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Faculty of Science

Aquatic insect assemblages in littoral zones of ponds and other man-made habitats

Ph.D. Thesis

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Annotation

This thesis focuses on aquatic insect and newt assemblages in fishponds and other man-made standing waters. It reviews the effects of fishpond management and restoration of post-mining sites on main aquatic taxa, with main focus on aquatic insects in the littoral zone. The next five chapters deal with long-term changes of the littoral habitats in fishponds and with various aspects of the importance of littoral habitats for aquatic organisms, mainly predatory insects and newts. The results are used to recommend management approaches aimed to increase biodiversity and conservation value of fishponds and other man-made habitats.

Declaration

I hereby declare that I am the author of this dissertation and that I have used only those sources and literature detailed in the list of references.

České Budějovice, 6.2.2021

Vojtěch Kolář

This thesis originated from a partnership of Faculty of Science, University of South Bohemia, and Institute of Entomology, Biology Centre CAS, supporting doctoral studies in the Hydrobiology study programme.

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List of papers and author's contribution

I. **Kolar V.,** K. Francová, J. Vrba, Boukal D. S. Habitat deterioration despite protection: long-term declines of littoral zones of fishponds in Czech nature reserves. (Manuscript)
VK designed the study (100%), collected, analysed and interpreted the data (90%) and led the writing of the first draft (80%).

II. **Kolar V.**, Boukal D. S. (2020) Habitat preferences of the endangered diving beetle *Graphoderus bilineatus*: implications for conservation management. *Insect Conservation and Diversity* 13: 480–494. DOI: 10.1111/icad.12433 (IF = 2.729).
VK participated in the planning of the study (80%), collected data in the field (100%), made first analyses and data interpretation (70%) and led the writing of the first draft (80%).

III. **Kolar V.**, Vlašánek P., Boukal D. S. The influence of successional stage on local odonate communities in man-made standing waters. (Manuscript)
VK participated in the planning of the study (90%), partly conducted the fieldwork (50%), analysed and interpreted the data (100%) and led the writing of the first draft (80%).

IV. **Kolář V.**, Tichánek F., Tropek R. (2017) Effect of different restoration approaches on two species of newts (Amphibia: Caudata) in Central European lignite spoil heaps. *Ecological Engineering* 99: 310–315. DOI: 10.1016/j.ecoleng.2016.11.042 (IF = 3.023).
VK participated in the planning of the study (70%), conducted all fieldwork (100%), participated in data interpretation (20%) and led the writing of the first draft (70%).

V. **Kolar V.**, Tichánek F., Tropek R. Evidence-based restoration of freshwater biodiversity after mining: Experience from Central European spoil heaps. (Manuscript)
VK participated in the planning of the study (70%), conducted all fieldwork (100%), participated in data analyses and interpretation (40%) and led the writing of the first draft (70%).

Co-author agreement

David Boukal, the supervisor of this thesis and co-author of Chapters I–III, fully acknowledges the contribution of Vojtěch Kolář as the first author and his contributions as stated above.

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Robert Tropek, the co-author of the Chapters IV and V, fully acknowledges the contribution of Vojtěch Kolář as the first author and his contributions as stated above.

RNDr. Robert Tropek, Ph.D.

Contents

~ Introduction ~

Thesis introduction

Aquatic insect assemblages in littoral zones of ponds and other man-made habitats

~ Overview ~

Freshwater habitats such as rivers, lakes, ponds and peat bogs are an important part of the global ecosystem because they are inhabited by more than 10% of all animal species (Stendera *et al.*, 2012; Darwall *et al.*, 2018). However, these habitats have been strongly affected by human activities and the impact on their biota has been increasing in the past decades. Changes in land use, eutrophication, introduction of invasive species, pollution, overexploitation, and flow modification are among the strongest negative factors affecting running and standing freshwater habitats (Dudgeon *et al.*, 2006; Darwall *et al.*, 2018; Reid *et al.*, 2019). Due to these factors or their combinations, 64-71% of the total global area of natural freshwater habitats were lost since 1900 (Davidson, 2014). This has led to a massive decrease in freshwater biodiversity, which is now faster than in terrestrial ecosystems (Dudgeon *et al.*, 2006; Stendera *et al.*, 2012).

On the other hand, human activity has created new habitats and habitat types, which may serve as surrogates for the vanishing natural biotopes (Sartori *et al.*, 2014; Kolozsvary & Holgerson, 2016). Surprisingly little is known about the main environmental drivers creating and affecting species composition in many man-made habitats such as fishponds and ponds in sandpits or spoil heaps (Stendera *et al.*, 2012), because the species may perceive and experience these habitats differently from their natural biotopes. Moreover, habitat requirements could vary between species and, within species, on larger spatial scales. This means that effective local conservation measures that work in one place may not work elsewhere, and conservation of one taxon may harm other taxa. For example, the habitat requirements of waterfowl differ from those of aquatic macrophytes or macroinvertebrates.

~ Effect of fishpond management on aquatic biota ~

Fishponds are the most common type of large standing waters in the Czech Republic. They represent man-made equivalents of natural shallow lakes and constitute half of the country's total current wetland area (Čížková *et al.*, 2013). Most fishponds in the Czech Republic are several hundred years old (IUCN, 1997). During that time, their management changed dramatically both in the Czech Republic and elsewhere in Central Europe. Until the end of the 19th century, fishponds were oligotrophic to mesotrophic due to the lack of intensive agriculture, moderate stocking with a range of fish species, and extensive management. Moreover, fishponds were regularly drained in summer or winter and left without water for several months to release mineral nutrients and to eliminate fish parasites and diseases (IUCN, 1997; Šumberová *et al.*, 2006; Francová *et al.*, 2019a). This undoubtedly contributed to a 'near-natural' status of many fishponds. Over the centuries, fishponds thus became secondary habitats for many species originally associated with peat bogs, small pools or waterlogged meadows (Kolář *et al.*, 2017; Kolar & Boukal, 2020).

At the end of the 19th century, fishpond management shifted to a more intensive operating mode characterized by the use of fertilization and stocking of monoculture of the common carp (*Cyprinus carpio*). This led to higher fish yields but also an increase in nutrient loading (IUCN, 1997; Potužák *et al.*, 2007). Since the 1960s, intensification of agriculture and major changes in land use lead to further eutrophication and even more intensive stocking and production of fish (Přikryl, 1996; Potužák *et al.*, 2007) that continue until today. As a result, most fishponds are now eutrophic or hypertrophic with a low standing stock of zooplankton characterized by small species (Fig. 1), common algal or cyanobacterial blooms, and occasional periods of hypoxia and anoxia. Moreover, many littoral areas with shallow water and extensive macrophyte beds were destroyed for the sake of maximum fish yields (Chapter I).

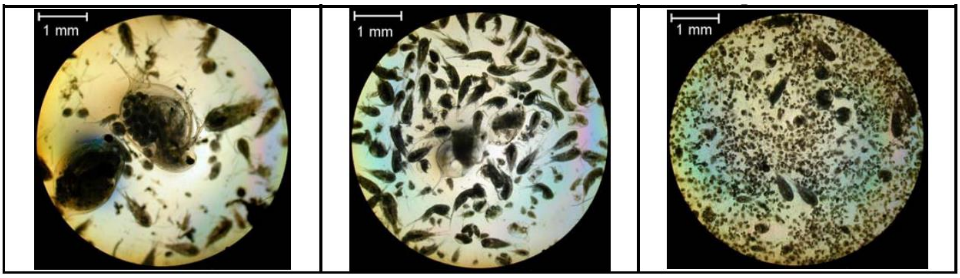

Fig. 1: Changes in zooplankton body size and species composition on the gradient of low (left) to high (right) planktivorous fish stock (according to Přikryl et al., 2004).

These changes in pond management undoubtedly led to decreases in local biodiversity in Central Europe and elsewhere. The declines have been only partially documented. Many studies focused on one taxon (e.g., birds: Pykal & Janda, 1994; Haas *et al.*, 2007, amphibians: Kloskowski, 2010, zooplankton: Přikryl, 1996; Potužák *et al.*, 2007, dragonflies: Hassall et al., 2012; Šigutová et al., 2015, macrophytes: Šumberová *et al.*, 2006; Francová *et al.*, 2019b, 2021) but some groups remain poorly studied. Aquatic insects are one of those groups; available evidence such as the extinction of the diving beetle *Dytiscus latissimus* in the 1960s and the decline of *Graphoderus bilineatus* in the Czech Republic (Hájek, 2004, Chapter II) suggests that the last period of intensification and major changes in land use in 1950s had a strong effect on local aquatic insect assemblages.

Ponds include three main types of habitat domains: littoral zone, and the benthic zone and water column of the open water area. The water column is inhabited mainly by phytoplankton, zooplankton and fish (Potužák *et al.*, 2007; Nieoczym & Kloskowski, 2014) and aquatic insects use this habitat only rarely (e.g., Corixidae). Benthic communities of the open water are dominated by oligochaete worms, leeches and dipteran larvae, especially chironomids (Miller & Crowl, 2006; Sychra *et al.*, 2010). Aquatic insects are most common in the littoral habitats together with gastropods, amphipods and amphibians (Nilsson & Svensson, 1995; Tolonen *et al.*, 2003; Kloskowski, 2010). Moreover, littoral zones are the main "hot spots" of fishpond biodiversity, especially when fish are present (Sychra *et al.*, 2010; Šetlíková *et al.*, 2016; Kloskowski *et al.*, 2020).

Aquatic invertebrate assemblages are influenced by many abiotic and biotic factors. Key abiotic factors include pH, temperature, water transparency, fluctuation of water column, and type of bottom. Key biotic factors include vegetation cover and heterogeneity and the species composition and biomass of stocked fish. Ponds in the Czech Republic are mostly stocked with common carp (*Cyprinus carpio*), sometimes together with other supplementary species such as pike (*Esox lucius*), grass carp (*Ctenopharyngodon idella*) and catfish (*Silurus glanis*) (Francová *et al.*, 2019a). Common carp negatively impacts the pond environment in multiple ways. Studies reporting very limited impact of common carp on invertebrate communities might have used inadequate sampling and statistical methodology (Šetlíková *et al.*, 2016) or low taxonomic resolution (Nieoczym & Kloskowski, 2014) that could conceal the differences in species diversity.

The effects of common carp on aquatic biota are both direct and indirect (Fig. 2; e.g., Parkos III *et al.*, 2003; Vilizzi & Tarkan, 2015). Increasing carp stock decreases the abundance and diversity of vascular plants (Broyer & Curtet, 2012; Francová *et al.*, 2019a, 2021) directly by digging in the sediment because carp could disrupt the ground as deep as 10 cm (Ivlev, 1961) to feed indiscriminately on invertebrates and new plant sprouts (Crivelli, 1983; Sidorkewicj *et al.*, 1999; Vilizzi & Tarkan, 2015).

This directly limits submerged plant growth and leads to elevated mortality through uprooting of individual plants. Moreover, carp also affects nutrient dynamics through its excretion that supports algal growth (dominated by cyanobacteria) and increases the suspended solids and nutrients in the water column (Matsuzaki *et al.*, 2007) especially in late season (Parkos III *et al.*, 2003). Thus, carp affects aquatic plants indirectly by increasing water turbidity, which decelerates plant growth and may in the long term contribute to the total destruction of the littoral zone (Matsuzaki *et al.*, 2007; Broyer & Curtet, 2012, Fig. 3, Chapter I).

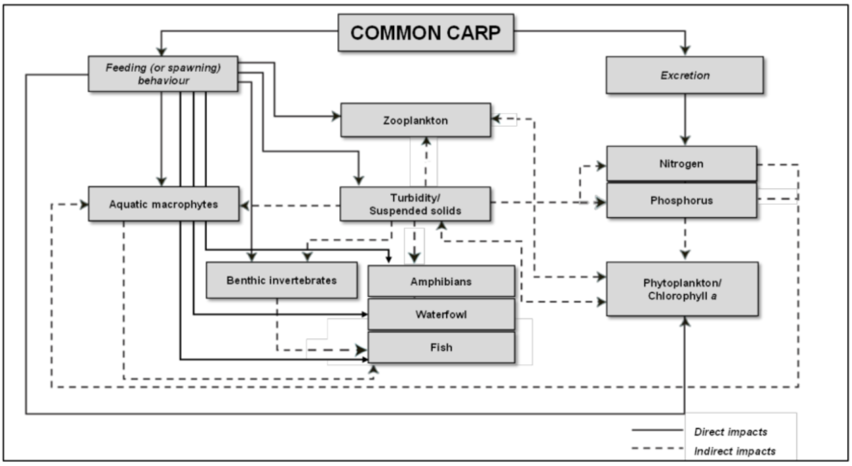

Fig. 2: Direct and indirect effects of common carp on the freshwater ecosystem (Vilizzi & Tarkan, 2015).

Fish in ponds negatively influence aquatic insect communities and amphibians. Insect and amphibian abundance and diversity decrease when fish are present (e.g., (Kloskowski, 2010; Kloskowski *et al.*, 2020), typically in favour of smaller species (Wellborn *et al.*, 1996; Tolonen *et al.*, 2003). In particular, ponds with less abundant plants or with high turbidity caused by high fish stock (see above) host fewer aquatic insects than ponds with vegetation (Tolonen *et al.*, 2003). Insects exploit vegetation as refuges from predators (Scheinin *et al.*, 2012; Kloskowski *et al.*, 2020) and many predatory insects (e.g., many dragonfly and damselfly larvae) prefer vegetation as perching sites for hunting (Klecka & Boukal, 2014; Kolar *et al.*, 2019). Moreover, some insect predators are visual hunters that cannot forage efficiently in turbid water. Finally, submerged and emerged plants serve as oviposition sites for some insect species (Inoda, 2011; Yee, 2014) and provides food either directly or indirectly by supporting the growth of periphyton (van Vondel & Dettner, 1997). Some groups of aquatic insects such as odonates, beetles and mayflies are absent or less abundant or less diverse in fishponds (Gee *et al.*, 1997; Tolonen *et al.*, 2003; Kloskowski, 2011a). On the other hand, invertebrate predators in fishponds are also less common and less active, which could potentially lead to an increase of their prey (Wellborn *et al.*, 1996; Kloskowski *et al.*, 2020). For example, some insect groups such as caddisflies or the common toad *Bufo bufo* can increase in abundance due to the absence of natural predators in fishponds (Manteifel & Reshetnikov, 2002; Kloskowski *et al.*, 2020).

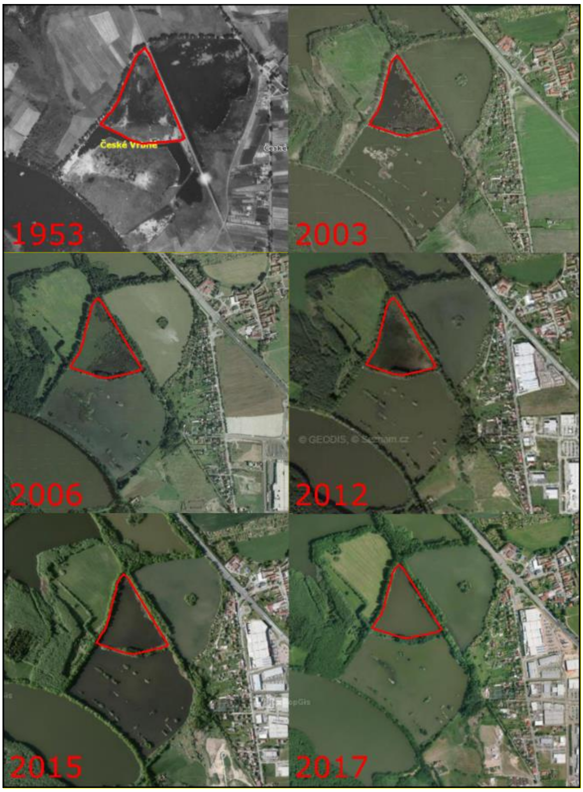

Fig. 3: Example of a decline in the vegetated littoral area in a fishpond in the last 70 years (red triangle = Bažina fishpond, part of the Vrbenské rybníky Natural Reserve). See Chapter I for a full analysis.

The above effects are usually mediated by the biomass and the age and size structure of the fish. Larger carp cause more disturbances in the bottom and in the littoral zone than smaller one-year old fish, with more severe consequences for the local biota (Kloskowski, 2011b; Nieoczym & Kloskowski, 2014). However, some aquatic insects such as aquatic bugs do not seem to respond to fish age. This could be explained by their ability to obtain their prey in turbid water in contrast to diving beetles or most dragonflies, or by the fact that fish do not prey on them (Papáček, 2001; Kloskowski, 2011b), which favours them under apparent competition with other groups. Moreover, some of the bugs (Corixidae) are polyphagous and increased eutrophication may enhance rather than diminish their food base.

Aquatic insect and amphibian assemblages in fishponds are further structured by biotic interactions within the communities, sometimes mediated by the fish. For example, predatory aquatic insects (mainly diving beetles, dragonfly larvae, and true bugs) and newts can be subject to indirect competition among themselves (Klecka & Boukal, 2014; Anderson & Semlitsch, 2016) and with the fish. The latter are usually better competitors because of their larger size, although large predator species can feed on fish fry (Papáček, 2001; Veselý *et al.*, 2017). High diversity of predatory aquatic insects can be maintained, e.g., through niche separation and use of different microhabitats (Anderson & Semlitsch, 2016; Kolar *et al.*, 2019). For all these reasons, it is still unknown to what extent fish stocking practices and other fishpond management decisions influence the local aquatic insect assemblages and relationships between the different trophic levels.

For example, one of the traditional forgotten fishpond management is periodic summer and/or winter drainage i.e., leaving the fishpond for part of the season on law water level or empty (IUCN, 1997; Francová *et al.*, 2019a). This enhances the decomposition of organic matter in aerobic conditions and thus increases fish production. It was also used to combat fish diseases and parasites in the past (Šumberová *et al.*, 2006; Francová *et al.*, 2019a) and nowadays to decrease non-native fish species (e.g., *Pseudorasbora parva*, *Lepomis gibbosus*, *Ameiurus nebulosus*). However, the effect of drainage is more often studied in the context of macrophytes (Arnott & Yan, 2002; Šumberová *et al.*, 2006): it is recommended as a suitable management option to increase the overall macrophyte diversity (Šumberová *et al.*, 2006; Broyer & Curtet, 2012; Francová *et al.*, 2019b) or to support some species, e.g., *Littorella uniflora* (Kolář *et al.*, 2017).

Pond drainage can also positively affect some zooplankton species, probably through the indirect effect of nutrient release to the water column (Hough *et al.*, 1991). The effect of drainage on aquatic and semi-aquatic macroinvertebrates is almost unknown (but see Meutter *et* *al.*, 2005). Drainage could favour pioneer species and thus one drainage pond in a fishpond system can increase local diversity. Finally, the aeration of bottom sediment can promote macrophyte growth and hence indirectly increase the macroinvertebrate densities (see above). This could then have a positive effect across the higher trophic levels up to the top predators such as birds.

~ Post-industrial sites as secondary habitats for freshwater species ~

Other common standing freshwater habitats in the modern European landscape are sites created after surface mining actions such as gravel, china clay and sandpits, and pond and lakes spontaneously or artificially created in the mine, spoil heaps and mine subsidence areas. Globally, mining-affected areas vary between 0.3% (Cherlet *et al.*, 2018) to 1% (Walker, 1999) of the land surface. Their effective management could create important ecosystems, which could support diverse freshwater organisms in the man-affected landscape.

Post-mining sites can indeed serve as important refuges for freshwater organisms including amphibians (Vojar et al., 2016, Chapter IV), zooplankton (Moreira *et al.*, 2016; Goździejewska *et al.*, 2018), insects (D'Amico *et al.*, 2004; Dolný & Harabiš, 2012; Pakulnicka *et al.*, 2015) or oligochaetes (Sowa & Krodkiewska, 2020). Typically, they offer ponds of various sizes characterized by a low level of eutrophication and relatively high morphological diversity (Hendrychová & Kabrna, 2016). The potential of such post-mining sites for biodiversity conservation depends largely on the applied restoration approach. In Central Europe, the most common restoration practice is technical reclamation consisting of surface remodelling by heavy machinery, its covering with fertile topsoil, planting of tree monocultures or sowing of species-poor productive grasslands, and often also a creation of artificial ponds and lakes (Tropek *et al.*, 2010; McCullough & van Etten, 2011; Hendrychová *et al.*, 2020) used for recreation and sometimes for intensive aquaculture (Mallo *et al.*, 2010). Examples of entirely or partly spontaneous succession are less common: the area is left without any modelling activities or partly modelled, and ponds are created naturally (Harabiš *et al.*, 2013; Fig. 4).

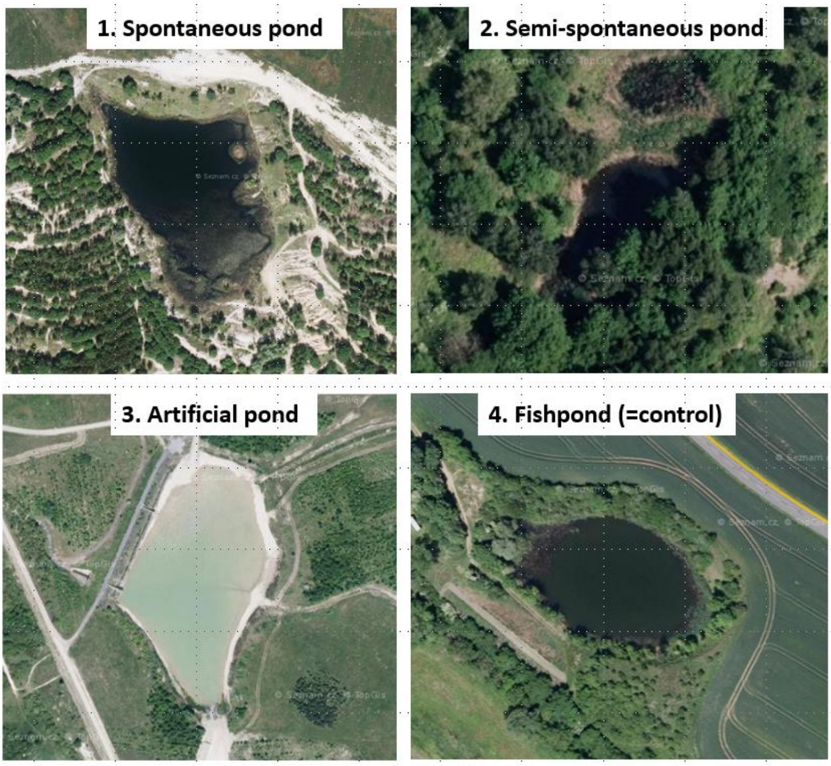

Fig. 4: Four main types of larger standing freshwater habitats in north-west Bohemia studied in Chapters IV and V: 1) spontaneous, 2) semi-spontaneous and 3) artificial pond at a spoil heap and 4) fishpond. Panels are on different scales (www.mapy.cz).

Numerous comparative studies showed that spontaneous succession is more effective than costly technical reclamation for the conservation of the terrestrial biodiversity of post-mining sites (Řehounková *et al.*, 2016; Moradi *et al.*, 2018), but similar knowledge for freshwater habitats is very limited. Recent studies have shown that spontaneous and semi-spontaneous succession leads to higher diversity and abundance of amphibians and dragonflies (Harabiš *et al.*, 2013; Vojar *et al.*, 2016). Moreover, artificially created ponds are often close to settlements and serve for recreation including legal or illegal fishing and fish stocking, which makes them similar to fishponds (V. Kolář, pers. obs., Chapters IV and V). They may also host invasive crayfish (Patoka *et al.*, 2016) and fish (V. Kolář, pers. obs.) that threaten the native biota.

Successional stage is another important driver of community composition in small ponds (Rahel, 1984; Layton & Voshell, 1991; Bloechl *et al.*, 2010, but see Gee *et al.*, 1997). Early stage succession, characterised by an open habitat with limited aquatic vegetation, is preferred by 'pioneer' species (Kehl & Dettner, 2003). These species have become rare or endangered because the modern Central European landscape lacks natural disturbances such as spring floods in river floodplains. The rate of succession is further driven by the amount of available nutrients, which has increased due to widespread eutrophication, making early stage succession habitats even scarcer.

Several studies showed that the presence of habitats in different successional stages is necessary to increase local biodiversity (e.g., plants: Teurlincx et al., 2018). Pools of different age are often present at post-industrial sites such as sandpits or spoil heaps, which suggests that these sites could harbour considerably diverse aquatic communities (Chapters III, IV, V). However, from the high number of studies which dealt with succession or reclamation activities at post-industrial sites (e.g., Tropek *et al.*, 2010; Řehounková *et al.*, 2016; Růžičková & Hykel, 2019) only some of them focused on aquatic taxa, mostly amphibians, dragonflies and one on benthic invertebrates (e.g., see Table 1 in Chapter V). Moreover, different types of ponds created during reclamation activities are often studied only in Central Europe as studies from other parts of the world usually only compare industrial and natural sites (Zhang *et al.*, 2019, 2020). Effective restoration should be based on thorough knowledge of habitat requirements (e.g., the type of pond and its preferred successional stage) of different groups to maximise the support of local biodiversity. Thus, more studies focusing on different taxa are needed to find and recommend specific restoration and management actions.

~ *Aims and scope of this thesis* ~

In this thesis, I focus on aquatic ectotherms occupying man-made habitats in the Czech Republic, especially fishponds and ponds at spoil-heaps and sandpits. As the study organisms, I chose predatory aquatic insects (beetles, heteropterans and odonates) that are the top predators in fishless habitats and their presence and abundance affects the whole community structure (Wellborn *et al.*, 1996). These species are also relatively rare and occur at lower densities. Thus, they could be used as bioindicators and sentinel species that reflect the biotic and abiotic changes in the ecosystem. While the main focus of my thesis is on predatory aquatic insects, I have also surveyed newts in post-industrial habitats because of their important role in community structuring and prominent status in the conservation of standing water habitats.

In **Chapter I**, I focus on the status of littoral zones in fishponds and their effective conservation. Littoral zones are an important part of the ecosystem and harbour most of the pond macroinvertebrate biodiversity. I use selected protected areas in South Bohemia as a case study to document the widespread decline of the littoral zone areas in the second half of the 20th century and to discuss the effectiveness of protected area status to stop or revert this process.

Effective conservation of endangered species requires good knowledge of their habitat requirements (Stewart *et al.*, 2007). In **Chapter II**, I deal with the protection of diving beetle *Graphoderus bilineatus* listed in NATURA 2000 (see above). Several other studies on the habitat preferences of *G. bilineatus* across Europe were published (Cuppen *et al.*, 2006; Iversen *et al.*, 2013), but these preferences may vary at large spatial scales. Thus, the same species may have different preferences on the opposite sites of its areal and more studies are necessary for its effective conservation. I assessed its habitat and microhabitat preferences and characterized the co-occurring water beetle communities in 82 pools and ponds in South Bohemia and compared my results to those from other countries.

In **Chapters III, IV** and **V**, I focus on newly created habitats in sandpits and spoil heaps and compare them to nearby fishponds as another common man-made habitat. I have studied dragonfly assemblages of early and late successional sandpit ponds (Chapter III) and newts (Chapter IV) and aquatic beetles and hemipterans (Chapter V) in ponds created during restoration. As stated above, effective restoration requires good knowledge of the habitat requirements of main groups, because in some cases the preferences of different species or higher taxa can be completely opposite. For this reason, Chapter V includes a synthesis of known habitat preferences of main groups of animals (both vertebrates and invertebrates) and aquatic macrophytes at spoil heaps and provides recommendations for management options that should lead to support the highest species diversity including rare aquatic species.

In sum, I hope that the five studies of aquatic taxa occupying the littoral zones of man-made habitats included in this thesis will increase our knowledge of their distribution and habitat requirements and contribute to their effective evidence-based conservation in the Czech Republic and elsewhere.

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~ Chapter I ~

Habitat deterioration despite protection: long-term declines of littoral zones of fishponds in Czech nature reserves

[Manuscript prepared for Biological Conservation]

Habitat deterioration despite protection: long-term declines of littoral zones of fishponds in Czech nature reserves

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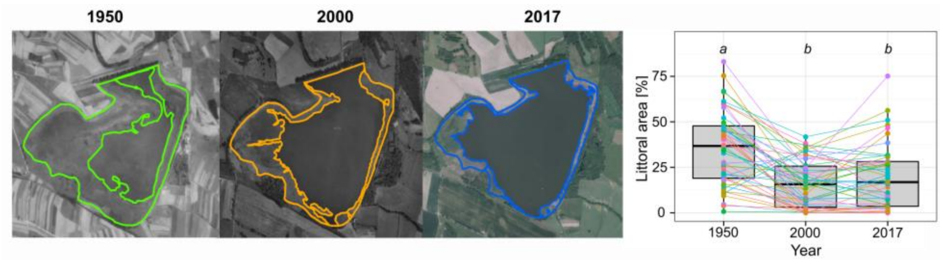
Highlights

- We evaluated long-term changes in the littoral zones of 46 fishpond reserves in Czechia.
- The area of littoral zone decreased markedly over time in most of the fishponds.
- Reserve duration, fishpond area and conservation target did not affect the trends.
- Changes in fishpond management are recommended for littoral zone recovery.

Graphical abstract



Abstract

Fishponds play a key role in current pondscape in many developed countries. Their littoral zones, supporting multiple ecosystem functions including the maintenance of aquatic and riparian biodiversity, have been adversely affected by the move towards more intensive aquaculture and widespread eutrophication in the middle 20th century. To counteract these changes, many fishponds received some protection, but its long-term efficiency has not been studied. Here we focus on the role of conservation status in protecting the area of littoral zones of fishponds in Czechia between the years 1950 and 2019. We found that the conservation status of these fishponds did not prevent habitat deterioration in most of the fishponds, especially during the second half of the 20th century. Moreover, we detected no significant effects of the reserve establishment year, fishpond area and conservation target on the littoral zones. This suggests that the conservation measures are insufficient across fishpond reserve types. We attribute the negative trends to persisting high fish stocks, especially of common carp, and eutrophication resulting from additional feeding, pond manuring, and ongoing nutrient inputs from the surrounding landscape and entire catchments. Sediment dredging and high grazing pressure by waterfowl in some reserves can further aggravate the situation. We conclude that effective protection of the littoral zones requires a paradigm shift towards less intensive fish stock management, more frequent summer drainage, and effective reduction of all nutrient inputs to increase the water quality. Such measures can help recover the littoral areas and the associated biota.

Keywords: Management, macrophytes, biodiversity, nature conservation, man-made habitats

~ Chapter II ~

Habitat preferences of the endangered diving beetle *Graphoderus bilineatus*: implications for conservation management

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Insect Conservation and Diversity

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Habitat preferences of the endangered diving beetle *Graphoderus bilineatus*: implications for conservation management

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Abstract. 1. Populations of the endangered diving beetle *Graphoderus bilineatus* are decreasing across Europe. Evidence-based conservation of its local populations requires good knowledge of its habitat requirements, but data from different countries are often incomplete or contradictory.

2. *Graphoderus bilineatus* was common until 1950s but then almost disappeared in the Czech Republic. Using data from a recent field survey in its core distributional area in the Czech Republic, we evaluate its habitat preferences at the habitat and microhabitat scale.

3. We found that extensively managed fishponds can provide similarly suitable habitats for *G. bilineatus* as do more natural habitats including floodplain and sandpit pools, while the species is typically absent in intensively managed fishponds. All else being equal, the species is more likely found in larger water bodies surrounded by other wetlands and is more often absent at sites in agricultural landscape.

4. We detected only weak preferences on the microhabitat scale. They suggested that *G. bilineatus* tends to occur in deeper water but closer to the shore and in microhabitats dominated by *Glyceria* or *Typha*. These microhabitat associations partly differ from those reported from other countries.

5. Moreover, *G. bilineatus* was found at localities with higher species richness of large-bodied aquatic beetles, both common and threatened, supporting the species status as an umbrella species for other aquatic macroinvertebrates.

6. Our findings provide guidelines for conservation management of currently known localities and other potentially suitable sites, including the creation of new ones. Finally, our study reinforces the Annex II species status of *G. bilineatus* in the Habitats and Species Directive.

Key words. Coleoptera, Dytiscidae, environmental factors, fishponds, insect conservation, NATURA 2000, oxbows, sand pits.

Introduction

Recent human activity has led to a large decrease of worldwide biodiversity in freshwater ecosystems (Darwall *et al*., 2018; Reid *et al*., 2018). These ecosystems are affected primarily by direct habitat destruction and modification caused by increasing eutrophication (Smith, 2003), invasive species (Simberloff *et al*., 2013), and increasing inputs of pollutants such as heavy metals, pharmaceuticals, and herbicides (Davies *et al*., 2008). These changes led to regional extinction of some aquatic insects including diving beetles (Bameul, 2013; Yee, 2014), which play an important role in structuring of local communities. Both larvae and adults of diving beetles are top predators that can modify local species composition, especially in fishless pools (Klecka & Boukal, 2012; Yee, 2014). Some diving beetles with highly

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specialised habitat requirements also serve as bioindicators of temporal pools, salinity, acidic waters, specific vegetation (e.g. *Sphagnum* in peat bogs) or water pollution (e.g. Ranta, 1982; Eyre *et al*., 1986; Alarie & Leclair, 1988; Juliano, 1991; Fairchild *et al*., 2003; Burghelea *et al*., 2011). This bioindicative value and population declines of many diving beetle species due to their sensitivity to environmental change thus lead to their inclusion in national Red lists across Europe.

On the pan-European scale, the NATURA 2000 network of protected sites was created to protect endangered taxa and ensure connectivity among sites in the modern fragmented landscape. The sites are designated under the Birds and Habitats Directives in order to protect selected endangered or endemic taxa and 'umbrella' species with specific biotope requirements, mostly assumed from Bern convention annexes II and III (Council of the European Union, 1992). Examples of such umbrella species among terrestrial insects include the butterfly *Phengaris arion* (Spitzer *et al*., 2009) and the longhorn beetle *Cerambyx cerdo* (Buse *et al*., 2008). However, the inclusion of some of the species is questionable as they do not serve as umbrella species (e.g. Ilg & Oertli, 2017), are no longer endangered, or were included in the list on the basis of simple identification (Bouchet *et al*., 1999; Leandro *et al*., 2017). Good understanding of (current) habitat preferences is therefore required to confirm the 'umbrella' status and deliver effective conservation of these species (Stewart *et al*., 2007).

Two rare and endangered diving beetles, *Dytiscus latissimus* and *Graphoderus bilineatus*, were also included in the EU Habitat Directive and the Bern Convention annexes (Foster, 1996a, 1996b). While *D. latissimus* is extinct in the Czech Republic (Hejda *et al*., 2017) and other surrounding countries (Hungary: Csabai, 2014, Slovakia: Holecová & Franc, 2001, Austria: Z. Csabai and M. Jäch, pers. comm.), *G. bilineatus* is considered endangered in the Czech Republic (Hejda *et al*., 2017). Nevertheless, their relevance as umbrella species has not been resolved, partly because their habitat preferences and associations with other aquatic macroinvertebrates are not fully understood.

Distribution, habitat requirements and conservation status of G. bilineatus

Graphoderus bilineatus is widely but patchily distributed across the western Palearctic Region from Spain, France and England to West Siberia, and from Croatia to South Fennoscandia (Nilsson & Holmen, 1995, Löbl & Smetana, 2003). Overall, its population trends are decreasing except in Northern and Eastern Europe (Huijbregts, 2003). In countries for which sufficient data exist, *G. bilineatus* populations were found to be more or less stable (Poland: Przewoźny & Lubecki, 2011; Gutowski & Przewoźny 2013; Przewoźny *et al*., 2014, Latvia: Kalniņš, 2006) or declining (Germany: Hendrich & Balke, 2005; Hendrich *et al*., 2011, the Netherlands: Huijbregts, 2003; Cuppen *et al*., 2006). It was relatively widespread in the Czech Republic until the 1960s, especially in areas with traditional fishpond aquaculture (the Třeboňská pánev basin and the Labe River floodplain, see Fig. 1), but then abruptly declined, presumably

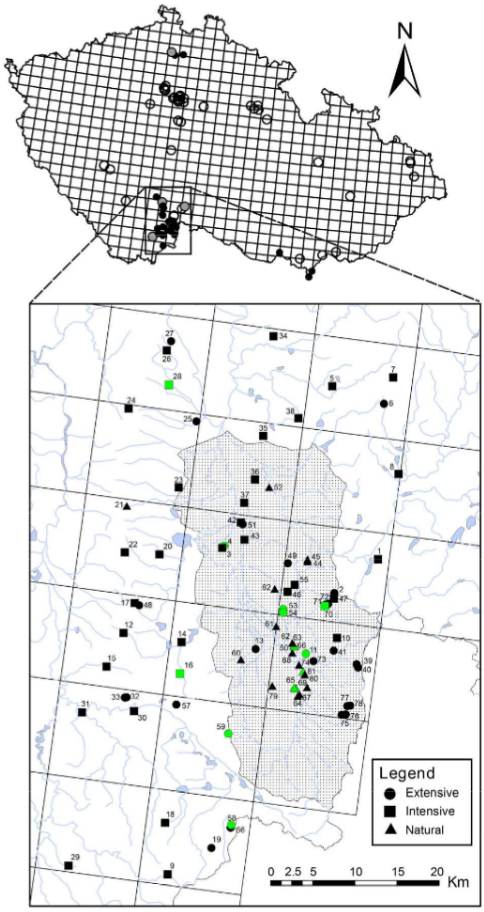

Fig 1. Historical and recent records of the diving beetle *Graphoderus bilineatus* in the Czech Republic, shown on the grid of the Czech faunistic grid mapping system (each square = 10 × 10 km). Black-filled circles = recent records since 2000, grey-filled circles = records between 1960 and 2000, empty circles = old records before 1960. Data from Hájek (2004), Boukal *et al*. (2007, 2012), Kolář *et al*. (2016, 2018, 2019) and the Species Occurrence Database of the Nature Conservation Agency of the Czech Republic (AOPK ČR, 2019). Magnified section shows the study sites. Green symbols = sites where *G. bilineatus* was found; black symbols = sites where *G. bilineatus* was not recorded (see Supporting Information Table S1 for more information). [Color figure can be viewed at wileyonlinelibrary.com]

due to the onset of more intensive agricultural and fishpond management (IUCN, 1997; Hájek, 2004; Potužák *et al*., 2007). The last population had been known from one extensively managed fishpond, the Vizír National Nature Monument in the Třeboňská pánev basin (Hájek, 2004), until additional sites were discovered after 2000 (Boukal *et al.*, 2007, 2012; Kolář *et al.*, 2016, 2018, 2019; Fig. 1).

The declines and national extinctions of *G. bilineatus* have been linked to landscape drainage, intensification of agriculture and increased pollution and eutrophication over the 19th and 20th century that lead, e.g., to its demise in Great Britain at the beginning of the 20th century (Angus, 1976; Yee, 2014). More recently, small isolated populations of *G. bilineatus* have also become threatened by non-native species: the invasive crayfish *Procambarus clarkii* was likely the last straw that lead to the demise of the remaining population of *G. bilineatus* in southern France in the 1990s (Bameul, 1994, 2013). Unfortunately, the lack of knowledge about the local habitat preferences of *G. bilineatus* hinders effective conservation measures and management recommendations that would preserve existing populations and enable the return of this species to many former parts of its historical distribution.

The species is found in a wide variety of habitats including lakes, peat bogs and ponds, usually within dense littoral zone (Nilsson & Holmen, 1995), but the preferences seem to differ across the species range (Foster *et al.*, 2016). Iversen *et al.* (2013) classified *G. bilineatus* habitats across Europe in two main categories: (i) mesotrophic or oligotrophic large lakes or canals with sparse vegetation (Galewski, 1975; Nilsson & Persson, 1989; Cuppen *et al.*, 2006), and (ii) lakes with sun-exposed shallow zones overgrown by littoral vegetation (Holmen, 1993; Nilsson & Holmen, 1995; Hendrich & Balke, 2005). Its populations are regularly found in vegetated ditches in the Netherlands (Cuppen *et al.*, 2006) and in oxbows along large rivers in Belarus (Moroz & Ryndevich, 2000), Croatia (Turić *et al.*, 2012), Hungary (Kálmán *et al.*, 2008; Csabai *et al.*, 2015), Baltic states and Sweden (Kalniņš, 2006; Iversen *et al.*, 2013; Vahruševs & Kalniņš, 2013) and Serbia (Mesaroš, 2012). Occasionally, specimens are found directly in rivers (Latvia: Kalniņš, 2006, Belarus: Moroz & Ryndevich, 2000, Poland, Sweden and Estonia: Iversen *et al.*, 2013). Many records from the Czech Republic came from fishponds with dense vegetation (Hájek, 2004), which can resemble lakes with exposed shallow littoral zones, i.e., the second category listed by Iversen *et al.* (2013).

In addition, published data suggest that the habitat requirements of *G. bilineatus* vary across its distributional area and may be related to small-scale environmental characteristics that cannot be fully characterised by the overall habitat type. However, quantitative data on the (micro)habitat requirements of *G. bilineatus* and their regional variation are surprisingly sparse and limited to a couple of studies from the Netherlands, Sweden, Poland and Estonia (Cuppen *et al.*, 2006; Iversen *et al.*, 2013).

To fill these gaps, we carried out a large field survey focused on *G. bilineatus* in the core area of its past and current distribution in the Czech Republic (Fig. 1), which is at the heart of its distributional range (Cuppen *et al.*, 2006). Our study is based on quantitative data collected at 82 sites using a standardised method that can be repeated elsewhere. We use the data to identify habitat preferences of *G. bilineatus* at the habitat and microhabitat scale and to test its relevance as a potential umbrella species for aquatic beetle assemblages. Finally, we use our findings to recommend possible management actions to support populations of this endangered species in Central Europe.

Methods

Study sites

Our study was conducted in the Třeboňsko Biosphere Reserve and its immediate vicinity in the southern Czech Republic (Fig. 1). Most of the area has been modified by human activities since the Middle Ages as large tracts of peat bogs, meadows and wetlands were converted to fishponds (Pokorný & Hauser, 2002). The fishponds (total area ca. 7500 ha) are mostly intensively managed (Albrecht, 2003), but natural habitats with minimum human impact such as peat bogs, oxbows and floodplain pools (including >500 permanent ones) along the Nežárka and Lužnice rivers occur throughout the area. In addition, secondary aquatic habitats have been created in flooded sand and gravel pits. Fishponds, flooded sand pits, and streams thus cover 15% of the Biosphere Reserve; the remaining landscape is dominated by forested areas (45%, mostly monocultures of *Pinus silvestris* or *Picea abies*) and agriculture (30%, mostly meadows and pastures), and only 10% of the area is urbanised (Albrecht, 2003).

During 2013–2017, we sampled 82 fishponds, oxbows, floodplain pools and sandpit pools that represent the most common habitat types in the study area (Table S1). The localities were visited in spring or autumn when *G. bilineatus* adults are most active to maximise the possibility of their detection at a given site (Cuppen *et al.*, 2006; D. Boukal & V. Křivan, unpubl. data).

Field surveys

We surveyed local water beetle assemblages with funnel traps baited with chicken liver (Balke & Hendrich, 1987; Hillsenhoff, 1991; Kolář *et al.*, 2017). Funnel traps are a standard method for sampling diving beetles (Klečka & Boukal, 2011) and amphibians (Madden & Jehle, 2013). The traps are more effective for large beetles (ca. >8–10 mm long) than other semiquantitative methods such as hand netting (Klečka & Boukal, 2011; Turić *et al.*, 2017). We used modified commercially available live bait funnel traps (dimensions $50 \times 22.5 \times 22.5$ cm or $80 \times 27.5 \times 27.5$ cm depending on water depth) covered with green nylon mesh (mesh size ca. 0.5 cm), with one entrance on each smallest side fitted with a funnel made of a cut-off top of a plastic bottle (2.5–3.5 cm inner entrance diameter) to guide the beetles inside the trap. Trap size and entrance diameter had no effect on *G. bilineatus* detection probability (binomial GLM: entrance diameter: $\chi^2_2 = 2.4$, $P = 0.31$; trap size: $\chi^2_1 = 0.4$, $P = 0.54$) and were thus not included in further analyses.

At each site, we placed 3–9 traps (mean ± SD = 5 ± 1, total $n = 407$ traps) in a roughly linear transect along the shore to proportionally cover local microhabitat heterogeneity such as different types of littoral zone, and exposed them for ca. 24 h (we usually set the traps in the morning and picked them up the next day during the morning). We always attempted to cover all potential microhabitats (including, e.g. 100% *Phragmites* stands or open water near the shore if they were present, although we knew that they usually harbour few or no diving beetle species). We aimed to maximise the likelihood of detecting *G. bilineatus*

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and other species rather than obtaining estimates of total population sizes at the given locality with the available collecting effort. For this reason, we avoided large tracts of open water and areas further away from the shoreline (more than ca. 3–40 m away depending on the steepness of the shore and water depth) because adults of *G. bilineatus* and other large aquatic beetles typically avoid such microhabitats (Nilsson & Söderberg, 1996; D. Boukal, V. Kolář et al., unpubl. data). The traps were set at least 5 m apart to ensure that they did not interfere with each other, and we thus treated the data from individual traps as spatially independent samples nested within the locality (see below for details). Upper part of each trap was kept above the water surface to avoid suffocation of the caught animals (Madden & Jehle, 2013; Kolář *et al*., 2017).

Trapped individuals of the beetle families Dytiscidae and Hydrophilidae were identified to species and released back immediately in the field to minimise disturbance; only some individuals from taxonomically difficult genera (e.g., *Agabus*, *Ilybius*) were killed and stored in 80% ethanol and identified in the lab using standard keys (Hansen, 1987; Nilsson & Holmen, 1995). The nomenclature follows Boukal *et al*. (2007) and the conservation status categories are taken from the latest Red list of the Czech Republic (Hejda *et al*., 2017).

At each site, we recorded environmental variables that we deemed potentially important for the species and that could be considered in conservation management and during the creation of new pools (Supporting Information Table S2). We divided the localities *a priori* into three main site types as a proxy of anthropogenic influence, ranked from the expected highest to lowest negative impact on *G. bilineatus* presence: (i) intensively managed fishponds including habitats with a visibly high fish stock or clear signs of supplementary feeding and/or fertilisation during the sampling visit ($n = 33$), (ii) extensively managed fishponds with a visibly low fish stock or without fish during the sampling visit ($n = 29$), and (iii) 'natural pools' including floodplain pools and sandpit pools created after sand or gravel mining ($n = 20$). Categories 1 and 2 thus include water bodies that can be drained and the water level adjusted by manipulation, while the water level at sites in category 3 is influenced only by natural processes.

We then characterised each locality with 16 landscape-level characteristics including the habitat area, altitude, proportions of five major landscape types in the immediate vicinity (i.e., proportional coverage of meadows, fields, forest, wetlands and urban areas) and five key characteristics of the shore ecotone (proportion of shoreline with aquatic and semiaquatic vegetation, average width of littoral vegetation, heterogeneity of the aquatic and semiaquatic vegetation as the number of dominant genera, presence of gradually sloping shoreline, and proportion of shoreline with trees), water transparency, and presence of fish. In addition, we measured water conductivity and pH with a WTW Multi 3430 multimeter (Weilheim, Germany), but the data were limited to 43 sites due to logistic constraints. We decided to omit these data from further analyses as the available pH and conductivity values correlated tightly with one or more habitat-level environmental variables (Supporting Information Table S3). We also omitted the presence of fish from further analyses as we could not obtain robust quantitative data on the total fish biomass and on the species and size composition of the current fish stock; the effect of fish was mostly captured by the locality type. Finally, we did not include altitude in the analyses due to the relatively narrow altitudinal range (only six localities at >550 m a.s.l., Supporting Information Table S2).

For each trap, we described the microhabitat scale characteristics with eight environmental variables: depth, distance from shore, and six biotic characteristics including the amount of detritus on the bottom (categorical) and the proportional cover of open water and four dominant macrophyte genera (*Phragmites*, *Carex*, *Typha*, *Glyceria*) around each trap (1 × 1 m).

Statistical analyses

Initial data exploration, all univariate models and their visualisations were implemented in R version 3.5.2 (R Core Team, 2018) and the multivariate analysis (PCA and DCA, see below) were conducted in CANOCO 5 (ter Braak & Šmilauer, 2012). To explore the environmental drivers of *G. bilineatus* presence at the habitat and microhabitat scale, we analysed the data using generalised linear models (GLMs, for the habitat scale) and generalised linear mixed models (GLMMs, for the microhabitat scale) with a negative binomial distribution with a log link function. Number of individuals at each locality or in each trap served as the dependent variable in both model types. We used the number of deployed traps as an offset in the GLMs to account the different number of used traps among localities, and locality as random intercept in the GLMMs.

Our dataset contained a large number of highly collinear explanatory variables for both spatial scales. We thus first reduced the number of continuous explanatory variables and described the main environmental gradients at both habitat and microhabitat level using principal component analyses (PCAs). We conducted two PCAs for the habitat level characteristics, one for the surrounding landscape types and another for the characteristics of shore ecotones, and two PCAs for the microhabitat level characteristics, one for the open water and dominant macrophyte cover around each trap and another for water depth and distance of the trap from shore. We kept the first 2–3 PCA axes from each PCA analysis as predictors in the subsequent analyses. We used the scree plot method (Jackson, 1993) to distinguish the PCA axes explaining most of the variability (surrounding landscape: *Landscape_PCA1* to *Landscape_PCA3*; shore ecotone: *Littoral_PCA1*, *Littoral_PCA2*; open water and macrophyte cover: *Vegetation_PCA1* to *Vegetation_PCA3*; water depth and distance from shore: *Depth_PCA1* and *Depth_PCA2*). The latter PCA did not reduce the dimension of the data but we used it to maintain a unified approach.

We then used a model selection approach in which we built a set of candidate models for both the habitat and microhabitat scale data, and used the corrected Akaike information criterion (AIC_c) to rank these models and identify the most parsimonious ones (Burnham & Anderson, 2002). We first fitted GLMs on the habitat scale with a linear combination of (a subset of) seven possible predictors: habitat type and surface area, *Landscape_PCA1* to *Landscape_PCA3*, *Littoral_PCA1* and *Littoral_PCA2*. Based on previous studies (Iversen *et al*., 2013) and our expectations, we expected that *G. bilineatus* presence at the habitat scale would vary with habitat type and surface area and proportion of nearby wetlands characterised by the *Landscape_PCA3* variable, and used these three habitat-level variables in all candidate models. This led to a set of $2^4 = 16$ candidate models differing in the use of *Landscape_PCA1*, *Landscape_PCA2*, *Littoral_PCA1* and *Littoral_PCA2* axes as explanatory variables (see Supporting Information Table S6). Preliminary inspection of our data further suggested that *G. bilineatus* was more likely absent in both very small and very large water bodies, and we thus included $\log_{10}$ (habitat surface area) as a second-order polynomial in all models. We decided not to include the number of traps per surface area as another predictor capturing a possible sampling effect that could explain the perceived absence in some of the largest intensively managed ponds. Number of traps varied much less than the surface area and the additional predictor would thus be strongly correlated with the inverse of the surface area.

We subsequently fitted the microhabitat scale data with a linear combination of the habitat-level predictors that were included in the most parsimonious model for the habitat-level data and up to six microhabitat-level predictors: amount of detritus, *Vegetation_PCA1* to *Vegetation_PCA3*, *Depth_PCA1* and *Depth_PCA2*. Based on previous studies (Nilsson & Söderberg, 1996; Cuppen *et al*., 2006; Kalniņš, 2006), we assumed that *G. bilineatus* presence would vary with the water depth and distance from shore, and used *Depth_PCA1* and *Depth_PCA2* in all candidate models (Supporting Information Table S6). This again led to a set of $2^4 = 16$ candidate models differing in the inclusion of the amount of detritus and *Vegetation_PCA1* to *Vegetation_PCA3* axes as explanatory variables.

We used the function *glmmTMB* from the package *glmmTMB* to analyse the GLMMs (v. 1.0.0; Brooks *et al*., 2017). In both analyses, we retained all plausible models with ΔAICc ≤ 2 (Burnham & Anderson, 2002), summarised them using the package *sjPlot* (v. 2.8.2; Lüdecke, 2014), checked model residuals using the package DHARMa (v. 0.2.7; Hartig, 2018), and visualised the most parsimonious model in the package *ggeffects* (v. 0.14.1; Lüdecke, 2018).

To describe the species assemblage of large-sized beetles of the families Dytiscidae and Hydrophilidae at each locality, we carried out a detrended correspondence analysis (DCA) of the species composition based on a matrix with 77 samples and 26 species. We were interested in overall richness of the community and thus transformed species abundances to presence vs. absence data (Supporting Information Table S4). The length of the gradient (3.8 SD units) justified the use of the unimodal method (Smilauer & Lepš, 2014). To explore whether *G. bilineatus* could serve as an umbrella species for local aquatic beetle assemblages, we tested whether species diversity and total abundance depended on *G. bilineatus* presence using a GLM with Poisson and quasipoisson distribution, respectively, to account for overdispersion in the data. We ran this analysis twice, once for all individuals and once only for species of conservation concern included in the Czech Red list (Hejda *et al*., 2017).

Results

Altogether, we found 74 individuals of *G. bilineatus* in 26 traps at 14 localities (51 males, 22 females and 1 unrecognised sex, see Fig. 1; Supporting Information Table S1). In addition to 11 new localities, we confirmed its presence at all three previously known sites included in our study, which suggests that our sampling effort was sufficient to detect the species presence. We found mostly one to two individuals at each locality, which is typical for this species in most European countries (Kalniņš, 2006; but see Volkova *et al*., 2013). Nevertheless, two new localities yielded more than 20 individuals (Supporting Information Table S1), implying strong local populations at these sites.

PCA analyses of environmental variables

The first PCA axis of proportion of major landscape types (*Landscape_PCA1*, 48.8% of variation explained in the landscape structure) described primarily the gradient from open meadow and urban habitats to ponds and pools in forest, while the second axis (*Landscape_PCA2*, 25.5%) covered a gradient from the semi-natural forest or meadow landscape to localities surrounded mainly by arable fields (Supporting Information Fig. S1a; Table S5). The third axis (*Landscape_PCA3*, 14.6%) reflected a gradient towards an increased proportion of nearby wetland biotopes.

The first PCA axis of shore ecotone (*Littoral_PCA1*, 37.3% of variation explained in shore ecotone) reflected the overall development of the littoral zone (Supporting Information Fig. S1b; Table S5). The second axis (*Littoral_PCA2*, 27.6%) captured mainly the gradient of shore steepness and proportion of trees around the shore.

At the microhabitat scale, the first PCA axis of open water and macrophyte cover (*Vegetation_PCA1*, 34.1% of variation explained) covered primarily the gradient from microhabitats dominated by *Typha* to those dominated by *Glyceria*, while the second axis (*Vegetation_PCA2*, 27.6%) corresponded mainly to a *Typha* to *Carex* dominance gradient (Supporting Information Fig. S2a; Table S5). The third axis (*Vegetation_PCA3*, 25.2%) reflected mainly microhabitat differences in the proportion of *Phragmites*.

Finally, the first PCA axis of water depth and distance from shore (*Depth_PCA1*, 55.2% of variation explained) corresponded mainly to increasing distance from shore, while the second axis (*Depth_PCA2*, 44.8%) corresponded mainly to increasing water depth (Supporting Information Fig. S2b; Table S5).

Habitat preferences of G. bilineatus

The probability of occurrence of *G. bilineatus* on the habitat scale as identified by the most parsimonious model differed significantly between site types (Table 1; Fig. 2). All else being equal, the species was more likely to be found in extensive fishponds and natural sites than in intensive fishponds, while we did not detect a significant difference between extensive fishponds and natural sites. All else being equal, the occurrence of *G. bilineatus* increased significantly with the surface area. Finally, *G. bilineatus* tended to be found more often more in habitats surrounded by a higher proportion of wetlands (i.e. increased with the value of *Landscape_PCA3*, Fig. 2).

Table 1. Plausible models of the effects of habitat on *G. bilineatus* abundance, with incidence rate ratios (mean and 95% CI) and significance (*P* values).

	Model 1		Model 2	
Predictors	Incidence rate ratios	*P*	Incidence rate ratios	*P*
(Intercept)	0.07 (0.02–0.29)	**<0.001**	0.05 (0.01–0.23)	**<0.001**
Intensive vs. Extensive	0.07 (0.01–0.50)	**0.008**	0.11 (0.01–0.83)	**0.03**
Natural vs. Extensive	19.46 (0.27–1401.92)	0.17	16.58 (0.30–921.00)	0.17
Log_{10}(Area)	26.17 (2.67–256.89)	**0.005**	23.82 (2.69–211.06)	**0.004**
$(\text{Log}_{10}(\text{Area}))^2$	1.01 (0.12–8.60)	0.99	0.92 (0.14–5.94)	0.93
Landscape_PCA3	3.84 (0.74–19.95)	0.11	4.63 (0.95–22.44)	0.057
Landscape_PCA2	–	–	0.31 (0.04–2.23)	0.25
Observations	82		82	
ΔAIC_c	0.0		0.8	

Intercept = 1-ha extensively managed pond; other predictors set at their mean value. Significant effects are in bold ($P < 0.05$).

The second parsimonious model was very similar. In addition to the same trends as identified by the most parsimonious model, it suggested a decreasing occurrence at sites surrounded by a larger proportion of arable fields (*Landscape_PCA2*) and a stronger, near-significant dependence of *G. bilineatus* on the proportion of surrounding wetland biotopes (Table 1).

Microhabitat preferences of G. bilineatus

Given the structure of the most parsimonious model for the occurrence at the whole-habitat level, we kept site type, surface area and the *Landscape_PCA3* variable as habitat-level predictors for the different models of the occurrence of *G. bilineatus* at the microhabitat scale (Fig. 3). The most parsimonious model showed that the occurrence at the microhabitat scale depended on the habitat-level characteristics in the same qualitative way as did the occurrence at the whole-habitat scale, although the differences between site types were no longer significant. Moreover, the occurrence at the microhabitat scale also tended to increase with water depth (*Depth_PCA1*) and decrease with distance from the shore (*Depth_PCA2*; Fig. 3; Table 2).

Two other plausible models further included local vegetation characteristics, although the relationships were not significant: *G. bilineatus* tended to be more likely found in microhabitats overgrown by *Typha* and without *Carex* and *Phragmites*

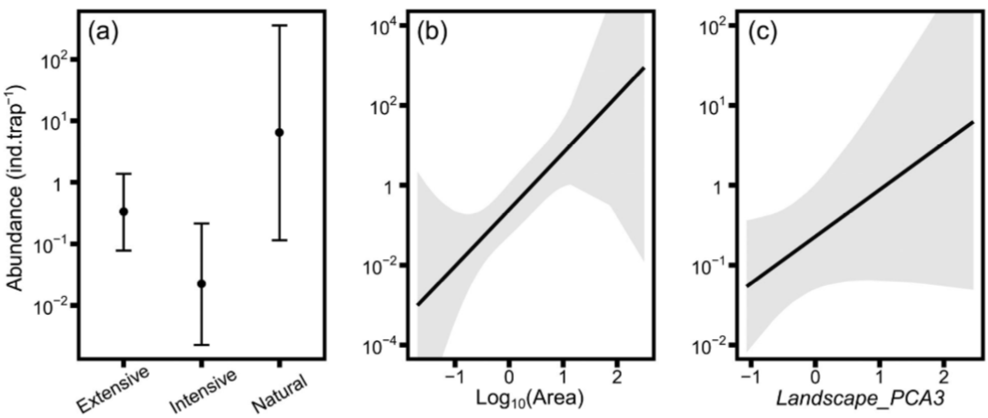

Fig 2. Predicted effects of environmental variables on *G. bilineatus* occurrence at the habitat level as identified by the most parsimonious model. Grey bands and error bars = 95% confidence intervals. Non-focal continuous trait values fixed at the mean value in the dataset (all panels); habitat type fixed to extensive fishpond (panels b and c). See Methods for details.

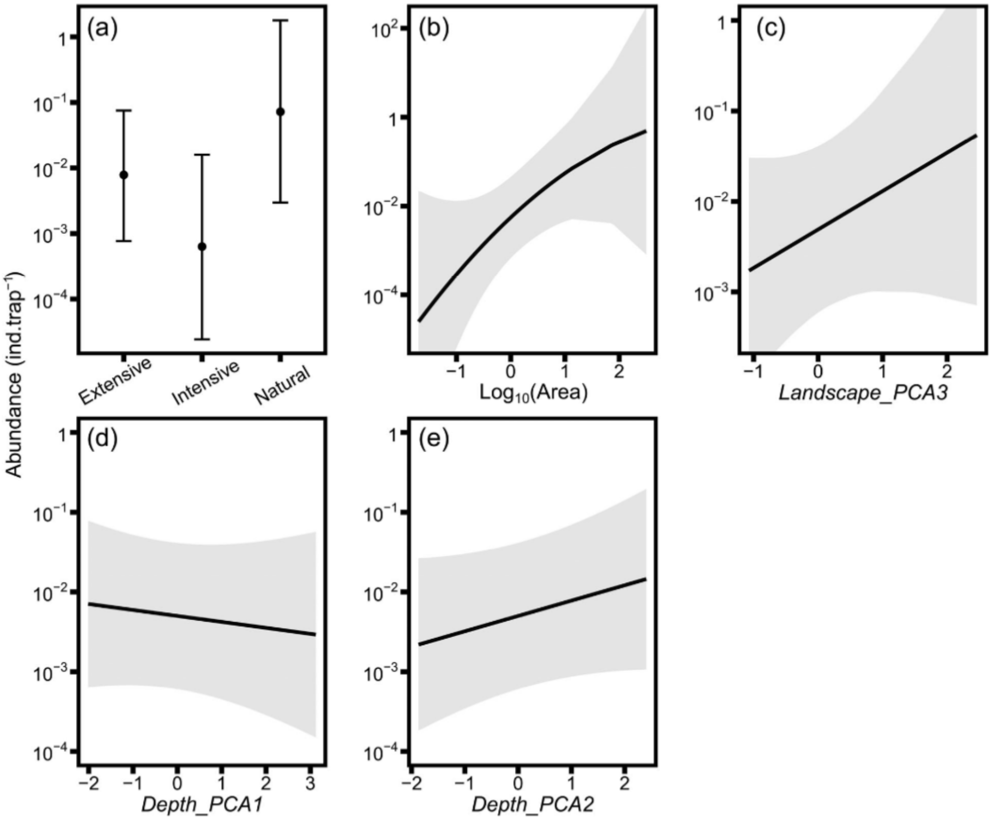

Fig 3. Predicted effects of environmental variables on *G. bilineatus* occurrence at the microhabitat level as identified by the most parsimonious model. Symbols and method to set non-focal trait values as in Fig. 2.

(*Veg_PCA2*) or in microhabitats overgrown with *Glyceria* and without *Typha* (*Veg_PCA1*; Table 2).

Co-occurring aquatic beetle communities

Species richness of large-bodied Dytiscidae and Hydrophilidae was higher at localities with *G. bilineatus* (Poisson GLM: $\chi^2_1 = 9.3$; $P = 0.002$). However, their abundance was not significantly higher when *G. bilineatus* was present (quasipoisson GLM: $F_{1,\,82} = 2.88$; $P = 0.09$). We found the same pattern for the Red-listed species (species richness: $\chi^2_1 = 4.8$; $P = 0.028$; total abundance: $F_{1,\,82} = 1.59$; $P = 0.21$).

DCA analysis of the co-occurring aquatic beetle assemblages explained 2.9% of the total explained variation. The intermediate position of *G. bilineatus* on both DCA axes implies that it is not associated with any extreme or unusual habitats and water beetle assemblages such as, e.g., *Rhantus grapii* in our dataset (Fig. 4). The latter species prefers densely vegetated water bodies in the Czech Republic (Boukal *et al.*, 2007). Adults of *G. bilineatus* were often found together with common species such as *Acilius canaliculatus*, *A. sulcatus* and *Dytiscus marginalis* and occurred more often with the congeneric *G. cinereus* than with *G. austriacus* and *G. zonatus*. Other relatively rare species such as *Hydaticus continentalis* and *H. aruspex* were also found frequently together with *G. bilineatus* (Fig. 4; Supporting Information Table S4).

Discussion

Conservation management of rare and endangered species should be based on quantitative evidence (Hochkirch *et al.*, 2013). *Graphoderus bilineatus* is one of the only two water beetles included in the NATURA 2000 species list and its conservation on the European scale is therefore of high

Table 2. Plausible models of the effects of microhabitat on *G. bilineatus* abundance, with incidence rate ratios (mean and 95% CI) and significance (*P*).

	Model 1		Model 2		Model 3	
Predictors	Incidence rate ratios	*P*	Incidence rate ratios	*P*	Incidence rate ratios	*P*
(Intercept)	0.01 (0.00–0.08)	**<0.001**	0.01 (0.00–0.09)	**<0.001**	0.01 (0.00–0.08)	**<0.001**
Intensive vs. Extensive	0.08 (0.00–1.41)	0.09	0.07 (0.00–1.14)	0.06	0.09 (0.01–1.55)	0.10
Natural vs. Extensive	9.56 (0.34–266.86)	0.18	8.29 (0.33–207.24)	0.20	8.16 (0.28–234.19)	0.22
Log_{10} Area	13.73 (1.36–139.03)	**<0.03**	13.00 (1.44–117.15)	**0.02**	12.64 (1.27–126.11)	**0.03**
$(\text{Log}_{10}\ \text{Area})^2$	0.72 (0.21–2.43)	0.60	0.79 (0.24–2.52)	0.69	0.74 (0.22–2.46)	0.62
Landscape_PCA3	2.65 (0.53–13.40)	0.24	2.44 (0.52–11.49)	0.29	2.66 (0.54–13.09)	0.23
Depth_PCA1	0.84 (0.45–1.58)	0.60	0.75 (0.38–1.47)	0.40	0.81 (0.42–1.56)	0.53
Depth_PCA2	1.56 (0.80–3.01)	0.19	1.59 (0.82–3.10)	0.17	1.58 (0.81–3.07)	0.18
Vegetation_PCA2	–	–	0.66 (0.28–1.55)	0.34	–	–
Vegetation_PCA1	–	–	–	–	1.20 (0.53–2.71)	0.67
Random effects						
σ^2	7.12		7.12		7.12	
τ_{00}	7.88_{Locality}		6.85_{Locality}		7.48_{Locality}	
ICC	0.53		0.49		0.51	
N	82_{Locality}		82_{Locality}		82_{Locality}	
Observations	407		407		407	
Marginal R^2/Conditional R^2	0.148/0.595		0.160/0.572		0.148/0.585	
ΔAIC_c	0.0		1.2		1.9	

Intercept = 1-ha extensively managed pond; other predictors set at their mean value. Significant effects are in bold ($P < 0.05$).

priority. So far, only two studies on *G. bilineatus* went beyond providing faunistic records with a general description of the habitat (the Netherlands: Cuppen *et al*., 2006; Sweden, Estonia and Poland: Iversen *et al*., 2013). This lack of quantitative data limits our ability to characterise and model habitat requirements of *G. bilineatus* and understand its responses to anthropogenic disturbances. Moreover, the apparent variation in habitat characteristics of *G. bilineatus* across its whole distributional area could be at least partly due to geographical variation in important environmental characteristics such as water conductivity or the composition of submerged vegetation. However, this variation across study sites are almost never reported; for a notable exception, see Cuppen *et al*. (2006).

Habitat preferences of G. bilineatus

Our results reiterate the key importance of habitat connectivity for *G. bilineatus* (Cuppen *et al*., 2006; Iversen *et al*., 2013). They suggest that the species mainly occurs in habitats surrounded by other wetlands such as fishponds, oxbows and peat bogs. These can serve as stepping stones during the colonisation of new suitable habitats (Fortuna *et al*., 2006) or be interconnected in one metapopulation. *Graphoderus bilineatus* has well-developed wings and flight muscles, but its flight efficiency is low compared to other congeners (Iversen *et al*., 2017). This species therefore needs a higher proportions of wetlands in the landscape for effective conservation. The stepping-stone effect is important for many aquatic insects, amphibians and macrophytes (Joly *et al*., 2001; Fortuna *et al*., 2006; Rannap *et al*., 2009; Hassall *et al*., 2012). Maintenance of habitat connectivity should be accompanied with effective protection of important habitats such as NATURA 2000 sites to avoid their isolation, which is still a real threat (Piquer-Rodríguez *et al*., 2012; Ferreira & Beja, 2013) and which could lead to the extinction debt of species that critically depend on such sites.

Our results further indicate that water bodies in agricultural landscape are mostly unsuitable for *G. bilineatus*. This can be due to reasons beyond the habitat connectivity issue. For example, higher input of nutrients and soil with agrochemical pollutants (Jones *et al*., 2004; Declerck *et al*., 2006; Wezel *et al*., 2013) leads to higher pH, which might be among the proximate causes of *G. bilineatus* absence as the species is found in acid waters throughout its northern and eastern range (Cuppen *et al*., 2006). We did not include pH directly in our models due to the missing data but in the subset of habitats with available pH, its value increased significantly with the proportion of fields surrounding the habitat. Moreover, intensive pond management

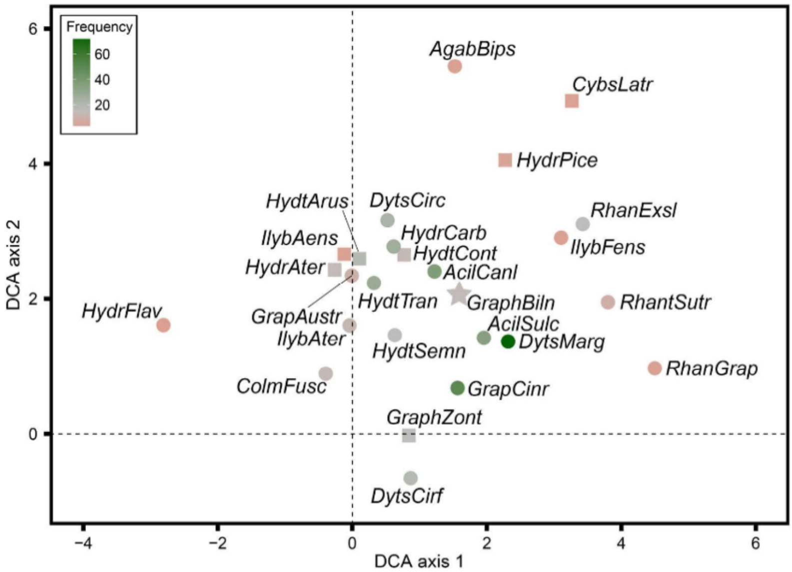

Fig 4. Indirect ordination diagram of species found together with *G. bilineatus* (DCA, total explained variation = 2.9%). Star = *G. bilineatus*; squares = species of conservation concern listed in the Czech Red list (Hejda *et al.*, 2017); circles = other species. Frequency of occurrence of each species in the dataset given by colour gradient. For abbreviations and Red list status see Supporting Information Table S2. [Color figure can be viewed at wileyonlinelibrary.com]

such as a high fish stock leading to degraded littoral zone, pond fertilisation and supplementary feeding with crop is more common in ponds in agricultural landscape, presumably due to their accessibility (V. Kolář & D. Boukal, pers. observation). All these factors can reduce the viability of *G. bilineatus* populations through decreased water quality, increased pressure from fish and reduced prey base.

We also found that *G. bilineatus* occurred more often in larger habitats, thereby confirming the conclusions by Iversen *et al.* (2013). Most notably, the species was often absent from ponds smaller than ca. 1 ha. However, this does not simply mean that 'bigger is better'. All of our findings of *G. bilineatus* in large, intensively managed fishponds came from shallow vegetated shoreline refuges, largely isolated from the main pond surface area. These refuges can harbour a rich local aquatic invertebrate community, and they are more likely to be found along the edges of larger fishponds. Our results highlight the importance of such refuges that may serve as stepping stones for aquatic insects during the colonisation of new habitats.

We found that natural water bodies (floodplain and sandpit pools) and extensively managed fishponds support *G. bilineatus* populations to a similar extent. Oxbows and floodplain pools often harbour rare species (Ward *et al.*, 2002; Turić *et al.*, 2012), and *G. bilineatus* is known from these habitats from other parts of Central Europe as outlined in the Introduction. On the other hand, *G. bilineatus* was usually absent from intensively managed fishponds in our study area. These ponds differed from extensively managed ones by high fish stocks (usually dominated by common carp), application of manure and a strongly degraded or entirely absent littoral zone. Other studies showed that the diversity of animals (Hartel *et al.*, 2007; Kloskowski, 2011) and plants (Bajer *et al.*, 2016; Francová *et al.*, 2019) in such ponds is low, especially when stocked with common carp.

Fishponds representing the most common habitat type in the study area are mostly harvested and emptied in autumn and then refilled once every 2–3 years (IUCN, 1997; Francová *et al.*, 2019), but local populations of diving beetles can survive this practise. For example, the Vizír fishpond Nature Reserve is regularly stocked with fish and emptied, yet it harbours a rich water beetle community including a strong *G. bilineatus* population (D. Boukal & V. Křivan, unpubl. data).

Among the natural sites, several records came from sand pits. We are aware of only one additional record of *G. bilineatus* from this type of post-industrial habitat from Germany, where it was found in a newly created sandpit lake, subsequently 'modified to the species requirements' (Weser, 2007; Koese *et al.*, 2008). We conclude that undisturbed oxbows and floodplain pools probably represent the historical natural habitat of *G. bilineatus* in Central Europe. The consequences of their loss and degradation across large areas have been partly diminished by the beetle's ability to utilise new secondary habitats such as extensively managed fishponds and newly created pools in sand pits.

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Microhabitat preferences of G. bilineatus

Littoral vegetation is an important part of aquatic biotopes and likely plays a key role in *G. bilineatus* life cycle. Submerged macrophyte stands often harbour more diverse fauna than open waters (Nilsson & Svensson, 1995; Tolonen *et al*., 2003; Declerck *et al*., 2011) because they serve as a refuge for aquatic invertebrates, amphibians and small fish (e.g., Eklöv & van Kooten, 2001; Klecka & Boukal, 2014). Submerged macrophytes may also enhance predation success of some insect predators (Klecka & Boukal, 2014; Kolar *et al*., 2019) including diving beetle larvae (Yee, 2010). Moreover, submerged plants increase available habitat surface and thus increase the diversity and abundance of prey base communities (Canion & Heck, 2009). Last but not least, macrophytes are indispensable for the reproduction of some dytiscids (Inoda, 2011a, 2011b) including the genus *Graphoderus*, which lays eggs above the water level in plant stems (Wesenberg-Lund, 1943).

In our study, *G. bilineatus* responded partly to aquatic vegetation as its probability of occurrence tended to increase with the cover of *Typha* or *Glyceria*. This is in line with other studies, in which *G. bilineatus* was mostly found in the littoral zone dominated by *Glyceria* (Olsvik, 1991; Cuppen *et al*., 2006). In other countries, the species also seems to prefer more natant vegetation such as *Nymphaea*, *Ceratophyllum*, *Elodea* and *Hottonia* (Sierdsema & Cuppen, 2006; Mesaroš, 2012) or reed banks (Koese *et al*., 2008; Hendrich *et al*., 2012). However, these studies only listed the macrophytes found at the localities with *G. bilineatus* without further details. Nevertheless, we also found the beetle at sites dominated by other vegetation (e.g., *Phragmites* and *Equisetum*, V. Kolář & D. Boukal, pers. obs.). We conclude that *G. bilineatus* is not tightly associated with a particular type of vegetation but aquatic macrophytes are important for its presence, similarly to other aquatic insects (Meutter *et al*., 2008; Declerck *et al*., 2011). The apparent preference for *Typha* and *Glyceria* could also be caused by the relative scarcity of the other plant genera, which made them unlikely to be selected by our analysis, or by other underlying microhabitat properties not covered by our analysis.

Our results further imply that *G. bilineatus* tends to prefer deeper water and microhabitats closer to the shoreline. This is in line with other studies that showed higher water beetle abundance and species richness in deeper pools (e.g., Nilsson & Holmen, 1995; Nilsson & Svensson, 1995). In the Netherlands, *G. bilineatus* was mostly found in channels at the depths of 75–100 cm (Cuppen *et al*., 2006). On the other hand, Kalniņš (2006) found *G. bilineatus* in traps placed in a shallow, 10–30 cm deep littoral zone. This suggests that the microhabitat preferences of *G. bilineatus* may vary geographically similarly to the habitat-scale preferences, and standardised data from different parts of its distribution area are needed to resolve this issue.

Co-occurring aquatic beetle communities

Water beetles found together with *G. bilineatus* were dominated by common species as in other countries (Kálmán *et al*., 2008; Hendrich *et al*., 2012; Przewoźny & Kot, 2014). Moreover, *G. bilineatus* occurred mostly at sites with higher species diversity and more species of conservation concern. This confirms that *G. bilineatus* is a suitable umbrella species for aquatic beetles as hypothesised by Gutowski & Przewoźny (2013) and reiterates the need to use multiple taxa to guide the prioritisation and site designation process in pond conservation. For example, amphibians can be poor predictors of the local diversity of other groups including aquatic insects, and ponds constructed for amphibians may be completely unsuitable for *G. bilineatus* and other species of conservation concern (Soomets *et al*., 2016; Ilg & Oertli, 2017).

Implications for conservation management and future directions

Our results imply that high habitat connectivity is crucial for successful conservation of *G. bilineatus*. Most records came from the Lužnice river floodplain characterised by many ponds and other water bodies. Eight of the newly discovered localities were also relatively further away (>10 km aerial distance) from the last known population at the Vizír fishpond, indicating a more widespread (meta)population that does not rely on subsidies from a single source.

Conservation efforts should thus focus on areas with an already high proportion of suitable sites. Habitat construction or restoration activities should concentrate within or nearby such areas and habitat management should aim at creating suitable local conditions, primarily through the support of more extensive fish farming and, wherever possible, maintenance of extensive littoral zones with submerged macrophytes. Such habitats could support diverse aquatic beetle communities including *G. bilineatus* and other species of conservation concern that depend upon near-natural habitats with well-developed littoral zone.

Our results further suggest that conservation activities can also target areas with post-mining sites such as abandoned sandpits. The channelisation of Czech as well other European rivers stopped the natural processes in the floodplains that maintained and created new oxbows (Tockner *et al*., 2009; Bojková *et al*., 2014). Current oxbows are mostly in a late succession stage characterised by excessive siltation and growth of shore trees, and their restoration to meet the habitat requirements of *G. bilineatus* would entail high costs and repeated maintenance unless it uses more systemic approaches towards re-wilding of river floodplains that have been implemented elsewhere in Europe (Friberg *et al*., 1998; Paillex *et al*., 2009), for example, through the support of self-sustained European beaver populations (Law *et al*., 2019).

Our study, like all other previous studies on the species, is based on adults. Nothing is known about the habitat and feeding preferences of *G. bilineatus* larvae and their sensitivity to environmental change such as increasing temperatures (Boukal *et al*., 2019), although their habitat and feeding preferences could differ from those of adults as reported for other diving beetles (e.g. Juliano, 1991; Klecka & Boukal, 2012; Yee, 2014). Yet, multiple *Graphoderus* species often cooccur in Central Europe and reliable identification of the larvae in the field without killing or damaging the individuals is nearly impossible (Galewski, 1975). Any field study of *G. bilineatus* larvae would thus have to rely on a currently unavailable, non-invasive method such as environmental

DNA that would also separate the life stages. Neither do we know if *G. bilineatus* specialises on specific prey similar to *Dytiscus latissimus* (Scholten *et al.*, 2018). Further studies examining the trophic relationships of *G. bilineatus* and habitat preferences of the larvae (once a suitable method emerges for the latter) would be vital to improve our understanding of their ecology and habitat requirements that may interfere with conservation efforts.

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Conflict of interest

The authors declare that there is no conflict of interest.

Author contributions

V.K. and D.S.B. designed the study. V.K. collected data in the field and analysed the data with additional input from D.S.B. V.K. wrote the first draft of the manuscript, and V.K. and D.S. B. made subsequent revisions.

Data availability statement

Data on beetle communities used and analysed in the current study are included in the Supplementary Material. Data on habitat characteristics are available from the corresponding author upon reasonable request.

Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1 List of surveyed sites with site ID used in Table S3 (ID), name of water (Name), nearest settlement (Municipality), number of the Czech faunistic grid mapping square (Square), date of sampling (Date), locality coordinates (GPS), site type, altitude (Alt), water surface area, number of traps used (N_{traps}), number of all recorded species (S), total number (N) and numbers of males (M) and (F) of recorded *G. bilineatus*. We did not sex the individual found at site ID 78.

Table S2: Summary of the environmental variables recorded on a) habitat and b) microhabitat scale in the four types of habitats. In categorical variables the number of replicates for each variable is presented. The proportional coverage of three major landscape types (meadows, fields, urban and wetlands including open waters) in the immediate vicinity within ca. 100 m distance of the water body, area and altitude measured or estimated from maps (Google Earth software), proportion of shoreline with aquatic and semiaquatic vegetation, presence of gradually sloping shoreline (on a relative scale, with 0% corresponding to entire shoreline with 90° slope and 100% to entire shoreline with 0° slope), proportion of shoreline with trees, and water transparency measured by Sneller tube and chemistry measured with WTW Multi 3430 multimeter. Fish presence estimated during the visit to the site. The set of predictors for the microhabitat scale contained water depth, distance of trap from the shoreline, the amount of detritus, and the proportional cover of open water and dominant macrophyte genera: *Phragmites*, *Typha*, *Glyceria* and *Carex* in the 1 × 1 m surroundings of each trap. Percentages = % of coverage. Conductivity and pH were measured only at 43 sites.

Table S3: Pearson correlations of conductivity and pH with habitat-level environmental characteristics. Significant results ($P < 0.05$) in bold; r = correlation coefficient; CI = 95% confidence interval.

Table S4: List of all large-bodied beetle species found at each locality (ID) including species name abbreviations used in ordination diagrams and their national conservation status (RL = National Red list; Hejda et al. 2017). EN – endangered; VU – vulnerable; NT – nearly threatened.

Fig S1: Principal components analysis (PCA) of (a) proportion of major landscape types surrounding each sampling site and (b) shore ecotone characterised by the proportion of shoreline with aquatic and semiaquatic vegetation, presence of gradually sloping shoreline, proportion of shoreline with trees, and water transparency in each sampling site. Proportions of variation explained by PCA axes: (a) axis 1 = 48.8%, axis 2 = 25.5%, axis 3 = 14.6%; (b) axis 1 = 37.3%, axis 2 = 27.6%, axis 3 = 14.9%. For additional details see Table S5.

Fig S2: Principal components analysis (PCA) of (a) the proportional cover of open water and dominant macrophyte genera around each trap and (b) water depth and distance of the trap from the shoreline. Proportions of variation explained by PCA axes: (a) axis 1 = 34.1%, axis 2 = 27.6%, axis 3 = 25.2%; (b) axis 1 = 55.2%, axis 2 = 44.8%. For additional details see Table S5.

Table S5: Eigenvalues of each variable used in PCA diagrams (Figs. S1 and S2).

Table S6: Values of ΔAIC_c, degrees of freedom (df) and Akaike weights (w) of the different models for habitat (a) and microhabitat scale (b). The most parsimonious and other plausible models are in bold. Model structure common to all models: (a) *G. bilineatus* ~ Habitat type + Log_{10}(area) + $\text{Log}_{10}(\text{area})^2$ + *Landscape_PCA3* + offset(ln (N_{traps})) and (b) *G. bilineatus* ~ Habitat type + Log_{10}(area) + $\text{Log}_{10}(\text{area})^2$ + *Landscape_PCA3* + *Depth_PCA1* + *Depth_PCA2* + (1|Locality); additional model terms given in the table.

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~ Chapter III ~

The influence of successional stage on local odonate communities in man-made standing waters

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Chapter III

The influence of successional stage on local odonate communities in man-made standing waters

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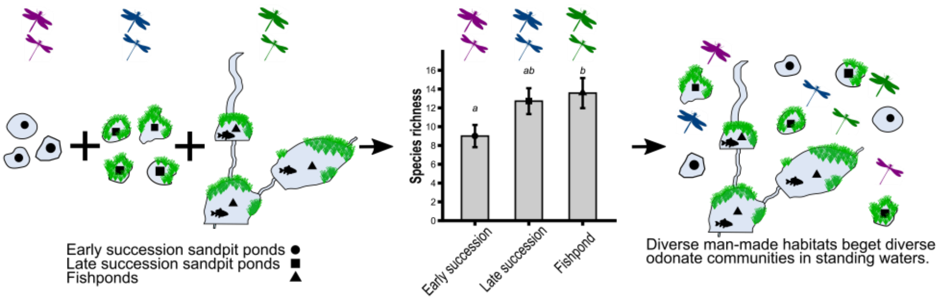
Highlights

- We compared odonate communities in sandpit ponds and fishponds.
- Community composition differed between habitat types despite similar diversity.
- Aquatic vegetation, water depth and bottom substrate shaped local communities.
- Diverse man-made habitats beget diverse odonate communities in standing waters.

Graphical abstract



Abstract

Man-made freshwater habitats are an important part of the European landscape, especially in areas with mostly absent or degraded natural habitats. To assess the role of different man-made standing waters in anthropogenic landscapes, we surveyed adult odonate communities in a cluster of 20 water bodies including fishponds and sandpit ponds in early and late successional stages. We found 25 odonate species (i.e., 47% of the fauna of the Czech Republic), but their presence differed significantly among the three habitat types. The highest species diversity, driven mainly by the presence of generalists, was found in fishponds. Sandpit ponds in an early successional stage hosted the least diverse communities dominated by pioneer and vagrant species. Specialist species occurred in both types of sandpit ponds, especially those in a late successional stage, more than in fishponds. Although the dragonfly biotic index did not differ among the three types of localities, all four species from the national Red list recorded during the study occurred only in sandpit ponds. The main environmental drivers of local odonate communities included the coverage of shoreline by emergent vegetation, water depth and bottom substrate; the latter two characteristics largely corresponded to the distinction between sandpit ponds and fishponds. We conclude that both sandpit ponds and fishponds play an important role in maintaining freshwater biodiversity that requires a mosaic of habitats in different successional stages.

Keywords: Odonata, fishponds, sandpits, post-industrial habitats, species richness, diversity, dragonfly biotic index

~ Chapter IV ~

Effect of different restoration approaches on two species of newts (Amphibia: Caudata) in Central European lignite spoil heaps

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Short communication

Effect of different restoration approaches on two species of newts (Amphibia: Caudata) in Central European lignite spoil heaps

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ABSTRACT

Post-mining sites often offer secondary habitats for various amphibians endangered in common agricultural landscapes. On the other hand, there is a general lack of quantitative studies on the effects of the common restoration practices on colonisation of such artificial freshwater habitats by amphibians. Here, we focus on two newts decreasing in Central Europe, *Lissotriton vulgaris* and *Triturus cristatus*, in pools within lignite (brown coal) spoil heaps in the western Czech Republic. We compared their abundances in pools established by technical reclamation, spontaneous succession, and their combination. In spring 2016, we sampled 29 freshwater pools in five spoil heaps and 10 fishponds in the surrounding agricultural landscape by funnel trapping. We captured 52 *L. vulgaris* and 138 *T. cristatus* in all the studied habitats together. As only two *L. vulgaris* and no *T. cristatus* were caught in fishponds, the high potential of pools in post-mining landscapes was confirmed. Both newt species generally avoided the artificially established pools, but the spontaneously established pools were equally suitable for them in both technically reclaimed and spontaneously developed heaps. *L. vulgaris* preferred more transparent water, higher cover of cattails and the pool placed in the forest, but with fewer trees on the pool banks, whilst *T. cristatus preferred narrower zone of littoral vegetation*, more trees on the pool banks, smaller water bodies and absence of fish. Such habitat preferences fully corroborate with natural habitats. The technical reclamation still prevails in restoration of post-mining sites in many regions. We reveal it is an unsuitable practice for amphibians, if not combined with natural succession processes.

1. Introduction

Various post-mining sites are known to serve as important refuges for numerous freshwater organisms (e.g., Harabiš and Dolný, 2015; Harabiš, 2016; Harabiš et al., 2013; Lewin et al., 2015; Michalik-Kucharz, 2008; Tichanek and Tropek, 2015, 2016), including amphibians (Lannoo et al., 2009; Vojar et al., 2016; Zavadil et al., 2011). Typically, they offer numerous pools of various sizes often characterized by a relatively very low level of eutrophication, which is one of the main causes of the standing freshwater biodiversity decrease in Europe, including amphibians (Zavadil et al., 2011).

The potential of such post-mining sites for biodiversity conservation strongly depends on the applied restoration approach. In Central Europe (Harabiš et al., 2013; Tropek et al., 2010), as well as in many other regions (Prach and Hobbs, 2008), the most common restoration practice is still represented by technical reclamation (i.e. remodelling of the surface by heavy machineries, its covering with fertile topsoils, and final planting of tree monocultures or sowing of species-poor productive grasslands; Prach and Hobbs, 2008; Tropek et al., 2010) and spontaneous succession. Although numerous comparative studies showed that spontaneous succession is much more effective for conservation of the terrestrial biodiversity of post-mining sites' biodiversity than costly technical reclamation (e.g. Prach and Hobbs, 2008; Šebelíková and Řehounková, 2016; Tropek et al., 2010), such knowledge on freshwater habitats is very limited, especially for amphibians. Moreover, a few existing detailed studies of dragonfly communities in lignite spoil heaps (Harabiš et al., 2013; Harabiš and Dolný, 2015; Tichanek and Tropek, 2015, 2016) have revealed that technically reclaimed freshwaters can harbour communities of a high conservation value as well. The situation of the freshwater habitats restoration thus

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seems to be more complicated, and more studies are still urgently needed for any effective restoration planning.

Here we present the first quantitative study on how the restoration approaches influence newts in any post-mining sites. Together with data on *Rana dalmatina* (Vojar et al., 2016), these are the only quantitative studies of amphibians under the target restoration approaches whatsoever. Although both studied newt species partly differ in their preferred microhabitat conditions, they both need rather smaller freshwater oligotrophic pools with sparse vegetation and without fish (Zavadil et al., 2011). *Lissotriton vulgaris* (Linnaeus, 1758) is a relatively common species of lower and middle elevations. Nevertheless, the recent decrease of its populations in Central Europe, especially in agricultural landscapes, has been described (Zavadil et al., 2011). *Triturus cristatus* (Laurenti, 1768) is much rarer and still decreasing in Central Europe (Zavadil et al., 2011). In Czechia, they are considered as nearly threatened and endangered, respectively, because of continuous destruction to their breeding habitats related mainly to water eutrophication, successional overgrowing followed by desiccation (terrestrification) of smaller water bodies, and intensification of fishpond management in the past decades (Zavadil et al., 2011). Both of them are protected by Czech legislation; *T. cristatus* is also included in the Annex II of the European Habitat Directive (i.e. "Natura 2000"). Although breeding or presence of both species in various post-mining and some other man-made sites has been documented repeatedly (e.g., Vojar et al., 2016; Zavadil et al., 2011), any knowledge on how they are influenced by restoration practices is very limited. The only existing study (Vojar et al., 2016), focussing on the effects of the two main restoration approaches on amphibians, does not include any abundance data on newts, which weakens its results. Moreover, its authors applied an oversimplified classification of restoration practices which could cause partly misleading interpretations (as we will discuss later).

In this study, we focus on abundances of the two newt species (as the only two amphibians in the study area effectively detectable by funnel-trapping) in freshwater pools in lignite spoil heaps formed by technical reclamation, spontaneous succession, and their combination. Abundances of both species in post-mining freshwater pools are also compared with fishponds in the adjoining landscape to assess the relative importance of the studied disturbed sites for them. Subsequently, we analysed also environmental characteristics of the pools preferred by the two newt species. Using a robust quantitative and standardised approach offers better generalisation of our results, important for the planning of effective post-mining landscapes restoration.

2. Methods

Our study was performed in the North Bohemian lignite basin, western Czechia, a lowland area historically covered by deciduous forests supplemented by relatively common open fens. Since the 19th century the basin has been substantially influenced by opencast lignite mining, resulting in more than 100 km^2 of large opencast mines and 150 km^2 of spoil heaps of presumably tertiary clays (Prach et al., 2011). More detailed information on the study area can be found in Hendrychová and Kabrna (2016). As a consequence of long-term intensive agriculture and industry, (semi)natural freshwater habitats are almost missing in the region; the most common small and middle-sized freshwater bodies in the whole area are represented by intensive fishponds in the common landscape and pools in (post)mining areas.

Amphibians were sampled in 29 freshwater pools in five lignite spoil heaps (Table 1) from 15 to 21 May 2016. From the seven amphibian species known from the studied spoil heaps (Vojar et al., 2016) only the two newt species entered our funnel traps.

Table 1
Summary of studied pools in the individual spoil heaps according to the applied restoration approach.

Spoil heap	GPS position	Habitat type	Studied pools	Range of habitat characteristics						*L. vulgaris* mean abundance	*T. cristatus* mean abundance
				Surface (m^2)	Littoral vegetation (m)	Banks inclination (%)	Fish[a]	pH	Water transparency (cm)		
Hornojiřetínská	N 50.5775°, E 13.5817°	*Spontaneous*	4	425–1476	0.5–21	0–70	2	8.5–8.7	30–50	0.0	12.0
		Semi-spontaneous	3	446–4563	0.5–2	40–90	2	8.6–8.7	25–35	0.0	23.3
Kopistská	N 50.5410°, E 13.6061°	*Semi-spontaneous*	2	1608–3446	2–3	10–40	1	8.8–8.9	40	3.0	4.0
Radovesická	N 50.5429°, E 13.8220°	*Spontaneous*	6	558–8432	0.5–2.5	0–90	0	8.5–9.1	30–52	1.5	0.8
		Semi-spontaneous	4	1229–4599	1–3	20–60	3	8.9–9	20–48	0.3	0.0
		Artificial	5	1186–32306	1.5–5	0–90	4	8.3–8.8	20–45	3.4	0.0
Růžodolská	N 50.5822°, E 13.6227°	*Semi-spontaneous*	2	501–3678	1.5–2	20–70	0	8.4–8.7	25–50	3.5	3.5
		Artificial	1	777	0.5	80	1	8.3	22	0.0	0.0
Velebudická	N 50.4908°, E 13.6088°	*Artificial*	2	7854–12965	1–3	50–60	2	8.6–8.9	40–45	0.0	0.0
Fishponds	–	*Fishponds*	10	1320–115304	0.1–3	0–90	10	8.6–9.4	8–45	1.2	0.0

[a] Number of pools with fish.

All the studied pools were selected to cover the main restoration approaches applied: *artificial* (i.e. artificially constructed pools in technically reclaimed parts of heaps), *semi-spontaneous* (i.e. spontaneously originated pools in technically reclaimed parts of heaps), and *spontaneous* (i.e. pools in non-reclaimed heaps left to spontaneous succession; Harabiš et al., 2013). The pools were selected to as equal covering of the heterogeneity of conditions as possible; all of them were more than 15 years old (i.e., enough time for colonisation by newts, Vojar 2006). In addition, 10 fishponds (i.e. the most common standing water bodies in the study region out of the (post)mining areas) were sampled in the agricultural landscape surrounding the spoil heaps to assess the relative conservation potential of the studied post-mining sites. The fishponds were selected as typical representatives of these human-made standing freshwater habitats in the region, and simultaneously to be close enough to the studied spoil heaps to avoid different conditions. For newts sampling, we used funnel traps (50–80 × 22.5–27.5 × 22.5–27.5 cm, 0.5 cm green mesh nylon, of 2.5–3.5 cm entrance diameter) baited by chicken livers, i.e. a standard method for sampling of amphibians, especially newts (Madden and Jehle, 2013), as well as other aquatic organisms. Each trap was exposed for 24 h. Our sampling effort was optimized according the studied pools' size: three traps for pools <4000 m^2 and five traps for pools >4000 m^2. The traps were placed to cover the whole habitat heterogeneity of the pools' littoral zone. The upper part of each trap was set above the water surface to avoid suffocation of caught animals (Madden and Jehle, 2013).

In addition to the restoration approach, each study site was characterized by water surface area (m^2), cover of surrounding (within 50 m) habitats (% of grassland, forest, crop field, and shrubland), cover of trees on the pool banks (%), average width (m) of littoral vegetation and its cover of banks (%), banks inclination (%), fish (presence vs. absence), relative cover of *Phragmites* and *Typha* (both in%), vegetation heterogeneity (number of plant genera with coverage >5%), water pH, conductivity ($\mu S.cm^{-1}$), salinity (ppt) and transparency by the Sneller's tube (cm).

All models and their visualizations were performed in R software (R Development Core Team, 2016). To reveal the effects of restoration approaches and the environmental factors on abundances of each of the studied newt species, four particular generalized estimated equations (GEE) models with the presumed Poisson-error distribution and log-link function were performed using the *geepack* package (Højsgaard et al., 2006). The environmental factors included into the final models were chosen via a manual forward selection process based on the Wald statistics ($p \leq 0.05$). The individual funnel traps within each study site were defined as pseudo-replications with an unstructured autocorrelation matrix. To select the most suitable autocorrelation structure, we used the Correlation Information Criterion (CIC) from the *MESS* package (Ekstrøm, 2011), which has been shown as the best indicator of the autocorrelation structure suitability. As no *T. cristatus* and only two *L. vulgaris* individuals of the studied newt species were recorded in the fishponds out of the spoil heaps, and no *T. cristatus* was recorded in the artificial pools, we compared newt abundances only between the three restoration approaches for *L. vulgaris*, and the spontaneous and semi-spontaneous pools for *T. cristatus*. Potential spatial autocorrelations in the data were tested using the Moran I criterion from the *Ape* package (Paradis et al., 2004); because no spatial autocorrelations were detected in the inter-site level, we did not consider those in the analyses.

3. Results and discussion

Altogether, we caught 52 individuals of *L. vulgaris* and 138 individuals of *T. cristatus*. Only two *L. vulgaris* and no *T. cristatus* were recorded in fishponds, evidencing thus that post-mining sites are much more important for both newt species. In the landscapes with strongly limited numbers of smaller (semi)natural water bodies, such as the study region, post-mining sites can thus be the most important strongholds of at least some amphibian species, as was already shown in numerous non-comparative studies (e.g., Galán, 1997; Lannoo et al., 2009; Vojar et al., 2016; Zavadil et al., 2011). Fishponds, typically characterised by intensive management and high fish abundance, are well-known to be less suitable for many amphibians (Brönmark and Edenhamn, 1994; Kloskowski, 2010; Landi et al., 2014) including the studied newt species (Skei et al., 2006; Zavadil et al., 2011). In the productive fishponds, especially amphibian larvae suffer from unsuitable water chemistry (especially high level of eutrophication; Kloskowski, 2010; Landi et al., 2014). Overabundant fish also destroy littoral vegetation as an important microhabitat for amphibian larvae and egg laying, compete with both adults and larvae for prey, and even prey on some amphibian species (Brönmark and Edenhamn, 1994; Hartel et al., 2007; Kloskowski, 2010).

Oppositely, pools in post-mining sites are usually oligotrophic because of very low nutrient content in the mined and/or heaped substrates (Doležalová et al., 2012). Together with the heterogeneity of the bottom and banks of such pools (Doležalová et al., 2012), it usually allows development of species-rich and heterogeneous communities of emergent plants, as well as aquatic invertebrates (Harabiš, 2016; Harabiš et al., 2013; Vojar et al., 2016). Simultaneously, abundances of fish are usually very low, if any (Doležalová et al., 2012; Harabiš, 2016; Harabiš et al., 2013).

3.1. Restoration approaches

We have proven that the restoration approach is highly important for both studied newt species. *L. vulgaris* was significantly less abundant in the artificially established pools within the technically reclaimed heaps (altogether 4 specimens) when compared to both spontaneous (18 specimens) and semi-spontaneous (28 specimens) pools ($df = 2$, $\chi^2 = 6.36$, $p = 0.042$; Fig. 1A). Simultaneously, no specimen of *T. cristatus* was found in these artificial pools, whereas it was relatively abundant in both spontaneous (53 specimens) and semi-spontaneous (85 specimens) pools. These results show fully artificial creation of freshwater pools during the technical reclamation as an highly inappropriate restoration approach for newts, which is fully corroborative with the only existing comparative study of amphibians from any post-mining sites (Vojar et al., 2016). On the other hand, abundances of *T. cristatus* ($df = 1$, $\chi^2 = 0.0584$, $p = 0.81$; Fig. 1B) as well as of *L. vulgaris* (the above mentioned GEE model; Fig. 1A) did not significantly differ between semi-spontaneous (i.e. the spontaneously developed pools within technically reclaimed heaps) and the spontaneous pools within the heaps fully left to spontaneous succession.

Such conclusions contradict with the study of amphibians from the same study area (Vojar et al., 2016), showing pools in the technically reclaimed heaps as generally less suitable for amphibians. This discrepancy could be explained by the oversimplified clasification of restoration status used by Vojar et al. (2016). They divided the pools in the studied heaps into two categories only – technically reclaimed and unreclaimed. However, according to our current, as well as previous (Harabiš et al., 2013), results, the two distinct types of pools are found in the technically reclaimed spoil heaps. These strongly differ in their habitat structure (Harabiš et al., 2013), as well as abundances of the studied newts. Any clustering of them together thus could show misleading results. Moreover, Vojar et al. (2016) incorrectly considered technically reclaimed heaps (at least large parts of the Kopistská spoil heap) as "unreclaimed". In fact, according to the information from the reclamation company, as well as from the author of the recla-

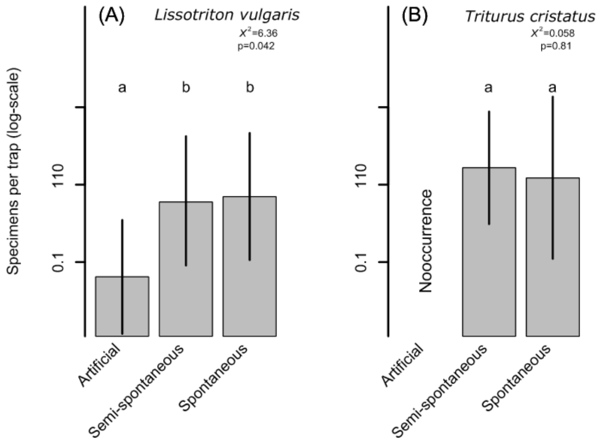

Fig. 1. Abundances of the two studied newts recorded in the studied pools created by the different restoration approach. Means and confidence intervals per trap are visualised. See Methods and Results for details of the used GEE models.

mation projects (S. Štýs, pers. comm.), this heap was technically reclaimed by remodelling of the surface, followed by shrubs and trees planting. In contrast, our more detailed evaluation of the applied restoration approaches showed that technical reclamation of larger sites can lead to development of valuable freshwater habitats if the pools are left for their semi-spontaneous development in unintentionally left terrain depressions. Such patterns have already been shown also for communities of dragonflies (Harabiš et al., 2013).

However, the revealed differences in the conservation potential of various restoration approaches only partly corroborates with the results of the only existing study of another group of freshwater organisms, analysing the effects of restoration on dragonflies in the same spoil heaps (Harabiš et al., 2013). Our study has closely followed the approaches of the cited dragonfly research (a large part of the studied pools even overlaped), allowing better comparisons of the results. The communities of dragonflies were equally rich in all of the three studied restoration approaches. Simultaneously, each of these methods showed some conservation potential as they harboured different threatened species (Harabiš et al., 2013). Together with the recent findings of the substantial conservation value of ditches draining the studied spoil heaps as another freshwater habitat established solely by technical reclamation (Harabiš and Dolný, 2015; Tichanek and Tropek, 2015, 2016), it seems that technically reclaimed heaps do not have a generally negative impact on freshwater biodiversity. This is in a strong contrast with numerous studies of terrestrial communities (e.g., Prach and Hobbs, 2008; Šebelíková and Řehounková, 2016; Tropek et al., 2010). On the other hand, contrary to the terrestrial habitats, the available data on the freshwater communities from post-mining sites are still highly limited, and more studies focusing on different taxonomical groups and other regions are necessary for better understanding the impact of various restoration practices on freshwater biodiversity.

3.2. Environmental characteristics

The two studied newts differed in their preferences for individual pools, which could be caused by various environmental factors. The GEE models revealed significantly positive associations of *L. vulgaris* (Fig. 2A–D) to surrounding forests (df = 1, Wald = 18.1, $p < 0.001$), coverage of *Typha* (df = 1, Wald = 13.2, $p < 0.001$) and water transparency (df = 1, Wald = 4.3, p = 0.038), as well as a significantly negative effect of trees at the pools' banks on the species abundance (df = 1, Wald = 10.3, p = 0.001; Fig. 2A). *T. cristatus* was significantly positively associated (Fig. 2E–H) with trees at the pools' banks (df = 1, Wald = 14.1, $p < 0.001$), whilst significantly negatively associated with water surface area (df = 1, Wald = 14.8, $p < 0.001$), littoral vegetation width (df = 1, Wald = 28.6, $p < 0.001$), and presence of fish (df = 1, Wald = 442.4, $p < 0.001$; Fig. 2B). All the significant associations were linear. On the other hand, the abundances of both newt species in the studied pools were positively correlated (Spearman's Rho correlation coefficient = 0.48, p = 0.008) and the differences were thus very probably caused by a different order of colinear characteristics entering the models (the correlation matrix is included in Appendix A in Supplementary material), so we thus interpret the results together for both newt species.

All the revealed associations can be easily related to the known biology of the species in their natural habitats. The newts often use forest habitats during the terrestrial phases, especially for overwintering (Skei et al., 2006; Vuorio et al., 2015). On the other hand, too many trees growing directly on the pool banks can decrease water temperature through shading, which can then slow down larval development (D'Amen et al., 2007) and decrease female oviposition (Dvořák and Gvoždík, 2009) in *Lissotriton*, whilst no such effect should be expected in *T. cristatus* (Gustafson et al., 2006). Both studied species are also known to prefer pools with relatively dense littoral and emergent vegetation where eggs are laid and both larvae and adults hide (Hartel et al., 2010, 2007; Joly et al., 2001; Stumpel and van der Voet, 1998). Transparent water is usually a sign of very low eutrophication, and simultaneously allows more effective foraging of newts (Kloskowski, 2010; Landi et al., 2014). Presence of fish is well-documented to repel newts from various freshwater pools (Binckley and Resetarits, 2003; Brönmark and Edenhamn, 1994; Hartel et al., 2007; Kloskowski, 2010), similarly to the general preference of both studied species to rather smaller pools (Zavadil et al., 2011). Such results show that newts use the surrogate habitats in the same way as the natural ones, and the principles well-described in restoration of amphibian breeding habitats in other landscapes should be applied during the restoration of secondary freshwater pools in post-mining sites.

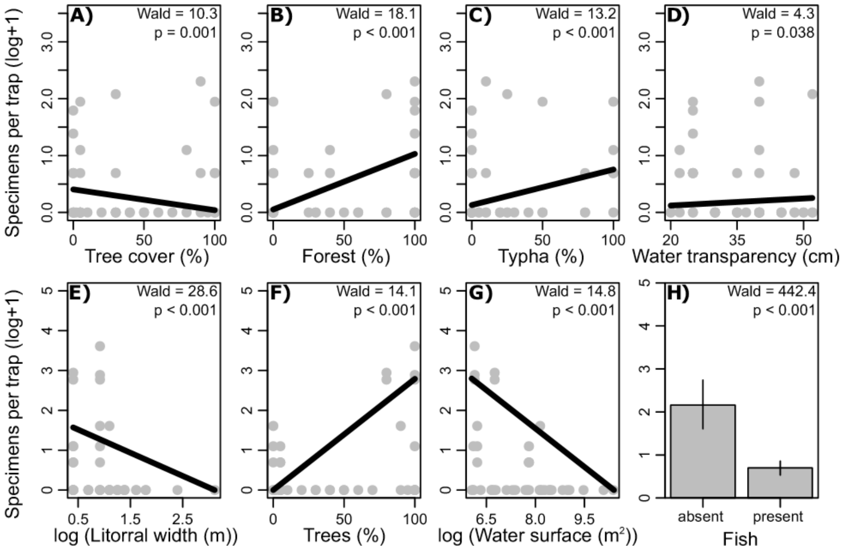

Fig. 2. Significant relationships between individual characteristics of the studied pools and abundances of *Lissotriton vulgaris* (A–D) and *Triturus cristatus* (E–H). The thick lines visualise the fitting of the significant variable, the dots are abundances of the studied newts per trap (see Methods for the tested models details).

4. Conclusions

We have confirmed freshwater pools in lignite spoil heaps as important habitats for both studied newt species, especially if compared with fishponds as one of the most common freshwater reservoirs in many European regions. We have also shown the applied restoration approach as the crucial factor for colonisation of pools by the newts. Despite the strong effort and high costs which are often invested into creation of artificial pools in post-mining sites, such artificial habitats were found as unsuitable for both species in our study. On the other hand, in contrast with terrestrial biodiversity, the technical reclamation of disturbed sites has no negative effects on the newts if the technical practices are appropriately combined with successional processes. Our results revealed spontaneously developed pools often offering suitable conditions for the newts, whether formed in reclaimed or non-reclaimed heaps. Leaving at least parts of spoil heaps for fully spontaneous succession should still be the main goal of restoration, considering cost effectivity as well as both terrestrial and freshwater biodiversity. In heaps or their parts which have to be technically reclaimed from some specific reasons (e.g. erosion risks, acid rock drainage, stream sedimentation, toxin leaks, and public safety issues), maintenance of randomly created terrain depressions, which can be potentially flooded during or after the restoration process, has a much higher potential to harbour threatened amphibians than artificially created pools.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecoleng.2016.11.042.

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Chapter V

~ Chapter V ~

Evidence-based restoration of freshwater biodiversity after mining: Experience from Central European spoil heaps

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Evidence-based restoration of freshwater biodiversity after mining: Experience from Central European spoil heaps

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Running title: Freshwaters habitats at post-mining sites

Abstract

1. Post-mining freshwater habitats can serve as secondary habitats for threatened species. Being globally plentiful, their efficient restoration should be based on detailed evidence, especially under the current global decline of freshwater biodiversity. Synthetic studies focusing on impact of restoration practice on freshwater communities are surprisingly rare even for the most common restoration approaches. Such lack of evidence limits the efficient habitat restoration in post-mining landscapes.
2. We combined a landscape-scaled field study of aquatic beetles and hemipterans in 29 freshwater pools at lignite spoil heaps in Czechia with a comparative synthesis of all 14 available datasets on freshwater communities at habitats created by coal mining in Central Europe. We compared diversity and conservation value of freshwater habitats created by the main restoration approaches, including technical reclamation, spontaneous succession, and their combination. Additionally, we analysed detailed influence of key habitat descriptors on their conservation potential.
3. Communities of aquatic beetles and hemipterans (1,384 adult specimens of 79 species) were richer in spontaneously and semi-spontaneously developed pools, which were also preferred by more red-listed species of both studied groups. The reviewed studies showed the same trend for amphibians, odonates, dipterans, and macrozoobenthos, although some technically created pools and drainage ditches harboured valuable communities of aquatic plants, odonates, and macrozoobenthos.
4. The conservation value of freshwater communities was driven by particular characteristics of the restored habitats, relatively independently of the general restoration approach. The key beneficial features were smaller area of restored water bodies, heterogeneous littoral vegetation with suppressed dominants, and heterogeneous bottom with low and mild banks. No fish should be introduced. The water surface should not be shaded by too many trees, but some forests in surroundings were beneficial.

5. *Synthesis and applications.* Efficient restoration of freshwater habitats at post-mining landscapes can create important secondary refuges for threatened biodiversity. Freshwater communities of high conservation value can be supported by all main restoration approaches if the heterogeneous habitats are created. Combination of technical reclamation with spontaneous succession seems to be the most efficient approach to maximise biodiversity of the restored freshwater habitats at coal-mining spoil heaps.

Keywords: aquatic insects, biodiversity conservation, freshwater communities, human-made habitats, post-industrial sites, restoration ecology, spontaneous succession

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2017 – 2019	Freshwater ectotherms under climate change: the role of phenotypic plasticity in life histories and trophic interactions (GAČR 17-15480S). Position: technician
2015 – 2016	Revision of current distribution of beetle species (Coleoptera) considered regionally extinct in the Czech Republic (TAČR TB020MZP048). Position: technician
2014 – 2016	Impact of predation risk and habitat complexity on the dynamics of macroinvertebrate community assembly in freshwater (GAČR 14-29857S). Position: technician
2012 – 2015	Mapping known and possible occurrence of *Graphoderus bilineatus* and confirming the occurrence of *Dytiscus latissimus* in the Czech Republic (within the program Monitoring a celoplošné mapování evropsky významných druhů jako podklad pro dokončení návrhu soustavy NATURA 2000 v ČR, AOPK ČR)
2013	How plastic are freshwater insects? Measuring growth, phenotypic plasticity and evolution in selected taxa (GAČR P505/10/0096). Position: technician

Fellowship

2019	University of Plymouth, prof. D. Bilton (2.5 months)

Field experience

2018 – present	Monitoring and mapping of selected species of plants and animals and inventories of protected areas in the Czech Republic (EIS: CZ.05.4. 27/0.0/0.0/17_078/0005239)
2018 – 2019	Leadership of field surveys of overlooked man-made habitats: understanding the drivers and patterns of freshwater biota in polluted standing waters (GAČR 18-159275)
2015 – 2016	Field surveys for the project 'Revision of current distribution of beetle species (Coleoptera) considered regionally extinct in the Czech Republic' (TAČR TB020MZP048)
2015	Inventories of odonates at peat bogs in the Šumava National Park
2012 – 2015	Mapping known and possible occurrence of *Graphoderus bilineatus* and confirming the occurrence of *Dytiscus latissimus* in the Czech Republic in the frame of the NATURA 2000 (CZ.1.02/6.1.00/10.06482)
2014	Field surveys on *Proterebia afra* butterfly in Greece

Teaching

University of South Bohemia in České Budějovice, Faculty of Science:
Field course of Hydrobiology
Ecology I – methods of insect sampling
Participation in Field Work courses
University of South Bohemia in České Budějovice, Faculty of Education:
Breeding of invertebrates – tutorial lecture

Students

Z. Lovčí 2018 – B.Sc. in Ecology of Ecosystems (University of South Bohemia in České Budějovice): *The impact of temperature on dragonflies metabolism and ontogenetic development.*

J. Adašević 2019 – Erasmus report (University of South Bohemia in České Budějovice): *Bioaccumulation of heavy metals in tissues of freshwater invertebrates at fly ash lagoons in the Czech Republic.*
Z. Lovčí 2020 – MSc. in Zoology, thesis co-supervisor (University of South Bohemia in České Budějovice): *Thermal preferences of aquatic ectotherms and their impact on species interactions*.

Author details based on Scopus

Number of publications in peer-reviewed journals with IF: 8
Total citations / self citations excluded: 49 / 47
h-index: 3

https://www.researchgate.net/profile/Vojtech_Kolar
https://scholar.google.cz/citations?user=IDkUjRkAAAAJ&hl=cs

Peer-reviewed publications with impact factor (IF)

Published or accepted:

Backhaus L., Albert G., Cuchietti A., Nino L. M. J., Fahs N., Lisner A., **Kolář V.**, Kermavnar J., Widmer S., Zimmermann Z., Rofrics N., de Bello F., Lepš J., García Medina N. (2021): Shift from trait convergence to divergence along old field succession, *Journal of Vegetation Science. In press*. DOI: 10.1111/jvs.12986

Kolar V., Boukal D. S. (2020): Habitat preferences of the endangered diving beetle *Graphoderus bilineatus*: implications for conservation management. *Insect Conservation and Diversity* 13: 480–494. DOI: 10.1111/icad.12433

Znachor P., Nedoma J., Hejzlar J., Seďa J., Komárková J., **Kolář V.**, Mrkvička T., Boukal D. S. (2020): Changing environmental conditions underpin long-term patterns of phytoplankton in a freshwater reservoir. *Science of The Total Environment* 710: 1–10. DOI: 10.1016/j.scitotenv.2019.135626

Kolář V., Boukal D., Sentis A. (2019): Predation risk and habitat complexity modify intermediate predator feeding rates and energetic

efficiencies in a tri-trophic system. *Freshwater Biology* 64: 1480–12491. DOI: 10.1111/fwb.13320

Vebrová L, van Nieuwenhuijzen A., **Kolář V.**, Boukal D. S. (2018): Seasonality and weather conditions jointly drive flight activity patterns of aquatic and terrestrial chironomids. *BMC Ecology* 18: 1–13. DOI: 10.1186/s12898-018-0175-y

Bartoňová A., **Kolář V.**, Marešová J., Šašić M., Šlancarová J., Sucháček P., Konvička M. (2017): Isolated Asian steppe element in the Balkans: habitats of *Proterebia afra* (Lepidoptera: Nymphalidae: Satyrinae) and associated butterfly communities. *Journal of Insect Conservation* 21: 559–571. DOI: 10.1007/s10841-017-9995-x

Patoka J., **Kolář V.**, Buřič M., Bláha M., Kalous L., Petrtýl M., Franta P., Tropek R., Petrusek A., Kouba A. (2016): Predictions of marbled crayfish establishment in conurbations realised: first report of its occurrence in the Czech Republic. *Biologia* 71: 1380–1385. DOI: 10.1515/biolog-2016-0164

Kolář V., Tichanek F., Tropek R. (2017): Effect of different restoration approaches on two species of newts (Amphibia: Caudata) in Central European lignite spoil heaps. *Ecological Engineering* 99: 310–315. DOI: 10.1016/j.ecoleng.2016.11.042

Unpublished:

Chmelová E., **Kolář V.**, Jan J., Carreira B. M., Landeira-Dabarca A., Otáhalová Š., Poláková M., Vebrová L., Borovec J., Boukal D. S., Tropek R. Valuable secondary habitats or hazardous ecological traps? Environmental risk assessment of minor and trace elements in fly ash deposits across the Czech Republic. *Environmental Science and Pollution Research. In review.*

Kolar V., K. Francová, J. Vrba, Boukal D. S. Habitat deterioration despite protection: long-term declines of littoral zones of fishponds in Czech nature reserves. Manuscript to be submitted to *Biological Conservation*.

Kolar V., Vlašánek P., Boukal D. S. The influence of successional stage on local odonate communities in man-made standing waters. Manuscript to be submitted to *Ecological Engineering*.

Kolar V., Tichánek F., Tropek R. Evidence-based restoration of freshwater biodiversity after mining: Experience from Central European spoil heaps. Manuscript to be resubmitted in *Journal of Applied Ecology*.

Lovčí Z., **Kolar V.**, Gvoždík L., Boukal D. S., The impact of thermal stratification on individual thermal preferences and predator-prey interactions in freshwater ectotherms. Manuscript to be submitted to *Animal Behaviour*.

Peer-reviewed non-IF papers

Kolář V. (2020): Vodní brouci (Coleoptera: Dytiscidae, Haliplidae, Heteroceridae, Hydrophilidae, Noteridae) v chráněných územích Louňov a Častrovické rybníky ve středních Čechách. *Bulletin Lampetra* 9: 23–33.

Waldhauser M. & **Kolář V.** (2020): Dvě nové lokality potápníka dvojčárého (*Graphoderus bilneatus*) na Českolipsku. *Sborník Severočeského Muzea, Přírodní Vědy* 38: 55–61.

Hanel L. & **Kolář V.** (2020): Náměty na pokusy a pozorování vodních živočichů ve školním akváriu VIII (chov vodomila černého a příbuzných druhů). *Biologie, Chemie a Zeměpis* 29: 2–12.

Kolář V., Boukal D. S., Sychra J., Straka M. (2020): Nálezy vodomila *Anacaena bipustulata* (Marsham, 1802) na postindustriálních lokalitách a jeho aktuální rozšíření v České republice. *Sborník Mosteckého Muzea*. *In press*.

Kolář V., Hadačová V., Kolář J., Hesoun P. (2019): Vodní brouci a ploštice vybraných maloplošných zvláště chráněných území jižních Čech III. *Sborník Jihočeského Muzea v Českých Budějovicích, Přírodní vědy* 59: 58–69.

Kolář V. & Hadačová V. (2017): Vážky a vodní brouci vybraných šumavských rašelinišť. *Silva Gabreta* 23: 19–32.

Kolář V. (2017): Výskyt potápníka *Bidessus grossepunctatus* (Vorbringer, 1907) v jižních Čechách. *Elateridarium* 11: 114–116.

Vlašánek P., **Kolář V.**, Tájková P. (2016): New records of *Gomphus pulchellus* on the eastern edge of its range in the Czech Republic (Odonata: Gomphidae). *Libellula* 35: 93–98.

Kolář V., Boukal D. S. (2016): Faunistické zprávy ze západních Čech – 8 Coleoptera: Dytiscidae. *Západočeské Entomologické Listy* 7: 11–13.

Kolář V., Hesoun P., van Nieuwenhuijzen A., Rozkopal M., Boukal D. S. (2016): Velcí vodní brouci a ploštice vybraných zvláště chráněných území jižních Čech. *Sborník Jihočeského Muzea v Českých Budějovicích, Přírodní vědy* 56: 88–93.

Kolář V., Tichánek F., Tropek R. (2015): Početná populace potápníka *Cybister lateralimarginalis* (De Geer, 1774) (Coleoptera: Dytiscidae) na mosteckých hnědouhelných výsypkách, *Elateridarium* 9: 160–162.

Kolář V., Hesoun P., Křivan V., van Nieuwenhuijzen A., Ondáš T., Rokzopal M., Boulkal D. S. (2015): Jaké typy rybníků preferují velcí potápníci a vodní ploštice? *Rybníky - naše dědictví i bohatství pro budoucnost*, příspěvěk ve sborníku z konference 18.-19.6.2015, David V. & Davidová T. (eds.)

Kolář V. (2014): Vodní brouci okolí Kačležského rybníka (Jindřichohradecko). *Sborník Jihočeského Muzea v Českých Budějovicích, Přírodní vědy* 54: 157–163.

Popular science papers

Blabolil P., Bartoň D., Kaštovský J., **Kolář V.**, Kreidlová V., Kučerová A., Vebrová L, Vrba J. (2020): Výchova mladých hydrobiologů na Jihočeské univerzitě v Českých Budějovicích. *Vodní hospodářství* 12: 24–26.

Kolář V. & Boukal D. (2020): Dobré a další zprávy o ochraně ohroženého vodního hmyzu: potápník dvojčárý v ČR. *Fórum Ochrany Přírody* 4: 41–45.

Hanel L. & **Kolář V.** (2020): Největší vodní brouk světa žije i v CHKO Blaník. *Pod Blaníkem* 24: 9–10.

Kolář V. & Boukal D. (2020): Komentář: Každý den jeden rybník - další hřebík do rakve vodním broukům. *Ekolist*. https://ekolist.cz/cz/publicistika/ nazory-a-komentare/vojtech-kolar-a-david-s.boukal-kazdy-den-jeden-rybnik-dalsi-hrebik-do-rakve-vodnim-broukum

Kolář V., Straka M., Sychra J., Boukal D. S. (2018): Vodní brouci jako zrcadlo našeho hospodaření s vodou. *Vodní hospodářství* 6: 6–11.

Kolář V., Ondáš T., Boukal D. (2016): Proč mizí vodní brouci (a jiný velký hmyz) z našich rybníků? *Fórum Ochrany Přírody* 3: 30–32.

Kolář V., Boukal D. (2015): Potápníci – nenápadní predátoři našich vod. *Živa* 6: 300–303.

International conferences

Kolář V., Boukal S. D., Sentis A. (2017): Habitat complexity and predation risk modify trophic interactions and energetic efficiency of intermediate predators. Symposium for European Freshwater Sciences (SEFS), June 2-7 2017, Olomouc, Czech Republic.

Kolář V., Ondáš T., Boukal D. S. (2016): What do diving beetles say about fishponds management? 2nd Central European Symposium for Aquatic Macroinvertebrate Research, July 3-8 2016, Pécs, Hungary.

Awards

2020	3rd place for best student presentation, Zoological days 2020, Olomouc: https://www.ivb.cz/vyzkum/zoologicke-dny/
2020	3rd place for best student presentation, Ph.D. conference of the Department of Ecosystem Biology, University of South Bohemia in České Budějovice: https://kbe.prf.jcu.cz/cs/news/vysledky-hodnoceni-doktorandskych-prezentaci-na-konferenci-doktorandu-kbe-konane-27-28-ledna-ve
2015	Živa award – best paper in Junior author category. *Potápníci – nenápadní predátoři našich vod*: https://ziva.avcr.cz/files/ziva/pdf/ceny-zivy-za-rok-2015.pdf
2015	M.Sc. thesis 1st place for best student presentation, M.Sc. & B.Sc. Conference of the Faculty of Agriculture, University of South Bohemia in České Budějovice
2012	B.Sc. thesis, 2nd place for best student presentation, M.Sc. & B.Sc. Conference of the Faculty of Agriculture, University of South Bohemia in České Budějovice

2014 B.Sc. thesis, 3rd place for best student work, Jihočeská ratolest projects for the protection of nature: https://www.krasec.cz/file.php?nid=16180&oid=6005533

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