



# Predation risk modifies habitat use and habitat selection of diving beetles (Coleoptera: Dytiscidae) in an Urban Pondscape

Wenfei Liao<sup>a,b,c,\*</sup>, Tommaso Zanca<sup>c,2</sup>, Jari Niemelä<sup>a,3,4</sup>

<sup>a</sup> Faculty of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, FI-00014 Helsinki, Finland

<sup>b</sup> School of Life Science and Technology, University of Electronic Science and Technology of China, Chengdu 610054, Sichuan, China

<sup>c</sup> Faculty of Science, University of Helsinki, P.O. Box 64, FI-00014 Helsinki, Finland

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## ABSTRACT

Urban freshwater ecosystems often involve the introduction of predator species that affect biodiversity via both direct and indirect effects of predation, altering the distribution of prey species. Yet, limited research has explored indirect effects on aquatic invertebrates in urban ponds. Here, we use Dytiscidae as our study taxon to investigate how predator-prey interaction modifies the habitat use and habitat selection of macroinvertebrates in ponds of an urban landscape. We sampled dytiscids in 11 ponds with, and 15 ponds without fish, in Helsinki, Finland, during 2018 – 2020, and emergent plant cover in pond margins as a proxy for the quantity of prey refuges. We found (i) at the pond scale, vegetation cover can mitigate the negative effects of predators on dytiscid species richness and abundance, and dytiscids prefer microhabitats with bulrush and sedges to microhabitats with no vegetation or common reeds, reflecting the importance of providing aquatic plants with high structural complexity as prey refuges. (ii) At the landscape scale, small-sized dytiscids favour fishless habitats, and the community-weighted mean body size of dytiscids has seasonal fluctuations, with smaller body sizes in May and June than in July in fishless ponds, indicating that dytiscids select habitats to regulate their investment in vigilance according to their life cycles. Our findings highlight that predation can alter the habitat use and habitat selection of aquatic invertebrates. Mitigating predation risk at both the habitat scale and the landscape scale is crucial to facilitate the fitness of aquatic invertebrates, especially small-sized species, to promote their diversity in urban ponds.

## 1. Introduction

Predator-prey interactions consider both direct effects of predators killing prey and indirect effects of predators scaring their prey in ecosystems (Brown, 1999). Studying the indirect effects of predator-prey interactions is a prey-centred approach that focuses on the responses of prey species to the stress and fear induced by predation, which includes many aspects, such as behaviours, physiology, and

\* Corresponding author at: Faculty of Biological and Environmental Sciences, University of Helsinki, P.O. Box 65, FI-00014 Helsinki, Finland.

E-mail address: [wenfei.liao@helsinki.fi](mailto:wenfei.liao@helsinki.fi) (W. Liao).

<sup>1</sup> 0000-0002-1583-0408

<sup>2</sup> 0000-0002-5752-5794

<sup>3</sup> Deceased

<sup>4</sup> 0000-0003-2420-7391

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life history traits (Lima and Dill, 1990; Brown et al., 1999; Ripple and Beschta, 2004; Tolon et al., 2009). Indirect effects of predators can modify habitat use and habitat selection of species by affecting both the fitness of individuals and trophic cascades (Brown et al., 1999; Creel and Christianson, 2008; Peckarsky et al., 2008; Peacor et al., 2020).

Indirect effects have inevitable effects on prey population (Werner and Peacor, 2003; Preisser et al., 2005; Sheriff et al., 2020). For example, the presence of predators increases vigilance in prey species and alters their behaviours, such as reducing foraging activities to avoid encountering predators, which may negatively affect the survival and reproduction of prey (Brown, 1988; Åbjörnsson et al., 1997; Laundré et al., 2010; Resetarits and Pintar, 2016; Kloskowski et al., 2020). Indirect effects of predation on prey species have been intensively studied in freshwater ecosystems since last century both in the field and in manipulated aquatic mesocosms (e.g., studies reviewed by Lima and Dill, 1990; Pintar et al., 2018; Pintar and Resetarits, 2021; Resetarits et al., 2021; Šigutová et al., 2022). Yet, limited research has explored such predation effects on aquatic invertebrates in urban ponds (but see Kloskowski et al., 2020).

'Pondscape' is a term similar to 'landscape' and is applied to a network of ponds in a landscape (Boothby, 1997). 'Pondscapes' have mainly been studied in urban contexts to improve the multifunctioning of urban ponds, regarding their potential role in providing nature-based solutions, such as supporting biodiversity (e.g. Gledhill et al., 2008; Noble and Hassall, 2015; Hill et al., 2018). Urban ponds often involve human disturbances, such as the intentional introduction of fish for recreational purposes (Liao, 2017) as well as unintentional introduction of alien species (Santana Marques et al., 2020). The introduction of predator species into aquatic ecosystems can change predator-prey dynamics via direct predation and indirect effects, such as inducing macroinvertebrates' behavioural responses to predation risk (Dahl and Greenberg, 1999; Schilling et al., 2009). The high predation risk in the presence of fish predators can restrict the capacity of ponds to support biodiversity and potentially the functioning of the pondscape (Liao et al., 2022). As indirect effects can affect community composition at the landscape scale (Wirsing et al., 2008), it is important to understand how different levels of predation risk affect macroinvertebrate communities and distributions, before making pondscape plans for biodiversity conservation.

In biodiversity research, species richness is a traditional and direct indicator of biodiversity, while the distribution of body size has been recently considered as another important measure of biodiversity. Body size is often correlated with species traits that influence extinction vulnerability, such as species' position in trophic levels, home ranges, and reproduction rates, which can be utilised to predict the extinction of species for conservation purposes (Woodward et al., 2005; Brose et al., 2017; Merckx et al., 2018; Rocha-Ortega et al., 2020). Fish predators tend to reduce macroinvertebrate species richness (Holtmann et al., 2018; Liao et al., 2020) and filter macroinvertebrate assemblages according to body size (Tate and Hershey, 2003). The availability of prey refuges, however, can mitigate predation pressure, which decreases the probability of prey extirpation and facilitates the coexistence of predator and prey (Sih, 1987; Ghosh et al., 2017). Aquatic plants are important spatial prey refuges for aquatic macroinvertebrates and can enhance invertebrate species richness (Denno et al., 2005; Law et al., 2019; Liao et al., 2023). Yet, little is known about how aquatic plants affect the habitat use and habitat selection of macroinvertebrates, nor if aquatic plants can enhance the coexistence of fish predators and small-sized prey species.

In this study, we use diving beetles (Dytiscidae) as our study taxon to investigate how predation risk affects the habitat use of aquatic invertebrates. More specifically, we investigate (1) the habitat use of dytiscids, i.e., how they use different microhabitats within a habitat, and (2) their habitat selection, i.e., what habitat they use in a pondscape. We use the diversity of dytiscids, i.e., species richness and abundance, as a reflection of dytiscids' habitat use and habitat selection. We use community-weighted mean body size as an indicator of species composition. As there is variance in the capacity for coexistence with fish between different dytiscid species and different stages in their life cycles, we hypothesize (1) different levels of predation risk modify dytiscids' habitat use at the pond scale; (2) different levels of predation risk affect dytiscid species' habitat selection at the pondscape scale.

## 2. Materials and methods

### 2.1. Study taxon

Dytiscids are a family of aquatic invertebrates that are prey to fish, while some large-sized species may also prey on small fish and may coexist with fish (Frelík, 2014; Liao et al., 2020). The body size of dytiscid adults varies across species from a few millimetres to less than 5 centimetres. The adults of most species can disperse via flight (Miller and Bergsten, 2016; Bilton, 2023). Dytiscid adults can be predators or opportunistic scavengers, while larvae are predators (Culler et al., 2023). Dytiscids are capable of detecting the presence of predators from both visual and chemical cues and changing their levels of vigilance to avoid predation (Åbjörnsson et al., 1997). They utilize aquatic plants for various functions, including prey refuges to avoid predation (Gioria and Feehan, 2023). In this study, we focused on adult dytiscids to study their habitat selection, because dytiscid larvae do not disperse between ponds.

### 2.2. Sampling methods

We surveyed 26 ponds at 11 sites in the Helsinki Metropolitan Area, Finland (60.2° N, 24.9° E). A site means an urban park. We conducted fieldwork in May, June, and July 2020. To sample dytiscids, we set 1-L activity traps, without bait, horizontally and operated the traps in water for 48 hours (Elmberg et al., 1992). The number of traps set in each pond was determined according to the perimeter of the pond; we set five traps in the pond with the shortest perimeter and 15 traps in the pond with the longest perimeter (Liao et al., 2020). We preserved dytiscid specimens in 70% ethanol until identification to the species level with a microscope in the laboratory. We followed Nilsson and Holmen (1995) and Bergsten et al. (2012) for the key and Nilsson and Hájek (2021) for the nomenclature. We obtained the species-specific body size by calculating the mean of the range of body length for each species from the

literature (Nilsson and Holmen, 1995). In this study, we collected data with the same method as Liao et al. (2022); therefore, we utilised part of the dytiscid community data collected in the same urban ponds during May and July 2018 and 2019 that has been published in Liao (2022), to form a larger dataset of dytiscid species richness and abundance at the pond scale.

Fish were the major predators of aquatic invertebrates in some of our study ponds, which caused different levels of predation risk to aquatic invertebrates, including dytiscids, in our study pondscape. We determined the presence or absence of fish in each pond by operating a fish trap in water for 24 hours during the first week of July every sampling year. The fish trap was totally submerged in water. No bait was used in the fish trapping. We recorded species, abundance, and body length of the trapped fish. Fifteen ponds were fishless, while 11 ponds had fish. The recorded fish species were Crucian carp (*Carassius carassius*), Prussian carp (*C. gibelio*), tench (*Tinca tinca*), European perch (*Perca fluviatilis*), and northern pike (*Esox lucius*). During the sampling years, the ponds with fish had 1.4 fish species on average, with a maximum of 3 species and a minimum of 1 species. The information on fish in 2018 and 2019 has been published in Liao et al. (2023) and the information in 2020 is described in Supplement 1.

We studied how dytiscids use habitats vegetated by emergent plants in the presence or absence of fish, because emergent plants are the main functional groups of aquatic vegetation in the margins of our study ponds. We visually estimated the percentage of vegetated pond margin per pond in May and July 2020. The vegetation consisted of both newly grown plants and remnant plants from the previous year. We also obtained vegetation data at the pond scale from a published dataset (Liao, 2020), which was collected with the same method as this study, to form a larger dataset.

We recorded microhabitat information regarding the cover of emergent plants to investigate how microhabitat quality affects dytiscid diversity. As little is known about the home range of dytiscids in water, we used 1 m × 1 m quadrats as our sampling area of microhabitats with the activity trap as the centre of each quadrat. We investigated four microhabitat types: 1. Microhabitats dominated by bulrush (*Typha* spp.), 2. By common reeds (*Phragmites australis*), 3. By sedges (Cyperaceae), and 4. Non-vegetated microhabitats. We chose the three plant groups because they were the predominant vegetation types in our study ponds and tend to form monocultures, each with a characteristic structure. We collected the data at the microhabitat scale during the first two weeks in May, June, and July 2020.

### 2.3. Data Analysis

To investigate how fish predators affect dytiscids' use of emergent plant cover in pond margins, we pooled the data from the traps in each individual pond during one sampling event, i.e., 48-hour sampling with activity traps each month, as a single observation. In total, we obtained 148 observations of dytiscid species richness and abundance at the pond scale during the three years of sampling. To investigate how dytiscids use the four types of microhabitats, we obtained data from 67 microhabitats without plants, 49 microhabitats dominated by bulrush (with mean percentage of vegetation cover  $\pm$  SD =  $42\% \pm 26\%$ ), 49 by sedges ( $57\% \pm 29\%$ ), and 28 by common reeds ( $48\% \pm 20\%$ ). In data exploration, no significant difference was found in the vegetation cover of the three vegetated microhabitat types in analysis of variance (ANOVA) with a Chi-square test.

We recorded 590 specimens during May – July 2020, with 166 specimens from ponds with fish and 424 specimens from ponds without fish, for the study of dytiscid body sizes. In ponds with fish, we obtained 57 specimens from bulrush microhabitats, 52 specimens from sedge microhabitats, 11 specimens from non-vegetated microhabitats, and 2 specimens from common reed microhabitats, respectively. With the species-specific body size collected from literature (Nilsson and Holmen, 1995), we calculated community-weighted mean body size with the sum of the species-specific body size of each specimen divided by the number of specimens recorded in each pond (Merckx et al., 2018), to investigate how fish predators filter dytiscid species and shape their distributions.

Because the fish dataset was small, we reduced it to the presence or absence of fish to enable us to build reliable models, without including biological data of the trapped fish. As dytiscid assemblages exhibit seasonal changes (Nilsson and Svensson, 1995; Bosi, 2001; Liao et al., 2020), we included the sampling months as a factor in the data analyses. We applied generalized linear mixed models (GLMMs) with Poisson distribution, to investigate how dytiscid species richness and abundance, respectively, responded to the emergent plant cover in the presence or absence of fish at the pond scale. In data exploration, we noticed there were potential interactions between emergent plant cover and the presence or absence of fish; therefore, the interaction was included as a covariate. As the sampling months had effects on dytiscid assemblages (Liao et al., 2023), we included the sampling months as a covariate in the model. We also included the number of traps as a covariate, because it was correlated with pond size, to balance the sampling effort in the pooled data of dytiscid species richness and abundance. As our observation might have been nested within sampling years, ponds and sites, we included them as random effects in the initial models. The full model is described in Appendix 1.

We applied Poisson GLMMs to investigate how dytiscid species richness and abundance, respectively, responded to microhabitats in ponds with fish (full models in Appendix 2). When the Poisson models were overdispersed, i.e. failed to deal with the higher variation than expected in the data, we simulated 10,000 datasets to ensure the overdispersion was not due to zero inflation, before applying GLMM with a negative binomial distribution (Zuur and Ieno, 2016).

We applied GLMMs with a gamma distribution to investigate how dytiscid community-weighted body size responded to the presence or absence of fish at the pond scale (full model in Appendix 3), and to microhabitat (full model in Appendix 4).

We conducted all data analyses using R software (R Core Team, 2020). We applied GLMMs with the 'glmmTMB' package (Brooks et al., 2017). We conducted a backward selection manually and chose the optimal model with the lowest AIC values (Zuur et al., 2009). We used the function 'drop1' with a Chi-squared test (R Core Team, 2020), to extract the p-value of covariates that are factors.

### 3. Results

During 2018 – 2020, we recorded 1515 individuals of 55 dytiscid species under 18 genera: 2 *Acilius* species, 7 *Agabus* species, 1 *Clemnius* species, 2 *Colymbetes* species, 1 *Cybister* species, 2 *Dytiscus* species, 2 *Graphoderus* species, 1 *Graptodytes* species, 1 *Hydaticus* species, 1 *Hydroglyphus* species, 15 *Hydroporus* species, 2 *Hygrotus* species, 1 *Hyphydrus* species, 10 *Ilybius* species, 1 *Laccornis* species, 4 *Rhantus* species, 1 *Suphrodytes* species, and 1 *Porhydrus* species. The list of species recorded during the sampling years is in [Appendix 5](#).

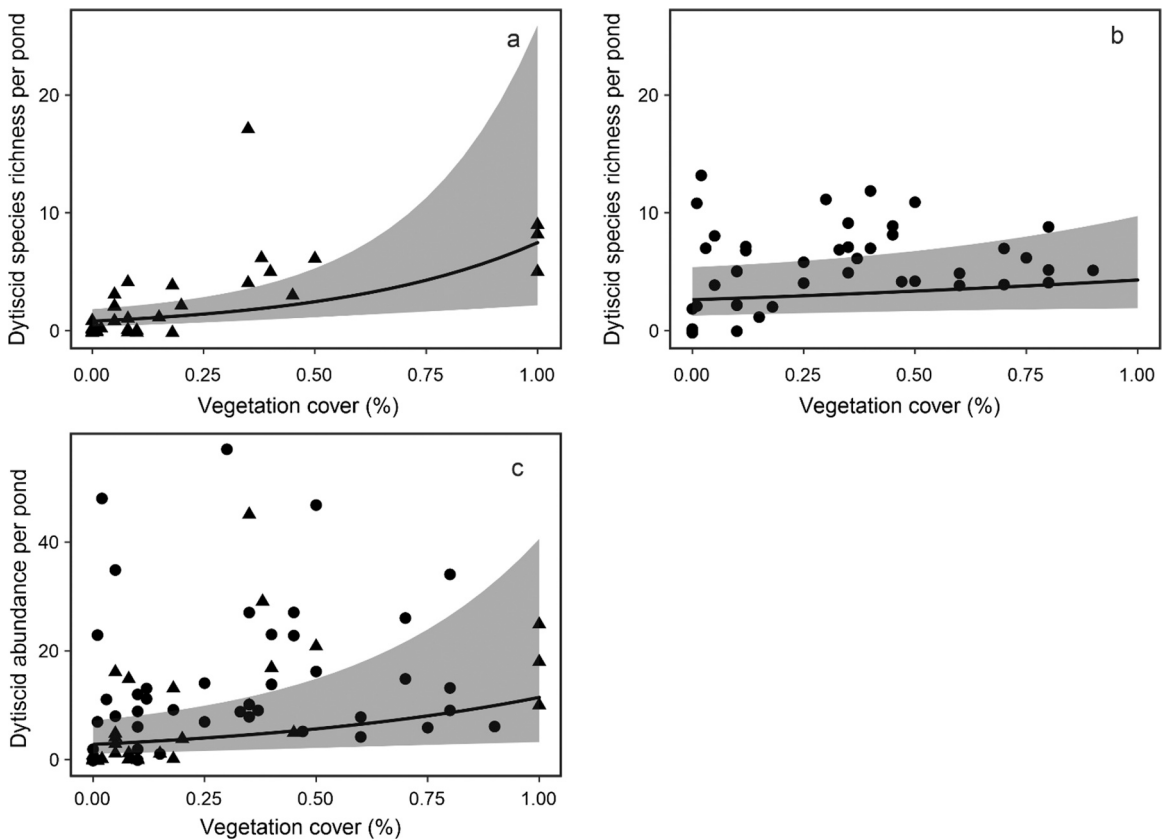
#### 3.1. Dytiscid species richness and abundance at the pond scale

Our optimal Poisson GLMM showed that, at the pond scale, there were more dytiscid species (Mean  $\pm$  Standard Deviation =  $2.5 \pm 3.6$  species in ponds with fish,  $5.3 \pm 3.5$  in ponds without fish) in May than in July ( $1.4 \pm 2.2$  in ponds with fish,  $3.9 \pm 3.6$  in ponds without fish,  $p$ -value  $< 0.001$ ). Ponds with fish had fewer dytiscid species than ponds without fish with marginal significance ( $p$ -value = 0.058; [Fig. 1](#)). Vegetation cover had a significantly more positive effect on dytiscid species richness in ponds with fish than in ponds without fish ( $p$ -value = 0.028; [Fig. 1](#), [Table 1](#)).

Our optimal negative binomial GLMM showed that dytiscids were more abundant in May ( $7.2 \pm 10.6$  in ponds with fish,  $13.6 \pm 13.5$  in ponds without fish) than in July ( $2.0 \pm 3.3$  in ponds with fish,  $9.6 \pm 10.0$  in ponds without fish,  $p$ -value  $< 0.001$ ). Dytiscid abundance was positively correlated with vegetation cover ( $p$ -value = 0.013; [Fig. 1c](#), [Table 2](#)). The presence or absence of fish, however, was not included in the model for dytiscid abundance, while the number of traps was excluded from the optimal model for both dytiscid species richness and abundance at the pond scale ([Table 1](#) & [Table 2](#)).

#### 3.2. Dytiscids in different microhabitats in ponds with fish

Our optimal model shows that dytiscid species richness was affected by microhabitat type ( $p$ -value = 0.018), and vegetation cover ( $p$ -value = 0.026). Non-vegetated microhabitats ( $0.1 \pm 0.4$  species) had significantly fewer dytiscid species than microhabitats dominated by bulrush ( $0.7 \pm 1.3$  species,  $p$ -value = 0.006) and by sedges ( $0.6 \pm 1.4$  species,  $p$ -value = 0.013; [Appendix 2](#)), but not significantly different from microhabitats by reeds ( $0.1 \pm 0.3$  species,  $p$ -value = 0.901). Dytiscid species richness is not statistically



**Fig. 1.** The effects of vegetation cover on dytiscid species richness in (a) ponds with fish and (b) ponds without fish, and on (c) dytiscid abundance at the pond scale. The triangles ( $\blacktriangle$ ) represent data collected in ponds with fish, and the filled circles ( $\bullet$ ) represent data collected in ponds without fish. The grey ribbons represent 95% confidence interval. Only data in May are shown in the plots; [Table 1](#) shows the results of July.

**Table 1**

The results of optimal Poisson GLMM for dytiscid species richness at the pond level. The absence of fish and July were set as the reference levels. The estimated random effects  $\sigma_{\text{year}}^2$  is 0.14<sup>2</sup>;  $\sigma_{\text{pond}}^2$  is 0.43<sup>2</sup>;  $\sigma_{\text{site}}^2$  is 0.86<sup>2</sup>.

	Estimate	SE	z-value	p-value
Intercept	0.64	0.36	1.77	0.075
May	0.46	0.12	<b>3.86</b>	< <b>0.001</b>
Fish	-0.66	0.35	-1.89	0.058
VegetationCover	0.15	0.10	1.50	0.131
Fish:VegetationCover	0.54	0.24	<b>2.193</b>	<b>0.028</b>

**Table 2**

The results of optimal negative binomial GLMM for dytiscid abundance at the pond level. July was set as the reference level. The estimated random effects  $\sigma_{\text{year}}^2$  is 0.21<sup>2</sup>;  $\sigma_{\text{pond}}^2$  is 0.76<sup>2</sup>;  $\sigma_{\text{site}}^2$  is 1.32<sup>2</sup>.

	Estimate	SE	z-value	p-value
Intercept	0.65	0.47	1.387	0.165
Vegetation Cover	0.44	0.17	<b>2.469</b>	<b>0.013</b>
May	0.78	0.18	<b>4.272</b>	< <b>0.001</b>

different in microhabitats dominated by bulrush from those by sedges (p-value = 0.864; Fig. 2a).

Non-vegetated microhabitats ( $0.2 \pm 0.5$  individuals) also had significantly lower dytiscid abundance than microhabitats dominated by bulrush ( $1.3 \pm 3.0$  individuals, p-value < 0.001) and by sedges ( $1.3 \pm 4.6$  individuals, p-value < 0.001), but not significantly higher than microhabitats by reeds ( $0.1 \pm 0.3$  individuals, p-value = 0.795). Dytiscid abundance was not statistically different in bulrush microhabitats compared to sedge microhabitats (p-value = 0.917; Fig. 2b).

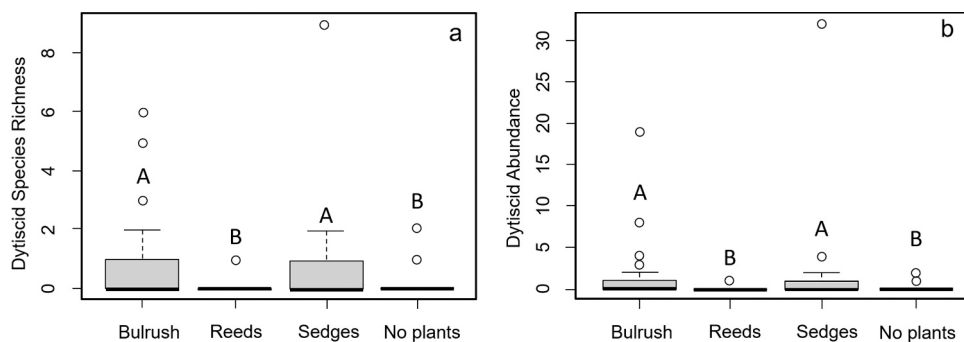
### 3.3. Dytiscid body size in ponds with and without fish

Our optimal Gamma GLMM model showed that the community-weighted mean body length of dytiscids was significantly affected by the presence or absence of fish (p-value < 0.001) and that the interaction between the presence or absence of fish and month was significant (p-value = 0.005; Fig. 3a, Table 3). Dytiscids in ponds with fish were of larger-sized species (mean  $\pm$  SD:  $13.7 \pm 9.0$  mm) than those in ponds without fish ( $6.2 \pm 5.6$  mm, p-value < 0.001; Fig. 3a, Table 3).

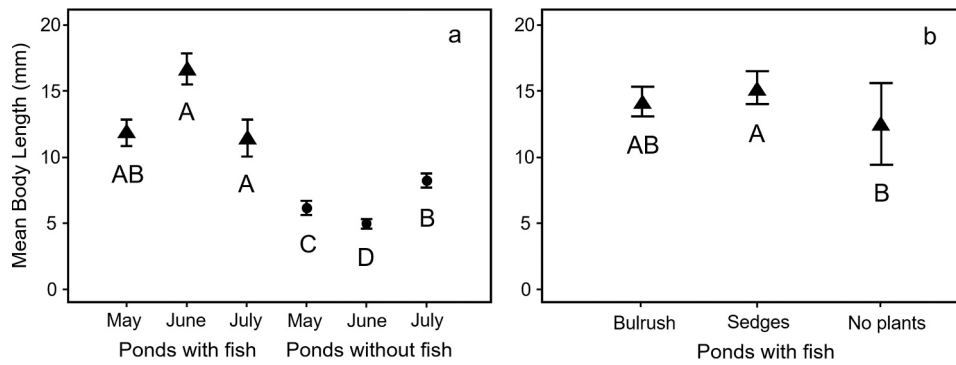
In ponds with fish, we recorded 11 individuals of 4 dytiscid species in the 67 non-vegetated microhabitats, 52 individuals of 15 species in microhabitats dominated by sedges, and 57 individuals of 13 species in microhabitats dominated by bulrush (Table 4). The community-weighted mean body length of dytiscids in non-vegetated microhabitats (mean  $\pm$  SD:  $12.5 \pm 10.3$  mm) was smaller than that of dytiscids in microhabitats dominated by bulrush ( $14.2 \pm 8.6$  mm, p-value = 0.048) and by sedges ( $15.3 \pm 9.0$  mm, p-value = 0.073). There was no significant difference in dytiscid body length between bulrush microhabitats and sedge microhabitats (p-value = 0.560, Fig. 3b).

## 4. Discussion

In this study, we investigated how two different levels of predation risk affect (1) dytiscid habitat use at the pond scale and (2) their



**Fig. 2.** Dytiscid species richness (a) and abundance (b) in four types of microhabitats in ponds with fish, i.e., microhabitats vegetated with bulrush, common reeds, and sedges respectively, and non-vegetated microhabitats. Labels with different letters indicate statistical significance. For example, bulrush microhabitats (labelled 'A') had significantly higher dytiscid species richness than non-vegetated microhabitats (labelled 'B'). The box denotes the data from Quantile 1 to Quantile 3; the black bar in each box denotes the median; the whiskers stand for the third quantile + 1.5 times interquartile range; the open circles denote observations that fall out of the whiskers.



**Fig. 3.** (a) The responses of dytiscid community-weighted mean body length to the presence or absence of fish. The triangles ( $\blacktriangle$ ) represent data collected in ponds with fish, and the filled circles ( $\bullet$ ) represent data collected in ponds without fish. (b) Dytiscid community-weighted mean body length at three different microhabitats in ponds with fish. Microhabitats with common reeds were excluded from the statistical analysis due to the unbalanced data (only two specimens were recorded). The error bars represent standard errors.

**Table 3**

Community-weighted mean body length of dytiscids from May to July 2020 in ponds with and without fish. SD means standard deviation. The categories labelled with the letter same letter indicates no statistical significance, whereas different letters indicate statistical significance.

Fish situation	Month	Number of beetles	Number of species	Body length (mm) $\pm$ SD
With fish	May	72	14	11.9 $\pm$ 8.4 <sup>AB</sup>
	June	66	13	16.7 $\pm$ 9.4 <sup>A</sup>
	July	28	13	11.5 $\pm$ 7.4 <sup>A</sup>
Without fish	May	122	27	6.1 $\pm$ 6.1 <sup>C</sup>
	June	189	26	4.9 $\pm$ 4.8 <sup>D</sup>
	July	113	21	8.2 $\pm$ 5.7 <sup>B</sup>

habitat selection at the pondscape scale. We found that, at the pond scale, the presence of fish had negative effects on dytiscid species richness, but not their abundance. Both dytiscid species richness and abundance are positively correlated with the increasing vegetation cover in the pond margins. In ponds with fish, dytiscid diversity is higher in microhabitats with bulrush and sedges than in non-vegetated microhabitats or in microhabitats with reeds, and microhabitat types have effects on dytiscid species traits. In the studied pondscape, dytiscid community-weighted mean body size is larger in ponds with fish than it is in fishless ponds, indicating changes in species composition related to body size at different levels of predation risk; dytiscid body size exhibits seasonal fluctuations in the two levels of predation risk, suggesting dytiscids select habitats to regulate their investment in vigilance according to their life cycles.

#### 4.1. Emergent plants mitigate predation risk and alter prey fitness

Animals regulate their levels of vigilance according to perceived predation risks, in order to balance their foraging opportunities (Brown, 1999). Our results show that, at the pond scale, there are fewer dytiscid species in the presence than in the absence of fish (Fig. 1a & b), reflecting higher predation pressure in ponds with fish than in ponds without fish, which is in accordance with previous studies (e.g., Hinden et al., 2005; de Mendoza et al., 2012). We found a stronger positive correlation between dytiscid species richness and vegetation cover in ponds with fish than in ponds without fish at the pond scale (Fig. 1a & b). Our result emphasizes the importance of aquatic plants as prey refuges in the presence of predators to mitigate predation risk for prey species. The availability of prey refuges can decrease the probability of attacks and increase the probability of survival after non-lethal attacks (Sih, 1987; Yee, 2010; Ghosh et al., 2017).

Aquatic plants can mitigate predation risk for aquatic animals, including dytiscids, which affects prey fitness (Nilsson and Holmen, 1995; Grabowski, 2004; de Mendoza et al., 2012; Ferrari et al., 2014). Our results show that both dytiscid species richness and abundance are positively correlated with the percentage of pond margins covered by emergent plants at the pond scale (Fig. 1a–c), which is different from the result of a previous study conducted at a smaller scale: At the microhabitat scale, dytiscid species richness and abundance have positive correlation with vegetation cover in ponds with fish, but no correlations in ponds without fish (Liao et al., 2023), reflecting that aquatic vegetation, as prey refuges, affect dytiscids' habitat use for survival. In this study, dytiscid species richness and abundance are positively correlated with vegetation cover at the pond scale, even under low predation risk, which reflects that aquatic plants alter other prey fitness components. Except for enhancing survival, aquatic plants also provide safe breeding sites (Jackson, 1958, 1960; Nilsson, 1987). For example, *Agabus* females lay their eggs in folded aquatic plant leaves (Jackson, 1958). The females of some *Ilybius* spp. have even evolved saw-like teeth in the terminal abdominal segment to insert eggs into living emergent plant tissues (Jackson, 1960). Survival and reproduction are both determinants of the population growth rate of prey species (Sheriff et al., 2020). The provision of aquatic plants is thus crucial to improve the fitness of prey species and facilitate the establishment of their populations, especially in urban ponds where aquatic invertebrates have more difficulties in dispersal than other landscapes

**Table 4**

Check list of Dytiscidae recorded in 2020, labelled with the four study types of microhabitats in ponds with fish: B represents bulrush; N represents non-vegetated; R represents reeds; S represents sedges. Information of species-specific life cycles is collected from Nilsson and Holmen (1995). Species of life cycle type 1 is univoltine spring breeder; type 2 is univoltine and breeds from summer to autumn; type 3 is semivoltine spring breeder.

Genus	Specific name	Life cycle	Ponds with fish				Ponds without fish			
			Microhabitats	May	June	July	May	June	July	
<i>Acilius</i>	<i>canaliculatus</i>	type 1	B, S	3	2	2	2		1	
	<i>sulcatus</i>	univoltine						1	2	
<i>Agabus</i>	<i>affinis</i>	type 1					5	1	1	
	<i>congener</i>	type 3					1	1		
	<i>fuscipennis</i>	type 2							2	
	<i>sturmii</i>	type 1	B, N, S	13	1		5	10	4	
<i>Clemnius</i>	<i>decoratus</i>	type 1					13	47	20	
<i>Colymbetes</i>	<i>paykulli</i>	larval development in late spring and summer					1			
<i>Cybister</i>	<i>lateralimarginalis</i>	type 1	B, N, R, S	5	7	1				
<i>Dytiscus</i>	<i>circumcinctus</i>	larval development in early summer	B, S	1	7		2	1		
	<i>marginalis</i>	larval development in early summer	B, S	3	2	1	2	2	2	
<i>Graphoderus</i>	<i>zonatus</i>	univoltine	B, S	1	14	6	1		3	
<i>Graptodytes</i>	<i>granularis</i>	type 1					13	11		
<i>Hydaticus</i>	<i>seminiger</i>	univoltine/type1?	B, S	4	7	2	8	10	8	
<i>Hydroglyphus</i>	<i>geminus</i>	-						1		
<i>Hydroporus</i>	<i>angustatus</i>	unknown					1	15		
	<i>erythrocephalus</i>	type 1					8			
	<i>gyllenhalii</i>	type 1					1		1	
	<i>incognitus</i>	type 1	B	5			14	12	9	
	<i>neglectus</i>	type 1					1			
	<i>palustris</i>	type 1	B, R, S	5		1	19	23	20	
	<i>planus</i>	type 1						1		
	<i>striola</i>	type 1	B	1			9	27		
	<i>tristis</i>	type 1					3	1	2	
	<i>impressopunctatus</i>	type 1						3	2	
	<i>inaequalis</i>	type 1	B, N, S	3	2	5	1	9		
	<i>Hyphydrus</i>	<i>ovatus</i>	type 1	S		1	3	1	1	1
	<i>Ilybius</i>	<i>aenescens</i>	-	S			1	2		
<i>angustior</i>		-						1		
<i>ater</i>		-	S		1	3		1	16	
<i>crassus</i>		-	B, S	6	1		1	4	3	
<i>erichsoni</i>		type 3							2	
<i>fuliginosus</i>		-						1		
<i>quadriguttatus</i>		-				1	1	2	12	
<i>subaeneus</i>		-					1			
<i>Laccornis</i>		<i>oblongus</i>	type 1						1	
<i>Rhantus</i>		<i>exoletus</i>	larval development in summer	S	10	8	1		2	
	<i>frontalis</i>	larval development from May to August	B, N, S	12	13	1	3	1	1	
<i>Suphrodytes</i>	<i>dorsalis</i>	-					3			

(Lundkvist et al., 2002; Horváth et al., 2009; Liao et al., 2022).

#### 4.2. Complex microhabitat structure modifies dytiscids' habitat use in the presence of fish

The structural complexity of aquatic vegetation plays a critical role in the diversity of aquatic invertebrates, especially under high predation risk (Nilsson and Söderberg, 1996; Tolonen et al., 2003; Nummi et al., 2021). We found in the presence of fish, bulrush and sedge microhabitats have higher dytiscid species richness and abundance than non-vegetated microhabitats and reed microhabitats (Fig. 2). The result that common reeds are not favoured by dytiscids is consistent with observations in other studies (Cuppen, 1983; Kolar and Boukal, 2020), although they occur in reed beds with rich *Sphagnum* mosses (Nilsson and Holmen, 1995). We assume that bulrush and sedges harbour more dytiscids than common reeds because their submerged parts have larger surface areas and more complex structures. We found no difference between the community-weighted mean body lengths of dytiscids in bulrush and in sedges (Fig. 3b, Table 4), reflecting that bulrush and sedges provide a similar level of structural complexity. We think the habitat use of dytiscids is associated with habitat structural complexity rather than particular macrophyte species, which is supported by other studies (e.g. Kolar and Boukal, 2020).

Levels of predation risk affect habitat use of aquatic macroinvertebrates due to the levels of vigilance necessary to avoid predators. Dytiscids are not unique in their response to the presence of fish predators. Other aquatic invertebrates, such as odonates, also use aquatic plants as prey refuges and perching sites (Peckarsky, 1982; Tolonen et al., 2003; Klecka and Boukal, 2014). Aquatic invertebrate diversity generally has a positive correlation with the species richness of aquatic plants that indicates vegetation structure complexity (Hassall et al., 2011; Gioria and Feehan, 2023; Law et al., 2019). Although urban ponds may involve intentional removal of aquatic vegetation to create tidy appearances (Hassall, 2014), retaining small patches of aquatic vegetation in a pond is necessary to

support urban biodiversity and ecosystem services based on biodiversity. In microhabitats with simple structures, such as common reed 'monoculture', adding some native plant species to form complex vegetation structures is a solution to enhance native communities and avoid the invasion of exotic species in urban ponds (Gomes et al., 2016; de Carvalho et al., 2022; Lozano et al., 2022).

#### 4.3. Predation pressure modifies dytiscids' habitat selection in pondscales

Predation risk induces trait responses of prey species, which affects habitat selection of animals (Resetarits and Wilbur, 1989; Kraus and Vonesh, 2010). Such risk-induced trait responses include behavioural, morphological, physiological, and life history responses (Peacor and Werner, 2001; Sheriff et al., 2020; Peacor et al., 2020). Our results show that many species, especially small-sized dytiscids, favour habitats with low predation risks in the study pondscape (Fig. 3a). The result is in accordance with the finding of Binckley and Resetarits (2005) that most water beetle species exhibit a strong preference for fishless habitats. Small-sized dytiscid species, such as *Hydroporus* spp., are incapable of producing defensive chemicals (Dettner, 2023). Lacking such physiological anti-predator capacity drives them to modify other traits, such as reducing activity in water or exhibiting predation-induced dispersal, to reduce predation risks (Åbjörnsson et al., 1997; Dahl and Greenberg, 1999; Kraus and Vonesh, 2010; Resetarits and Pintar, 2016). These predation-induced behaviours, such as avoidance of habitats with fish, have been found also in other aquatic invertebrates, such as Hydrophilidae and Culicidae (Crespo, 2011; Pintar et al., 2018; Resetarits et al., 2021).

Risk-induced trait responses can be different among species even within the same family. In our study, we found that the presence or absence of fish is not included in the optimal model for dytiscid abundance at the pond scale (Fig. 1c; Table 2), indicating that some species are capable of coexisting with fish and establishing populations in ponds with fish. Such differences between dytiscid species can be because medium to large-sized dytiscid species, such as *Agabus* spp. and *Dytiscus* spp., are capable of producing defensive chemicals, such as steroids and pregnanes, to anesthetize and even kill their predators (Miller and Mumma, 1975, 1976; Gerhart et al., 1991; Schaaf et al., 2000). Also, large-sized dytiscids and their larvae can even be predators of small fish (Liao's personal observation; Frelik, 2014), which ecological role is another explanation for the larger community-weighted mean body length in ponds with fish than in ponds without fish. Other taxa of aquatic invertebrates may exhibit different behaviours as responses to predators. For example, whirligig beetles (Gyrinidae) form large aggregations in mixed species groups to enhance environmental scanning and help detect fish predators faster than having small groups (Vulinec and Miller, 1989; Watt and Chapman, 1998), which may add diversity of certain taxa to a local habitat. Different risk-induced trait responses among prey species, therefore, can lead to different aquatic community compositions at the pondscape scale.

Risk-induced trait responses of prey species in their life history, an aspect of non-consumptive effects of predators, can also shape community compositions at the landscape scale. Our results show that the community-weighted mean body size of dytiscids exhibits seasonal fluctuations both in ponds with and without fish (Table 3, Fig. 3a), which may have resulted from the different levels of vigilance necessary to balance survival and reproduction in the life history of species. Most of the dytiscid species recorded in our study ponds are spring breeders with summer larvae (Table 4; Nilsson and Holmen, 1995). Mating exposes animals, including dytiscids, to high predation risks (Arnqvist, 1989; Bergsten et al., 2001), and dytiscid larvae can be vulnerable to fish predation (Kraus and Vonesh, 2010). To maximise their fitness, dytiscid adults need to select habitats suitable for breeding. For instance, females of small-sized *Hydroporus* spp. exhibit strong preferences for oviposition in fishless habitats, despite tanks with fish having higher food availability for dytiscid larvae (Brodin et al., 2006), reflecting the fear of females for predation and the non-consumptive effects on their fecundity (Sheriff et al., 2020). The cost of breeding, therefore, may have also contributed to dytiscids' selection of habitats with low predation risks, manifesting seasonal changes in their species composition.

Non-consumptive effects of predation play a role as important as direct predation and modify patch use and habitat selection of prey species due to the ecology of fear (Brown et al., 1999; Laundré et al., 2001; Ripple and Beschta, 2004; Wirsing and Ripple, 2011; Sheriff et al., 2020). Fear induces the change of aquatic invertebrate species traits, such as fast development of larvae with small body sizes in the presence of predators (Peckarsky et al., 2002), and their behavioural responses of aquatic invertebrates, including predation-induced dispersal that drives them to seek habitats with low predation risk (McCauley and Rowe, 2010; Baines et al., 2014; Dettner, 2019). One limitation of our study is that we did not directly measure the fear of dytiscids. Future studies should investigate their chemical responses to the presence of predators, in order to understand the theory 'ecology of fear' and how 'pondscape of fear' alters habitat use and habitat selection of aquatic invertebrates.

#### 4.4. Implications for aquatic biodiversity conservation

Aquatic vegetation, as spatial prey refuges, can promote the coexistence of fish and aquatic invertebrates (Denno et al., 2005; de Mendoza et al., 2012; Law et al., 2019; Liao et al., 2023). In urban landscapes, ponds may suffer from an array of internal and external environmental changes. For example, internally, the habitat structure of urban ponds may be simplified due to tidy appearances preferred by many urban residents (Hassall, 2014; Ngiam et al., 2017), which can impede the survival and reproduction of aquatic invertebrates, especially in the presence of fish predators. Externally, urban landscapes involve many deceptive features, such as glass and car roofs, that mislead dispersing aquatic invertebrates (Nilsson, 1997; Horváth et al., 2009). Provision of favourable habitat features may decrease the necessity of dispersal induced by predation at the local scale while facilitating the establishment of aquatic invertebrates at the pondscape scale.

Urban ponds often involve introduced fish for ecosystem services or are invaded by alien fish species, such as Prussian carps in some of our study ponds, which increases predation risks for aquatic invertebrates (Copp et al., 2005; Weyl et al., 2010; Lucas and Polidoro, 2019). To mitigate the negative effects of predators, it is crucial to provide (1) patches with native aquatic plants with high structural



complexity at the pond scale, to facilitate the coexistence of fish and aquatic invertebrates and to reduce predation-induced dispersal, and (2) wetland habitats with low predation risks at the landscape scale, such as ponds with a high percent of emergent vegetation cover and/or fishless ponds, to support the fitness of aquatic invertebrates and the establishment of stable urban populations. Supporting high native biodiversity is crucial to enhance socio-ecological values of urban pond networks.

### Authors' contributions

WL designed the study, collected and analysed data, and led the writing. TZ helped WL search and comprehend important literature and commented on the manuscript critically for important intellectual contents. JN supervised WL, and commented and revised the contents and structure of the manuscript critically.

### CRedit authorship contribution statement

**Niemelä Jari:** Writing – review & editing, Supervision, Resources. **Liao Wenfei:** Writing – original draft, Visualization, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Zanca Tommaso:** Writing – review & editing, Validation.

### Declaration of Competing Interest

All authors declare no conflict of interest.

### Data availability

Data used in this study is available on <https://doi.org/10.23729/6001c8fe-3387-4923-8d3f-8875a6a805c6>.

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### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2024.e02801](https://doi.org/10.1016/j.gecco.2024.e02801).

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