander loss, since they had a stronger predatory pressure on macroinvertebrates at earlier stages than at later stages, in relation to the change in their diet towards bigger preys as amphibian larvae as they grow (Rudolf & Van Allen, 2017, Takatsu, 2022). The habitat also seemed important, since loss of salamander larvae from streams altered macroinvertebrate community in different ways than those individuals from ponds due to feeding preferentially on different taxa, although the loss of both of them increased their abundance (Ptatscheck et al., 2025). Lastly, interactions between macroinvertebrates and amphibians can be relevant, as their effects are caused by trophic cascades and they are shaped by the identity of each species. For example, two caddisflies increased their survival after salamander loss when considered individually, however, in the presence of both, only one of them increased their survival after salamander loss, since it preyed on the other one but was more vulnerable to salamander predatory pressure, which induced a net higher survival of the prey caddisfly in salamander presence (Wissinger et al., 1999). But those effects are also observed in the interactions among urodeles. The loss of one salamander increased macroinvertebrate abundance, but in ecosystems with a greater urodele, the loss of both had no effect, since the bigger one did not feed mainly on macroinvertebrates, but preyed on the smaller salamander, reducing its predatory pressure on macroinvertebrates (Bayer & Lowe, 2021). A different example is that the loss of two salamanders had no effect on macroinvertebrates when taken into account individually, but the loss of both in ecosystems where they were previously significantly increased invertebrate abundance and richness, due to their use of different microhabitats for foraging, which avoided invertebrates from sheltering in the other type of substrate to shelter (Keitzer & Goforth, 2013).

Leaf litter decomposition can be affected by urodele loss through two complementary pathways. Urodele loss increases leaf litter decomposition due to the lack of consumptive effects on macroinvertebrates that induce trophic cascades, mainly when they were in their early and medium developmental stages (Rudolf & Van Allen, 2017). But urodele loss can also reduce leaf litter decomposition due to non-consumptive effects without changes in macroinvertebrate or aquatic hyphomycete community, but altering macroinvertebrate feeding behaviour, inducing a shift from a predominantly leaf litter diet in salamander presence to periphyton grazing activity in their absence, as macroinvertebrates prefer feeding on periphyton, but leaf litter provided a safer refuge to avoid salamander predation (Alonso et al., 2024b).

Urodeles loss was observed to slow down nutrient cycling in similar ways to anuran loss. Urodele feeding on invertebrates release part of those nutrients through excretion, with their higher activity benefitting nutrient cycling due to their higher consumption and excretion rates (Munshaw et al., 2013). However, most research is needed, since the studies are scarce and the loss of single species have rendered opposite effects on nutrient concentrations in water (Arribas et al., 2014, Holomuzki et al., 1994).

Effects of urodele loss on ecosystem metabolism have shown contradictory outcomes in the two studies analysing it. The absence of effects of salamander loss on primary production or respiration have been linked to the low primary production and high dependence of allochthonous resources in those streams, which reduces the influence of trophic cascades of instream species (Rubbo et al., 2012). However, in less heterotrophic environments, salamander loss increased respiration and primary production due to the

consumption of grazers, as invertebrates and tadpoles that feed on periphyton, controlling metabolism through trophic cascades, but the effect was only observed in early and intermediate development stages and disappeared on later ones, showing again the importance of the developmental changes of amphibians on ecosystem functioning (Rudolf & Van Allen, 2017).

CONCLUSIONS AND FUTURE DIRECTIONS

In this review, we summarized the results of 129 studies about effects of amphibians on freshwater ecosystem structure and functioning. Despite the dramatic decline that amphibians are suffering worldwide, knowledge about impacts of amphibian loss on freshwater ecosystems is still very limited, and most studies have focused on a few families and ecosystems, producing important biases and knowledge gaps. Despite finding some consistent effects for some variables, as an increase in periphyton, macrophyte and metaphyton biomass after anuran loss, most effects described in the literature were highly variable, and often modulated by species traits (e.g., feeding mode and body size), but also by variation within species, as differences in size, sex or development stage (Davenport et al., 2025, Rudolf & Van Allen, 2017, Takatsu, 2022). And effects of urodeles were generally more variable compared to those of anurans (Bayer & Lowe, 2021, Stemp et al., 2022), which could be related to the more complex mechanisms involving trophic cascades that controlled the studied variables, but also to the lower number of urodele studies. The review evidenced large differences across amphibian species in relation to their effects on freshwater ecosystems, and that variability among species shows the importance of understanding the pathways through which the traits of each species determine the outcome of their loss, especially in those variables that have shown a greater range of responses, for example, phytoplankton, zooplankton and macroinvertebrates in the case of anurans. It is also important to note that some outcomes depended not only on the amphibian species lost, but also on the experimental conditions due to the specific characteristics of the ecosystem and the interactions among the different species of the community. These results allow to point out the main gaps on research on the ecological effects of amphibian loss. Firstly, research have been strongly biased towards some groups, while other have been understudied. Urodeles have received much less attention than anurans, and even within that group, most studies have focused on two families (Ambystomatidae and Salamandridae) in North America and on the effects of their loss on macroinvertebrates. Species from other families and locations, as well as effects on other ecosystem compartments, are still scarce. Research on anurans also presents some gaps, with many papers focusing on three families (Ranidae, Bufonidae and Hylidae) and, again, in North America, whereas other taxa and other continents, especially Asia, Africa and Oceania, still remain underrepresented. Another gap is related to the type of ecosystem. Most studies were conducted in mesocosms simulating ponds, and there has also been extensive research on total amphibian depletion through stream sampling. Thus, despite some isolated studies from lakes, paddy fields or cave streams, ecosystems different from ponds and headwater streams have received scarce attention. Lastly, given that the effects of amphibian loss are highly related with the other components of the community, it is very relevant to use real-case scenarios and prioritize field experiments with actual communities and natural conditions, with predictions about which species are likely to disappear (e.g., as a results of habitat loss, climate change, invasive species or infection by pathogens), and which ones to remain. Overall, investigations about how amphibian loss impacts freshwater ecosystems should continue implementing realistic scenarios and widening its scope to include less studied ecosystems and taxonomic groups, to reach a comprehensive understanding of the consequences of plausible extinctions and to improve conservation and management measures to mitigate those effects.

AUTHOR CONTRIBUTIONS

A.A.:Conceptualization, investigation, methodology, visualization, writing - original draft, writing – review and editing; L.B.: Conceptualization, methodology, writing – review and editing; J.B.:

Conceptualization, methodology, visualization, writing – review and editing.

CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

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