



# Between-habitat distributions of pond tadpoles and their insect predators in response to fish presence

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**Abstract** Between-habitat distributions of prey shared by multiple predators depend on habitat use by the predators, whose own distributions may interact. We used a large-scale, whole-system natural experiment to examine distributions of anuran tadpoles and insect predators between pond microhabitats with contrasting complexity (open water vs emergent littoral vegetation) in drainable ponds that were either kept fishless or stocked with fish. Total relative densities of insect predators did not significantly differ with respect to the fish status of the ponds. Individual anuran taxa responded variously, but only fish-tolerant *Bufo bufo* densities were higher in the presence of fish. The densities of both insect predators and tadpoles showed positive interactions between fish presence and the use of complex littoral habitat. The habitat shift to littoral vegetation could be indirectly amplified by fish adverse impact on submerged macrophytes, the main structured microhabitat in open-water areas. Irrespective of mechanisms of fish effects (direct consumption, behavioral deterrence or alteration of

habitat conditions), aggregation of both tadpoles and insect predators in littoral vegetation may put tadpoles at greater risk of predation by insects, a potentially important factor of amphibian mortality in waters containing fish.

**Keywords** Antipredator response · Habitat complexity · Non-consumptive effects · Predator–prey interactions · Littoral vegetation · Spatial behavior

## Introduction

Distributions of predators and prey across space can have major community-level consequences (Krivan, 1997; Lima, 2002). Predation has been demonstrated to alter habitat use and distribution of prey organisms (e.g., González & Tessier, 1997; Dupuch et al., 2009; Hanisch et al., 2012). Much attention has been given to the influence of multiple predators on prey populations and the role of interactions among predators in shaping predator–prey relationships (reviewed in Sih et al., 1998) because effects of multiple predators can depart from predictions based on pairwise relationships (e.g., Soluk & Collins, 1988; Wissinger & McGrady, 1993; McCoy et al., 2012; Palacios et al., 2018). In aquatic systems, predators that typically forage actively in simple open habitats are hampered by vegetation, and thus complex-structured microhabitats may relax their

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predation pressure on prey populations (Crowder & Cooper, 1982; Heck & Crowder, 1991). Multiple predators interact with one another, including intra-guild predation (IGP), as well as with habitat complexity (González & Tessier, 1997; Swisher et al., 1998; Anderson & Semlitsch, 2016). Prey shared by multiple predators should choose among habitats according to their use by top predators and by mesopredators, whose own spatial distributions are dependent on the distribution of top predators.

Fish are notorious for their strong top-down impacts on freshwater communities; the occurrence of some macroinvertebrates and amphibian larvae is limited to waters where fish are absent (Schilling et al., 2009; de Mendoza et al., 2012; Holbrook & Dorn, 2016). Predatory effects of fish can be confounded by a plethora of indirect interactions, including alteration of habitat conditions ('ecosystem engineering') in some species (Parkos et al., 2003; Matsuzaki et al., 2007). Predaceous insects, as mesopredators, may respond to predation risk from fish, as well as to cues of prey, while both fish and insects send danger cues to lower trophic levels (Burks & Lodge, 2002; Inoda, 2012). Prey shared by fish and insect predators may be capable of distinguishing among their cues and correspondingly fine-tune their antipredator behavior (Semlitsch & Reyer, 1992; Van Buskirk, 2001; Relyea, 2003; Smith & Awan, 2009). The different modes of prey detection and capture by fish and aquatic insects correspond with their habitat use. Most fish predators are visually oriented (Healey, 1984). Their ability to capture prey decreases in structurally complex habitats formed by macrophytes (e.g., Crowder & Cooper, 1982; Savino & Stein, 1982; Diehl & Kornijów, 1998), although small-bodied fish or fish that ambush rather than chase prey are less affected, or not at all (Diehl & Kornijów, 1998; Eklöv & VanKooten, 2001; de Mendoza et al., 2012). Consequently, prey should prefer vegetated or otherwise structured habitats in the presence of fish (Fairchild & Holomuzki, 2005; Hanisch et al., 2012, but see Gunzburger & Travis, 2005; Smith et al., 2009). Although predatory insects use visual cues as well, many taxa rely greatly on tactile or chemical information to detect prey (e.g., Richards & Bull, 1990; Inoda, 2012). Predatory insects use aquatic vegetation as a perch site, where they ambush their prey; moreover, as they are typically smaller than fish predators, they may display better maneuvering ability

in structurally complex habitats (Heck & Crowder, 1991; Fairchild & Holomuzki, 2005). Many insect predators have been reported to easily alternate their habitat and foraging strategies; in structured habitats insects can shift between active foraging and a sit-and-wait mode, depending on the density, activity and evasiveness of prey and on interference from other predators (Akre & Johnson, 1979; Formanowicz, 1982; Johansson, 1991; Michel & Adams, 2009). Consequently, insect predators display higher abundance and diversity in structurally complex, vegetated habitats than in open water (Semlitsch & Reyer, 1992; Babbitt & Tarr, 2002; Rennie & Jackson, 2005; but see McCauley, 2008). Their prey, i.e., amphibian larvae, have in turn been observed to avoid vegetation when insect predators were present (Rubbo et al., 2006; Smith & Awan, 2009). The presence of chemical defenses in amphibian larvae may prove critical for sorting among habitats, as these defenses can vary in effectiveness against different types of predators; some species may perform better in habitats dominated by fish (Kats et al., 1988; Manteifel & Reshetnikov, 2002; Üveges et al., 2019). Also, fish are gape-limited feeders (Sibbing, 1988), and tadpoles of some species may grow large enough to become invulnerable to fish predation, while insects with piercing mouthparts are less size-limited (Culler et al., 2014).

Responses of aquatic prey to the presence of multiple predators are generally inferred from small-scale experimental studies on specific prey species, whose relevance to natural complex and species-rich communities is often unclear (Wilbur & Fauth, 1990; Anderson & Semlitsch, 2016). Given the strong predatory pressure of fish and insects on amphibian larvae, the lack of field research on their natural distributions within ponds differing in predator assemblages is surprising. Although they do not allow for inference on individual species interactions, community-level field studies taking into account natural habitat complexity would not only verify the results from artificial experimental environments, but also provide vital information for wetland conservation management. Here, we examined spatial distributions of anuran tadpoles and their insect predators between open water as a simple habitat and emergent littoral vegetation as a complex habitat in the presence or absence of fish in semi-natural ponds. Both tadpoles and insects, especially those active when foraging, are at risk from fish (e.g., Healey, 1984; Henrikson, 1990;

Kloskowski, 2011a; de Mendoza et al., 2012). Based on the differences in hunting modes and population size structure, we assumed that fish would pose a greater threat to predatory insects and their shared prey (tadpoles) in the less structured open-water habitat than in emergent vegetation (de Mendoza et al., 2012). On the other hand, tadpoles are under stronger predation pressure of sit-and-wait foraging insects in the emergent littoral vegetation and should be capable of better evading their attacks in open water (Formanowicz & Bobka, 1989; Smith & Awan, 2009; see also Relyea, 2001). Therefore, we predicted that compared to fishless ponds, in ponds containing fish the between-habitat distributions of insect predators and tadpoles vulnerable to fish would be skewed towards emergent littoral vegetation. Conversely, chemically defended *Bufo bufo* tadpoles, which are tolerant of fish but vulnerable to at least some predatory insects (Laurila, 1998; Manteifel & Reshetnikov, 2002; Kloskowski, 2011b), were expected not to alter their behavior in response to fish and to stay mainly in open water (Laurila et al., 1997; Smith et al., 2009).

## Materials and methods

### Study system

The research was conducted in open ponds used for extensive culture of cyprinids, mainly common carp *Cyprinus carpio*, in south-eastern Poland (51° 17–33' N, 22° 15–26' E). The ponds were normally filled and stocked in spring, and in autumn they were drained and the fish were harvested. The surface area of the ponds used in the study varied between 1 and 14 ha, except one pond of 18 ha. Water depth was fairly uniform across the pond, although it typically became shallower towards the shore. Mean depth ranged from 0.7 to 1.3 m over the sampling period. We used filled but unstocked ponds (“fishless ponds”) and stocked ponds (“fish-containing ponds”) to carry out a large-scale natural experiment comparing the distributions of amphibian larvae and their insect predators between pond microhabitats. We sampled 35 ponds, in spring 2012 (14 ponds) and 2013 (21 ponds); 17 ponds were fishless and 18 ponds contained fish. Each pond was used only once in the study. While natural fishless and fish-containing ponds often differ in depth and

hydroperiod (Wellborn et al., 1996), the advantage of our approach was that with the exception of some individual variation (size area, emergent vegetation cover) among ponds, the two types of ponds did not substantially differ in any morphological or environmental characteristics, i.e., fish effects were separated from environmental effects. All study ponds were situated in an agricultural landscape interspersed with small forest patches and were enclosed by a network of grassed levees and ditches. Given the homogeneity of the surrounding terrestrial matrix, we did not expect any sampling biases resulting from landscape-related variation in species abundance. The fish-containing ponds were stocked from March 23 to April 24. Screens of 2–3 mm mesh at water intakes prevented wild fish from entering the ponds via supplied water. Fish populations were fairly uniform among stocked ponds and consisted of 1- and 2-year-old cyprinids, mainly common carp (approx. 80–95% of total stock biomass; stocked at individual mass of approx. 40–410 g). Additionally, small amounts (stock biomass of individual species typically < 10 kg/ha) of other carp species were stocked, i.e., grass carp *Ctenopharyngodon idella*, bighead carp *Hypophthalmichthys nobilis*, and crucian carp *Carassius carassius*. Total fish stocking densities in the ponds (about 100–280 kg/ha) were similar or lower than the natural densities attained by cyprinids in shallow eutrophic lakes (Scheffer, 2004). The stocked fish were large enough to present a predation risk to amphibian larvae and their insect predators in the ponds. Common carp is primarily benthivorous, not specialized in the capture of fast-moving prey due to the lack of grasping teeth (Sibbing, 1988). However, it is an opportunistic feeder, readily foraging on non-benthic invertebrates and amphibian larvae and able to heavily suppress their populations via both consumptive and non-consumptive effect (Parkos et al., 2003; Rahman et al., 2010; Kloskowski, 2011a).

### Habitat division into open water and complex littoral habitat

The ponds supported dense beds of emergent macrophytes along the shores, composed mainly of *Phragmites australis*, *Typha angustifolia*, *T. latifolia* and *Schoenoplectus lacustris*, usually several meters wide but occasionally extending up to 100 m. Stem density in the overgrown areas varied between 72 and 182

stems  $\text{m}^{-2}$  (based on counts of green and the previous year's dried-up stems in 20 ponds, using a  $0.5 \text{ m} \times 0.5 \text{ m}$  frame at eight evenly distributed sites in the vegetated littoral zone per pond). The emergent littoral vegetation was difficult for larger fish to access (cf. Sychra et al., 2010), although its coverage was not uniform, with small poorly vegetated patches inside the macrophyte beds. The percentage of pond area covered by emergent macrophytes did not differ between ponds with and without fish (mean  $28.8 \pm \text{SE } 3.8\%$  vs  $31.3 \pm 3.5\%$ ,  $t_{33} = 0.51$ ,  $P = 0.610$ ). Owing to the overall shallowness of the ponds, under favorable conditions submerged macrophytes could occur across the entire bottom area. Nonetheless, during the study period there was an irregular yet distinct border in each pond between two roughly homogenous habitats: emergent vegetation belts along the shore (henceforth "littoral habitat") and open-water areas.

#### Sampling of predatory insects and amphibian larvae

Pond insects and tadpoles were captured using funnel activity traps between May 15 and May 19, 2012 and between May 17 and June 4, 2013 (when the season was delayed due to later ice-out), a period coinciding with the peak of larval amphibian occurrence in the ponds (Kloskowski, 2009). Trapping was used because traps effectively sample aquatic insects and tadpoles, including highly mobile species, in dense vegetation (cf. Becerra Jurado et al., 2008; Kloskowski, 2009), and also are not affected by the diel activity patterns of the sampled animals. The traps were made of 1-L plastic cylinders 220 mm in length with funnels about 100 mm at the base and 23 mm at the entrance (for details on trap construction see Nieoczym & Kloskowski, 2015). The traps, placed on the bottom for 24 h, were approximately evenly spaced across each pond, in pairs, 5–15 m in opposite directions from the outer edge of emergent macrophytes (towards the shore and the center of the pond). In each pond 10 traps were set in open water and 10 traps in the littoral habitat. Trapped tadpoles were determined to species (except for "water frogs" *Pelophylax* sp. and "brown frogs" *Rana temporaria* and *R. arvalis*, which were identified to genus) and released. They were roughly measured to be less than 40 mm total length. Predatory insects retrieved from

the traps were preserved in 70% alcohol and later identified under a  $10 \times$  microscope and measured. Trap catches are presented as numbers of individuals per 10 traps.

We classified *Notonecta glauca* and *Ranatra linearis* (Heteroptera), larval Anisoptera and Dytiscidae, and larger-sized ( $\geq 15 \text{ mm}$  body length) adult dytiscids as predators ("insect predators") on amphibian larvae (Formanowicz & Bobka, 1989; Henrikson, 1990; Tate & Hershey, 2003; Klecka & Boukal, 2012). Other potential invertebrate predators, predaceous Hirudinea, Zygoptera larvae, and *Ilyocoris cimicoides* (Heteroptera), were either captured only exceptionally or deemed too small to exert significant predatory pressure on tadpoles (Klecka & Boukal, 2012).

Besides *Pelophylax* and *Rana* frogs, amphibian species trapped in the ponds were *Bombina bombina*, *Pelobates fuscus*, *B. bufo*, *Bufo viridis* and *Hyla orientalis*. Omitted from the analyses were urodels (*Triturus cristatus* and *Lissotriton vulgaris*), which were rarely observed in the ponds. The anuran species occurring in the ponds are considered prone to fish predation (Kloskowski, 2011a; Buschendorf et al., 2016), except *B. bufo* tadpoles, which, due to the production of defensive toxins, are less susceptible to fish than to insect predators (Laurila, 1998; Manteifel & Reshetnikov, 2002; Üveges et al., 2019) and whose response to fish predation risk diverges in that they typically display shoaling behavior (Watt et al., 1997; but see Anholt et al., 1996 and Laurila et al., 1998 for experiments in which *B. bufo* tadpoles have exhibited spatial avoidance of predators). Species palatable to fish may vary in antipredator behavior and susceptibility to individual fish species (Stauffer & Semlitsch, 1993; Teplitsky et al., 2003; Buschendorf et al., 2016).

#### Environmental measurements

Environmental variables which could potentially affect habitat selection by insect predators and tadpoles (Kholin & Nilsson 1998; Thurnheer & Reyer, 2001; Sychra et al., 2010) were measured concurrently with insect/tadpole sampling. Submerged vegetation was collected using a Bernatowicz rake in 10 haphazardly selected open-water locations, roughly evenly spaced. Plants were dried to a stable biomass and weighed to 0.001 g. We calculated dry plant biomass per bottom area unit ( $\text{g m}^{-2}$ ) as a proxy for habitat complexity. The dominant species were *Chara* sp.,

*Stuckenia pectinata* and *Potamogeton lucens*. Other environmental variables were measured in the mid-water column, at about 30–50 cm above the bottom in both habitats, close to the trapping sites. Water temperature, oxygen concentration and conductivity were measured using a CX-401 ELMETRON meter. Total suspended solids (TSS) were estimated (PASTEL-UV SECOMAM spectrophotometer set to a 200–300 nm wavelength; means from three samples per habitat per site were calculated) because common carp causes an increase in suspended solids in the water through bioturbation and excretion of waste products (Matsuzaki et al., 2007), whereas macrophytes reduce suspended solid concentrations (reviewed in Scheffer, 2004). Samples were transported on ice to the laboratory and immediately analyzed.

### Statistical methods

To assess the effects of fish and habitat complexity on insect predator and tadpole densities in the two pond habitats, we used generalized linear mixed effects models (GLMMs) with a log link and negative binomial distribution. Year was considered as a random factor. Since two data points (catches in open water and in littoral vegetation) were obtained from each pond, pond identity was entered as another random factor. Owing to low occurrence of Anisoptera larvae (recorded in only 6 ponds) and predatory Heteroptera (recorded in 5 ponds), we pooled them with dytiscids in the analyses. We ran separate GLMMs for individual anuran taxa; the two least common species, *B. viridis* and *B. bombina*, which occurred exclusively or mainly in fishless ponds (see “Results”), were omitted because their sample sizes and distributions did not allow for meaningful analyses. Submerged vegetation abundance in open water was highly related to fish presence (GLMM with identity link function and normal distribution of errors; see “Results”), and therefore it was not included as a fixed variable in the density distribution models. However, its effect on proportional habitat use by insect predators and the anuran taxa for which models on their relative densities were constructed was evaluated using GLMMs with a logit link and a binomially distributed error term. The number of individuals captured in open water was treated as a binomial response, while the total number of individuals recorded in the pond was the binomial

denominator. Abiotic water parameter differences with regard to fish presence/absence and habitat type were also tested with GLMMs (identity link, normal errors). A Bonferroni correction for multiple testing was not applied (Moran, 2003). Significance levels were set at  $P = 0.05$ . All analyses were conducted in GenStat v. 15 (VSN International Ltd.).

### Results

Up to 8 species of insect predators were recorded in trap samples in each pond. The most common were dytiscids (adults or larvae), *Agabus* sp., present in 12 (34%) ponds, *Cybister lateralimarginalis* and *Rhantus latitans*, each recorded from 9 (26%) ponds). *Sympetrum* sp. had the highest frequency of occurrence in Anisoptera samples—4 (11%) ponds. The most commonly occurring anurans were *B. bufo*, recorded in 25 (71%) ponds, *P. fuscus*, observed in 23 (66%) ponds, *Pelophylax* sp., in 18 (51%) ponds, *H. orientalis*, in 16 (46%) ponds, and *Rana* frogs, in 15 (43%) ponds. The less commonly found species showed a strong negative response to fish presence; *Bufo* tadpoles occurred in only 9 ponds, all of them fishless, and *Bombina bombina* in 9 fishless ponds and 2 fish-containing ponds.

The total relative densities of insect predators were not affected by fish presence/absence in the ponds, although there was a marginally significant tendency for insects to achieve higher densities in fish-containing ponds (Table 1, Fig. 1A). The relative densities of anuran taxa varied with respect to fish presence; *B. bufo* was clearly more abundant in ponds with fish, and the densities of *P. fuscus* and *H. orientalis* were significantly lower in fish-containing ponds than in fishless ponds, while *Pelophylax* and *Rana* frog densities did not differ between ponds with and without fish (Table 1). The main effects of habitat complexity indicated that insect predators and *Rana* tadpoles were more numerous overall in the littoral habitat, while *P. fuscus* and *Pelophylax* tadpoles preferred open-water habitat. A similar but only marginally significant tendency was found for *B. bufo* (Table 1). The relative densities of insect predators and all anuran taxa for which individual analyses were possible, including *B. bufo*, showed positive interactions between fish presence and the use of littoral habitat (Table 1, Fig. 1A–F).



Of the physical and chemical water parameters, conductivity and TSS were higher in fish-containing ponds than in fishless ponds; also, conductivity was higher overall in the littoral habitat, while oxygen concentration was greater in open water (Tables 2, 3). Submerged macrophyte biomass (log-transformed) showed a strong negative dependence upon fish presence (Wald  $\chi^2 = 12.72$ ,  $df = 1$ ,  $P < 0.001$ ; mean biomass  $3.3 \pm SE 0.8 \text{ g m}^{-2}$  in fishless ponds vs  $1.7 \pm 0.8 \text{ g m}^{-2}$  in fish-containing ponds). Submerged macrophyte biomass did not affect the proportional habitat use by insect predators (Wald  $\chi^2 = 0.07$ ,  $df = 1$ ,  $P = 0.793$ ); however, the use of open water was highly positively related to submerged vegetation in all anuran species, including *B. bufo* (binomial GLMMs; Wald  $\chi^2 \geq 16.22$ ,  $df = 1$ , all  $P < 0.001$ ), except *P. fuscus*, for which the relationship only approached significance (Wald  $\chi^2 = 2.72$ ,  $df = 1$ ,  $P = 0.099$ ).

## Discussion

### Between-habitat distributions

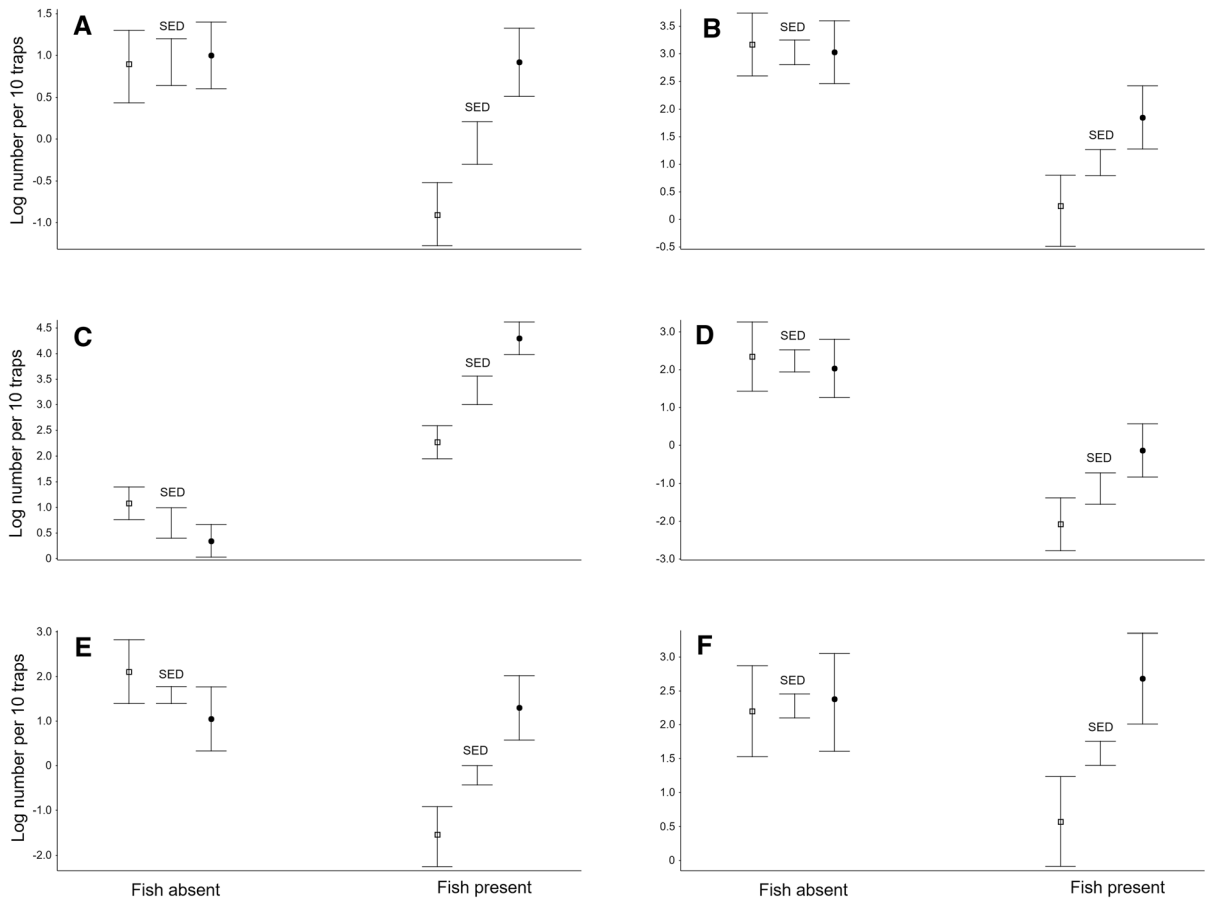
Both insect predators and tadpoles of all anuran taxa for which reliable analyses could be obtained occurred at relatively higher densities in the complex littoral habitat than in open water when fish were present in the ponds. The conventional explanation for reduced insect or tadpole densities in the presence of fish is predation. Actually, the within-pond distribution of insects and amphibians could to some extent be a passive process, in that they were disproportionately decimated by fish in open water (Crowder & Cooper, 1982). However, given the broad evidence that many insects and larval amphibians are adapted to minimize risk of predation via microhabitat shifts (e.g., Pierce, 1988; Formanowicz & Bobka, 1989), we argue that direct predation was unlikely to be the main mechanism (cf. Hanisch et al., 2012) and that spatial anti-predatory behavior might contribute to the observed distribution patterns as well. Also, we cannot rule out

**Table 1** Results of GLMM analyses (Poisson errors, log link function) of the effects of fish presence/absence and habitat type on relative densities of insect predators, fish-intolerant

anuran tadpoles and fish-tolerant *Bufo bufo* tadpoles, with pond identity and year as random factors

Relative densities	Predictor	Estimate (SED)	F-ratio	df	P
Insect predators	Fish status (absent, present)	0.00, - 2.18 (0.73)	3.03	1, 34.7	0.091
	Habitat (open water, littoral)	0.00, 0.03 (0.31)	5.64	1, 34.0	0.023
	Interaction fish presence $\times$ habitat	0.00, 1.96 (0.69)	5.20	1, 34.0	0.029
<i>Pelobates fuscus</i>	Fish status (absent, present)	0.00, - 2.93 (0.81)	7.18	1, 32.6	0.011
	Habitat (open water, littoral)	0.00, - 0.15 (0.45)	4.56	1, 32.6	0.040
	Interaction fish presence $\times$ habitat	0.00, 1.75 (0.65)	7.27	1, 32.6	0.011
<i>Bufo bufo</i>	Fish status (absent, present)	0.00, 1.20 (0.64)	26.99	1, 33.3	< 0.001
	Habitat (open water, littoral)	0.00, - 0.73 (0.59)	3.20	1, 33.2	0.083
	Interaction fish presence $\times$ habitat	0.00, 2.76 (0.81)	11.53	1, 33.2	0.002
<i>Hyla orientalis</i>	Fish status (absent, present)	0.00, - 4.43 (0.86)	30.51	1, 33.1	< 0.001
	Habitat (open water, littoral)	0.00, - 0.32 (0.59)	0.69	1, 28.0	0.414
	Interaction fish presence $\times$ habitat	0.00, 2.26 (1.04)	4.73	1, 28.0	0.038
<i>Rana</i> sp.	Fish status (absent, present)	0.00, - 1.62 (0.45)	2.61	1, 31.9	0.116
	Habitat (open water, littoral)	0.00, 0.18 (0.35)	20.58	1, 33.0	< 0.001
	Interaction fish presence $\times$ habitat	0.00, 1.92 (0.50)	14.57	1, 33.0	< 0.001
<i>Pelophylax</i> sp.	Fish status (absent, present)	0.00, - 3.66 (0.96)	2.14	1, 31.7	0.153
	Habitat (open water, littoral)	0.00, - 1.06 (0.38)	5.02	1, 32.7	0.032
	Interaction fish presence $\times$ habitat	0.00, 3.91 (0.57)	47.06	1, 32.7	< 0.001

Standard errors of differences are given in parentheses



**Fig. 1** GLMM predicted mean ( $\pm$  SE) densities of insect predators (A), *Pelobates fuscus* (B), *Bufo bufo* (C), *Hyla orientalis* (D), *Pelophylax* sp. (E) and *Rana* sp. larvae (F) in open-water (open squares) and littoral (filled squares) habitat of

fishless and fish-containing ponds. The vertical lines between means represent standard errors of differences of means (SED) for comparisons between habitats within ponds

**Table 2** Results of GLMM analyses (normal errors, identity link) of the effects of fish presence/absence and habitat type on physicochemical parameters of pond water

Parameter	Predictor	Estimate (SED)	F-ratio	df	P
Temperature ( $^{\circ}$ C)	Fish status (absent, present)	0.00, - 2.18 (0.73)	0.06	1, 33	0.811
	Habitat (open water, littoral)	0.00, 0.03 (0.31)	0.97	1, 34	0.331
Oxygen concentration ( $\text{mg l}^{-1}$ )	Fish status (absent, present)	0.00, 7.81 (3.93)	3.95	1, 33	0.055
	Habitat (open water, littoral)	0.00, - 17.08 (3.75)	20.71	1, 34	< 0.001
TSS ( $\text{mg l}^{-1}$ )	Fish status (absent, present)	0.00, 12.09 (5.95)	4.13	1, 33	0.050
	Habitat (open water, littoral)	0.00, - 0.43 (1.56)	0.08	1, 34	0.782
Conductivity ( $\mu\text{S cm}^{-1}$ )	Fish status (absent, present)	0.00, 58.18 (23.24)	6.27	1, 33	0.017
	Habitat (open water, littoral)	0.00, 10.03 (2.96)	11.50	1, 34	0.002

Insignificant interactions were dropped from the models. Standard errors of differences are given in parentheses

**Table 3** GLMM means ( $\pm$  SE) of abiotic parameters measured in open water and in the vegetated littoral habitat

Parameter	Fish absent		Fish present		SED
	Open water	Vegetation	Open water	Vegetation	
Temperature ( $^{\circ}\text{C}$ )	28.9 $\pm$ 0.5	29.1 $\pm$ 0.5	29.2 $\pm$ 0.5	29.2 $\pm$ 0.5	0.5
Oxygen concentration ( $\text{mg l}^{-1}$ )	16.1 $\pm$ 3.8	5.8 $\pm$ 3.7	30.5 $\pm$ 3.8	7.0 $\pm$ 3.7	5.3
TSS ( $\text{mg l}^{-1}$ )	26.6 $\pm$ 4.3	27.7 $\pm$ 4.3	39.7 $\pm$ 4.4	38.3 $\pm$ 4.3	4.8
Conductivity ( $\mu\text{S cm}^{-1}$ )	291.9 $\pm$ 16.8	302.6 $\pm$ 16.6	350.8 $\pm$ 16.3	360.1 $\pm$ 16.5	17.0

SED average standard error of differences

that in the presence of fish some of the insect predators, such as large-bodied adult dytiscids, which are less vulnerable to fish due to individual size and a hard cuticle, did not seek shelter but were attracted to the structured vegetation by the abundance of prey behaviorally avoiding fish. The tendency of insects and amphibian larvae to stay in the littoral, usually more shallow zone could also be affected by micro-habitat preferences based on abiotic characteristics, especially a preference for warmer water (Thurnheer & Reyer, 2001; Tolonen et al., 2001; Hampton, 2004). The relationships between temperature selection and predation avoidance in tadpoles can be complicated by a number of factors, including tadpole developmental stage and species-specific forms of behavioral thermoregulation (Brattstrom, 1962; Wollmuth et al., 1987; Ultsch et al., 1999). However, abiotic conditions, including water temperature, were similar between pond microhabitats, presumably due to similar depth and the largely unrestricted water exchange between the littoral and the open-water zone, except that oxygen concentrations were higher in open water, likely due to the stronger mixing action of waves (cf. Přibáň & Šmíd, 1978; Sychra et al., 2010). Conductivity was consistently higher in the littoral habitat than in open water, but the average difference was about  $10 \mu\text{S cm}^{-1}$ , which was unlikely to reflect any important contrasts in biotic or abiotic conditions. In shallow waterbodies such as these ponds, thorough mixing of the water occurs frequently, so horizontal gradients in chemical parameters or phytoplankton between habitats are unlikely to persist in the long term; however, the presence of submerged macrophytes may influence littoral-pelagic exchange (Barko & James, 1998). Nevertheless, interactions between predation and modification of

food resources by opportunist fish such as common carp are complex. Fish may increase pond resource levels through bottom-up effects (Horppila et al., 1998). When carp predation on tadpoles is precluded, environmental conditions for larval development in carp-dominated ponds can be more favorable than in the absence of fish, presumably mainly because bottom stirring by carp leads to resedimentation, facilitating tadpole access to re-suspended food particles (Kloskowski, 2011b). However, as indicated by the similar TSS levels, carp benthic feeding was unlikely to disproportionately increase tadpole resources in the littoral habitat relative to open water. Periphyton can be an important food source for amphibian larvae (Diaz-Paniagua, 1987; Brönmark et al., 1991; see also Dupuch et al., 2009), attracting them to vegetated littoral areas, but most larval anurans are primarily suspension-feeding omnivores (Seale & Wassersug, 1979; Petranka & Kennedy, 1999).

We expected *B. bufo* tadpoles to exhibit the opposite spatial response to taxa more prone to fish predation. However, despite the overall higher densities in fish-containing ponds than in fishless ponds, in the presence of fish *B. bufo* were relatively more numerous in the littoral zone, a modification of habitat use that was likely to enhance encounters with insect predators (Formanowicz, 1982; Tate & Hershey, 2003; Smith & Awan, 2009). Interpretation of this pattern is not straightforward, although the behavior is fairly consistent with the findings of Semlitsch & Gavasso (1992) in experimental settings, where *B. bufo* responded to both *Dytiscus* larvae and vertebrate predators by shifting from open water to the edges of experimental containers (see also Porej & Hetherington, 2005). The observed overall strong association



with littoral vegetation could be accounted for by the feeding preferences of larval *B. bufo* (Diaz-Paniagua, 1987). Another possible explanation is that their distribution was shaped by fish predation (avoidance) after all, as *B. bufo* tadpoles are not fully protected from fish; their susceptibility may increase in the presence of tadpoles of palatable species, which dilute the protective effect of *B. bufo* chemical defenses (Kaczmarek et al., 2018).

As trap efficiency depends on the activity of the sampled animals, our results may be confounded by the differential activity levels of tadpoles in the uneven presence of different types of predators and in habitats with varying complexity (Becerra Jurado et al., 2008). Since activity increases prey exposure to vertebrate predators, tadpoles should show lower activity levels under predation risk from fish than from insects in fishless habitats (reviewed in Wellborn et al., 1996; Smith & Awan, 2009). However, tadpoles of some anurans reduce their activity in the presence of insect predators as well (Laurila et al., 1998). Activity of insect predators typically decreases in the presence of fish, but the behavioral responses are species-specific and dependent on habitat structure (Pierce, 1988; Warfe & Barmuta, 2004). Activity traps are likely to underestimate sit-and-wait foraging insects (Hampton & Friedenber, 2002; Michel & Adams, 2009). Activity traps deployed for 24 h provide a cumulative picture of insect and tadpole distribution over this sampling period, unbiased by potential changes in activity and between-habitat shifts from day to night. On the other hand, potentially strong variation in spatial distribution between habitats over a short temporal scale (Hampton & Friedenber, 2002; Hampton, 2004), with important consequences for predator–prey dynamics, may remain concealed.

Pooling *Pelophylax* and *Rana* species to genera for analyses could mask inherent species differences in oviposition site preferences and habitat use by larvae (Berger, 1977; Kuzmin, 1999). Still, we assumed that, within their genera, the studied ranid species are genetically and ecologically similar enough (Van Buskirk, 2003) to display a common response to fish predation risk (Semlitsch & Reyer, 1992; Stauffer & Semlitsch, 1993). The consistent effects of the interactions of fish presence with habitat in models for all individual anuran taxa supported the general supposition that anuran species lacking chemical defenses shifted to complex habitat refugia (cf. Kats et al.,

1988). Similarly, given the wide range of foraging modes among closely related members of the insect community and their varied effectiveness as predators of tadpoles, treatment of all taxa as equal in the analyses is an oversimplification. However, the within-pond distribution patterns of insect predators appeared common to a wide array of taxa simply because in the presence of fish they were virtually absent from open water, so independently of foraging mode, they posed a threat to tadpoles only in vegetated littoral areas. Habitat selection by tadpoles may change with increased body size, as their mortality due to predation by size-limited predators, including fish such as common carp, is typically concentrated during the first weeks of larval life (Travis et al., 1985; Van Buskirk, 2001; Smith & Awan, 2009; Kloskowski, 2011b). However, this could not introduce a significant interspecific bias, because the studied species which metamorphose at a large size, such as *H. orientalis*, *P. fuscus* or *Pelophylax* sp., are late breeders, achieving large body size later in summer (Kloskowski, 2009), and during the sampling period tadpoles of all species studied were relatively small.

In shallow ponds and lakes, the open-water zone is not an entirely simple habitat because submerged vegetation provides structure offering shelter and additional food resources, such as detritus (Carpenter & Lodge, 1986), and thus it can affect invertebrate and tadpole distributions. The adverse impact of fish on submerged macrophytes (reviewed in Scheffer, 2004), which in our study presumably resulted from the feeding activity of common carp but also of the small numbers of co-occurring herbivorous grass carp (Matsuzaki et al., 2007; Kloskowski, 2011a; Francová et al., 2019), could additionally drive distribution shifts by predatory insects and tadpoles due to the loss of the principal structured microhabitat in the open-water area (Parkos et al., 2003). Littoral vegetation is resistant to fish because it is based on the well-rooted remains of the previous year's emergent macrophytes.

#### Potential combined effects of fish and insect predators

In the present study, we did not attempt to assess the individual or combined influence of fish and insect predators on tadpole mortality. The densities of some anuran taxa were clearly lower in ponds containing fish, suggesting that multiple predator types induced

greater mortality than invertebrate predators alone in the fishless ponds. However, larval amphibian abundance in ponds is to a large extent determined by the non-random choice of oviposition site by adult females, aimed at minimizing the risk of predation to larvae; the presence of fish typically elicits a strong avoidance response (reviewed in Buxton & Sperry, 2016). Anuran discrimination among oviposition sites appears to be confirmed by the virtual absence of *B. bombina* and *B. viridis* and the low overall densities of *P. fuscus* and *H. orientalis* in fish-containing ponds; however, we cannot rule out rapid tadpole elimination by actual predation.

If tadpole spatial distribution in ponds with fish resulted primarily from behavioral responses to simultaneous threats from fish and insect predators, the preference for vegetated littoral areas over open-water habitat indicates that fish posed a more imminent danger (cf. Krupa & Sih, 1998; Relyea, 2003). This may appear trivial given the size and total biomass domination of fish in the ponds (see also Semlitsch & Gavasso, 1992; Tate & Hershey, 2003). However, Anisoptera larvae and dytiscids are no less dangerous predators, able to cause significant tadpole mortality (Wilbur & Fauth, 1990; Gunzburger & Travis, 2005; Anderson & Semlitsch, 2016) and we are inclined to argue that, irrespective of causal factors behind within-pond tadpole distribution, habitat shift to littoral vegetation might increase larval amphibian vulnerability to sit-and-wait insect predators (Soluk & Collins, 1988; see also Bofill & Yee, 2019) as well as to widely foraging insects, which in the absence of fish would have fed in open water (Culler et al., 2014). Thus, fish presence can improve the conditions for insect predators that are themselves less vulnerable to fish than other mesopredators. The conflict between spatial responses to different predators does not necessarily result in overall risk enhancement, because prey may switch to other compensatory defenses (Krupa & Sih, 1998). Tadpole use of a structurally complex habitat may serve as a generalized defense reducing the risk of predation by some insects as well (Babbitt & Tanner, 1998; Babbitt & Tarr, 2002; Kopp et al., 2006; see also Michel & Adams, 2009).

Enhanced co-occurrence of insect predators in complex habitats may reduce their total abundance due to intensified IGP (reviewed in Culler et al., 2014; Ramos & Van Buskirk, 2012). Similarly, fish can indirectly mitigate insect predation on tadpoles via

IGP as well as behavioral effects, e.g., interference or reduced insect activity in the presence of fish (Wisinger & McGrady, 1993; Warfe & Barmuta, 2004; but see González & Tessier, 1997). However, as fish foraging is hampered by thick vegetation, fish IGP and interference with insect foraging can be insufficient to reduce total predation rates (by all predators) on tadpoles (Sih et al., 1998; Finke & Denno, 2002; see also Swisher et al., 1998).

## Conclusions

Natural experiments and observational studies of multiple predator effects are inferior to well-controlled, artificial-setting experiments in separating and explaining causal relationships; however, they deal with attributes of real systems, such as vast arrays of predators and prey or natural habitat complexity, and thus provide meaningful research and management insights. Here, in a large-scale, whole-system study, we found a strong influence of fish on the distribution of tadpoles and their insect predators between pond microhabitats. Insect predators and larval anurans displayed varying microhabitat preferences; overall, insects and *Rana* tadpoles were relatively more numerous in littoral habitat, while *P. fuscus* and *Pelophylax* tadpoles were relatively more abundant in open water (cf. Teplitsky et al., 2003). Also, differences in relative densities of individual anuran taxa between ponds with and without fish indicate their differential vulnerability to fish (Kats et al., 1988; Teplitsky et al., 2003). Nonetheless, insects and tadpoles showed a common distribution pattern, with increasing relative densities in littoral habitat in response to fish. While this is a speculative inference, as we did not estimate insect predation on anurans, we wish to draw attention to a potentially important indirect non-consumptive effect of fish: aggregation in complex vegetation in response to fish may put tadpoles at greater risk from insect predators, which are also driven to the same habitat by fish predation pressure. The use of emergent littoral vegetation may be particularly intensified in systems where open-water submerged macrophytes are adversely affected by fish. Our findings illustrate the importance of sampling various microhabitats during surveys of macroinvertebrates or larval amphibians in water bodies with heterogeneous vegetation. Maintenance of vegetated habitat is often proposed as a key

management action to support pond biodiversity (Porej & Hetherington, 2005; Hartel et al., 2007; Kenison et al., 2016). Our data corroborate this recommendation, as predatory insects and anuran tadpoles shifted to littoral vegetation in the presence of fish. However, further community-level research is warranted to assess the potential emergent effects (sensu Sih et al., 1998) of fish and insect predation on amphibian larvae in relation to habitat complexity, because in fish-dominated ecosystems macrophyte refugia may be less effective in reducing total predation risk than expected.

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