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Faculty of Science

Role of habitat complexity and predation in the structuring of aquatic communities

Ph.D. Thesis

Mgr. Pavel Soukup

Supervisor: doc. Ing. MgA. David Boukal, Ph.D.
Department of Ecosystem Biology, University of South Bohemia
Institute of Entomology, Biology Centre of the Czech Academy of Science

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Annotation

This thesis focuses on the roles habitat complexity and predation play in the structuring of aquatic communities. Chapter one provides an overview of the way habitat complexity structures communities separately, and by altering predator prey interactions in all aquatic habitats. The following two chapters examine their combined effects using different predator-prey pairs and time scopes: short-term laboratory experiments and a medium-term mesocosm experiment.

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, 28. 1. 2022

Pavel Soukup

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. **Soukup P. R.**, J. Näslund, J. Höjesjö, Boukal D. S. (2022) From individuals to communities: habitat complexity affects all levels of organization in aquatic environments. *WIREs Water*, DOI: 10.1002/wat2.1575 (IF=6.1)
PRS participated in conceiving the conceptual framework (50%), lead the literature review (90%) and writing of the first draft (70%).

II. Mocq J.*, **P. R. Soukup***, J. Näslund, Boukal D. S. (2021) Disentangling the nonlinear effects of habitat complexity on functional responses. *Journal of Animal Ecology*, DOI: 10.1111/1365-2656.13473 (IF=5.09).
*PRS participated in designing Experiment 1 (20%) and Experiment 2 (80%), co-conducted the experiments (50%), and contributed significantly to data analyses (30%) and writing of the first draft (50%). * = equal contribution to the manuscript.*

III. **Soukup P. R.**, V. Kolář, Boukal D. S. Invasive crayfish predation risk and habitat complexity effects on community assembly in small standing waters. (Manuscript)
PRS participated in designing the experiment (30%), lead the experiment (60%), partially analyzed the data (50%), and wrote the first draft (80%).

Co-author agreement

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

doc. Ing. MgA. David Boukal, Ph.D.

Contents

Introduction

Thesis introduction

Role of habitat complexity and predation in the structuring of aquatic communities

Overview

Small water bodies are well defined, relatively contained habitats with great potential for ecological research (De Meester *et al.*, 2005). They range from ephemeral pools, hosting only the fastest developing invertebrates, to permanent ponds with established communities structured into several trophic levels (Wellborn, Skelly & Werner, 1996). Community structure is shaped by both biotic and abiotic conditions.

Among the biotic interactions, predation is especially important in aquatic ecosystems, where fewer herbivorous interactions take place and saprophagy and detritivory is less prominent due to a relative lack of organic detritus (Hui, 2012). Apart from bottom-up biotic effects (i.e., the level of local primary productivity and its effects on higher trophic levels), aquatic communities are primarily shaped by predation. Predation is an important, top-down biotic factor for community assembly, as predators influence the community both directly (consumption of prey) and indirectly (e.g., via trophic cascade, Nyström, Svensson & Lardner, 2001). Predators can even influence habitat use or foraging activity of lower trophic level individuals via trait-mediated interactions (Bernot & Turner, 2001).

Abiotic factors include psychical and chemical characteristics of water, such as viscosity and temperature. Habitat complexity is an important and omnipresent abiotic factor. It describes the arrangements of structural elements withing a habitat (Kovalenko, Thomaz & Warfe, 2012). The water column is utilized three-dimensionally by aquatic organisms, suggesting that habitat complexity can be an especially important abiotic factor in aquatic environments (Tokeshi & Arakaki, 2012).

Taken together, habitat complexity and predation are ubiquitous and strong drivers of community assembly and structure in small standing waters by causing both bottom-up and top-down changes. Considerable body of research has aimed to uncover effects of habitat complexity and predation on community structure and assembly. Despite that, the role habitat complexity plays in moderating the effects of predation on community structure and assembly remains incompletely understood. Their interplay needs to be studied on individual, population a community levels and on a variety of time scales.

Factors affecting the structure and assembly of aquatic communities

Factors affecting community dynamics vary in time. The establishment and colonization of a newly formed habitat is described by community assembly. Community assembly describes how and why a set of species ends up inhabiting a particular locality (Weiher *et al.*, 2011). Processes underpinning the assembly are partially deterministic. We can describe them by a set of 'assembly rules', which depend on a few quantifiable variables, most importantly the local/regional species pool size, and the local abiotic and biotic conditions (Cody & Diamond, 1975). Contrary to these mechanistic expectations, similar conditions can give rise to different communities (Drake, 1991). This is because multiple assembly trajectories can be derived from the same species pools and abiotic conditions due to the timing of species invasions and the innate stochasticity of interspecific interactions (Chase, 2003). The nonlinearity of biological processes further increases the role of stochasticity in early phases of colonization (nonlinear processes like predator's functional response, Holling 1966; selection of oviposition habitats, Holzer and Lawler 2015, Blaustein et al. 2004; likelihood of dispersion, De Bie et al. 2012).

Early biotic interactions are key to establishing new communities, when a more stable food web is only beginning to form, and trophic chains consolidate from the bottom up (Drake, 1991). Predator presence is an early key factor influencing community assembly (Vonesh *et al.*, 2009). Small water bodies can form very rapidly e.g., as rain-filled puddles. Even these rapidly formed 'islands' of aquatic environment can be quickly colonized by predators, although ephemeral ponds host smaller predator density (Hill *et al.*, 2017) and usually only invertebrate predators (Wellborn *et al.*, 1996). Early presence of predators can have direct (e.g., reducing mesopredator abundance, Boersma *et al.*, 2014) and indirect effects on community assembly (e.g., habitat selection, Kraus & Vonesh, 2010). Overall, predator effects affect the community top-down and may have cascading effects across multiple trophic levels. On the other hand, habitat complexity, i.e. the arrangement of physical structures and their features in habitats

(Kovalenko *et al.*, 2012) modifies community assembly bottom-up by providing microhabitats and modifying predator-prey interactions. Both habitat complexity and predation have been recognized as key factors influencing community assembly in small standing waters and I focus on their effects on community structure and assembly in this thesis.

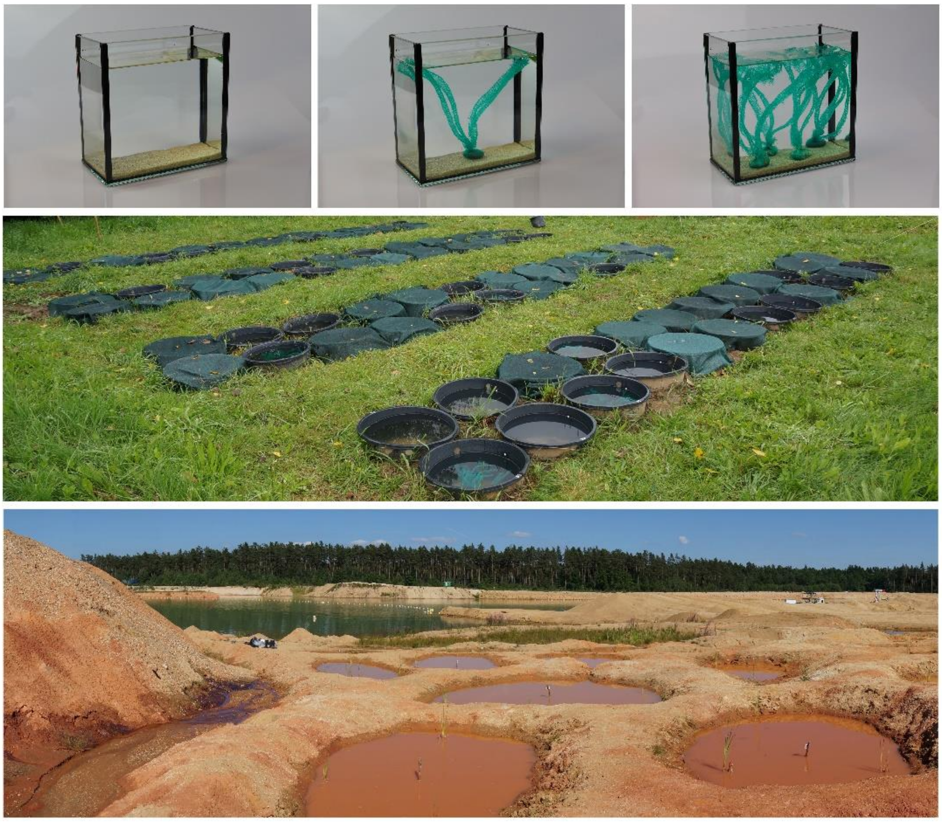

Figure 1: Examples of experimental designs: controlled laboratory microcosm (top row, used in Chapter II), mesocosm experiment open to colonization (middle, used in Chapter III), long-term field experiment (bottom, e.g., Vebrová *et al.*, 2018).

Linking individual traits to aquatic community structure

Recent development of size- and other trait-based approaches has also changed the way researchers formulate their questions and characterize the processes and outcomes of community assembly (Boukal, 2014), including the role of habitat complexity and predation risk in the structuring of communities. Functional traits are characteristics of organisms that influence their fitness, including not only morphology but also behaviour (Nock, Vogt & Beisner, 2016). Differences in community structure are commonly inferred from taxonomic identity and abundance. Traits such as individual size (Gilljam *et al.*, 2011; Miller & Rudolf, 2011), trophic position (Vonesh *et al.*, 2009), habitat utilization (Klecka & Boukal, 2014) and activity (Start & Gilbert, 2019) can, however, provide important insights into the underlying mechanisms.

Body size is an especially important trait in aquatic invertebrates, since they grow several orders of magnitude during ontogeny and this drives changes in trophic position and ecosystem functioning of individuals of the same species (Rudolf & Rasmussen, 2013). Many traits, including trophic position, microhabitat use, dispersion mode, often change during individual ontogeny and can be therefore partially accounted for by size. That being said, even size related effects can be species specific, indicating a combination of analyses is preferable to either species- or size-centric approach alone (Rudolf *et al.*, 2014). Examining the community through a combination of taxonomic and functional perspective can prove more useful for answering certain questions. For example, higher densities of juvenile trout were seen in streams by Höjesjö *et al.* (2015), suggesting complex environment is better for the trout population. However, the increased trout density probably led to depletion of prey, greater intraspecific competition, and slower individual growth. Höjesjö *et al.* (2015) would not have detected that if they did not sample the population and measure the size of the individuals repeatedly.

Considering functional traits including body sizes can therefore help us make better predictions of the effect of predators on community structure (Start & Gilbert, 2019) and more efficient habitat management decisions (Kelley *et al.*, 2018).

Methodologies to study community structure and assembly

Having established habitat complexity and predation as key factors influencing the structure and assembly of aquatic communities above, let us consider methods of elucidating these effects. Various experimental approaches have been used (Figure 1). Highly controlled laboratory experiments can help identify mechanisms underlying observed changes in community assembly (Kneitel & Chase, 2004). This approach is suitable to describe individual behaviour and interactions between key species on shorter time scales (e.g., Buxton *et al.*, 2020). Extrapolating results from laboratory into natural setups is, however, difficult. Population and community level consequences are best understood in natural setups, such as longer-term mesocosm studies and field experiments (Pintar & Resetarits, 2020). Understanding all levels of organization (individual, interaction, community) in a study system therefore requires combining results from focused short-term and wider-scope long-term studies.

For example, mosquitoes are well known for their oviposition habitat selection, as they can avoid ponds inhabited by predators when predator-free ponds are available (e.g., Silberbush & Blaustein, 2011). Preferences for conspecific presence appear to shape oviposition habitat selection in females of the genus *Aedes* (Albeny-Simões *et al.,* 2014). In the field, however, selection of oviposition habitats can be driven solely by resource availability (Fader & Juliano, 2014). More natural set-ups can therefore help test hypotheses generated from lab results. Combinations of laboratory trials and mesocosm or field experiments are therefore required for both mechanistic and realistic explanations of community assembly in small standing waters.

In what follows, I discuss the main effects of habitat complexity and predation on community assembly and structure in more detail. Although separate sections are dedicated to both these effects, they do often co-occur in nature, as I will point out where appropriate.

Effects of habitat complexity on community assembly and structure

Habitat complexity, described as the arrangement of physical structures and their features in habitats (Kovalenko *et al.*, 2012), is an abiotic factor shaping community structure and assembly. Its effect is particularly important in aquatic environments, as higher density of water allows for more three-dimensional utilization of space (Tokeshi & Arakaki, 2012). Examples of complex habitats include zones of dense macrophytes in standing waters and nearshore marine habitats (Wolters *et al.*, 2018), living or dead mussel beds in freshwater and marine habitats (Kobak *et al.*, 2016), and root and driftwood banks in running waters (Smokorowski & Pratt, 2007).

Habitat complexity has two main provisioning effects on the community. Firstly, it divides space, which can create refuges (e.g., from fish predation for *Gammarus*, Grutters et al. 2015), ovipositing sites (e.g., dragonfly laying eggs in emergent aquatic plants, Lutz and Pittman 1968), and perching sites (e.g., dragonfly larvae gaining access to pelagic prey, Mocq *et al.* 2021). Secondly, it usually also increases surface area available for biofilm development. This can increase primary production, which is then carried to higher trophic levels by grazers (Wolters *et al.*, 2019). As a result, communities established in structurally complex habitats are usually more diverse and species rich, although the relative importance of various habitat complexity effects are likely specific to each habitat and largely undocumented (reviewed by Ortega, Thomaz, and Bini 2018). Similarly, many taxonomic groups thrive in higher abundances in structurally complex habitats. Examples include more algae cover developing on more complex plastic macrophyte models (Wolters *et al.*, 2019), more frog eggs laid in ponds with high vegetations density (Holzer & Lawler, 2015), and more abundant beetles in pools with denser vegetation and in complexity-bearing habitats within them (Gómez Lutz, Kehr & Fernández, 2015).

Complex habitats are to some degree connected to living organisms, whose biotic interactions are not considered when discussing the effects of habitat complexity alone. Inorganic sources of habitat complexity include substrate rugosity or refuge density (Jermacz *et al.*, 2015), and artificial macrophyte models (Wolters *et al.*, 2019) or even non-mimicking structures (Crooks, Chang & Ruiz, 2016). The latter are used to separate habitat complexity effects from biotic interactions in experiments.

Ecological systems do not always gradually respond to environmental change. In particular, nonlinear responses can lead to chaotic behaviour or ecological regime shifts (Scheffer *et al.*, 2001; Carpenter *et al.*, 2011). Therefore, when possible, working with a gradient of habitat complexity with three or more levels is desirable. However, many studies have examined the effects of habitat complexity on community assembly only on a binary (presence-absence) scale. This may lead to incomplete or false conclusions about the role of habitat complexity in community assembly. For example, functional responses that describe the dependence of prey killed by a predator on prey density (Holling, 1966) can take many possible shapes when a gradient of habitat complexity is considered (Mocq *et al.*, 2021). Predation rates are commonly expected to decline in structurally complex habitats due to the availability of refuges and lower encounter rates (Fulan & Anjos, 2015; Schmidt-Drewello *et al.*, 2016) but this may not always hold. For predators which change hunting strategies in high complexity (e.g., fish, Stahr & Shoup, 2015; dragonfly larvae, Mocq *et al.*, 2021), there might be a low habitat complexity peak of predation efficiency which later declines in higher habitat complexity levels. This would be a unimodal response to a habitat complexity gradient. Likely all habitat complexity effects can only be linear within a narrow range of complexities. When a broad range of naturally occurring habitat complexity levels are considered, more complicated relationships are likely to be uncovered (Soukup *et al.*, 2022).

While we can summarise the effects of habitat complexity as a provider of shelter and surface area (Tokeshi & Arakaki, 2012), divider of territories (Bilhete & Grant, 2016) and overall positive influence on abundance, biomass and diversity (St. Pierre & Kovalenko, 2014; Czarnecka, 2016) of aquatic organisms, some areas remain relatively sparsely understood. Ecosystem engineers interact with different components of habitat complexity (e.g., crayfish benefit from increased habitat complexity, Corkum & Cronin, 2004; they increase it by excavating banks but decrease it by disturbing macrophytes, Carreira, Dias & Rebelo, 2014), and their activity can have long-term feedbacks, which remain largely unknown.

Habitat complexity can greatly effect community assembly and colonization (Flecker & David Allan, 1984). Due to methodological difficulties, few colonization experiments examining community assembly in habitats of different habitat complexity are known in lotic systems (unlike manmade reefs in marine environments, e.g., Hylkema *et al.*, 2020), presenting an opportunity for further inquiry. Additionally, natural habitats span a wide range of complexity, from barren bottoms to dense a diverse macrophyte beds (Tokeshi & Arakaki, 2012). Since habitat complexity often significantly modifies predator prey interactions (e.g., Fulan & Anjos, 2015), efforts should be made to quantify the intensity of these effects on a finer scale of habitat complexities.

Effects of predation on community assembly and structure

Predators can alter the course of community assembly both directly and indirectly. The direct lethal effects stem from the killing and usually also consumption of the prey. Prey preferred by the predator are hence less likely to become established in the community (Liebold, 1997), and predation may also mediate competitive interactions among different species of prey, e.g., through apparent competition (Dijoux & Boukal, 2021). Functional responses are often used to express direct lethal effects of predators on a gradient of prey densities (Holling, 1966). This is beneficial for various modelling efforts. Precise descriptions of functional responses allow the analysis of species rich ecosystems, which are otherwise prone to chaotic dynamics (Williams & Martinez, 2004). Functional responses may help in formulating effective strategies for the removal of alien species (Boukal, Sabelis & Berec, 2007). Interestingly, habitat complexity can sometimes change functional response shapes from destabilizing Type II to stabilizing Type III, qualitatively changing predator prey dynamics (Barrios-O'Neill *et al.*, 2015).

Non-lethal effects are invoked by the mere presence of a predator (Figueiredo *et al.*, 2018). The terms 'consumptive' and 'non-consumptive' are also used to describe these two kinds of effects (McCauley, Rowe & Fortin, 2011). Notably, the consequences of unsuccessful attacks (e.g., maimed, forewarned prey) can be considered 'consumptive', although technically also 'non-lethal'. Additionally, predator effects can be described as 'direct', when exacted by the predator's activity, or 'indirect' for secondary changes arising from direct effects (e.g., O'Connor *et al.*, 2012). Direct effects arise from so-called density-mediated interactions (more predators eat more prey), while indirect effects can be attributed to trait-mediated interactions (any number of predators stimulates defensive strategies in prey, Preisser, Bolnick & Bernard, 2005).

The trophic cascade is a prime example of an indirect predator effect, in which the effects of predation propagate down to lower trophic levels (Figure 2). In food chains, we should see alternating negative and positive effects, radiating top-down from the predator (Power, 1990). For instance, predatory fish can have negative effects on herbivorous consumers such as zooplankton (Hrbáček, 1962; Dodson, 1974) and subsequently a positive indirect effect on the primary producers such as algae (Vonesh *et al.*, 2009). Introducing a piscivore into such a system lengthens the trophic chain and reverses the trophic cascade (Carpenter, Kitchell & Hodgson, 1985). Once established, cascade effects are persistent until a change in the trophic structure occurs (Bell, Neill & Schluter, 2003). In small ponds, both fish and invertebrate predators can cause cascading effects (dragonfly larvae: Stav, Blaustein & Margalit, 2000; rainbow trout and signal crayfish: Nyström, Svensson & Lardner, 2001).

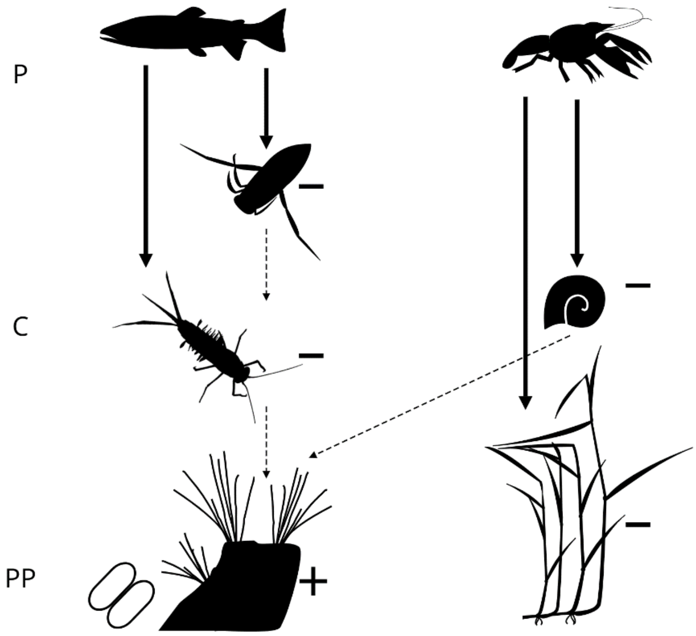

Figure 2: Examples of trophic cascades in freshwater systems. Fish or invertebrate predators prey on consumers. This indirectly increases biomass of primary producers, such as epiphytic algae. Here trout feed on insects, including predators and grazers, thereby increasing periphyton biomass (left column). Although the trout may eliminate some insect predators (intraguild predation), their overall effect on grazers can still be negative. Omnivorous predators also consume primary producers, partially compensating the cascading effects. Here a crayfish feeds on aquatic snails and rooting plants. Examples inspired by results reported in (Nyström *et al.*, 2001). Thick solid arrows = direct predator effects, thin dashed arrows = indirect predator effects. Only interactions directly related to the described trophic cascades are represented. Signs (+, –) indicate overall effects of the top predator presence on the biomass of pictured groups. P = predators, C = consumers, PP = primary producers and bacteria. Design and illustrations by Pavel Soukup.

Indirect effects of predation can also contribute to a trophic cascade. For example, damselflies avoid oviposition in bromeliad phytotelmata next to which a stuffed bird was placed to invoke top predator risk (Breviglieri, Oliveira & Romero, 2017). Consequently, aquatic meso-predator abundance increased in bromeliads devoid of damselfly larvae that are top predators in the local food web. This led to a lower scraper abundance, which could have meant lower decomposition rates and stunted bromeliad growth in the long term. A perceived risk of predation and oviposition avoidance was thus enough to create cascading effects across both terrestrial and aquatic environments.

The importance of non-consumptive effects depends on several factors. Besides the taxonomic identity and functional traits of interacting organisms, the intensity of non-consumptive effects can scale predictably with predator body size as shown in aquatic hemipteran predators (Krenek & Rudolf, 2014). Moreover, differences in prey sensory ability and habitat characteristics can drive the strength of non-consumptive effects (Smee, Ferner & Weissburg, 2008). Finally, antipredator behaviour may not be efficient in environments with multiple predators, as seen by mosquito larvae not diving when simultaneously under threat of predation by *Aeshna*, *Agabus* and *Aquarius* (Meadows, Owen & Snyder, 2017). Alternatively, prey can adjust their behaviour to the predator perceived most dangerous in environments with multiple predators (*Rana sylvatica* tadpole, Relyea, 2003).

All the effects outlined in the previous paragraphs can occur simultaneously in natural ecosystems. Nonetheless, their separation promotes clarity in communication, allows us to design experiments isolating the individual facets of predator effects and helps obtain a better mechanistic understanding of overall predator effects. Non-consumptive effects can be studied by exposing focal organisms to visual or chemical predator cues to simulate predator risk (e.g., Turner, Bernot, and Boes 2000). Captive or otherwise incapacitated predators can be introduced in the environment (e.g., Turner *et al.*, 2000) and even dummy predators can evoke measurable effects (competitive behavior in trout, Kalleberg, 1958).

Chemical cues are apparently most impactful for aquatic invertebrate prey (Adler & Drew Harvell, 1990; Ferrari, Wisenden & Chivers, 2010). These indirect effects commonly include growth of defensive appendages (Barnhisel, 1991), changes in larval development (McCauley *et al.*, 2011), changes in oviposition habitat selection (Resetarits, 2001; Blaustein, Blaustein & Chase, 2005), habitat use (Oram & Spitze, 2013), activity, feeding and other behavioural alternations (e.g., Sih, 1992), which can negatively affect the prey population (Preisser *et al.*, 2005).

Predator-prey interactions are easily one of the most studied ecological phenomena, aquatic environments notwithstanding. Functional responses can quantify predation intensity in specific predator-prey pairs (e.g., Cuthbert *et al.*, 2019). Factors including temperature (Wasserman *et al.*, 2016) and habitat complexity can alter predator's functional response (Barrios-O'Neill *et al.*, 2015). Functional response shape was shown to change from Type II to Type three in certain predator prey pairs (Alexander *et al.*, 2012) but not for others (Anderson, 2001; Wasserman *et al.*, 2016). A decrease in attack rate in complex habitats can be attributed to the provision of refuges to prey (Barrios-O'Neill *et al.*, 2015) but a decrease in handling time is sometimes also reported (Alexander, Dick & O'Connor, 2013) and it is unclear why predators should take more time to process food in more complex environments. Available research is mostly evaluating functional responses in binary habitats (simple vs. complex), while we would expect a more complicated responses to take place in nature (e.g., a low threshold for the effect to manifest, and a high threshold levelling off the effect, or even reversing it). Despite the importance habitat complexity plays in predator-prey interactions, relatively little is known about the qualitative and quantitative changes to functional response. Similarly, the trophic cascade is well documented for piscivorous fish in ponds and lakes (e.g., Vašek *et al.*, 2013), but cascades caused by indirect predator effects, or by omnivorous predators can be harder to detect (Figure 2). Knowledge about the various modifying effects of habitat complexity on direct and indirect predator effects might prove important for our understanding of the role of habitat complexity and predation risk in community assembly.

Aim and scope of this thesis

In this thesis I focus on selected aspects of the role of habitat complexity and predation risk in community assembly in small standing bodies. I chose invertebrate predators as my focal group, since they are top predators in small fishless standing water bodies (Wellborn *et al.*, 1996). I combine different levels of focus to deal with the topic. I conducted a review of the role of habitat complexity in community assembly to identify potential areas of interest. I further ran a semi-natural open colonization mesocosm experiment to identify the effects of habitat complexity and predation risk at the community level and controlled laboratory experiments to elucidate the effects of habitat complexity on the predator behaviour and the strength of predator-prey interactions.

In **Chapter I**, I review habitat complexity effects on individuals, their interactions, and entire communities in all aquatic environments. This review provides a conceptual framework that covers both the effects of habitat complexity on the different levels of biotic organizations and all possible feedback loops that may enhance of diminish the direct effects. I reviewed 208 recent studies dealing with habitat complexity in aquatic environments and examined their results and reasoning in the spirit of this framework. This allowed me to identify understudied areas and suggest possible directions for future research. Among other things, this review showed that the role of habitat complexity is often studied using only 2-3 levels of habitat complexity, which prevents the quantification of any nonlinear effects of habitat complexity on community assembly.

To address this question, I examine predator-prey interactions on a more gradual gradient of habitat complexity in laboratory microcosms in **Chapter II**. We used dragonfly (*Aeshna cyanea*) larvae feeding on phantom midge (*Chaoborus obscuripes*) larvae as a case study. *Aeshna* larvae are visual predators that commonly employ a ‘sit-and-wait’ ambush strategy (Pritchard, 1965). Using a population-level experiment with five levels of habitat complexity (submerged plant mimics), we described the dependence of the parameters of the functional response linking prey consumption to prey density (Holling, 1966) on the range of habitat complexity levels. To complement the data and provide more mechanistic explanations of the results from the population-level functional response experiment, I also conducted an individual-level behavioural experiment in which I recorded *Aeshna* behaviour while feeding on *Chaoborus* larvae in arenas with varying habitat complexity. We combined the population- and individual-level approach to identify plausible models of the effect of habitat complexity on functional response parameters, and reviewed previous experiments to advance our understanding of the role of habitat complexity in functional responses in 2D and 3D environments.

In **Chapter III**, I focus on the effect of an invasive crayfish *Orconectes limosus* and habitat complexity on early stages of community assembly. I set up small outdoor mesocosms with crayfish and plastic plant models to mimic natural submerged plants and followed the colonization process for 29 days. I measured the abundance and biomass responses of the colonizing macroinvertebrates to habitat complexity and predation risk. I used well established allometric equations to estimate biomass from length measurements (e.g., Benke *et al.*, 1999; Johnston & Cunjak, 1999). Size measurements were automated using algorithms which extract length estimates from even complicated outlines of invertebrates (e.g., longest-shortest path, originally intended for measuring shoot lenghts of brached plants Polder *et al.*, 2010, Figure 3). Acquiring individual-level data from long-term or large-scale experiments remains difficult. The above-mentioned methods helped me show that the consumptive and nonconsumptive effects of the omnivorous crayfish on early stages of community assembly are relatively minor and manifested only in the altered size structure of the community. In this case, the assembly was driven more by the effects of habitat complexity.

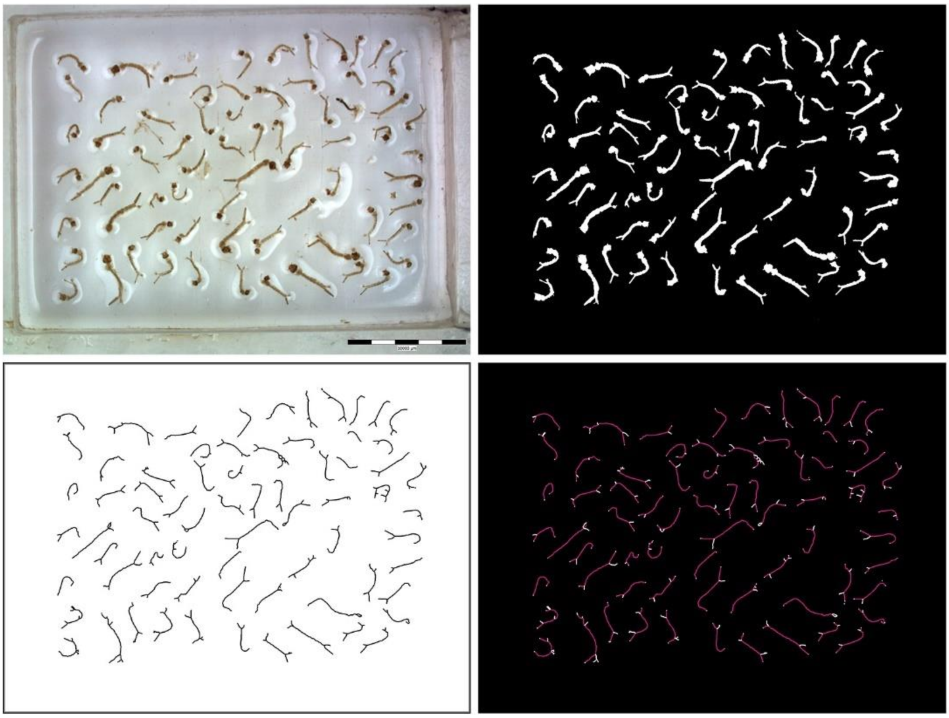

Figure 3: Automated length measurement procedure for aquatic insects. Pictures of separated individuals are taken with a stereomicroscope (top left), binary (i.e., black and white) image is created using a black threshold (top right), skeletons for each object are calculated (bottom left) and pruned to find the longest shortest path, which closely corresponds to the body length of the individual (up to ~10% error). See also Chapter III for details.

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Chapter I

From individuals to communities: habitat complexity affects all levels of organization in aquatic environments

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OVERVIEW

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From individuals to communities: Habitat complexity affects all levels of organization in aquatic environments

Pavel R. Soukup[1,2] | **Joacim Näslund**[3] | **Johan Höjesjö**[4] | **David S. Boukal**[1,2]

[1]Faculty of Science, Department of Ecosystem Biology, University of South Bohemia, České Budějovice, Czech Republic

[2]Czech Academy of Sciences, Biology Centre, Institute of Entomology, České Budějovice, Czech Republic

[3]Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Drottningholm, Sweden

[4]Department of Biological & Environmental Sciences, University of Gothenburg, Gothenburg, Sweden

Correspondence
David S. Boukal, University of South Bohemia, Faculty of Science, Department of Ecosystem Biology, Branišovská 1760, České Budějovice 370 05, Czech Republic.
Email: dboukal@prf.jcu.cz

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Abstract

Habitat complexity describes a wide array of spatial distribution patterns of physical structures in habitats. It affects aquatic ecosystems on multiple levels from individuals (e.g., foraging behavior) to species interactions (e.g., predation, prey selection) and entire communities (e.g., biodiversity, food web structure). We present a conceptual framework to classify these effects and use it to summarize recent advances in the field. We identify three main research gaps and limitations preventing a full synthesis of the effects of habitat complexity on aquatic communities and ecosystems. Habitat complexity is often characterized using ad hoc measures, which limits cross-experimental comparison and meta-analytical and modeling approaches. The effects of habitat complexity on communities and ecosystems can also involve feedback loops on lower levels of organization including the habitat complexity itself. Such ecological feedbacks can influence habitat formation and amplify or mitigate the direct effects of habitat loss and simplification or habitat restoration on populations and communities, yet are surprisingly little understood. Finally, most studies examine habitat complexity on the presence-absence scale. This limits our ability to recognize nonlinear responses across habitat complexity gradients, which occur in many contexts in aquatic habitats. Since nonlinear responses can stabilize or destabilize population and community dynamics, we call for the use of a higher resolution of habitat complexity in future studies. We conclude that currently degraded habitats offer exciting opportunities for combining restorative efforts with research that could combine multi-level experiments and monitoring to improve our understanding of the role of habitat complexity across aquatic ecosystems.

This article is categorized under:
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KEYWORDS
behavior, biodiversity, ecological feedbacks, food webs, habitat complexity, habitat restoration, predation

1 | INTRODUCTION

Habitat complexity (hereafter "HC") is an ecologically intuitive concept used to describe a wide array of spatial distribution patterns of physical structures and their features in habitats (Tokeshi & Arakaki, 2012; Box 1). In aquatic ecology, spatial elements related to HC range from the density and fractal dimension of macrophytes to the rugosity and grain size of the substrate (Kovalenko et al., 2012). Higher density and viscosity of water, as compared to air, allow aquatic habitats to be utilized in all three dimensions, enhancing the importance of HC in aquatic environments (Tokeshi & Arakaki, 2012). HC affects aquatic living systems directly and indirectly from individuals to species interactions to entire communities and ecosystems (Kovalenko et al., 2012). HC has ramifications for environmental protection (Brogan & Relyea, 2015), wildlife management (Czarnecka, 2016; Smokorowski & Pratt, 2007), aquaculture and fisheries (Näslund & Johnsson, 2016; Stoner et al., 2011), and disease prevention (Cuthbert et al., 2019). The popularity of HC as a research topic is further increased by its relative ease of use in experimental setups and environmental applications (e.g., Nyström et al., 2001; Höjesjö et al., 2015).

In their influential article, Kovalenko et al. (2012) provided a cross-ecosystem overview of HC types and gave examples of different methods of quantifying complexity. Other articles focused on the effects of HC in specific habitats. For example, Orth et al. (1984) and Horinouchi (2007) summarized the effects of HC on predator-prey relationships in sea grass beds, Mitchell and Harborne (2020) covered them for coral reefs, and Teagle et al. (2017) described the habitat-forming effects of kelp in kelp forests. In freshwater ecosystems, specific types of HC, such as wood debris (Crook & Robertson, 1999; Smokorowski & Pratt, 2007) and submerged vegetation (Jeppesen et al., 1997), have been investigated in detail. Several HC effects have been extensively examined across aquatic environments, including behavioral changes (Mikheev et al., 2010; Shumway, 2008), fish welfare (Näslund & Johnsson, 2016), abundance and species richness (Ortega et al., 2018), individual body size (Robson et al., 2005), and both nonconsumptive (Mitchell & Harborne, 2020) and overall predator effects (Horinouchi, 2007). Despite occasional methodological differences, HC effects are comparable across aquatic environments, since many parallel ecosystem types exist in freshwater, brackish, and marine systems. To provide a broad and interdisciplinary perspective of HC in aquatic environments, we cover studies from all types of aquatic systems.

Numerous ecological effects on communities and ecosystems have been attributed to HC across environmental contexts and spatial scales from zooplankton in urban ponds (Fontanarrosa et al., 2019) to cetaceans in coastal seas (De Rock et al., 2019). A ubiquitous effect of HC on ecosystems follows from its bottom-up effects on community structure and energy flows in the food web (Diehl, 1992). Increasing surface area and spatial separation coinciding with increasing HC create new microhabitats for more individuals and species (e.g., Teagle et al., 2017). Larger surface area can increase periphyton growth, which provides resources for higher trophic levels and potentially increases food chain lengths (Warfe & Barmuta, 2006). HC also modifies behavior in multiple ways, for example, by inducing hunting mode changes (Michel & Adams, 2009) and refuge use (Orrock et al., 2013), and by modifying territorial behavior (Church & Grant, 2019). This can alter trophic and competitive interactions (e.g., Schmidt-Drewello et al., 2016), stabilize food webs, and increase overall biomass and diversity (Ortega et al., 2018).

These effects may also create feedback loops via habitat formation or evolutionary change (Shumway, 2008; Wathen et al., 2019). Here we integrate the evidence across individual, interaction, and community levels to highlight the different pathways in which HC affects aquatic ecosystems including the feedback loops (Figure 1) and synthesize recent advances in HC research in freshwater and marine environments. To do so, we focused on articles published in years 2015–2020. By querying the Web of Science database (Clarivate Analytics, Philadelphia, last updated 31 December, 2020) for "habitat complexity" AND (marine OR *water OR aquatic) we arrived at 555 studies, of which 365 were excluded as irrelevant, leaving 190 for review. Complementary searches using the Google Scholar search engine (Google LLC, Mountain View) yielded 28 additional studies whose subject matched closely our topics. To maintain brevity, only selected illustrative studies are discussed in the main text alongside other key references; see Supporting Information for details on all 218 studies. We have used a similar approach to populate Figure 2 with main reviews; see Supporting Information for additional details on data acquisition (Box 1).

2 | EFFECTS OF HC ON INDIVIDUALS

The effects of HC on individuals can be both direct and indirect (Figure 1). Probably the most intuitive aspect of HC is its ability to directly *provide shelter* from physical disturbances, *break up the living space and increase surface area* for organismal settlement (Figure 1, arrow 1). This aspect has been thoroughly covered in recent articles (Tables 1 and S1)

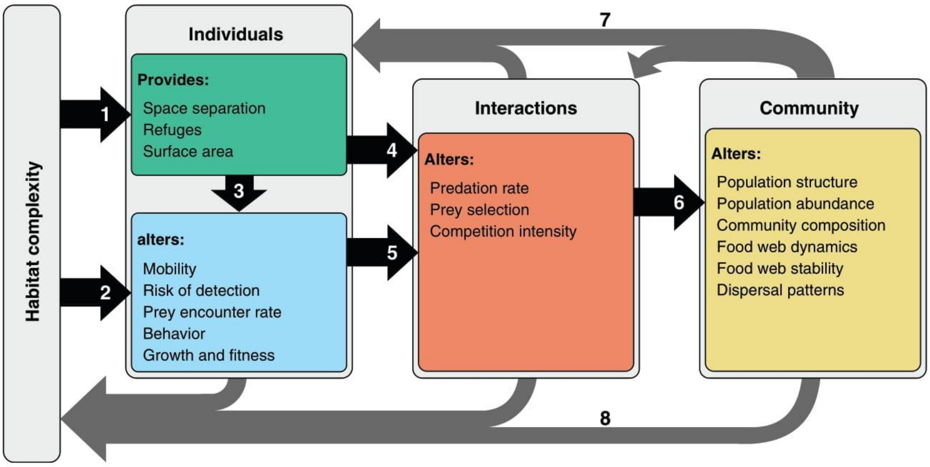

FIGURE 1 Overview of the conceptual framework linking the effects of HC on individuals (arrows 1–3) to species interactions (arrows 4 and 5) and communities (arrow 6). Individuals are affected by provision of niches (arrow 1) and by modifications of their behavior, growth and other fitness components, including reproduction and fecundity (arrow 2). Provisional effects of HC can have further indirect effects on modified individual behavior, chances of being detected and ability to detect (arrow 3). Changes in space and altered traits of individuals affect species interactions (arrows 4 and 5). Community-level changes induced by HC (arrow 6) may feedback on individuals and species interactions, and changes in species interactions induced by HC may feedback on individual behavior and fitness components (arrow set 7). Changes at all levels of biotic organization may feedback on HC (arrow set 8). Note that arrow 6 combines all possible effects at the individual level and the level of species interactions

and past reviews (Figure 2). Researches mostly describe this effect by stating modifications made to increase HC such as the number of added structures (Wasserman et al., 2016), which is common in laboratory, or what kind of material was used to enrich the complexity of the environment (Dennis et al., 2018), common in *in situ* field studies. In controlled environments, researchers manipulate HC by transferring natural complexity generators or their models to create gradients with ad hoc established units of complexity. Examples include variable density of eelgrass (*Zostera marina*) shoots (Hovel et al., 2016; Voigt & Hovel, 2019), or a given amount of wood debris added per unit of area (Czarnecka et al., 2019; Enefalk & Bergman, 2016). In field studies, habitat characteristics are commonly described on a semi-quantitative scale, for example, by the amount and type of macrophytes (e.g., Anderson, 2019). However, a quantitative, context-independent overview of the provisioning effects remains elusive as the studies typically do not quantify added surface area, refuge volume/count or similar HC metrics (see below for exceptions).

Several methods were devised to measure habitat provisioning by the different types of HC, including fractal dimension (Tokeshi & Arakaki, 2012) and habitat heterogeneity (Carvalho & Barros, 2017), and to specify HC quantity (Dibble & Thomaz, 2006) and quality (Warfe et al., 2008). Fractal dimension can describe the dimensionality of the environment (Flores et al., 2016; Grutters et al., 2015). Various indices can quantify habitat provisioning by macrophyte beds using their architecture (Lillie & Budd, 1992) or interstitial distance between structures like stems or branches (Dibble et al., 1996). Surfaces can be characterized by rugosity derived from the ratio between the distance of two points measured by following the bottom and the distance measured directly point-to-point (Trebilco et al., 2015). Finally, directly measured surface area of structures and volume of the environment occupied by them can provide an unbiased environmental predictor of the extent of habitat provisioning (Warfe et al., 2008). Niche diversity created in complex environments is better described by habitat heterogeneity. Since habitat heterogeneity can have different effects on functional and taxonomic diversity and its definition is often overlooked or repurposed to fit a given experimental design, care must be taken when generalizing individual studies (reviewed by Carvalho & Barros, 2017). This diversity of HC metrics means that direct quantitative comparisons across HC studies remain challenging. More widespread use of suitable cross-context HC metrics in articles on all aspects of HC in aquatic ecosystems will be indispensable for future meta-analyses and quantitative syntheses.

Publication	A1	A2	A3	A4	A5	A6	A7	A8	HR
Seraphim et al. (2020)	●	○	○	●	●	●			●
Mitchell and Harborne (2020)				●	●				
Kovalenko (2019)						●			
Ortega et al. (2018)						●			
Teagle et al. (2017)	●			○	○	●			
Näslund and Johnsson (2016)	●	●	●						
Czarnecka (2016)	●	●	●			●			○
Kovalenko et al. (2012)	●	○	○	●	●	●	●		○
Tokeshi and Arakaki (2012)	●	○				●			
Mikheev et al. (2010)		●	●	●	●				
Shumway (2008)	●	○					○		
Smokorowski and Pratt (2007)		●				●			●
Horinouchi (2007)		●		●	●	○			
Robson et al. (2005)		●		○	○	●			
Statzner and Moss (2004)	●					●			
Crook and Robertson (1999)	○	●	○	○	○	●			○
Turner et al. (1999)	○			○	○	○			●
Charton and Ruzafa (1999)	○	○		○	○	●			○
Orth et al. (1984)	●	●		○	○	●			

FIGURE 2 Focus of selected main reviews and meta-analyses related to HC in aquatic habitats. Columns A1–A8 correspond to arrows 1–8 in Figure 1 and column HR corresponds to habitat restoration. Full circle: main focus of the review, open circle: discussed at length, no symbol: only noted in passing or omitted. See Supporting Information for details

HC also directly *alters individual mobility* (Figure 1, arrow 2) and the *behavior of individuals* (Figure 1, arrow 2). Both effects are well covered in the literature (Tables 1 and S1, Figure 2). Individual movements can be obstructed by physical barriers in the environment, leading to, for example, lower prey escape probability (Hovel et al., 2016). However, animals such as odonate larvae can also benefit from increased HC if the complexity-forming structure provides support or better grip for moving and repositioning (Folsom & Collins, 1984; Klecka & Boukal, 2014). Furthermore, territorial fish defend smaller territories in more complex environments, likely due to visual separation of competitors or greater relative quality of territories in complex environments (see below; Bilhete & Grant, 2016; Kalleberg, 1958). These contrasting observations highlight the context dependence of HC effects and key role of functional traits of the species in this dependence, which is another promising area for future studies.

HC can also modify other individual traits that may contribute to *fitness*. For example, Costa-Pereira et al. (2016) reported different morphologies of a characin fish (*Astyanax lacustris*) inhabiting river segments of differing HC. Individual bluegill sunfish (*Lepomis macrochirus*) living in the physically complex littoral zone develop larger brains than pelagic conspecifics (Axelrod et al., 2018). Since brain size can affect cognitive abilities (Buechel et al., 2018, guppies *Poecilia reticulata*), HC may contribute to changes in cognitive functions (Shumway, 2008, African cichlid

BOX 1 Terminology used to describe habitat complexity

Habitats can be considered complex in various features (patterns or gradients in temperature, nutrient content, etc.) in both space and time. Here we focus on habitat structural complexity, that is, the complexity of structural elements in space and their features (Tokeshi & Arakaki, 2012).

Terminology used to describe HC and its components differs among study systems. Despite the convergence toward HC as a catch-all term describing spatial distribution patterns of physical structures in habitats, terms like substrate heterogeneity, topographical complexity, or habitat architecture are also used within context of studies where more descriptive terminology promotes clarity (Kovalenko et al., 2012). However, omitting the term "habitat complexity" altogether in an article can make it difficult to find by interested readers. For these reasons, HC has become a typical "umbrella" term in ecological research focusing on the effects of spatial structuring of the physical habitat on biota.

In aquatic environments, examples of HC sources include substrate rugosity, particle size, and interstitial space, macrophyte, macroalgal or coral density, percentage cover, height and fractal dimension, and physical refuge or predator free space availability. Depending on the scale at which the focal organisms interact with their habitat, HC can take the form of large-scale sea structures or tiny pores in substrate particles.

Other terms like habitat heterogeneity or environmental heterogeneity are sometimes used instead of HC, but they also include the diversity of habitat types in the broader environment, rather than the distribution of spatial elements in a particular habitat. Interpretation of results of individual studies should consider these terminological differences.

TABLE 1 Number of recent studies (2015–2020) on different aspects of HC. Total articles = 218 (see Table S1 for details)

Level of organization	HC effect	Number of studies
Individuals	Divides space, provides refuges or substrate for periphyton (Figure 1, arrow 1)	30
	Alters mobility, predator/prey detection or feeding behavior (Figure 1, arrow 2)	74
	Modifies individual behavior, mobility and predator/prey detection due to additional niches, refuges, or increased energy flow (Figure 1, arrow 3)	64
	Any individual level effects (arrows 1–3)	*166*
Interactions	Modifies interaction strength due to additional niches, refuges, or substrate for periphyton growth (Figure 1, arrow 4)	71
	Modifies interaction strength due to altered mobility, predator/prey detection, or feeding behavior (Figure 1, arrow 5)	72
	Any interaction level effects (arrows 4 and 5)	*74*
Community	Habitat provisioning, alterations of individual-level properties and modified interactions strengths lead to altered community composition/dynamics (Figure 1, arrow 6)	141
Feedbacks	Interactions or community dynamics altered by HC create feedbacks on individuals or interactions (Figure 1, aggregate arrow 7)	15
	Communities, interactions, or individual traits affected by HC feedback on HC (Figure 1, aggregate arrow 8)	8
	Any feedbacks (arrows 7 and 8)	*18*

fishes). Predator-induced use of refuges can also have negative effects on growth, activity and fecundity (Orrock et al., 2013), suggesting delayed, long-term costs of immediate protection in the prey.

Habitat provisioning by HC can also *indirectly modify individual behavior*, the *ability to detect* other organisms and the *risks of being detected* (Figure 1, arrow 3). While many recent articles focused on these indirect effects (Tables 1 and S1), they are not covered in many comprehensive reviews (Figure 2), suggesting that a more detailed analysis of this topic is due. Indirect effects of HC on behavior greatly depend on functional traits such as microhabitat use and foraging tactic (Klecka & Boukal, 2014). Ambush predators prefer hunting in complex environments to gain perching conditions and/or to avoid detection by the prey (Miyashita et al., 2016). Other predators avoid complex environments where their mobility or ability to recognize prey is impaired (De Fouw et al., 2016). Yet others respond to altered HC by changes in their hunting mode to optimize their success. For example, some fish species switch from rapid cruising to a less active, but equally successful, sit-and-wait strategy in more complex habitats (largemouth bass: Stahr & Shoup, 2015; brown trout: Enefalk & Bergman, 2016).

Predator reaction distance (Murray et al., 2016) often decreases with increasing HC. Prey thus prefer more complex habitats to avoid detection by predators, but also to gain access to resources (conspecific prey: Stahr & Shoup, 2015; heterospecific prey: Kenison et al., 2016; Tano et al., 2017). This preference may occur even without predator cues (Ajemian et al., 2015) and can also affect oviposition (mosquitoes: Bond et al., 2005; amphibians: Holzer & Lawler, 2015).

3 | EFFECTS OF HC ON INTERACTIONS

The direct and indirect effects on individuals discussed above can modify other ecologically relevant performance traits, affecting interactions between conspecifics and heterospecifics. Direct evidence of such effects are typically drawn from behavioral observations of predators (Enefalk & Bergman, 2016; Michel & Adams, 2009) and prey (Ajemian et al., 2015) in environments with different HC levels, as both provisioning and altering effects of HC can modify *predator–prey interactions* (Figure 1, arrows 4 and 5). The two types of effects have received comparable attention measured by their coverage in reviews (Figure 2) and recent articles (Tables 1 and S1).

The relative ease of laboratory predation experiments has led to abundant data on HC effects on predator–prey relationships. Most commonly, the effect of HC on predation is measured by prey consumption in environments of different complexity. HC levels in some of these studies include only simple versus complex environments (e.g., De la Parra et al., 2016; Fulan & Anjos, 2015; Gregor & Anderson, 2016; Schmidt-Drewello et al., 2016). The increasing use of HC gradients (Carroll et al., 2015; Lee et al., 2017) is commendable as it better reflects natural conditions and may reveal nonlinear dependence of trophic interactions on HC, with consequences on population and community stability (Mocq et al., 2021). Many possible response shapes can however occur for HC effects, ranging from no/constant response to linear and various types of nonlinear responses (Figure 3). Linear responses reported by some studies (e.g., Li et al., 2019) are conditional on having a limited range of HC. In practice, adding more complexity either has a diminishing effect on the response and the HC effect levels off toward high HC (Mocq et al., 2021), or the effect is reversed at high HC levels and leads to a concave-down relationship between HC and the response as in the prey selectivity of the characin fish *Serrapinnus notomelas* (Figueiredo et al., 2015). Some studies also report a binary, presence-absence effect of HC. That is, the response is independent of the amount of HC as in the predation mortality of *Cypricercus* ostracods (Figueiredo et al., 2015). The latter case is a special type of a sigmoidal/stepwise response to HC.

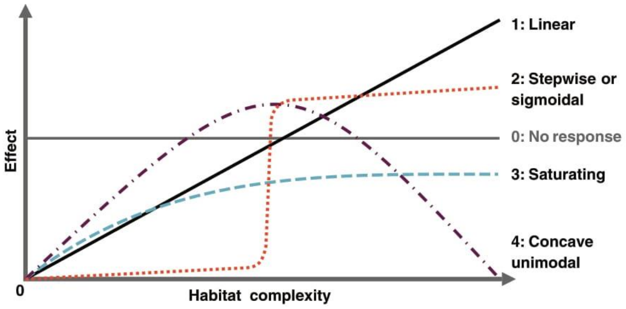

FIGURE 3 Hypothetical examples of qualitative response shapes along a HC gradient. Linear response excludes the lack of response ("no response"). Note that the effect can be positive or negative; for example, the linear response represents both increasing and decreasing responses to increasing HC

Predation rates are often expected to decline in more complex environments due to fewer encounters with prey in both marine (Bishop & Byers, 2015; Carroll et al., 2015; Hovel et al., 2016; Miyashita et al., 2016) and freshwater environments (Figueiredo et al., 2015; Grutters et al., 2015; Huang et al., 2016; Schmidt-Drewello et al., 2016). However, these expectations depend on predator and prey microhabitat use and predator foraging tactics (Klecka & Boukal, 2014) and may be further modified by case-specific variables such as the physical characteristics of the submerged plants providing the HC (Grutters et al., 2015). Other factors, such as temperature (Wasserman et al., 2016) or predation risk posed by a higher-level predator (Kolar et al., 2019) can modify the baseline effect so that it only manifests in high temperatures or depends on intermediate predator identity. Finally, HC may not alter trophic relationships at all, as found in an intraguild predation system with dragonfly and beetle predators (Carter et al., 2018).

Prey selection, a key process affecting the strength of predator–prey interactions, can be altered by HC. In some cases, prey preferences are HC-independent (De la Parra et al., 2016). Alternatively, all prey types are consumed equally in simple environments, while some are more accessible in complex environment facilitating prey preference (Fulan & Anjos, 2015, *Erythemis* dragonfly nymphs). Increasing HC may also interfere with prey selection: characin fish prefer midge larvae over ostracods in low and zero complexity environments, but are unselective in a high complexity environment, possibly due to low encounter rates with either prey motivating nonselective feeding (Figueiredo et al., 2015). HC can also affect prey selection indirectly, for example, when wading birds adjust their feeding location to time of year and HC to maintain capture success (Lantz & Cook, 2015). HC can further modify prey selection by altering predation risk perception of intermediate predators. For example, the characid fish *Astyanax lacustris* preferred pelagic prey (*Daphnia magna*) in the presence of the native piscivorous wolf fish (*Hoplias* aff. *malabaricus*) in a complex but not in a simple habitat. In the absence of piscivorous fish or in the presence of non-native piscivorous cichlid fish (*Astronotus crassipinnis*), no preference was seen in either habitat (Figueiredo et al., 2018).

Complex habitats also modify *competitive interactions*, for example, by dampening territorial behavior and competitor encounter rate. That is, more complex habitats can support larger populations per unit of area, with important consequences for conservation and management of exploited populations (Bilhete & Grant, 2016). Complex habitats can also be a limiting resource *per se*. For example, small gammarid individuals inhabit less complex, suboptimal substrates to avoid competition with larger conspecifics (Kobak et al., 2015). Large redband parrotfish (*Sparisoma aurofrenatum*) males prefer to defend highly rugose reef territories and territories with higher quality algae, indicating that highly complex reef sections represent high quality territories (Catano et al., 2015). In sum, individual-level effects of HC can lead to changes in both trophic and non-trophic interactions.

Large-scale environmental characteristics that extend beyond the focal habitat can further *modulate the effects of HC on individuals and their interactions*. For example, the relative effect of HC is more difficult to interpret in complex natural streams with drifting prey. Here dominant individuals might occupy favorable upstream feeding territories (Hughes, 1998) and reduce drifting food items through filtering interference with less competitive individuals (Nilsson et al., 2004). Detailed foraging-based models (reviewed by Piccolo et al., 2014) that incorporate food availability, spatial distribution, and foraging, growth and survival of individual fish are thus required to understand the impact of HC on drift-feeding fishes. Increasing HC is likely to indirectly weaken intraspecific competition for food in this system, with rank-specific consequences for individual fish if complex environments provide more refuges and foraging opportunities for subordinate individuals whereas dominant individuals can monopolize the opportunities in less complex environments (Höjesjö et al., 2004).

4 | COMMUNITY LEVEL CONSEQUENCES OF CHANGES IN HC

Changes at the levels of individuals and interactions underpin HC-driven differences in *community composition, food web dynamics and dispersal patterns* (Figure 1, arrow 6). These topics have been extensively covered in recent reviews and articles (Figure 2, Tables 1 and S1). In brief, communities in more complex habitats are usually more diverse. This effect on *biodiversity* occurs across different types of HC and levels of taxonomic resolution (reviewed by Ortega et al., 2018), and can extend to functional diversity (Milesi et al., 2016).

Increased number and quality of living spaces leads to higher *abundances* across taxa and habitats such as amphibians in ponds (Holzer & Lawler, 2015; Kenison et al., 2016), invertebrates in moss patches (Wulf & Pearson, 2017), fish in streams (Donadi et al., 2019; Massicotte et al., 2015), and shrimps in sea meadows (Bartholomew & Burt, 2015) and in kelp assemblages (reviewed by Teagle et al., 2017). Available living space can be represented by the volume protected from tidal forces (Orland et al., 2016) or stream currents (Milesi et al., 2016), both of which lead to increased colonization and chances of survival, explaining higher abundance.

(Carpenter et al., 2011). Given that studies of such feedbacks require long-term data across several levels of organization, it is not surprising that these HC-mediated ecological feedbacks continue to receive only limited attention (Figure 2, Tables 1 and S1).

Among other things, such feedbacks can alter individual growth and fitness components. For example, Höjesjö et al. (2015) reported more juvenile brown trout (*Salmo trutta*) in better condition in stream segments with increased HC, while the fewer trout in control sections grew faster. These counter-intuitive patterns could result from a decrease in territorial aggressive behavior in the high HC, driven by more shelters, and a release from density-dependent food limitation in the low HC. Interestingly, studies on aquacultured Atlantic salmon (*Salmo salar*) indicate that higher complexity can decrease growth rates even when food is unlimited, likely as an effect of the fish prioritizing sheltering over feeding in what may be perceived as a threatening environment (Rosengren et al., 2017). Studies on yet other fish (Herdrich et al., 2018; Lee et al., 2017) and amphibian species (Kenison et al., 2016) found no dependence of individual growth on HC despite positive effects on individual survival or population size. This suggests that additional resources in complex environments can offset the negative effect of increased population density on individuals. More generally, such feedback loops can mask the direct provisioning and altering effects of HC on individuals, which may lead to the false conclusion that HC does not affect individuals if the concomitant effects on the population and community level are ignored.

Various components of HC are themselves products of biogenic processes (shell hash, bivalve beds, macrophytes, coral reefs) or subject to manipulation by organisms inhabiting the environment. This creates potential feedbacks that can modify local environmental complexity (Figure 1, arrow set 8). We are aware of no systematic review of these feedbacks (Figure 2), and their coverage in recent articles is limited and to some extent anecdotal (Tables 1 and S1). For example, solution holes in marine karst habitats attract grouper fish who then enlarge them or excavate new ones to use as a refuge (Ellis et al., 2017). Recovering algal canopies (Ørberg et al., 2018), corals (Roth et al., 2018), mussel beds (Commito et al., 2014), oyster reefs (Brumbaugh & Coen, 2009), and macrophytes (Webb et al., 2016) are typical examples of self-promoting HC. If HC is an aspect of live biomass, it is difficult to separate how much of this feedback lies in biotic processes (e.g., corals producing more polyps via budding) and how much is the net complexity effect (e.g., even a dead coral reef is suitable for the attachment of coral larvae).

Different forms of HC or complexity-creating organisms in one location can act in synergy or interfere. For example, seagrass patches grow better on reefs with higher rugosity (Catano et al., 2016; Lyon et al., 2019), but coral recruitment can be slowed in seagrass patches (Roth et al., 2018). Taller reefs resist sedimentation and enable oyster populations to survive. As oyster shells also contribute to reef height, populations with critical mass can reach growth escape velocity and stabilize themselves (Colden et al., 2017).

In particular, HC-mediated ecological feedbacks were mapped in aquatic vegetated areas (reviewed in Maxwell et al., 2017). Aquatic vegetation traps sediment and nutrients, and can improve water clarity, which contributes to further development of submerged vegetation and therefore further increase in HC. Dense plant growths can also dampen bottom substrate erosion (Fonseca & Koehl, 2006) and decrease sediment grain size by capturing fine sediment (Bouma et al., 2009), leading to a negative feedback between the vegetation and substrate coarseness. Moreover, many vegetation-associated communities are partially shaped by non-trophic interactions with the habitat-forming organisms (van der Zee et al., 2016). In fact, HC-generating species enhance food web complexity in various aquatic ecosystems (Borst et al., 2018) and all macrophyte HC generators feedback negatively on their own biomass as they attract and shelter grazers (e.g., Valentine & Duffy, 2006). Separating the HC effects from the overall biotic and structural effects might prove beneficial to conservation efforts, since increasing HC by adding artificial structures is a common management practice (e.g., reefs, Paxton et al., 2017), and some effects manifest in artificial and even nonmimicking structures (Crooks et al., 2016; Degraer et al., 2020).

Ecosystem engineers can also generate positive or negative feedbacks on HC. Beavers increase HC by dam building and tree-felling (Wathen et al., 2019) and by modifying streamflow and stream-bank erosion patterns (Dauwalter & Walrath, 2018). Since beavers select habitats based on terrestrial characteristics related to HC (wood and macrophytes, Wang et al., 2019), we consider beaver activity to be a HC feedback. Invasive species such as zebra mussels also preferentially settle in complex environments and later transform and enhance its complexity introducing new effects on invertebrates (Cobb & Watzin, 2002). Similarly, crayfish benefit by increased foraging rates and decreased territoriality in more complex environments (Corkum & Cronin, 2004) and then increase HC by burrowing or decrease it by macrophyte elimination (Paglianti & Gherardi, 2004). Marine bivalves have an overall positive effect on species abundance, but the effects depend considerably on bivalve traits and environmental context (Bateman & Bishop, 2017). In sum, these studies demonstrate that complex habitats have the potential to lose, gain or retain complexity via ecological feedbacks.

HC effects on *species richness* are not necessarily directly proportional to increased abundance. For example, both artificial and natural moss patches in a stream hosted more diverse invertebrate communities than riffles and pools (Wulf & Pearson, 2017). Despite that, fewer colonists inhabited the artificial moss patches, which were presumed less complex than their natural counterparts. In that study, a certain level of complexity thus seemed necessary to provide refugia and nurseries for the invertebrates.

The commonly reported *biomass* increases in complex habitats can be driven by changes in abundance due to bottom up processes such as increased periphyton growth (Warfe & Barmuta, 2006) and alterations of size spectra (reviewed by Robson et al., 2005). For example, Trebilco et al. (2015) observed eight-times lower biomass of small fish in low-rugosity reefs compared to high-rugosity reefs, which likely served as refuges of the small fish from predation. This lead to a more evenly distributed size spectrum and larger total biomass in more complex reefs.

HC-driven changes in community composition and species interactions can alter *food web dynamics*. Cascading effects in the food web mediated by trophic and non-trophic interactions can be magnified (Grabowski et al., 2008), dampened (Brogan & Relyea, 2015) or unaffected (Katano, 2013, big-scaled redfin fish *Tribolodon hakonensis*) by HC depending on its role in the ecosystem. Interference between intermediate predators, for instance, can be reduced in complex environments and lead to more targeted predation of basal consumers (Grabowski et al., 2008). These effects can be further modified by the different origins and roles of HC in the pelagic and benthic mesohabitats. For example, Brogan and Relyea (2015) noted how macrophyte presence mitigates cascading effects in the planktonic food chain: zooplankton decline after a pesticide application led to an algal bloom in habitats without macrophytes, but the bloom was prevented in macrophyte presence due to shading. This example illustrates the intricacy of using HC as a general concept when discussing effects on aquatic ecosystems.

Predator functional responses, which describe predator feeding rates as a function of prey density, have a strong effects on *food web stability* (Abrams & Roth, 1994). Prey refuges created in more complex environment are expected to lead to a shift from Type II to Type III functional responses, which have a stabilizing effect on food web dynamics by making extinction events less likely (Oaten & Murdoch, 1975). Barrios-O'Neill et al. (2016) thus predicted higher population stability for prey living on complex substrates than for prey on simple substrates based on extensive predation experiments with multiple species and size classes of freshwater predatory fish and crustaceans. However, most laboratory studies suggest that Holling Type II functional response, with the propensity to destabilize food web dynamics, is most common across taxa and different types and levels of HC (Mocq et al., 2021). Shifts from Type II to Type III are rare and come mainly from experiments on marine taxa (Alexander et al., 2012; Barrios-O'Neill et al., 2016; Long & Whitefleet-Smith, 2013). On the other hand, HC effects on key functional response parameters, attack rate and handling time, appear to differ between 2D and 3D environments (for details see Mocq et al., 2021).

Community composition and dynamics are contingent on *community assembly*, that is, the history of colonization and connected stochastic effects (Drake, 1991). Dispersal is a crucial component of community assembly and plays an important role even in mature communities (Chase, 2010). HC modifies dispersal patterns both directly via habitat preference and oviposition choices made by mobile species, and indirectly by changes in individual fitness and intra- and interspecific interactions, as discussed above. For example, adult amphibians prefer to vocalize, mate and deposit eggs in complex environments (Holzer & Lawler, 2015). Some macrophyte species are essential for aquatic insects as oviposition substrate (dragonflies: Lutz & Pittman, 1968; diving beetles: Inoda, 2011), reiterating the need for more detailed descriptions of HC. In general, highly complex habitats often indicate resource-rich environments and may therefore be preferred dispersal and oviposition targets. On the other hand, the presence of conspecifics can also indicate favorable conditions, and predator presence can be associated with mature environments. Both of these signals are often independent of HC, explaining relative lack of HC-related habitat choice during oviposition in many taxa (Resetarits, 1996).

Finally, "islands" of increased HC can also serve as *stepping stones* and allow species with limited dispersal abilities to spread across otherwise barren environments. This has ramification for habitat restoration efforts. For example, construction of artificial reefs can facilitate spread of species and alter community structure around such reefs (Keller et al., 2017). Importantly, this could also apply to the spread of invasive species, which needs to be considered in environmental management programs.

5 | HC-MEDIATED ECOLOGICAL FEEDBACKS

HC effects on species interactions and communities feedback on individuals and their interactions (Figure 1, arrow set 7). These feedbacks can be either stabilizing or destabilizing, and potentially lead to ecological regime shifts

6 | CONCLUSIONS AND POSSIBLE FUTURE DIRECTIONS

6.1 | Level of focus: effects of HC on biota versus feedback effects

In this review, we presented a conceptual framework to classify the effects of HC in aquatic ecosystems and used it to summarize recent advances in the field. The different links between HC, individuals, species interactions and communities remain unevenly covered, although we found no complete gaps of evidence for our conceptual framework (Figure 2 and Table 1). HC-mediated feedbacks on lower levels of biotic organization (Figure 1, arrow set 7) and feedbacks of local biota on HC (Figure 1, arrow set 8) received the least attention. Despite the methodological challenges mentioned above, focusing on the role of feedbacks has ample potential for future studies given the possibility of ecological surprises in the rapidly changing world. Ecological surprises are defined as "changing population numbers or community compositions that were unanticipated or even diametrically opposed to expectations from past observations, experiments, or theories" (Doak et al., 2008). Such surprises may also be generated by nonlinear ecological feedbacks as demonstrated by abrupt ecological regime shifts (Carpenter et al., 2011; Maxwell et al., 2015).

Relatively few recent studies also documented the provisional aspects of HC (Figure 1, arrow 1). This is surprising, since manipulative experiments create conditions with different HC and should therefore be *a priori* well informed on the physical characteristics of their design. Apart from the provisional aspects, the bottom-up effects of HC on individuals, species interactions and communities have received ample attention in the past. The direct and indirect pathways in which HC affects individuals (Figure 1, arrows 2 or 3) are often studied together (Tables 1 and S1) but rarely resolved. This hampers a full mechanistic understanding of individual-level HC effects. The same is true for interaction- and community-level consequences and even potential feedbacks.

Interaction-level effects of HC continue to be tested in all aquatic environments, with predator–prey interactions constituting the majority of inquiries. On the other hand, the effects of HC on non-trophic interactions including, for example, intra- and interspecific competition and predator interference remain patchily covered (notable exception: salmonids in streams; Höjesjö, 2017). Most studies also use a taxonomy-centered approach (e.g., Schmidt-Drewello et al., 2016), while the use of individual body size (Carroll et al., 2015) and other functional traits remains rare (Grutters et al., 2015). Our understanding of the modifier aspects of other abiotic conditions on the various HC effects also remains fragmentary (e.g., light: Diehl, 2006; temperature: Wasserman et al., 2016). Community-level effects are commonly concerned with abundances and diversity. Despite a strong consensus on the positive effect of HC on diversity, the mechanistic explanations are often not discussed (Ortega et al., 2018). All these topics thus represent promising areas for future studies.

6.2 | Quantification of HC

We suggest that future research should strive for a more widespread use of established quantitative descriptions of HC. In agreement with the recent consensus (Carvalho & Barros, 2017; Kovalenko et al., 2012; Tokeshi & Arakaki, 2012) we call for accurate and standardized descriptions of HC that can be interpreted even beyond their original scope. Accurate description of HC parameters would enable easier replication of experimental designs and cross-experimental comparison (Kovalenko et al., 2012), facilitate meta-analytical and modeling efforts, and provide further data to estimate the provisioning effect of HC. Macrophytes and their analogues can be measured to determine their fractal complexity (Wolters et al., 2019), fractal dimension of substrates can be calculated (Jermacz et al., 2015), and indices of habitat architecture (Lillie & Budd, 1992), plant architecture (Grof-Tisza et al., 2017) or interstitial space can be given (Dibble et al., 1996). Modern imaging techniques can be used to reconstruct 3D environments, leading to accurate description of HC on larger scales (Asner et al., 2020; de Mazzuco et al., 2020).

6.3 | Resolution of HC gradients

The resolution at which HC is studied strongly affects our ability to detect and quantify the effects of HC on biota. This resolution varies between studies (Table 2). Most manipulative studies only test 2–3 levels of HC (i.e., presence/absence of the complexity-generating structure, with the presence sometimes split into a "low" and "high" HC treatment). Field research usually describes HC-generating structures such as macrophytes, woody debris, or other submerged structures quantified using various indices on a continuous, ordinal, or semiquantitative scale.

TABLE 2 HC resolution in individual studies

HC levels	2	3	4	5	6	Variable
Number of studies	71	47	22	12	4	60

Note: HC levels, number of quantitative levels of HC used in the study; variable, continuous or semiquantitative scale of HC (see Table S1).

At least three levels of HC are needed to distinguish between the main qualitative responses to HC (Figure 3), but more levels are advisable to allow for detection of threshold- or optimum effects of HC (Mocq et al., 2021). Ecological systems are complex, with many variables and agents at play even in simplified settings (Doak et al., 2008). In such systems, nonlinear responses to HC can cause chaotic behavior or ecological regime shifts (Carpenter et al., 2011; Scheffer et al., 2001). For instance, vegetated habitats can be vulnerable to small changes in initial plant biomass (Maxwell et al., 2015). Processes like bioerosion in coral reefs (Davidson et al., 2018) and predator–prey dynamics (Sarnelle, 2003) can be sensitive to threshold conditions. Description of potential nonlinear HC effects are thus indispensable to accurately describe dispersal patterns, predator–prey interaction, food web stability, and community dynamics under environmental changes that involve alterations of HC.

6.4 | Spatial and temporal scales of HC

HC and the corresponding variation of complexity-generating elements inherently vary across spatial scales from the microhabitats relevant, for example, for colonization of substrates by sessile organisms to larger spatial scales that characterize the entire ecosystem (reviewed by Tokeshi & Arakaki, 2012). In the context of our framework, most questions related to individuals and interactions and the underlying mechanisms are scale specific, such as the effect of HC on predation rates measured in controlled environments in which factors at other scales are purposefully ignored (e.g., Barrios-O'Neill et al., 2016). However, a comprehensive understanding of the patterns and functionality of HC in an ecosystem context requires data from multiple scales (Tokeshi & Arakaki, 2012), because aspects of HC that are not measured outside of the focal habitat may have influence. As a hypothetical example, fish diversity on a focal patch might not depend on its HC (contrary to, e.g., Lyon et al., 2019) but on the HC of the neighboring patches if more complex habitats supported reproduction of more fish species and all juvenile fish always dispersed away from the natal site before settlement to a random patch. For these reasons, a multiscale perspective should also be used when designing and evaluating the effectiveness of aquatic reserves and/or restoration activities (Charton & Ruzafa, 1999).

Another relevant but often overlooked aspect is the temporal variation of HC at the given spatial scale. This is particularly important in highly dynamic environments such as tidal shore areas but also in environments that vary seasonally such as ponds, streams, or seagrass meadows with rich submerged macrophytes (Gallardo et al., 2017; Henderson et al., 2017; Vowles & Kemp, 2019). Organisms in these environments must either tolerate a wide range of HC, possess physiological and behavioral adaptations to the more or less rapidly changing HC, or the whole community composition may covary with HC over time, for example, through seasonal species turnover (Gallardo et al., 2017), even if the ultimate drivers of the turnover may be unrelated to HC. Identification of key habitat-specific adaptations and functional traits that enable species to withstand such changes in HC would be particularly useful for restoration efforts that strive for rapid recovery of degraded aquatic ecosystems.

6.5 | Importance of HC in habitat management and restoration

HC is a key component to consider within the management of aquatic environments, since homogenization and simplification of aquatic environments are common consequences of human impact. This may come through loss of vegetation beds in lakes and shallow sea areas, sedimentation over coarse substrate and reefs, removal of large epibenthic organisms and destruction of sea bottom by trawling and dredging, and channeling and dredging of rivers (e.g., Turner et al., 1999; Waycott et al., 2009; Wohl, 2005). At the other end of the complexity spectrum, excessive complexity in the form of vegetation overgrowth is also a HC-related and often anthropogenic issue (Stallings et al., 2015). All these changes typically lead to decreased diversity and abundance of fish and other taxa, and are thus considered negative (Czarnecka, 2016; Smokorowski & Pratt, 2007). HC can also be increased, intentionally or not, by human constructions in the water (e.g., oil platforms, wind turbines, bridge foundations, groynes, jetties, and shipwrecks), which may attract or repel certain species (e.g., Consoli et al., 2015; Meyer-Gutbrod et al., 2019) and feedback on the local ecosystem.

As HC is an integral habitat property, conservation and resource maintenance efforts need to consider HC effects on target species, communities, and habitats to accurately predict what happens if HC is altered (Hall et al., 2018; Hartel et al., 2007; Kovalenko et al., 2012). Similarly, responsible planning and execution of ecological restoration requires good knowledge of the HC in the unaltered reference condition for a given environment, and how deviations from this state affects the current community (Bekkby et al., 2020; Palmer et al., 2010; Violin et al., 2011; Wohl, 2005). This reiterates the need to understand how HC affects the different levels of the ecological community, recognizing that the effects may be nonlinear and involve feedbacks (Seraphim et al., 2020).

To gain this complex knowledge, combinations of long- and short-term experiments across laboratory-, mesocosm-, and natural systems coupled with standardized monitoring of any restoration activities may be necessary (Statzner & Moss, 2004). Such multi-level studies can help us disentangle underlying mechanisms of the role of HC on biota (Holzer & Lawler, 2015; Voigt & Hovel, 2019) and provide robust evidence base for the use of HC alterations in nature conservation, restoration, and management (Donadi et al., 2019; Foote et al., 2020; Shafer & Bergstrom, 2010). Currently degraded habitats may offer particular opportunities for combining research and restorative efforts, ascertaining both large arenas for multi-level experiments and monitoring of the effects with benefits for both researchers and managers.

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CONFLICT OF INTEREST

All authors declare no conflict of interests.

AUTHOR CONTRIBUTIONS

Pavel R. Soukup: Conceptualization (equal); data curation (lead); formal analysis (equal); investigation (equal); methodology (equal); visualization (lead); writing – original draft (lead); writing – review and editing (equal). **Joacim Näslund:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); investigation (equal); methodology (equal); validation (equal); visualization (supporting); writing – original draft (supporting); writing – review and editing (equal). **Johan Höjesjö:** Conceptualization (supporting); data curation (supporting); formal analysis (supporting); funding acquisition (equal); investigation (supporting); methodology (supporting); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting).

DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

ORCID

Pavel R. Soukup https://orcid.org/0000-0002-9930-2388
Joacim Näslund https://orcid.org/0000-0003-1091-2225
Johan Höjesjö https://orcid.org/0000-0001-5706-1400
David S. Boukal https://orcid.org/0000-0001-8181-7458

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SUPPORTING INFORMATION

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Supplementary information for “From individuals to communities: habitat complexity affects all levels of organization in aquatic environments”

Pavel R. Soukup, Joacim Näslund, Johan Höjesjö, David S. Boukal

Conceptual framework and data acquisition

We have constructed the overall structure of the conceptual Figure 1 from first-principles thinking. That is, we considered all possible links between different levels of biotic organisation including individuals, their interactions and populations and communities. We assumed that environmental conditions can directly affect only individuals, and their effects on interactions and higher levels of biotic organisation are mediated through the individual level. We also considered all possible feedback loops between the different levels. Examples of the effects included Figure 1 are based on previous reviews and our own literature review and represent the most common or typical effects demonstrated or hypothesized in the literature.

We focused on papers published in years 2015-2020. By querying the Web of Science database (Clarivate Analytics, Philadelphia, last updated 31 December 2020) for “habitat complexity” AND (marine OR *water OR aquatic) we arrived at 555 studies, of which 365 were excluded as irrelevant for the subject of this review, leaving 190 for review. Complementary searches using the Google Scholar search engine (Google LLC, Mountain View) yielded 28 additional studies whose subject matched closely our topics.

Additional search terms (“structural complexity”, etc.) inflated the list of results several times but most of the additional articles (i.e., those that were not found by using the search terms included in the paper) were irrelevant for the subject of this review as they included papers on terrestrial biota and otherwise irrelevant hits. Note that many papers using more specific terms throughout the article such as “woody debris” (Farina et al., 2016), “habitat structure” (Montag et al., 2019) or “vegetation” (Lucon-

Xiccato, 2019) refer to “habitat complexity” at least once in the introduction, abstract or keywords. For these reasons, we chose the narrow but robust search term “habitat complexity”.

We assigned studies from this collected bibliography (Table S1) to the different levels and relationships of our conceptual framework. Our classification was based on both quantitative evidence (even inconclusive) and reasoning illustrated by the relationship to explain a result in the given study. This allowed us to identify knowledge gaps and to suggest future lines of research.

We used the same approach to identify the main reviews and populate Fig. 2. That is, we queried the Web of Science database (Clarivate Analytics, Philadelphia, last updated 31 December 2020) for ("habitat complexity" OR “habitat heterogeneity”) AND (marine OR *water OR aquatic) AND (review OR meta-analysis OR metaanalysis) and included all papers published before 2021, i.e. we did not limit the search to the 6-year window as in Table S1. This approach yielded 97 studies, from which we selected nine papers that focused on at least one of the forward or feedback links between habitat complexity and the local biota (arrows A1–A8 in Fig. 1). Complementary searches using the Google Scholar search engine (Google LLC, Mountain View) yielded 10 additional reviews and meta-analyses.

Table S1: List of reviewed studies, sorted alphabetically by the first author's last name. **Reference** = short citation, see full record below. **HC type (levels)** = type of habitat complexity used; maximum number of independent levels used is given in brackets (var = variable amount along a HC gradient). **Method** = broad categorization of the method and data analysed in the paper. **Organisms** = predators and prey (if any) examined in the study. Organisms from different trophic levels are separated by a "×" sign. **Environment and scale =** categorical information describing: aquatic environment (lotic, lentic, marine or special), spatial scale (microcosm, mesocosm, field and combinations), time scale (minutes, hours, days, weeks, months or years) and region (Africa, Asia, Europe, Arctic, Australia, Latin America, North America or multiple continents). Time scale refers to data collection period or experimental length. When multiple studies are reported in a single paper, the longest value is reported here. **Conclusion** = key results of the study concerning habitat complexity. **A** = Relationships depicted by arrow numbers A1–A8 in Fig. 1 in the main text that were examined in the study. Relationship entries are based on both quantitative evidence (even inconclusive) and reasoning illustrated by the relationship to explain a result in the given study. Abbreviations: HC = habitat complexity, FR = functional response.

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Agudo-Adriani *et al.*, 2016	*Acropora cervicornis* coral structural parameters (var)	community survey	reef fish	marine, field, hours, Latin America	Length, volume, the number of peripheral branches and average number of branches explain 40% of the variability of community structure and over 60% of variability of abundance and richness of fish.	6
Aguilar-Medrano & Arias-González, 2018	coral cover (var)	visual census	reef fish	marine, field, years, Latin America	Variation in HC is a significant factor related to fish richness and functional diversity.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Ajemian, Sohel & Mattila, 2015	*Zostera marina* macrophyte analogue (2)	habitat selection observations	*Perca fluviatilis* × *Gasterosteus aculeatus*	marine, mesocosm, minutes, Europe	Prey prefers vegetated habitats, especially in high turbidity. Prey is less active in turbid environments. Prey uses HC as refuge after predator introduction, especially in high HC.	2, 3
Alexander *et al.*, 2015	macrophyte analogue (4)	counting survived prey, modelling FR	*Micropterus salmoides* × *Poecilia reticulata*	lotic, mesocosm, hours, Africa	Less prey is consumed in high HC compared to all other levels. FR always type II. Handling time and attack rate increases in high HC.	4, 5
Anderson, 2019	turbidity, macrophytes (var)	frog survey	*Rana draytonii*	lentic, field, years, North America	Probability of *R. draytonii* presence increases with vegetation presence and is further associated with moderate turbidity.	6
Strain *et al.*, 2020	seawall tiles, live oyster (2)	community survey	reef community	marine, field, months, Australia	Species density of sessile invertebrates and the percentage cover of oysters does not differ between complex and seeded tiles. Flat unseeded tiles support fewer invertebrates and oysters.	6
Axelrod, Laberge & Robinson, 2018	habitat type (2)	brain mass measurement	*Lepomis macrochirus*	lentic, field, years, North America	Individuals from littoral habitats with dense vegetation have larger brains relative to their size compared to individuals from pelagic rocky habitats.	7
Barrios-O’Neill *et al.*, 2016	substrate type (3)	counting survived prey	fish × *Chelicorophium curvispinum*	lentic, microcosm, hours, Europe	HC mediates the strength of body-mass predator prey relationships and modulates destabilizing interactions.	4, 5, 6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Bartholomew & Burt, 2015	artificial habitat (3)	community survey	seagrass biota	marine, field, weeks, Asia	Shrimp abundance increases with HC in fall.	5, 6
Beal *et al.*, 2020	shell hash or gravel addition (3)	counting and measuring survived prey	*Carcinus maenas* × clams	marine, field, years, North America	Neither shell hash nor gravel mitigate negative effects of predation on clam populations.	6
Beatty *et al.*, 2020	substrate type (3)	counting survived prey	*Pacifastacus leniusculus* × gammarids	lentic, mesocosm, hours, Europe	Under crayfish predation, amphipod survival varies with species, substrate type and the interaction of the two.	4, 5
Beatty, Ryan & Morgan, 2019	woody debris (var)	community survey	*Cherax cainii*	lentic, field, months, Australia	*C. cainii* is more commonly found in areas with woody debris.	6
Bilhete & Grant, 2016	substrate gravel or gravel with stones (2)	behavioural observations, growth rate measurements	*Salmo salar* juvenile × stream biota	lotic, field, minutes, North America	Aggressiveness, feeding rate and territory size is smaller in high HC. Growth rate is not affected by HC.	2, 3, 4, 5
Birck *et al.*, 2019	macrophyte analogue, rock & driftwood (3)	behavioral observation	native fish predators × *Oreochromis niloticus* juveniles	lotic, microcosm, days, Latin America	HC did not influence predatory efficiency of fish predators.	2, 4, 5
Bishop & Byers, 2015	*Gracilaria vermiculophylla* macroalgae, *Crassostrea virginica* shell (3)	counting survived prey, colonization	*Callinectes sapidus* × *Panopeus herbstii*	marine, field & mesocosm, days, North America	Fewer prey (*P. herbstii*) colonize patches with predators (*C. sapidus*). Prey survival is greatest in *C. virginica* oyster beds, lower in algae and lowest in mud. Predator presence deters prey from inhabiting less complex substrates.	2, 3, 4, 5, 6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Bodmer *et al.*, 2017	natural habitats (2)	behavioral observation	shadow stimulus × *Diadema antillarum*	marine, mesocosm, minutes, Latin America	Predator avoidance behavior of *D. antillarum* is comparable in both habitats differing in percentage scleractinian coral cover.	2, 3
Bolduc *et al.*, 2020	macrophytes (var)	community survey	zooplankton	lentic, field, years, North America	Submerged aquatic vegetation influences zooplankton functional groups and diversity indices.	1, 6
Bolduc, Bertolo & Pinel-Alloul, 2016	macrophytes (var)	community survey	zooplankton	lentic, field, weeks, North America	Aquatic vegetation increases functional diversity and total biomass of the zooplankton community.	6
Bolton *et al.*, 2018	crevice volume (3)	video recording, colonization	reef predators × reef biota	marine, field, months, Au	Predation pressure increases with crevice size.	2, 3, 4, 5, 6
Bradford *et al.*, 2020	seawall tiles, live oyster (4)	community survey	seawall community	marine, field, months, Asia	More complex tiles have greater cover and species richness of sessile epifauna. Tiles seeded with oysters facilitate recruitment of the same species.	6
Bradley, Gladstone & Gribben, 2018	*Caulerpa filiformis* macrophyte (2)	visual census	reef fish	marine, field, months, Australia	Fish richness and abundance do not differ among habitat types.	6
Brito, Michelan & Juen, 2021	macrophytes (var)	community survey	dragonfly larvae	lentic, field, months, North America	Limnological variables are more important for dragonfly community composition than habitat complexity.	6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Brogan & Relyea, 2015	*Elodea canadensis* macrophyte (4)	community survey	lentic community	lentic, mesocosm, months, North America	Densities of *E. canadiensis* converged over the course of the experiment. Rotifers reach higher population densities in high HC. Less periphyton grows in high HC. HC prolongs time to metamorphosis and decreases mass at metamorphosis in amphibians. Fewer snails inhabit high HC environments.	6
Buxton *et al.*, 2020	*Cyperus* sp. stalks (3)	counting survived prey	*Anisops sardea*, *Enithares chinai* × *Culex pipiens* larvae	lentic, microcosm, hours, Africa	More *C. pipiens* larvae are consumed in multiple predator treatments in the absence of HC. HC modifies multiple predator effects differently for pairs of predators, reducing prey risk with multiple *A. sardea* compared to *E. chinai*.	4, 5
Cáceres *et al.*, 2020	coral cover (var)	community survey	fish community	marine, field, weeks, Latin America	Complex reefs host fish assemblages with greater functional and ecological diversity.	6
Cai *et al.*, 2019	habitat type (5)	fish community survey	fish	lentic, field, months, Asia	Richness, diversity and number of species differs with season, vegetation type and depth.	2, 3, 6
Callaway, 2018	reef units from various rock (4)	community survey	benthic fauna	marine, field, months, Europe	Different reef units have variable abiotic properties. Community structure and species richness is best explained by the volume of interstitial space and trapped sediment.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Campos *et al.*, 2020	artificial kelp reefs (2)	community survey	reef community	marine, field, months, Latin America	Kelp promotes biomass of specific species and functional groups. Artificial reefs promote construction of biogenic structures and increase HC.	6, 7, 8
Carminatto *et al.*, 2020	habitat assessment score (var)	community survey	fish community	marine, field, months, Latin America	Fish assemblages vary with HC. More complex reefs host more fish of higher species richness.	1, 6
Carroll, Jackson & Peterson, 2015	seagrass macrophyte analogue (5)	counting survived prey	crabs × *Argopecten irradians*	marine, mesocosm, days, North America	HC increases survival in all predator setups. Predator identity and predator & prey size determines the slope of the relationship.	4, 5
Carter, Vodopich & Crumrine, 2018	macrophyte analogue (2)	counting survived prey	*Cybister fimbriolatus*, *Anax junius* larvae × *Pachydiplax longipennis* larvae	lentic, mesocosm, days, North America	Prey consumption was lower in high HC for 4 out of 6 size combinations for both predators. Intraguild predation does not depend on HC.	4, 5, 6
Carvalho, Loiola & Barros, 2017	amount of sediment fractions (4)	community survey	benthic fauna	marine, field, weeks, Latin America	Diversity of sediment fractions does not influence benthic fauna diversity and abundance.	6
Catano *et al.*, 2015	reef structure (var)	behavioral observations	*Sparisoma aurofrenatum*	marine, field, minutes, North America	Males in lower HC reefs choose high HC territories. Males in higher overall HC choose smaller territories.	2, 3
Catano *et al.*, 2016	rugosity of reefs (2)	behavioral observations	*Mycteroperca bonaci* × herbivorous reef fish	marine, field, hours, North America	Seagrass grazing by herbivorous fish decreases in the presence of predator (*M. bonaci*) decoy. This effect is more pronounced in high HC areas and abates with distance from the decoy.	2, 3, 4, 5, 8

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Champion, Rosenfeld & Shadwick, 2018	substrate type (3)	counting survived prey	*Rhinichthys cataractae* × Ephemeroptera, Simuliidae, Chironomidae	lotic, microcosm, hours, North America	Prey capture efficiency of *R. cataractae* declines with current velocity for all prey taxa and substrate types. Foraging efficiency does not depend on substrate type, except for fewer mayflies being consumed on unembedded substrate in medium velocity.	4, 5, 6
Chandler, Gorman & Haas, 2016	macrophyte analogue (3)	counting survived prey	*Procambarus evermanni* × *Lithobates sphenocephalus*, *Pseudacris ornata*	lentic, mesocosm, months, North America	Tadpole grow faster in predator treatments and in more complex treatments. HC does not mitigate predator effects.	2, 4, 5
Cheminée *et al.*, 2015	concrete blocks (4)	community survey	fish community	marine, field, months, Europe	Recruits of *Coris julis* fish occur significantly more often in complex habitats.	2, 3
Chhor *et al.*, 2020	erosion armouring implements (3)	community survey	lake biota	lentic, field, months, North America	Overall biotic diversity does not vary between habitats, more macrophytes grow on natural shorelines, fish and benthic communities differ among habitats.	6
Choi *et al.*, 2015	macrophytes (var)	community survey	epiphytic microcrustaceans	lentic, field, years, Asia	Distribution of epiphytic microcrustaceans differs among macrophyte species.	6
Choi *et al.*, 2016	habitat type (4)	community survey	zooplankton	lentic, field, months, Asia	Zooplankton density is higher in vegetated habitats, especially in the mixed vegetation zone.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Church & Grant, 2019	macrophyte analogue (2)	behavioral observation	*Amatitlania nigrofasciata*	lentic, microcosm, minutes, North America	Dominant *A. nigrofasciata* individuals select and defend complex habitats.	2, 5
Clausing, Phillips & Fong, 2020	substrate rugosity (var)	community survey	algal community	marine, field, years, Australia	HC accounts for most changes in species abundance, obscuring underlying effects of nutrient addition.	6
Clemente *et al.*, 2019	macrophyte analogue (2)	community survey	invertebrate colonization	lentic, field, weeks, multiple continents	Communities in subtropics and temperate zones related to HC types differ. More periphyton grows on floating HC in subtropics and in temperate lakes.	6
Colden, Latour & Lipcius, 2017	man-made reefs of varying height (6)	population survey	*Crassostrea virginica*	marine, field, years, North America	Reefs higher than 30 cm promote long term *C. virginica* survival, whereas lower reefs allow gradual degradation of *C. virginica* populations.	6, 7, 8
Collins *et al.*, 2015	reef relief, volume, origin (3)	population survey	*Epinephelus itajara*	marine, field, years, North America	More *E. itajara* individuals inhabit artificial habitats over natural ones. Abundance of *E. itajara* correlates with high relief and volume.	6
Consoli *et al.*, 2015	shipwrecks (2)	community survey	fish community	marine, field, North America, Europe	Artificial structures host more abundant and species rich communities compared to control sites.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Corser & Wilcox, 2019	habitat metrics (var)	population survey	*Salmo trutta*	lotic, field, months, North America	Local *S. trutta* population uses almost all woody debris, boulders, undercut bank and submerged vegetation habitats available. Different size classes utilize different habitats.	2, 3, 6
Costa-Pereira *et al.*, 2016	habitat type (2)	morphological measurements	*Astyanax lacustris*	lotic, field, years, Latin America	Individual *A. lacustris* captured in habitats of different HC have different body morphologies.	2, 7
Crane *et al.*, 2019	macrophyte analogue (2)	behavioral observation	(alarm cues) × *Pimephales promelas*	lentic, microcosm, days, North America	Risk cues reduce *P. promelas* movement in both HC treatments. Low HC leads to reduced movement of *P. promelas* regardless of cues.	2
Crooks, Chang & Ruiz, 2016	macrophyte analogue and plastic army men (5)	habitat preference	*Palaemon macrodactylus*	marine, microcosm, hours, North America	*P. macrodactylus* shrimps prefer environments with more structures regardless of their organization in space (simple, branched, non-mimic).	1, 2, 3
Cuthbert *et al.*, 2019a	substrate presence (2)	counting survived prey	freshwater turtles × *Gammarus pulex*, Chironomid larvae	lentic, microcosm, minutes, Europe	Substrate presence reduces the magnitude of FR for both prey types in four freshwater turtles commonly kept as pets (*Trachemys scripta scripta*, *T. s. troostii*, *Sternotherus odoratus*, *Kinosternon subrubrum*).	4, 5
Cuthbert *et al.*, 2019b	*Schoenoplectus brachyceras* macrophyte stalks (3)	functional response	*Anisops debilis* × *Culex pipiens* larvae	lentic, microcosm, minutes, Africa	Attack rate decreases stepwise with increasing HC.	4, 5

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Cuthbert, Dick & Callaghan, 2018	plastic caps (2)	functional response	*Macrocylops albidus, M.fuscus, Megacyclops viridis* × *Culex quinquefasciatus* larvae	lentic, microcosm, hours, Europe	High HC decreases attack rate. Handling time is not affected, and FR shape remains Type II.	4, 5, 6
Czarnecka *et al.*, 2019	woody debris (2)	counting survived prey, behavioral observation	*Perca fluviatilis* × *Gammarus fossarum*	lentic, mesocosm, minutes, Europe	HC retards predation on dark nights but not during illuminated nights or during dusk. Fish activity is not influenced by HC.	3, 4, 5
da Silva-Pinto *et al.*, 2020	macrophyte analogues, shelter (2)	behavioral observation	*Stegastes fuscus*	marine, laboratory, minutes, Latin America	Barren habitat and warmer water temperature decrease the frequency of agonistic displays in *S. fuscus*.	2, 3
Dang *et al.*, 2020	reef rugosity (var)	community survey	coral community	marine, field, months, Asia	Small scale HC correlates positively with juvenile coral abundance. Large scale HC correlates negatively with juvenile coral abundance.	6, 8
Dauwalter & Walrath, 2018	habitat type (2)	electrofishing, habitat assessment	*Lepidomeda copei*	lotic, field, years, North America	Beaver activity creates more complex streamflow where *L. copei* occur more often. Other HC components are also associated with *L. copei* occurrence.	6
Davies, Briones-Fourzán & Lozano-Álvarez, 2019	habitat assessment score (var)	community survey	(PaV1 virus) × *Panulirus argus*	marine, field, week, Latin America	Seagrass coverage may increase the probability of infection by PaV1 virus in *P. argus*.	1, 2, 3, 5

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Davis *et al.*, 2017	benthic structural complexity (3)	community survey	mollusc community	marine, field, months, Australia	Species richness and overall diversity increases in highly complex habitats.	6
de Fouw *et al.*, 2016	sea grass (2)	observation of behavior	*Calidris canutus* × *Loripes lucinalis*	marine, microcosm, minutes, Africa	HC increases handling time and decreases searching efficiency of predators.	2, 3, 4, 5
De la Parra, Sarma & Nandini, 2016	*Egeria densa* macrophyte (2)	counting survived prey	*Rhionaeschna multicolor* larvae × mix of invertebrates	lentic, microcosm, hours, Latin America	Prey consumption by *R. multicolor* larvae is lower in high HC.	2, 3, 4, 5
De Rock *et al.*, 2019	seabed shape (var)	occurrence analysis	cetaceans	marine, field, years, Africa	Modelled habitat suitability for some cetaceans correlates with HC.	2, 6
Dennis *et al.*, 2018	various concrete mixes (3)	algae cover and taxonomy	algae community	marine, field, months, Europe	Hemp and shell enriched blocks host more diverse algal communities with a larger live cover.	6
Ding *et al.*, 2015	substrate complexity (var)	community survey	Cichlidae	lentic, field, weeks, Africa	Habitats with higher rugosity host more functionally and taxonomically diverse communities.	6
Donadi *et al.*, 2019	large wood debris (var)	community survey	stream fish	lotic, field, years, Europe	Presence of large woody debris correlates with higher abundance of *Salmo trutta* juveniles. Neither *S. salar* nor sculpin fish were affected by HC.	6
Duarte, Mota & Dias, 2020	macroalgae (4)	community survey	molluscs	marine, field, years, Latin America	Higher HC enhances associated mollusc abundance, richness and diversity.	1, 6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Eggertsen *et al.*, 2020	coral reef outcrops and their features (var)	community survey	reef fish	marine, field, weeks, Australia	Seascape configuration and macroalgae influence rates of herbivory and abundance of parrotfish.	2, 4, 5, 6
Eisele, Madrigal-Mora & Espinoza, 2021	rugosity (var)	community survey	fish community	marine, field, years, Latin America	Season, HC, temperature and sampling location best predict species richness and abundance. Species richness and abundance increases with increased HC.	6
Ellis, Coleman & Koenig, 2017	solution holes density (var)	community survey	*Epinephelus morio* × reef fauna	marine, field, years, North America	*E. morio* occupy on average 55% of solution holes. *E. morio* increase solution holes sizes. *E. morio* presence is correlated with higher abundance and species richness of mobile fauna.	1, 6, 7, 8
Enefalk & Bergman, 2016	fine wood (3)	behavioral observations	*Salmo trutta* juveniles × *Chironomus* larvae	lotic, mesocosm, minutes, Europe	*S. trutta* activity declines and sheltering time increases in complex environments. Fewer attack take place in high HC, but capture rate is unaffected.	2, 3, 4, 5
Farina *et al.*, 2016	macrophyte cover fragmentation (4)	counting survived prey	(natural predation) × *Paracentrotus lividus*	marine, field, weeks, Europe	*P. lividus* survival is lower in continuous habitat types as opposed to low/high fragmentation and rocky habitats. Predation pressure differs among habitats (fish vs. whelks).	4, 5
Ferrari *et al.*, 2018	high-resolution surface rugosity (var)	baited video surveys	reef fish	marine, field, weeks, Australia	High-resolution surface rugosity explained 16% of variance of fish abundance. HC effects on abundance are species specific. Patterns are consistent across functional groups.	6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Ferreira Barbosa *et al.*, 2019	macroalgae (3)	community survey	molluscs	marine, field, weeks, Latin America	HC of 3 algal species was determined, *Sargassum polyceratium* being most complex. Taxonomic and functional richness and abundance of algae-associated molluscs correlates with algal complexity.	1, 6
Figueiredo *et al.*, 2016	turbidity (2)	counting survived prey	*Hoplias* aff. *malabaricus* × *Moenkhausia forestii* × midge larvae	lotic, mesocosm, hours, Latin America	Predation rate of the intermediate predator (*M. forestii*) is decreased by turbidity and unaffected by top predator presence.	4, 5
Figueiredo *et al.*, 2018	macrophyte analogue (2)	counting survived prey	*Astronotus crassipinnis*, *Hoplias* aff. *malabaricus* (non-lethal effects only) × *Astyanax lacustris* × *Daphnia*, *Chironomus* larvae	lotic, mesocosm, minutes, Latin America	Prey survival is increased in high HC. To a lesser degree, high HC increases survival even when non-native predator is present, but not when native predator is. In the presence of a native piscivorous fish in vegetated habitat, pelagic prey is preferred. Otherwise, no selectivity is observed.	4, 5, 6
Figueiredo, Mormul & Benedito, 2015	*Egeria najas* macrophyte (5)	counting survived prey	*Serrapinnus notomelas* × *Chironomus* larvae, *Cypricercus*	lotic, mesocosm, hours, Latin America	Any amount of HC decreases prey consumption. *Chironomus* is preferred as prey in low or no HC treatments, but no preference occurs in high HC.	2, 3, 4, 5
Flores *et al.*, 2016	*Ceratophyllum* macrophyte analogue (2)	leaf mass loss, FPOM production	*Gammarus pulex, Asellus aquaticus, Cyclops viridis* × *Alnus glutinosa* leaf litter	lentic, microcosm, weeks, Europe	Loss of leaf mass by grazing is not affected by HC. All species perform equally, and polycultures do not differ from monocultures. pH decreases in high HC setups.	1, 4, 5

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Flynn *et al.*, 2020	mussel shells and macroalgae (3)	counting survived prey	*Carcinus maenas* × small *Carcinus maenas* or *Panopeus herbstii*	marine, laboratory and field, hours, North America	In both field and laboratory experiments, only the most complex habitat (mussel and macroalga combination) provided more protection to small *C. maenas* or *P. herbstii* crabs from large *C. maenas* predation.	4, 5
Fonseca & Tanaka, 2015	macrophytes (2)	community survey	invertebrate community	lotic, field, months, Latin America	Greater abundance of invertebrates can be found in grass patches in the wet season. In the dry season, diversity is lower in the grass patches. All functional groups other than scrapers are more abundant in grass patches at all sampling times.	6
Fontanarrosa *et al.*, 2019	plankton refuge with floating or submerged plants (2)	community survey	fish × zooplankton	lentic, mesocosm, months, Latin America	Phytoplankton and zooplankton communities diverge in time among treatments. Zooplankton prefers to hide in the traps and avoid open water.	2, 3, 4, 6
Foo *et al.*, 2021	reef rugosity (var)	community survey	reef fish	marine, field, years, North America	Different factors best predict changes in biomass for different functional groups. Generally, increases in rugosity correspond with increases in biomass with all functional groups of fish but especially grazers.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Fulan & Anjos, 2015	*Pistia stratiotes*, *Salvinia auriculata* macrophytes (2)	counting survived prey	*Erythemis* larvae × Chironomidae and Elmidae larvae	lentic, microcosm, days, Latin America	All prey was consumed in zero HC. Presence of *Pistia* reduces prey consumption to about 50%, presence of *Salvinia* to about 60%.	2, 3, 4, 5
Gallardo *et al.*, 2017	*Salvinia biloba*, *Egeria najas* macrophytes (2)	community survey	macroinvertebrate community	lentic, field, months, Latin America	More complex habitats support more diverse and more abundant macroinvertebrates.	6
Garner *et al.*, 2019	reef complexity (2)	community survey	fish community	marine, field, months, North America	Combination of habitat characteristics including HC influences fish community structure.	1, 2, 6
Gehrels *et al.*, 2017	substrate type (6)	counting survived prey	*Carcinus maenas* × juvenile *Carcinus maenas*	marine, field & mesocosm, hours, North America	Juvenile *C. maenas* mortality rates gradually decrease with increasing habitat complexity both in mesocosm and field enclosure experiments.	4, 5
Geraldi, Bacheler & Kellison, 2019	substrate relief (var)	trapping and recording fish	reef fish	marine, field, years, North America	More fish appear on video with increasing HC, but fewer can be caught in traps.	6
Gething *et al.*, 2020	substrate type (4)	community survey	macroinvertebrate community	lotic, field, weeks, Europe	Different substrate types support a distinct macroinvertebrate community with varying degrees of heterogeneity.	6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Glaspie & Seitz, 2018	substrate type (4)	counting survived prey	*Callinectes sapidus* × *Mya arenaria*, *Mercenaria mercenaria*	marine, field & mesocosm, days, North America	In the field, predator exclusion decreases clam mortality, especially in the two more complex substrates (sand, seagrass). In the laboratory *Mya* may retain a low-density refuge from predation even with the loss of structurally complex habitats.	4, 5
Gómez Lutz, Kehr & Fernández, 2015	habitat type (3)	community survey	*Tropisternus* spp.	lentic, field, months, Latin America	More complex ponds host more *Tropisternus* beetles, and more can be caught in vegetated microhabitats.	2, 3, 6
Granzotti, Muniz & Gomes, 2018	macrophytes (3)	video recording, counting survived prey	*Hoplerythrinus unitaeniatus* × *Moenkhausia forestii*, × *Chironomidae* larvae	lotic, mesocosm, hours, Latin America	HC and *H. unitaeniatus* presence did not influence total prey consumption. More *M. forestii* individuals preyed on *Chironomidae* in the absence of *H. unitaeniatus*. M. forestii survival increased with HC in the presence of *H. unitaeniatus*. *H. unitaeniatus* switches to sit-and-wait strategies with increasing HC. *M. forestii* form shoals and seek cover in HC in the presence of the *H. unitaeniatus*.	1, 2, 3, 4, 5
Gregor & Anderson, 2016	different sized rocks, artificial habitat (3)	counting survived prey	*Paralabrax clathratus* × *Lythrypnus dalli*	marine, field & mesocosm, days, North America	Fish survival increases with rock size. Low predator access and low interstitial space promote prey survival. Prey prefer low predator access habitats only when predator is present.	1, 2, 3, 4, 5

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Grof-Tisza *et al.*, 2017	macrophytes and macrophyte analogues (2)	exuviae survey, behavioral observation, counting survived prey	naturally occurring birds × *Sympetrum corruptum* larvae	lentic, field, days, North America	*Sympetrum* exuviae are more commonly found on plants with defences and more complex plants. Larvae choose to moult on complex plants, cages or plants with defenses. Mechanical defenses and plant complexity decrease avian predation on moulting larvae.	1, 2, 3, 4, 5
Grutters *et al.*, 2015	native and non-native macrophytes and their analogues (3)	counting survived prey	*Cyprinus carpio* juveniles, *Anax imperator* larvae × *Daphnia*, *Gammarus* and damselfly mix	lentic, mesocosm, minutes, Europe	Carp consumes invertebrate prey in all densities of both native and non-native plants. Under *Anax* predation, *Gammarus* survival is greater if any HC is available. Shoot fractal dimension and rigidity (usually high in macrophyte analogues) alter prey survival in complex environments.	1, 4, 5
Guo *et al.*, 2020	artificial habitat (2)	community survey, counting survived prey	*Clarias gariepinus* × fish community	lotic, field and laboratory, months, Asia	Artificial habitats increase species richness, abundance and diversity in field and improve survival of juvenile fish under predation in laboratory.	4, 5, 6
Hao *et al.*, 2017	macrophytes and their analogues (3)	community survey	periphyton community	lentic, mesocosm, months, Asia	Natural plants host less periphyton than artificial ones. Periphyton density and biovolume generally increases with HC.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Hasselquist *et al.*, 2018	various metrics, including substrate heterogeneity (var)	community survey	macrophyte, diatom and invertebrate biota	lotic, field, days, Europe	Sediment heterogeneity and beaver wood increases macroinvertebrate species richness and abundance. Some aspects of HC are correlated with additional community characteristics.	6
Hatcher *et al.*, 2019	submerged structures (var)	community survey	fish community	lentic, field, years, North America	Mudflats with submerged structures harbour more fish of a higher range of sizes. Community composition differs in complex and barren mudflats.	6
Henderson *et al.*, 2017	macrophyte and habitat metrics (var)	community survey	fish	marine, field, months, Australia	Species richness is predicted by the distance to mangroves and seagrass areas, shoot density and seagrass biomass.	6
Herdrich *et al.*, 2018	large wood debris (2)	core sampling, electrofishing, otolith measurement	*Salvelinus fontinalis*	lotic, field, months, North America	*S. fontinalis* population density and biomass are higher in high wood streams. Growth rate is not affected by HC.	6, 7
Hill, 2016	macrophytes and exclusion cage (3)	community survey, counting survived prey	*Micropterus salmoides* *Hemichromis letourneuxi* and other fish	lotic, field & mesocosm, years, North America	Water level and HC predicts fish abundance in the field. HC increases prey survival in mesocosms.	4, 5, 6
Ho *et al.*, 2018	macroalgae cover (var)	habitat assessment, visual census	reef fish	marine, field, years, Asia	Fish density and species richness correlate with seagrass coverage and distance from coral reef.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Höjesjö *et al.*, 2015	macrophyte analogues (2)	population survey	*Salmo trutta*	lotic, field, months, Europe	Emerged 0+ *S. trutta* abundance, condition and overall biomass is higher in high HC. Low HC habitats host only few but larger and heavier *S. trutta*. HC has no effect on 1+ year old *S. trutta*.	6, 7
Holzer & Lawler, 2015	invasive and native macrophytes (5)	community survey, behavioral observation	*Pseudacris regilla*, other colonizing taxa	lentic, field & mesocosm, months, North America	More larvae and calling males of *P. regilla* are found in canary grass (*Phalaris arundinacea*) habitat. Average *P. regilla* tadpole survival is greater in canary grass. Algal primary production and water quality is not affected by HC. Predator and competitor communities are similar among treatments with plants and differ from plant-free controls.	2, 3, 6
Hovel *et al.*, 2016	macrophyte analogue, *Zostera marina* (3)	behavioral observations, counting survived prey	*Heterostichus rostratus* × *Hippolyte californiensis*	marine, mesocosm, minutes, North America	Prey consumption is independent of HC. Predators move less in epiphyte-enhanced shoots in both shoot densities. Predator strikes are more likely to success in low HC. In high HC prey attempts to escape the predator less often.	2, 3, 4, 5
Huang *et al.*, 2016	*Hydrilla verticulata* macrophyte (3)	counting survived prey	*Procambarus clarkia* × *Rhodeus sinensis*	lentic, microcosm, hours, Asia	Prey consumption decreases with HC and increases with prey density.	4, 5
Hunt *et al.*, 2019	3D reef structure (var)	visual census	*Pterois* spp. fish	marine, field, months, Latin America	*Pterois* individuals prefers broad-scale, rather than fine-scale, HC.	2, 3

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Hylkema *et al.*, 2020	artificial reefs (4)	community survey	reef fish	marine, field, months, Latin America	Artificial reefs host richer and more abundant fish communities than bare sand. Reefs providing more shelter volume host an even higher fish abundance and biomass.	1, 6
Ilarri *et al.*, 2018	shell type diversity (3)	invertebrate colonization	river biota	lotic, field, months, Europe	Heterogeneous treatments attract higher density of individuals of higher species richness and functional diversity than homogenous treatments.	6
James *et al.*, 2019	habitats of varying complexity (var)	gut content analysis	*Rhabdosargus holubi*	marine, field, months, Africa	*Rh. holubi* successfully utilizes habitats with varying complexity. Diet differs according to habitat.	1, 2
Jermacz *et al.*, 2015	substrate coarseness, macrophytes and their analogues (5)	behavioral observation	*Pontogammarus robustoides*	lentic, mesocosm, minutes, Europe	*P. robustoides* prefers coarser substrate, juveniles slightly less so than adults, and the most complex plants. Juveniles prefer natural plants over artificial analogues.	1, 2, 3
Kenison *et al.*, 2016	naturally occurring macrophytes, branch bundles (2)	community survey	naturally occurring fish × *Ambystoma macrodactylum* larvae	lentic, field, months, North America	Vegetation density increases the probability of capture of *A. macrodactylum* in trout populated ponds but decreases it in trout-free ponds. Added HC has no effect on growth rate, morphology or metamorphosis of *A. macrodactylum* larvae.	2, 3, 7

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Kerry & Bellwood, 2015	coral canopy (4)	community survey	reef fish	marine, field, years, Australia	Coral canopy influences fish assemblages. Removing canopy reduces large fish diversity and abundance, especially for some groups.	6
Kloskowski, Nieoczym & Stryjecki, 2020	dry plant biomass	community survey	natural predators × tadpole	lentic, field, months, Europe	The use of open or complex habitat is species specific. Only *Bufo bufo* densities were higher in the presence of fish.	2, 6
Kobak *et al.*, 2016	*Dreissena polymorpha*, substrate type (3)	counting survived prey	*Babka gymnotrachelus*, *Proterorhinus semilunaris* × *Chironomus* larvae	lotic, microcosm, minutes, Europe	Predators eat most *Chironomus* larvae on sandy substrate. *P. semilunaris* feeds in mussel beds more efficiently than *B. gymnotrachelus*. Abundance of *Chironomus* increases in mussel beds.	2, 3, 4, 5
Kobak, Jermacz & Dzierzyńska-Białończyk, 2015	substrate coarseness, macrophytes and their analogues, *Dreissena* sp. (6)	behavioral observation	*Dikerogammarus villosus*	lentic, mesocosm, hours, Europe	*D. villosus* prefers coarser substrate, juveniles slightly less so than adults. *D. villosus* prefers the most complex macrophytes, adults slightly less so than juveniles. All *D. villosus* always prefer mineral particles over macrophytes. *D. villosus* prefers stones rather than living *Dreissena* mussel beds.	1, 2, 3
Kolar, Boukal & Sentis, 2019	macrophyte analogue (2)	counting survived prey	predation risk cues × *Ischnura*, *Libellula* and *Sympetrum* larvae × *Daphnia*	lentic microcosm, hours, Europe	More prey is eaten in high HC in the absence of predation risk cues, except for *Sympetrum*.	4, 5

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Kornijów, Measey & Moss, 2016	*Nuphar lutea* macrophyte (3)	community survey	*Perca fluviatilis* × pond biota	lentic, field, months, Europe	Benthos abundance and biomass is highest in medium HC and lowest in high HC. Fish presence decreases total invertebrate biomass. Perch feed on plankton and floating leaves but avoid petioles.	2, 3, 4, 5
Krabbenhoft, Burdett & Turner, 2017	dry leaf litter (2)	invertebrate colonization, gut content analysis	young-of-the-year fish × invertebrate community	lotic, mesocosm, weeks, North America	Total invertebrate density did not differ between HC treatments. Fish prey preference is independent on the presence of leaf litter.	4, 5, 6
Kristensen *et al.*, 2015	mussel beds (2)	community survey	fish community, eelgrass	marine, field, months, Europe	Addition of mussel beds increases abundance and diversity of fish even though most mussels are killed by starfish.	6
Kuhnen *et al.*, 2019	mariculture structures (var)	community survey	fish community	marine, field, months, Latin America	Low HC leads to elevated fear in minnows. Risk cues reduce movement in both HC treatments.	2
Lantz & Cook, 2015	*Utricularia* macrophyte (3)	recording behavior	wading birds × *Gambusia holbrooki*	lentic, field, days, North America	Wading birds prefer more complex habitats early in January and less complex habitats in April. Bird foraging efficiency is not influenced by HC.	2, 3, 4, 5
Lazic *et al.*, 2018	natural habitats (var)	visual census	*Hippocampus hippocampus* and *H. guttulatus* seahorses	marine, field, years, Europe	Seahorses of both species are more often found in habitats assumed more complex.	1, 2, 8
Leclerc & Viard, 2018	macrophyte analogue (3)	colonization of substrate	marine biota × fouling community	marine, field, months, Europe	HC does not influence species richness, abundance and composition of the fouling community.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Leclerc *et al.*, 2016	*Laminaria hyperborea* kelp strata (4)	community survey	kelp forest biota	marine, field, months, Europe	Richness and biomass of fauna and flora differ between *Laminaria* kelp strata.	6
Ledbetter & Hovel, 2020	eelgrass and bryozoan analogues (6)	counting survived prey, behavioral observation	*Heterostichus rostratus* × *Hippolyte californiensis*	marine, laboratory and field, hours, North America	*H. rostratus* prefers to forage in a clean eelgrass model habitat rather than bryozoan seagrass model habitat. Increased eelgrass density reduces foraging efficiency. Survival of tethered *H. californiensis* does not depend on HC in the field.	2, 3, 4, 5
Lee *et al.*, 2017	exclosure (4)	counting survived prey	*Coreoperca herzi* × *Rhynchocypris oxycephalus*	lotic, mesocosm, weeks, Asia	Exclosures increase survival and decrease vulnerability of *R. oxycephalus* to predation. HC did not influence growth rate of *R. oxycephalus*.	4, 5, 7
Lemay *et al.*, 2021	seaweed morphotypes (5)	community survey	microbial community	marine, field, days, North America	Morphological characteristics of seaweeds can impact their microbiome by altering the way they come into contact with microbes, independent of biotic interactions.	6
Leslie *et al.*, 2017	*Spartina maritima*, *Zostera capensis* macrophytes (3)	community survey, behavioral observation	*Rhabdosargus holubi*	marine, field, months, Africa	*Zostera capensis* has higher stem density and dimensionless indices than *Spartina*. Biomass of both plant species is comparable. Behavior of *R. holubi* differs between habitats and more complex habitats host more *R. holubi* individuals.	1, 2, 3, 6
Li *et al.*, 2019	coarse woody debris (var)	community survey	invertebrate community	lotic, field, days, Asia	HC increases taxonomic and functional diversity of invertebrate communities.	6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Liao, Yeh & Mok, 2015	macrophyte shoot density (4)	community survey	meiofauna community	marine, field, hours, Asia	Meiofauna abundance, diversity and community structure differ between habitats. HC increases abundance and diversity of meiofauna.	6
Lisney, Collin & Kelley, 2020	habitat metrics (var)	morphological measurements	*Melanotaenia australis*	lotic, field, months, Australia	Populations of *M. australis* inhabiting low HC habitats have on average smaller, more dorsally located eyes.	7
Loke & Todd, 2016	concrete tiles with constant surface area (4)	community survey	colonization	marine, field, months, Asia	Abundance and species richness are highest in tiles with “pits”. More complex variants underline this effect.	6
Loke *et al.*, 2019	concrete tiles (3)	community survey	colonization	marine, field, months, Asia	Covered complex tiles host more organisms of higher species richness than uncovered complex tiles and control tiles.	6
Lopes *et al.*, 2015	macrophytes (2)	community survey	fish community	lotic, field, hours, Latin America	Fish density is decreased by vegetation density. Densely vegetated patches host more species-rich communities.	6
Lowe *et al.*, 2019	reef slope and rugosity (var)	community survey	reef fish community	marine, field, years, Australia	Structural complexity of benthos best predicted wrasse density. Declines in HC and hard coral cover leads to abundance declines in many species.	6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Lucon-Xiccato, 2019	macrophytes (2)	behavioral observation	*Pelophylax esculentus*	lentic, microcosm, minutes, Europe	Alarm cues obtained from *P. esculentus* tadpoles raised in vegetated areas have variable effect on *P. esculentus* tadpoles, whereas cues obtained from *P. esculentus* tadpoles raised in sparsely vegetated areas decrease activity in the tadpoles.	2, 3
Lv *et al.*, 2019	*Potamogeton crispus* macrophyte (var)	community survey	algae community	lentic, field, months, Asia	Macrophyte cover (%) and epiphytic algal richness are correlated.	6
Lyon *et al.*, 2019	reef structure of artificial reefs (var)	community survey	reef fish, eelgrass	marine, field, months, North America	Reef rugosity correlates positively with seagrass density. Complex reefs host most diverse communities of fish, whereas less complex reefs host more abundant communities of fish.	6, 8
Margiotta *et al.*, 2016	oyster shells and living oyster trays (3)	invertebrate colonization	several crab species (*Eurypanopeus depressus*, *Panopeus herbstii*, *Petrolisthes armatus*)	marine, field, months, North America	Densities of oyster spat and *P. armatus* increase with rugosity. *E. depressus* densities increase with rugosity and with *Brachiodontes exustus* mussel densities. *P. herbstii* is evenly distributed regardless of rugosity.	1, 2, 3, 6
Marin Jarrin *et al.*, 2015	field locations of presumed varying complexity (2)	gut content analysis, zooplankton community	*Perca flavescens* × zooplankton	lentic, field, years, North America	Habitat heterogeneity caused by the Maumee River plume during the spring season does not affect zooplankton community composition, density of larval yellow perch, its diet or foraging behavior.	2, 3, 4, 5, 6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Massicotte *et al.*, 2015	macrophytes, EVI (enhanced vegetation index) (var)	field survey, satellite imaging	*Perca flavescens*	lentic, field, years, North America	Probability of observing *P. flavescens* larvae increases in environments with high EVI measure.	2, 3, 6
Matias *et al.*, 2015	habitat fragmentation intensity (3)	invertebrate colonization	invertebrate community	marine, field, weeks, Europe	Animal assemblages are not affected by habitat fragmentation intensity.	6
Matsuda *et al.*, 2015	macrophytes (var)	community survey	Ostracoda	combined, field, weeks, Latin America	Some ostracod species are associated with vegetation of higher fractal dimension.	1, 6
Mayer-Pinto, Matias & Coleman, 2016	synthetic turf (2)	community survey	benthic community	marine, field, weeks, Australia	Newly colonized assemblages vary among different habitat types. Contaminants mediate the increase of richness caused by HC.	6
Mazão & Bispo, 2016	substrate (2)	invertebrate colonization	colonization	lotic, field, weeks, Latin America	Substrate complexity does not alter species composition in riffles and pools.	6
Mazzuco, Stelzer & Bernardino, 2020	rugosity (var)	community survey	benthic community	marine, field, months, Latin America	Diversity and composition of benthic assemblages are regulated by rugosity and temperature.	1, 6
Medeiros & Henry-Silva, 2017	*Egeria densa*, *Chara indica* macrophytes (2)	behavioral observation	*Melaniodes tuberculata*	lentic, microcosm, hours, Latin America	Snails prefer grazing on *E. densa*, which is more complex than *Ch. indica*.	1, 2, 3, 4, 5

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Mendez, Schwindt & Bortolus, 2015	*Balanus glandula* structures (3)	community survey	invertebrate community	saltmarsh, field, months, Latin America	HC increases diversity, species richness and abundance of macroinvertebrates. Different communities establish in habitats of varying complexity.	6
Mendo *et al.*, 2015	*Hincksia sordida* algae (var)	community survey, predation trials	natural predation × *Pecten fumatus*	marine, field, weeks, Australia	Predation risk of *P. fumatus* is lower in areas with intermediate algal biomass. *P. fumatus* density is independent on algal biomass.	4, 5, 6
Meyer-Gutbrod *et al.*, 2019	oil platform structures (var)	community survey	fish community	marine, field, years, North America	Fish utilize oil platform structures unevenly, internal horizontal crossbeams being the most attractive.	2, 3,
Michaels & Preziosi, 2015	macrophytes and macrophyte analogues (4)	behavioral observations, individual measurement	*Agalychnis callidryas* tadpoles	special, microcosm, weeks, Europe	Both artificial and live plants increase *A. callidryas* size at metamorphosis. Larval period is shortened in high HC. Leaping behavior is rare in HC treatments.	2, 3
Milesi, Dolédec & Melo, 2016	slate blocks (2)	community survey	invertebrate colonization	lotic, field, months, Latin America	Heterogeneous slate blocks host more organic matter and invertebrates of higher functional diversity. Large, predatory or shredder and collector invertebrates are more common on heterogeneous slate blocks. Scrapers and case-building organisms are prominent on homogeneous substrates.	1, 6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Miyashita, Paul Richardson & Emmett Duffy, 2016	algae *Gracilaria*, *Crassostrea virginica* shells (2)	observation of behavior	*Crangon septemspinosa*, *Palaemonetes pugio*, *Callinectes sapidus* × *Americamysis bahia*	marine, mesocosm, weeks, North America	All three predators are more effective in high HC. HC alone does not affect mysid abundance or microalgal biomass. *P. pugio* and *C. sapidus* only prey on mysids in high HC. *C. septemspinosa* and predator polyculture (one of each species together) suppress mysids regardless of HC. *C. septemspinosa* is the most effective predator regardless of HC. *C. sapidus* survive better in high HC.	2, 3, 4, 5, 6
Montag *et al.*, 2019	coarse woody debris (var)	community survey	stream biota	lotic, field, months, Latin America	HC correlates with species richness. Various habitat characteristics are associated with species richness in different groups.	6
Morris *et al.*, 2017	concrete flowerpots on seawalls (2)	visual census	reef fish	marine, field, months, Australia	Flowerpots have no consistent effects on fish assemblages.	6
Murray, Stillman & Britton, 2016	substrate (2)	behavioral observations	*Rutilus rutilus* × food pellets	lentic, microcosm, North America, Europe	HC decreases reaction distance of predators. Fewer prey is consumed in high HC. Turbidity reduces consumption rate and increases search time.	2, 3, 4, 5
Nay *et al.*, 2020	coral (2)	behavioral observation	*Chromis atripectoralis*	marine, laboratory, hours, Australia	When presented with environments with multiple temperatures, *Ch. atripectoralis* chose to inhabit high HC environments even slightly outside of the preferred temperature range.	2, 3

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Newman *et al.*, 2015	reef complexity (5)	community survey	reef biota	marine, field, North America, Latin America	HC correlates positively with species richness.	6
Nichols, Segui & Hovel, 2015	algae cover (2)	community survey, behavioral observation, counting survived prey	natural predation × *Strongylocentrotus* spp.	marine, field, months, North America	*Strongylocentrotus* mortality is higher in no-cover treatments during the day. Night-time predation is not affected.	2, 3, 4, 5
Nunes, Sampaio & Barros, 2015	rugosity of reefs (var)	behavioral observation	diver (spearfishing mimic) × reef fish	marine, field, North America, Latin America	Escape behavior of reef fish varies between species and habitats. Fish in high HC often hide in holes rather than flee in a group.	3
Ohira *et al.*, 2015	stream depth and velocity (var)	community survey	fish community	lotic, field, months, Asia	Species richness correlates with HC.	6
Olson *et al.*, 2019	*Zostera marina* macrophyte, adjacent habitat (3)	trawling, observations, gut content analysis	*Sebastes* spp. fish	marine, field, months, North America	Rockfish recruitment is higher in most complex meadows or in meadows adjacent to kelp forests. HC dampens the positive effect of kelp proximity.	6
Ørberg *et al.*, 2018	rock rugosity, macroalga cover (4)	individual measurement	molluscs and barnacles	marine, field, years, Arctic	Algal canopy and rock rugosity facilitate recolonization and increase species richness.	6, 7, 8

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Orland *et al.*, 2016	*Laminaria hyperborea* kelp (var)	CT scan of kelp holdfasts	kelp-associated invertebrates	marine, field, North America, Europe	Volume and age of kelp holdfasts correlates strongly with abundance and richness of invertebrate colonist. Community composition is usually dominated by one group.	1, 6
Osório *et al.*, 2019	macrophyte analogue (2)	periphyton community survey	periphytic colonization	lentic, field, weeks, Latin America	Species richness, diversity and density of periphyton is greater on complex macrophyte analogues. Community composition varies among HC treatments.	6
Paxton *et al.*, 2017	artificial and natural reef structures (4)	visual census	reef fish	marine, field, years, North America	Reef rugosity varies among reef structures and increases fish abundance and species richness.	6
Paz Cardozo *et al.*, 2021	macrophyte biomass (3)	community survey	*Moenkhausia forestii*	lotic, field, days, Latin America	Individual specialization in diet and morphology is greatest in *M. forestii* populations inhabiting sites with low to intermediate macrophyte biomass.	7
Perkins *et al.*, 2020	rugosity (var)	habitat imaging	barren habitat	marine, field, years, Australia	Barrens are more likely to develop in areas with higher reef rugosity.	1, 6
Phillips & Prestie, 2017	sampling baskets placed on different substrates (2)	invertebrate colonization	macroinvertebrate community	lentic, field, months, North America	Different species of invertebrates colonize sampling baskets in varying densities based on the substrate underneath the baskets.	6
Pilotto *et al.*, 2016	woody debris (2)	community survey	invertebrate community	lotic, field, months, Europe	Invertebrates are most abundant directly on or near wood logs. Wood-rich habitats host most diverse invertebrate communities.	6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Pitcher & Soluk, 2016	habitat connectedness and macrophyte analogue (2)	counting survived prey	*Anax junius* larvae, *Lepomis cyanellus* × amphipods, snails and damselflies	lentic, mesocosm, hours, North America	HC decreases *A. junius* predation on amphipods. *A. junius* and *L. cyanellus* combined consume more prey than predicted from their individual consumption regardless of HC.	2, 3, 4, 5
Porreca *et al.*, 2020	macrophyte analogue (2)	counting survived prey, morphological analysis	*Micropterus salmoides* × *Pomoxis* spp.	lentic, field, hours, North America	Morphological differences in *Pomoxis* species alter their predator evasiveness. *P. nigromaculatus* are more successful at evading capture in vegetation and *P. annularis* are more successful at evading capture in open water.	4, 5, 7
Price *et al.*, 2019	coral (var)	community survey	coral community	marine, field, days, Europe	Coral cover correlates closely with measured rugosity. Diversity of the coral community plateaus with rugosity. Proportion of dead to live coral does not matter to coral community structure.	1, 2, 3, 6
Rek & Kwiatkowska, 2016	habitat type (3)	acoustic measurements	Rallid birds	lentic, field, days, Europe	Signals of species inhabiting less complex habitats have longer transmission ranges than signals of species inhabiting more complex habitats	?
Ren *et al.*, 2019	macrophyte analogue (5)	prey mass and count consumed, growth rate	*Siniperca chuatsi* × *Cirrhinus mrigala*	lentic, mesocosm, weeks, Asia	Any amount of vegetation increases prey (*C. mrigala*) consumption and weight gain of *S. chuatsi* compared to barren habitats.	4, 5

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Renick *et al.*, 2015	macrophyte analogue (3)	counting survived prey, behavioral observation	*Gasterosteus aculeatus* × *Atherinops affinis* larvae	marine, mesocosm, minutes, North America	Predation increases with increasing HC. Pesticide exposure and habitat structure reduces prey aggregative behavior.	2, 3, 4, 5
Reynolds *et al.*, 2018	*Zostera marina* macrophyte (var)	counting eaten tethered prey	natural predators × site-specific amphipods and gastropods	marine, field, hours, multiple continents	Predation on amphipods decreases with increasing seagrass shoot density and latitude.	4, 5
Riquelme-Pérez *et al.*, 2019	*Lessonia trabeculata* macroalga kelp (2)	community survey, baited predation observation	piscivorous fish × fish	marine, field, months, Latin America	Fish richness and predation pressure is independent of habitat type. More fish can be seen on barren ground.	2, 3, 4, 5, 6
Roth *et al.*, 2018	reef rugosity (2)	community survey	reef biota	marine, field, months, Asia	Algae-dominated habitats experience slower coral recruitment. Coral-dominated habitats host higher fish biomass.	6, 7, 8
Schmidt-Drewello *et al.*, 2016	leaves (2)	counting survived prey	*Gasterosteus aculeatus* × *Echinogammarus berilloni*, *Gammarus fossarum*, *G. pulex*	lotic, microcosm, hours, Europe	*G. aculeatus* prefers native prey (*G. fossarum, G. pulex*) over invasive prey (*E. berilloni*) in complex environment; both prey types are consumed similarly in absence of HC. Predation decreases in high HC. *E. berilloni* are better protected by HC than native prey.	2, 3, 4, 5
Schweitzer & Stevens, 2019	coverage of biogenic organisms (var)	community survey	reef fish	marine, field, years, North America	Fish abundance is correlated with proportion of total cover by biogenic structures.	2, 3, 6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Selfati *et al.*, 2018	artificial habitat (2)	fishing effort and visual census	Epinephelinae (groupers)	marine, field, weeks, Africa	Artificial habitats host a significantly higher grouper density than natural habitats.	6
Smith, Quist & Hardy, 2016	habitat metrics (var)	community survey	fish community	lotic, field, years, North America	Species richness increases with HC.	6
Sohel & Lindström, 2015	algal turbidity (2)	behavioral observation	*Sterna hirundo* silhouette × *Gasterosteus aculeatus*	marine, mesocosm, months, Europe	Smaller proportion of *G. aculeatus* individuals flees into shelter and leaves the feeding area in turbid water.	2
Sridharan & Namboothri, 2015	root density and canopy cover (var)	community survey	fish community	lotic, field, months, Asia	Root density and canopy cover does not affect fish abundance and species richness.	6
Stahr & Shoup, 2015	*Justicia americana* macrophyte (2)	recording behavior	*Micropterus salmoides* × *M. salmoides* juvenile	lentic, mesocosm, minutes, North America	Juvenile survival increases with HC. Predators are less active in HC. Attacks are more successful in no HC treatments. Juveniles avoid adults in absence of HC but hide in complex structures regardless of predation risk.	2, 3, 4, 5
Stahr & Shoup, 2016	macrophyte analogue (5)	observation of behavior	*Micropterus salmoides* × Chironomidae larvae	lentic, microcosm, minutes, North America	*M. salmoides* consumed prey equally regardless of HC.	4, 5
Stephan *et al.*, 2019	*Eichhornia crassipes* (2)	community survey	zooplankton community	lentic, mesocosm, weeks, Latin America	Floating macrophytes increase diversity by providing habitats for complementary functional groups to pelagic species.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Strain *et al.*, 2021	concrete tiles (3)	colonization	artificial structure biota	marine, field, months, global	Effects of HC on biodiversity are variable across different functional groups and local abiotic and biotic conditions.	6
Taira *et al.*, 2020	concrete tiles (2)	community survey	shoreline community	marine, field, months, Asia	Plots with enhanced HC host a greater abundance and species richness of fish. More biotic cover in complex habitats attracts epibenthic feeding fishes.	2, 3, 4, 5, 6
Tano *et al.*, 2017	macroalgal beds and seagrass meadows (var)	fish and habitat survey	fish	marine, field, months, Africa	Macroalgal beds host more juvenile fish than seagrass meadows.	6
Tavares *et al.*, 2017	macrophyte analogue (2)	counting emerged individuals	*Hyphessobrycon eques* × larvae of Coenagrionidae	lentic, mesocosm, weeks, Latin America	Coenagrionid larvae emerge sooner and have lower mortality in high HC.	6
Taxböck *et al.*, 2020	diversity of substrates (var)	community survey	diatom community	freshwater, field, years, Europe	Diatom species richness increased with elevation of springs and habitat diversity.	6
Thiriet *et al.*, 2016	habitat type (4)	community survey	reef fish	marine, field, weeks, Europe	Diversity and abundance of fish is highest in the most complex habitat and lowest on barren ground.	6
Tornwall, Swan & Brown, 2017	substrates in sampling baskets (2)	invertebrate colonization	macroinvertebrate community	lentic, field, weeks, North America	Species richness increases in time and differs between low and high HC treatments in headwater streams. In the main-stem waters these differences disappear after about 4 weeks.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Torres, Giri & Collins, 2018	macrophytes (3)	habitat and decapod community survey	freshwater decapods	lotic, field, North America, Latin America	Body sizes, abundances and sex ratios of different species are affected by the presence of macrophytes. Some are more abundant in floating vegetation, while others in vegetation-free and emerged vegetation waters.	6
Tramonte *et al.*, 2019	macrophyte analogue (2)	grazing activity measurement	*Melanoides tuberculata*, *Aylacostoma chlorotica* × algae community	lotic, mesocosm, hours, Latin America	Native grazer (*A. chlorotica*) consumption is constant in both HC treatments, but invasive grazer (*M. tuberculata*) consumes less algae in the high HC treatment.	1, 2, 3, 4, 5, 6
Trebilco *et al.*, 2015	rugosity, kelp characteristics (var)	community survey	fish community	marine, field, years, North America	Higher rugosity correlates with greater density of smaller fish and greater total fish biomass. Higher kelp stipe density increases overall biomass across the entire size spectrum. Size spectra predictions can be obtained from habitat characteristics.	6
Tsunoda & Mitsuo, 2018	naturally occurring macrophytes (var)	gut content analysis	*Micropterus salmoides* × pond biota	lentic, field, North America, Asia	Vegetation cover is associated with lesser fish consumption.	4, 5
Tuntiprapas, Rattanachot & Prathep, 2021	seagrass (var)	community survey	*Thalamita crenata*	marine, field, months, Asia	*T. crenata* abundance increases with seagrass cover.	6
Turnbull *et al.*, 2018	reef heterogeneity (var)	visual census	reef biota	marine, field, years, Australia	Fish abundance and biomass increases with increasing HC.	6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Ushiama *et al.*, 2019	concrete tiles and epibiota (3)	community survey	fish community	marine, field, months, Australia	Fish interaction time and feeding varies based on tile structure and epibiota. HC does not affect diversity or number of observed fish.	2, 4, 5, 6
van Hal, Griffioen & van Keeken, 2017	submerged wind farm structures (3)	community survey	coastal fauna	marine, field, months, Europe	Fish are generally attracted to submerged artificial wind farm structures. The structures have negligible effect on aggregation.	2, 3, 6
van Lier *et al.*, 2018	multiple habitat metrics (var)	habitat assessment, visual census	labrid fish	marine, field, months, Au	Certain habitat metrics related to HC are associated with labrid fish diversity, functional trophic groups and live stage structure.	6
Villegas *et al.*, 2019	kelp macroalgae (2)	community survey	kelp forest fish	marine, field, months, Latin America	Forested plots host more fish. Fish in kelp patches utilize rock microhabitat more than water column or kelp.	2, 3, 6
Voigt & Hovel, 2019	*Zostera marina* macrophyte (2)	community survey, grazing trials	*Alia carinata*, *Hippolyte californiensis*, gammarids × epiphytic algae	marine, field & mesocosm, weeks, North America	Grazing impact is higher in high HC. Epiphytic algal abundance is reduced by grazing in high HC but not low HC. More grazers colonize high HC areas.	4, 5, 6
von Nordheim *et al.*, 2018	macrophyte analogue (3)	artificial fertilization	*Clupea harengus*	marine, field, years, Europe	Fertilization rates are high and independent on HC. In late spawning season, egg mortality is higher in the least complex habitats.	1, 4, 7
Vowles & Kemp, 2019	naturally occurring macrophytes (var)	electrofishing, tagging	*Salmo trutta* fish	lotic, field, years, Europe	Macrophyte cover has no significant effect on trout density, which is best predicted by depth instead.	6

Reference	**HC type (levels)**	**Method**	**Organisms**	**Environment and scale**	**Conclusion**	**A**
Wagner, Weber & Wahl, 2015	naturally occurring wood debris (5)	behavioral observations	*Esox masquinongy* juvenile	lentic, field, months, North America	*E. masquinongy* juveniles prefer to inhabit sites with decaying wood of intermediate structural complexity.	2, 3
Wasserman *et al.*, 2016	*Cyperus eragrostis* macrophyte stalks (3)	counting survived prey, FR model	*Enithares sobria* × *Daphnia longispina*	lentic, microcosm, hours, Africa	Across temperatures, more prey is eaten in high HC treatments. HC increases attack rate (except in 14 °C where it decreases handling time instead).	4, 5
Webb, Schultz & Dibble, 2016	naturally occurring macrophytes (2)	plant community survey	pond biota	lentic, field, years, North America	Community composition and overall plant biomass is not affected by herbicide (except for recession of invasive plants).	2, 3, 4, 5
Weber & Weber, 2020	habitats with different HC (var)	long term radio-monitoring	*Esox masquinongy*	lentic, field, months, North America	*E. masquinongy* individuals select complex habitats according to their ability. Systems with more complex habitats promote post-stocking survival and reduce overall movement.	2, 3, 4, 5, 6
White & Brown, 2015	habitat type (2)	behavioral observation	Gobiidae	marine, microcosm, minutes, Australia	Gobiids from complex habitats can learn to navigate mazes more quickly, make fewer errors and use macrophyte structures as landmarks more often than gobiids from simple habitats.	2, 3
White & Walsh, 2020	wood blocks (2)	community survey	macroinvertebrate community	lotic, field, weeks, Australia	HC increases abundance of most taxa but less so in urban streams. HC increases taxon richness in rural streams but less so in urban streams.	6

Reference	HC type (levels)	Method	Organisms	Environment and scale	Conclusion	A
Wilson *et al.*, 2015	*Hydrilla verticillata* macrophyte (var)	behavioral observation	*Lepomis* spp.	lentic, field, years, North America	Fewer fish can be seen with increasing HC.	2, 3
Wolters *et al.*, 2018	macrophytes (3)	macrophyte and macro-invertebrate survey	stream macroinvertebrates	lotic, field, months, Europe	Macroinvertebrate species richness, diversity and functional richness increases in more complex plants.	1, 6
Wolters *et al.*, 2019	macrophytes and their analogues (3)	periphyton cover estimate, taxonomic analysis, growth trials	periphytic community, *Cloeon dipterum*, *Haitia acuta*	lentic, mesocosm, weeks, Europe	Algal cover is lower on living macrophytes than on artificial ones. Complex artificial macrophytes have much higher algal cover than simple ones. Different natural plants cultivate different algal communities. *H. acuta* grew faster in *E. densa* macrophyte treatment. Both invertebrates grew in all treatments, except for *C. dipterum* in the simple artificial macrophyte treatment.	1, 6
Wulf & Pearson, 2017	*Hypnodendron* moss and its analogue (4)	community survey	stream biota	lotic, field, weeks, Au	Fewer invertebrates colonize artificial moss compared to live moss. Size structure and richness is similar in both substrate types.	6

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Chapter II

Disentangling the nonlinear effects of habitat complexity on functional responses

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Chapter II

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RESEARCH ARTICLE

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Disentangling the nonlinear effects of habitat complexity on functional responses

Julien Mocq[1,2] | **Pavel R. Soukup**[1,2] | **Joacim Näslund**[1,3] | **David S. Boukal**[1,2]

[1]Faculty of Science, Department of Ecosystem Biology & Soil and Water Research Infrastructure, University of South Bohemia, České Budějovice, Czech Republic

[2]Biology Centre, Institute of Entomology, Czech Academy of Sciences, České Budějovice, Czech Republic

[3]Department of Aquatic Resources, Institute of Freshwater Research, Swedish University of Agricultural Sciences, Drottningholm, Sweden

Correspondence
Julien Mocq
Email: julien.mocq@gmail.com

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Abstract

1. Structural complexity of habitats modifies trophic interactions by providing refuges and altering predator and prey behaviour. Nonlinear effects on trophic interaction strengths driven by these mechanisms may alter food web dynamics and community structure in response to habitat modifications. However, changes in functional response, the relationship between prey density and feeding rate, along habitat complexity (HC) gradients are little understood.
2. We quantified functional responses along a HC gradient from an entirely unstructured to highly structured habitat in a freshwater system, using dragonfly larvae (*Aeshna cyanea*) preying on *Chaoborus obscuripes* larvae. To disentangle mechanisms by which changes in HC affect functional responses, we used two different approaches—a population-level and a behavioural experiment—applied an information theoretic approach to identify plausible links between HC and functional response parameters, and compared our results to previous studies.
3. Functional response shape did not change, but we found strong evidence for nonlinear dependence of attack rate and handling time on HC in our study. Combined results from both experiments imply that attack rate increased stepwise between the unstructured and structured habitats in line with the threshold hypothesis, because the predators gained better access to the prey. Handling time was lowest at an intermediate HC level in the population-level experiment while the direct estimate of handling time did not vary with HC in the behavioural experiment. These differences point towards HC-driven changes in foraging activity and other predator and prey behaviour.
4. Most previous studies reported stepwise decrease in attack rate in line with the threshold hypothesis or no change with increasing HC. Moreover, changes in the handling time parameter with HC appear to be relatively common but not conforming to the threshold hypothesis. Overall, increased HC appears to, respectively, weaken and strengthen trophic links in 2D and 3D predator–prey interactions.
5. We conclude that detailed understanding of HC effects on food webs requires complementary experimental approaches across HC gradients that consider predator foraging strategies and predator and prey behaviour. Such studies can also help guide conservation efforts as addition of structural elements is frequently used for restoration of degraded aquatic habitats.

Julien Mocq and Pavel R. Soukup contributed equally to the manuscript.

KEYWORDS

Aeshna, attack rate, *Chaoborus*, dimensionality of predator–prey interactions, habitat domain, handling time, refuge, threshold hypothesis

1 | INTRODUCTION

Habitat structure is a ubiquitous environmental feature that underlies the diversity and composition of local communities (Newman et al., 2015; Thomaz et al., 2008). More structured habitats typically host more abundant and diverse communities (e.g. Heck & Wetstone, 1977; Jeffries, 1993; Newman et al., 2015), but see August, 1983; Reichstein et al., 2013). Habitat structure encompasses habitat heterogeneity, defined as the diversity of structural elements, and habitat complexity (hereafter 'HC'), defined as a multidimensional element consisting of qualitative and quantitative components, such as the type and density of macrophyte leaves in freshwaters or corals and macroalgae in the marine environment (Carvalho & Barros, 2017; Kovalenko et al., 2012).

Understanding the links between HC and community structure and functioning has important implications for conservation and management of habitats and ecosystems. Community responses to habitat alteration can be nonlinear (Tokeshi & Arakaki, 2012) and may include rapid deterioration or even catastrophic regime shifts (Scheffer et al., 2001). For example, marine macrofaunal community richness decreased strongly with decreasing HC of coral reefs, which contrasted with limited community-level responses above a certain HC threshold (Newman et al., 2015). Such results suggest that community-level responses to HC could be reduced to the presence–absence scale, but the responses and underlying mechanisms across longer gradients of HC are incompletely understood (Tokeshi & Arakaki, 2012).

Changes in trophic interactions (Dean & Connell, 1987; Kovalenko et al., 2012), along with less diversified niches (Jeffries, 1993) and smaller amounts of total food and habitat area (Fontoura et al., 2019; Parker et al., 2001), drive community responses to habitat simplification. Trophic interactions determine the fluxes of energy and nutrients within food webs and their alterations can thus have cascading effects on the structure and stability of the underlying communities (Berlow et al., 2004). The 'threshold hypothesis' supported by numerous experiments posits that predation rates and anti-predator behaviour changes nonlinearly along HC gradients (Gotceitas & Colgan, 1989). Food web structure and dynamics may not respond to HC alterations outside a critical HC range, but even small changes in HC within that range could incur strong population- and-community-level responses.

Functional responses (Holling, 1966) are central to studies linking trophic interaction strengths to food web dynamics and stability. Three parameters describe the most common functional response shapes (Figure 1): the Hill exponent characterizing the

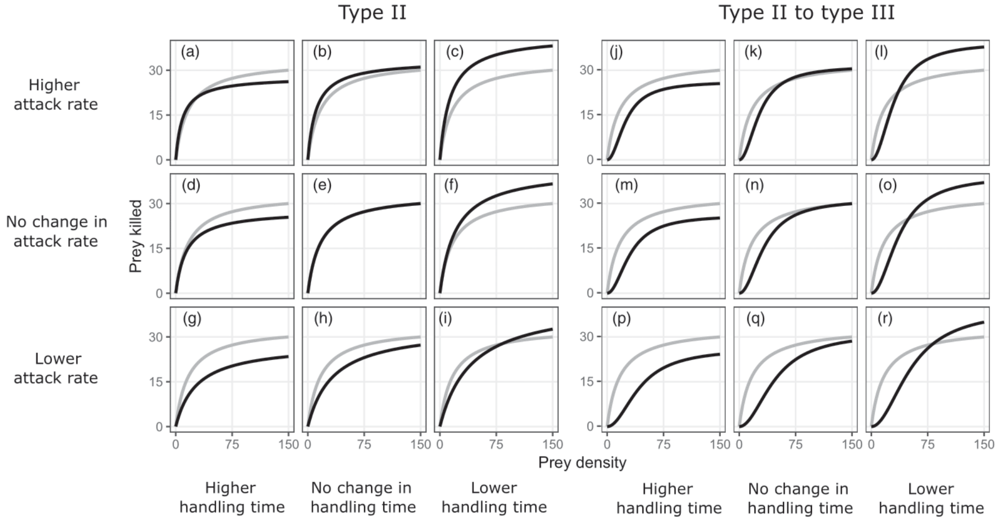


FIGURE 1 Possible responses (black lines) of a type II functional response (grey line) to changes in HC. These include no response (e), changes in handling time and/or attack rate without a shift to type III response (a–d, f–i), and changes from type II to type III (j–r). All curves based on the formula $y = (aN^b)/(1 + ahN^b)$, with baseline parameter values of attack rate (a–i: $a = 2$, j–r: $a = 0.028$) and handling time (a–i: $h = 0.03$, j–r: $h = 0.032$) altered by 50% (a) or 20% (h) according to the panel label. The Hill exponent was set to $b = 1$ for panels a–i and $b = 2$ for panels j–r

functional response shape, the attack rate corresponding to the slope of the functional response at low prey densities, and the handling time whose inverse determines the maximum impact of the predator at high prey densities (e.g. Barrios-O'Neill et al., 2015; Kalinkat, Schneider, et al., 2013). The shape and parameter values of functional response strongly influence the stability of consumer–resource interactions and population equilibria, and hence are of great importance in studies of population dynamics, community stability and effects of invasive species (Barrios-O'Neill et al., 2015; Boukal et al., 2007; Williams & Martinez, 2004).

HC can modify the shape and magnitude of functional responses by altering the attack rate, handling time or the Hill exponent (Figure 1). Using a modified Rosenzweig–MacArthur model as an example, some of these changes can destabilize predator–prey dynamics (Figure 1a–c) while others may have a stabilizing (Figure 1h,j–r) or either effect (Figure 1d,f,g,i) depending on the numerical values of model parameters (Boukal et al., 2007). The underlying proximate mechanisms include changes in predator or prey distribution in space, behavioural changes, movement interference and altered ability of predators to exploit prey driven by predator and prey habitat domains and relevant functional traits (Boukal, 2014; Gotceitas & Colgan, 1989; Klecka & Boukal, 2014).

Three broad types of such mechanisms have been recognized. First, impediments to predator movement or visual detection of the prey can decrease the attack rates (Figure 1g–i; Hauzy et al., 2010; Long et al., 2012; Manatunge et al., 2000). Second, HC can create perching sites for the predator (Klecka & Boukal, 2014) or compromise prey movement and visual range (Hauzy et al., 2010; Manatunge et al., 2000) and hence increase the attack rates (Figure 1a–c). Third, prey refuges in more complex habitats ('refuge effect'; Alexander et al., 2012; Lipcius & Hines, 1986) can change type II to type III functional response because some but not all prey can escape predation by using these refuges (Figure 1j–r). Interestingly, we lack mechanistic explanations for the surprisingly common observations of HC-dependent handling time with or without a concurrent change from type II to type III (Figure 1a,c,d,f,g,i,l,m,o,p,r; e.g. Kalinkat, Brose, et al., 2013; Lipcius & Hines, 1986; Wasserman et al., 2016). This parameter includes the predator's ability to process and digest captured prey that should be independent of HC but also other biological processes and activities (Jeschke, 2007; Li et al., 2018) that may vary with HC. For example, more frequent failed predation attempts or longer periods of predator inactivity increase handling times.

The impact of HC on functional responses is usually studied on the presence–absence scale or a scale with a structurally simple habitat and two levels of HC and rarely consider the HC as a gradient (Table S1). To date, only four studies included four HC levels (terrestrial: Hoddle, 2003; Kalinkat, Brose, et al., 2013; marine: Anderson, 2001; freshwater: Alexander et al., 2015), and one study used leaves of five terrestrial plant species differing in trichome density that we interpret as HC levels (Barbosa et al., 2019). These studies used different taxa and experimental set-ups and reached different conclusions on the effect of HC on functional responses. Changes in functional responses along more gradual gradients of HC are thus poorly understood and we lack tests of the 'threshold hypothesis' in a dynamical setting. This hampers a robust understanding of the qualitative and quantitative effects of habitat alteration on trophic interactions and community structure.

To fill this gap, we carried out laboratory experiments to estimate the parameters of a functional response along a gradient of five HC levels ranging from an entirely unstructured to highly structured habitat. We used dragonfly *Aeshna cyanea* larvae feeding on phantom midge *Chaoborus obscuripes* larvae; both species frequently co-occur in nature. While the dragonfly larvae are climbers that hunt mainly visually with a sit-and-wait ambush strategy (Pritchard, 1965), *Chaoborus* larvae occupy the water column (Pastorok, 1981). The theory summarized above predicts two outcomes for this combination of predator and prey domains and predator foraging strategy: (a) increasing attack rates as the habitat transitions from simple to more complex because the predators gain better access to prey in the water column (Klecka & Boukal, 2014), followed by decreasing attack rates due to impeded access to the prey in highly structured habitat and (b) possible change from type II to type III functional response due to a 'refuge effect' in highly structured habitats.

2 | MATERIALS AND METHODS

We combined two complementary approaches to functional response estimation, with their own strengths and weaknesses, yet almost never used simultaneously, to obtain robust results: a population-level approach that estimates the parameters from prey mortality measured in feeding experiments conducted at multiple prey densities, and a behavioural approach in which the attack rates and handling times are estimated directly by observing the predation process (Hauzy et al., 2010; Hossie & Murray, 2010).

2.1 | Experiment 1

We first conducted a population-level experiment at five HC levels in a temperature-controlled room (mean ± *SD*: 19.7 ± 0.25°C, 18L:6D photoperiod) on 8–16 September 2016. Predators and prey were collected in small fishless forest ponds (49°4′59.078″N, 14°23′30.756″E) near České Budějovice, Czech Republic. *Chaoborus* larvae (4th instar, mean ± *SD* wet mass $8.18 \pm 1.34 \times 10^{-3}$ g) were acclimated in 10-L plastic buckets and fed ad libitum with zooplankton (*Daphnia* sp.) for 1–2 days prior to the experiment. *Aeshna* larvae (wet mass 0.154 ± 0.02 g, range 0.120–0.188 g) were acclimated individually in 150-ml plastic cups and fed ad libitum with *Tubifex* worms for 2–3 days prior to the experiment. Before the experiment, each *Aeshna* was weighted to the nearest 0.1 mg (ABT 120-5DM analytical balance; KERN & SOHN GmbH, Balingen, Germany) and starved for 24 hr.

Feeding trials were run in translucent plastic boxes (length × width ×height = 16 cm × 12 cm × 12 cm) filled with 1.5 L (9 cm depth) of tap water continuously aerated for 24 hr. A 1-mm layer of fine quartz sand (grain size

~0.3 mm) was added to provide a bottom substrate. Arenas were separated by cardboard walls to prevent visual interference among predators. We placed $N_p = 0, 1, 2, 4$ or 8 plastic plant models in the arena to create a HC gradient. Each plant model consisted of four strips of green plastic mesh (18 cm long, 2 cm wide, 1.5 mm mesh size) tied to a small stone (2–3 cm diameter; Figure S1). Index of complexity of individual 'plants' I_{hv} equalled 9.4 ± 1.6 (mean ± *SD*, $n = 8$)—measured as $I_{hv} = f_h/l_h + f_v/l_v$, with f_h and f_v the mean numbers of interstices intercepted per meter, respectively, along the horizontal and vertical axes, and l_h and l_v the mean lengths of interstices in meters, respectively, along the horizontal and vertical axes (Dibble et al., 1996).

We quantified the functional response at each HC level on a gradient of seven prey densities (N_0 = 2, 4, 8, 16, 32, 64 and 128 individuals). Prey were released into the arena 30 min before the experiment, after which the predator was added and allowed to forage for 8 hr. Afterwards, we noted the location of each predator, removed it and counted surviving and dead prey. All predators and prey were used only once. Arenas, sand and plastic plant models were used repeatedly but thoroughly rinsed with boiling water to eliminate chemical cues between subsequent trials.

We ran 8–10 replicates of predation trials for every combination of HC and prey density (N_{tot} = 279). Background prey mortality, assessed in 4–7 control replicates for each combination of HC and prey density, was low (proportion of dead individuals: mean ± *SD* = 0.02 ± 0.05, n = 161) and independent of HC and initial prey density (quasi-binomial GLM: HC, p = 0.53; prey density, p = 0.48). We thus ignored background prey mortality in the analyses.

2.2 | Experiment 2

In all, 18 *Aeshna* larvae (mean ± *SD* wet mass 0.346 ± 0.048 g, range 0.275–0.475 g) and their prey (4th instar *Chaoborus*, mean ± *SD* wet mass $9.45 \pm 1.69 \times 10^{-3}$ g) were collected from the same location as above in September 2017. Prior to the experiment, the animals were treated identically as in Experiment 1, including a 24-hr starvation period of the predators.

The experiment was run in thermal cabinets (Lovibond BSK ET 650; Tintometer GmbH, Dortmund, Germany) at 20°C (mean ± *SD* = 20.3 ± 0.2°C) and simulated daylight conditions. We used glass aquaria with nearly the same volume as in Experiment 1 (1.44 L, length × width × height = 15 cm × 8 cm × 15 cm, 12 cm water depth), allowing side video recording. Trials were run at three HC levels: none ($N_p = 0$ plant models per arena), low ($N_p = 1$) and high ($N_p = 4$). Each individual *Aeshna* was trialled in one level of HC at two prey densities (6 and 24 prey individuals, order of prey treatment randomized) over a 4-day period: each individual was starved during day 1, used in the first trial and subsequently fed *at libitum* on day 2, starved on day 3, and trialled again on day 4. The set-up including the acclimation procedure was otherwise identical as in Experiment 1. We ran 36 trials in total (3 HC levels × 2 prey densities × 6 replicates per experimental conditions).

Prey were introduced into the arena 30 min before the predator. Its behaviour was recorded with PK-910H HD 1080p webcams (A4TECH; Taipei, Taiwan) at 30 frames per second for 50 min. Observations started after the introduced predator stopped swimming and settled onto a surface, indicating it has calmed and begun to search for prey. Its behaviour was then recorded for 40 min or until the handling of the last prey captured in the 40-min interval was completed. The camera was placed perpendicularly to the centre of the arena's wider side; two opposing cameras were used in the high complexity treatment to prevent unobserved predation events.

Four categories of predator behaviour were manually scored using BORIS v5.1.3 (Friard & Gamba, 2016): (a) substrate preference, defined as proportions of total time spent on the wall, bottom and on plant models, all rounded to the nearest second; (b) predator attack towards a prey, visible as a rapid extension of the mouthparts; (c) handling time, defined as time elapsed since prey capture to the last cleaning movement of the predator's mouthparts before its whole-body movement or another attack on prey and (d) duration of a foraging bout, defined as time interval from the start of the trial or the end of previous prey handling to the next successful attack or the end of the trial. We used the ratio between the number of successful and failed predator attacks to calculate the probability of successful prey capture and foraging bout durations to estimate attack rates (see below). Four events with zero handling time were excluded from the attack rate and handling time analysis, assuming that the predators were not hunting during prey handling.

2.3 | Data analyses

We used a model selection approach for the data from each experiment, and compared a suite of models covering all possibilities outlined in Figure 1 similar to Kalinkat, Brose, et al. (2013). We also compared the estimates of attack rate and handling time from the two experiments. We ran all analyses in R 3.6.2 (R Development Core Team, 2019).

Data from the population-level Experiment 1 were analysed with packages BBMLE (Bolker & R Development Core Team, 2017) and EMDBOOK (Bolker, 2016). We first distinguished between Type II and Type III functional response at each level of habitat complexity *HC*, expressed on a relative scale as $HC = N_p/8$. We used the logistic regression between the proportion of eaten prey N_e/N_0 and the initial prey density (Juliano, 2001):

$$\frac{N_e}{N_0} = \frac{\exp\left(P_0(HC) + P_1(HC)N_0 + P_2(HC)N_0^2 + P_3(HC)N_0^3\right)}{1 + \exp\left(P_0(HC) + P_1(HC)N_0 + P_2(HC)N_0^2 + P_3(HC)N_0^3\right)}, \quad (1)$$

where N_e is the number of prey eaten and the HC-specific parameters P_i(HC) are determined with the maximum likelihood method (Juliano, 2001). While P_1(HC) < 0 characterize a Type II functional response, P_1(HC) > 0 and P_2(HC) < 0 identify a Type III functional response for given *HC*. We have also attempted to fit models with a variable Hill exponent, but these models did not converge (results not shown).

We found only Type II functional response at each level of HC and thus used Rogers equation to account for prey depletion (Rogers, 1972). To detect possible nonlinear effects of HC on attack rate *a* or handling time *h*, we considered 18 models of increasing complexity with HC-dependent parameters *a*(HC) and *h*(HC) (Table S2). Models (1)–(9) assumed that *a*(HC) and *h*(HC) are constant or scale linearly (i.e. $a(\mathrm{HC}) = a_0 + a_1 HC$ and/or $h(\mathrm{HC}) = h_0 + h_1 HC$) or as a second-order polynomial with HC (i.e. $a(\mathrm{HC}) = a_0 + a_1 HC + a_2 HC^2$ and/or $h(\mathrm{HC}) = h_0 + h_1 HC + h_2 C^2$). Models (10)–(12) described a stepwise change in the attack rate (i.e. $a(0) = a_{V0}$ and $a(\mathrm{HC}) = a_{V1}$ for $HC > 0$) combined with a constant, linear or unimodal dependence of handling time on HC. Models (13)–(15) further generalized models (10)–(12) using a linear relationship $a(\mathrm{HC}) = a_{V1} + a_V\ HC$ for $HC > 0$ with a maximum attack rate at $N_P = 1$ for negative a_V values. Finally, models (16)–(18) assumed that the attack rate or handling time vary freely across HC levels, that is, $a(\mathrm{HC}) = a_{Vj}$ or $h(\mathrm{HC}) = h_{Vj}$ for *j* artificial 'plants' ($j = 0, 1, 2, 4$ and 8). Model (1) corresponds to no effect of HC on the functional response, models (10–12) correspond to a qualitative, presence–absence driven effect of HC on attack rate, models (13–15) correspond to an initial increase in attack rate followed by a possibly decelerating or negative effect of HC on attack rate in more complex habitats and model (18) with HC-specific parameters is closest to the approach taken in many previous studies (Tables S1 and S2).

Prey consumption increased with predator size *W* even within the relatively narrow preselected size range. We accounted for this effect in models (1)–(18) by incorporating allometric scaling of handling time and attack rate as $a(HC, W) = a(\mathrm{HC})\cdot W^b$ and $h(C, W) = h(\mathrm{HC})\cdot W^c$, where *b* and *c* are the respective allometric exponents (Weterings et al., 2015), yielding a modified Rogers equation:

$$N_e = N_0 \left(1 - \exp\ \left(a\,(HC)\,W^b\,\left(N_e h\,(HC)\,W^c - T\right)\right)\right), \qquad (2)$$

where the number of eaten prey N_e depends on initial prey density N_0, duration of experiment *T* and the parameters outlined above. We used Lambert-W function to solve the equation (Bolker, 2008). Each model was fitted by maximum likelihood estimation (Bolker, 2008) and all 18 models ranked by their Bayesian information criterion (BIC) values (Brewer et al., 2016). We considered models with $\Delta\mathrm{BIC} \le 2$ as plausible alternatives to the most parsimonious model (Burnham & Anderson, 2002).

We characterize the magnitude of the HC effect in each functional response parameter *r* ($r = a$ or h) of each plausible model by calculating the largest relative change $\Delta r = \min_{HC}(\ln(r(\mathrm{HC})/r(0)))$ if $r(\mathrm{HC}) \le r(0)$ or $\Delta r = \max_{HC}(\ln(r(\mathrm{HC})/r(0)))$ if $r(\mathrm{HC}) \ge r(0)$ across the four increased HC levels. We used the same approach to extract data from previous studies (Table S1). We also fitted the log-transformed $\log_{10}(N_e + 1)$ data as advised by Uszko et al. (2020) with nonlinear least squares regression to verify that our results are robust; the maximum-likelihood method was unable to produce parameter estimates for these data. We do not report parameter values estimated from the log-transformed data as they lack direct interpretation and cannot be compared to previous studies.

We then used the data from Experiment 2 to analyse the effects of HC and prey density on the microhabitat use (i.e. proportions of time spent on the wall, bottom and artificial plants when present), probability of a successful attack, number of eaten prey, handling time and attack rate of the predators. In each analysis, we constructed a set of candidate models and used BIC to identify the most parsimonious and plausible models as in Experiment 1. Candidate models for all four response variables covered all possible combinations of HC and prey density as fixed-effect predictors, including their statistical interactions (Table S3). Prey density was included as a linear covariate and HC as a linear (*HC*, scaled as $HC = N_p/4$), quadratic ($HC + HC^2$, scaled as $HC = N_p/4$) or binary (HC_{bin}, set to 0 if $HC = 0$ and to 1 if $HC = 1$ or 4) covariate. This yielded 11 candidate models for all analyses except the effect of artificial plants on microhabitat use (5 candidate models due to plant absence at $HC = 0$). We used scaled initial prey density ($N_0/24$) in the analyses of microhabitat use, probability of prey capture, number of eaten prey and handling time, and scaled prey density at the time of attack ($N_t/24$) in the analysis of attack rate to account for possible effects of prey depletion.

Data on microhabitat use, handling time, probability of prey capture and number of eaten prey from Experiment 2 were fitted with linear mixed models (LMMs) and generalized linear mixed models (GLMMs) using the LME4 package (Bates et al., 2015) with a random replicate effect nested within predator identity to account for variation among individual replicates and predators. Data on microhabitat use and the probability of a successful attack were analysed using binomial GLMMs with logit link function. Data on handling time were analysed using a LMM with a log-transformed response, and the number of eaten prey was analysed using a Poisson GLMM with a log link function. Preliminary inspection of the data showed that the number of eaten prey did not change but handling time decreased with predator weight *W*. To facilitate comparison of both experiments, we included $\ln(W^c)$ as an offset in the analyses of handling time from Experiment 2, using the mean value of *c* estimated by Equation 1 in all 18 functional response models weighted by the BIC model weights reflecting their relative parsimony (see Table S2). DHARMA package version 0.2.7 (Hartig, 2020) was used to validate model residuals and test for the lack of over- and underdispersion and for influential outliers in the most parsimonious models. Table S5 was generated in *sjPlot* version 2.8.2 (Lüdecke, 2021).

We used survival analysis for the right-censored attack rate data from Experiment 2. Duration of foraging bouts used to estimate the attack rates did not visibly vary with predator weight unlike in Experiment 1, presumably due to smaller size range in Experiment 2. We thus did not correct for predator body size in this analysis. Data were first fitted with parametric frailty models to account for repeated measures within trials (PARFM package version 2.7.5; (Munda et al., 2012)) and then re-fitted with a parametric survival model (FLEXSURV package version 0.7.1; Jackson, 2016) with the same covariates as the most parsimonious parametric frailty model to obtain the treatment-specific, size-corrected attack rate estimates (see Text S2 for details).

3 | RESULTS

3.1 | Experiment 1: Population-level estimates

We only found support for type II functional responses (all P_1(HC) ≤ 9.56, Table S4). The estimated attack rate exponents *b* were systematically positive (weighted mean ± *SD* = 1.68 ± 0.42, range 1.05–2.51) and handling time exponents *c* systematically negative (weighted mean ± *SD* = −1.13 ± 0.17, range −1.37 to −1.00), suggesting a consistent effect of varying body sizes of the individual predators across the models and HC levels.

Our analysis identified three plausible models for the dependence of attack rate *a* and handling time *h* on HC with untransformed data (Table 1; Table S1). The most parsimonious model (6) included a constant attack rate and a concave-up dependence of handling time on HC with a minimum corresponding to ~30% reduction at intermediate HC levels (N_p ~ 4, $\Delta h = -0.35$). Other plausible models (10) and (12) included a stepwise, up to twofold increase in attack rate (model (10): $\Delta a = 0.67$, model (12): $\Delta a = 0.41$) with the transition from a structurally simple ($HC = 0$) to more complex habitats ($HC > 0$), and a constant or unimodal dependence of handling time on HC (Figure 2). Functional responses based on the three plausible models were all similar and their fit to the data overlapped with the functional response based on separate fitting of the data for each HC level with model (18), especially for $N_p = 2$ and 8 (Figure 3; Figure S2). Analysis based on log-transformed data ranked these three models in the same order but gave less support to models (10) and (12). Models (1–4) assuming constant values or a linear dependence of attack rate and handling time on HC were not supported by the data (Table 1; Table S1). The predators almost always sat on the artificial plants at the end of the feeding trial (98.2% of the replicates with $N_p > 0$). In the absence of the plants, they mostly sat on the wall (80% of the replicates).

3.2 | Experiment 2: Estimates derived from behavioural data

Our model selection approach revealed only 1–2 plausible models for each of the five response variables. Based on these models, predator microhabitat use varied with HC but not with prey density (Tables S3 and S5). We observed the same shift in microhabitat use from walls to artificial plants as perching sites when the plants were present (Figure 4a) as in Experiment 1. As HC increased, the proportion of time spent by the predators on artificial plants increased while proportions of time spent on the walls and on the bottom decreased.

Prey handling times in Experiment 2 (mean ± *SD* = 39.9 ± 23.3 s, range 5.6–144.2 s, $n = 115$) were independent of HC (Tables S3

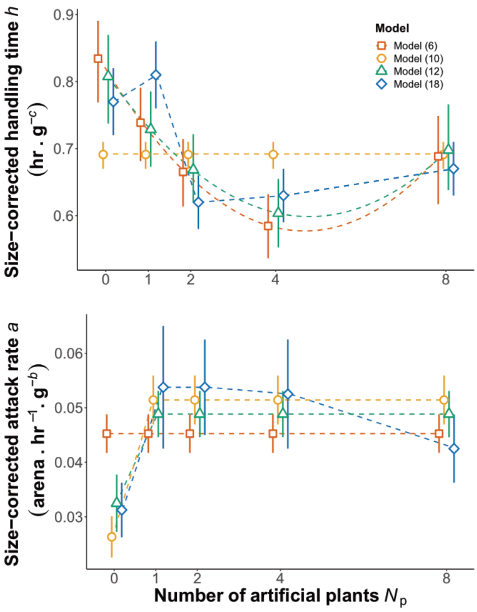
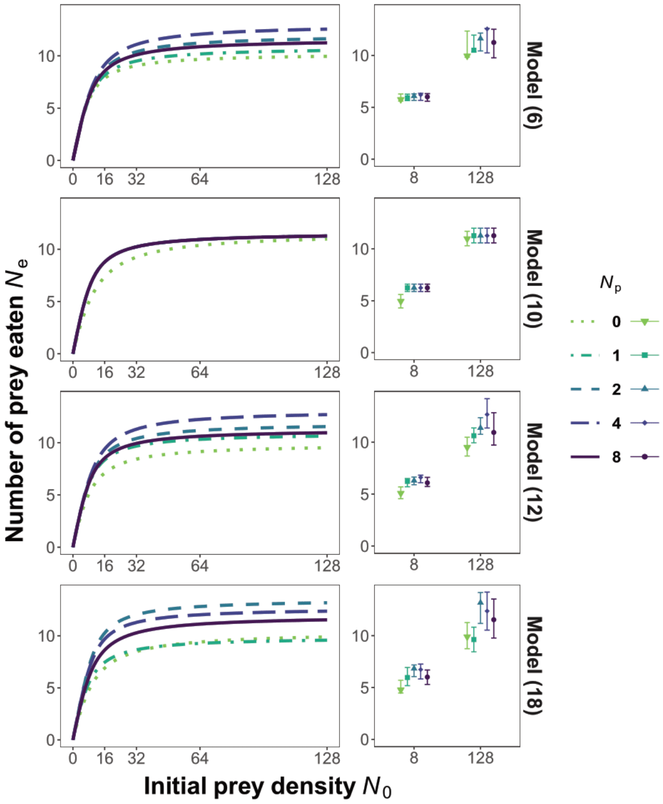


FIGURE 2 Dependence of size-corrected attack rate *a* and handling time *h* from Equation 2 on HC (N_p, number of artificial plants) in the most parsimonious model (6) and plausible models (10) and (12). Model (18) estimating *a* and *h* separately for each HC level illustrated for comparison. Estimates shown as mean ± 95% confidence interval. See Table S2 for the respective values of the allometric exponents for attack rate (*b*) and handling time (*c*)

TABLE 1 Summary of plausible models of the effect of HC on attack rate *a* and handling time *h* from the analyses using untransformed and log-transformed data. Ln(*L*) = log-likelihood; ΔBIC = difference of the BIC value from that of the most parsimonious model; W_{BIC} = model weight based on BIC value. See Section 2 for details

		Untransformed data					Log-transformed data			
Model	Model structure	*df*	Ln(*L*)	ΔBIC	W_{BIC}	Rank	Ln(*L*)	ΔBIC	W_{BIC}	Rank
(6)	constant *a* quadratic *h*	6	−568.1	0	0.359	1	189.3	0	0.710	1
(12)	stepwise *a* quadratic *h*	7	−565.8	1.0	0.220	2	189.8	4.7	0.069	2
(10)	stepwise *a* constant *h*	5	−571.9	2.0	0.135	3	184	5.1	0.056	3

FIGURE 3 Dependence of the functional response of *Aeshna* feeding on *Chaoborus* on HC gradient, fitted with the three parsimonious models (6), (10) and (12) and with the most complex model (18). Left column: mean prey consumption, right column: means with 95% bootstrapped confidence intervals at $N_0 = 8$ and 128; see Table 1 and Table S2 for details. Note that model (10) yields identical functional response curves for $N_p = 1–8$



and S5). With predator size fixed to the mean mass in Experiment 1, the predicted size-corrected handling times based on Experiment 2 (mean = 88.0 s, 95% CI = 76.0–101.8 s) were much lower than the minimum handling time estimates from Experiment 1 (model (6), $N_p = 4$: mean = 2,104 s, 95% CI = 1,931–2,278 s, Figure 2) and this relationship remained unchanged across a wide range of plausible size-scaling exponents of handling time (Figure S3).

The most parsimonious models further showed that the probability of a successful attack increased sharply with HC, especially at the low prey density (Tables S3 and S5, Figure 4b). Number of eaten prey and attack rate increased with prey density and were higher in structurally complex environments, but did not differ between trials with 1 and 4 artificial plants (number of eaten prey: Tables S3 and S6 and Figure 4c; attack rates: Table S3 and Text S2) while the numbers of prey attacks were highest at low HC ($N_p = 1$) and lowest at no HC ($N_p = 0$, details not shown; compare Figure 4b,c). The estimated size-corrected attack rates in the absence of artificial plants ($N_c = 6$ ind. arena^{-1}: $a = 0.15$ arena.hr^{-1}, 95% CI = 0.07–0.30 arena.hr^{-1}; $N_c = 24$ ind.arena^{-1}: $a = 0.37$ arena.hr^{-1}, 95% CI = 0.18–0.74 arena.hr^{-1}) were comparable to those from Experiment 1 but became significantly higher than in Experiment 1 when artificial plants were present ($N_c = 6$ ind.arena^{-1}: $a = 1.16$ arena.hr^{-1}, 95% CI = 0.86–1.55 arena.hr^{-1}; $N_c = 24$ ind.arena^{-1}: $a = 2.91$ arena.hr^{-1}, 95% CI = 2.20–3.80 arena.hr^{-1}).

4 | DISCUSSION

The diversity of observed effects of HC on functional responses (Figure 1, Text S1 and Table S1) points towards the importance of predator and prey functional traits and other habitat characteristics in determining how gradual changes in HC alter predator–prey interactions and population dynamics. Their synthesis is currently hampered by the relative paucity of suitable data and lack of standardized methods to assess the dependence of functional responses on HC.

Our study systematically explored quantitative changes in functional response along a HC gradient. We used a model selection approach, which enables a direct comparison of different relationships between HC and functional response parameters (Long et al., 2012;

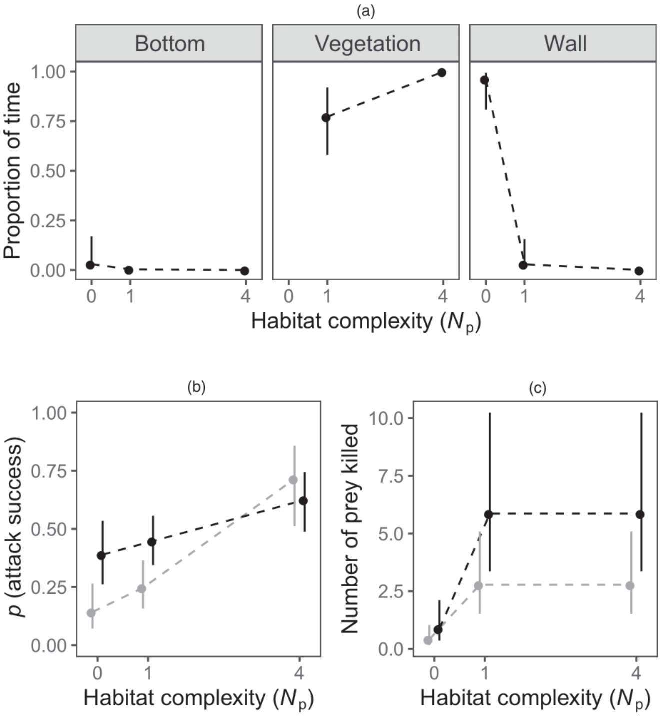


FIGURE 4 Predicted effects of HC (N_p, number of artificial plants) on (a) predator microhabitat use, (b) probability of a successful attack and (c) number of successful attacks in Experiment 2 based on the most parsimonious models. In panels (b) and (c), the initial prey density N_0 is 6 (grey) and 24 (black) ind.arena^{-1}. Circles = mean predicted values; error bars = 95% CIs based on fixed effects

Rall et al., 2012) and provides a general framework to test the relevance of various underlying mechanisms. We demonstrated that HC can have substantially nonlinear effects on functional responses, and the combination of the population-level and behavioural approaches allowed us to identify possible underlying mechanisms. While some effects observed in our experiment and previous studies are in line with the 'threshold hypothesis' (Gotceitas & Colgan, 1989), we also identified more complex relationships between HC and functional response parameters driven by changes in predator behaviour and foraging performance.

4.1 | Dependence of functional response shape on HC

We observed only type II functional responses across all HC levels. Categorical functional responses, used also in our study, may not detect subtle changes in functional response curvature driven, for example, by prey refuge use in more complex environments or by increased presence of movement obstacles that hinder predators (Barrios-O'Neill et al., 2015; Hauzy et al., 2010). However, only the 'pelagic' prey in our experiment likely perceived the added HC only as obstacles. Type II functional responses are common in aeshnid larvae (Johansson & Johansson, 1992; Van Buskirk et al., 2011); only Hossie and Murray (2010) observed a shift from type II to type III in *Anax* larvae when HC generated by sufficient amount of leaf litter provided refuge for the tadpole prey.

Changes in the functional response shape along a HC gradient (Figure 1j–l) were detected or suspected in only 10 out of 40 tested predator–prey pairs in previous studies with relevant data (Table S1), thereby suggesting that increased HC may not stabilize predator–prey and food web dynamics through the prey refuge effect as often as previously thought. This should however be confirmed by long-term experiments under more natural conditions as most studies reported in Table S1 used more or less artificial laboratory settings.

4.2 | Dependence of attack rate on HC

We expected to observe maximum attack rates at intermediate HC levels, at which the benefits of improved access to the prey (Klecka & Boukal, 2014) in less used part of the arenas (Uiterwaal et al., 2019) would dominate over costs of limited prey detection and movement hindrance (Gotceitas & Colgan, 1989). While the population-level data were congruent with this expectation, the most parsimonious models identified no change or a stepwise increase of attack rate between none and low HC (i.e. zero and one artificial plant). Behavioural data also followed the latter threshold pattern. Observed differences in size-corrected attack rates in our two experiments are consistent with experimental duration. The population-level experiment ran longer, which typically leads to lower and potentially more realistic estimates of attack rate due to more time spent on foraging-unrelated activities, for example, due to satiation (Li et al., 2018).

HC-specific differences in the attack rate estimates from both experiments thus imply that *Aeshna* larvae forage more efficiently in the presence of artificial plants. Although the relationship between macrophyte density and attack rate of aeshnid larvae would likely be more gradual in natural habitats with larger volumes, our results lend further support to the 'threshold hypothesis' (Gotceitas & Colgan, 1989) and to the possibility of nonlinear responses of freshwater communities to habitat alterations driven by changes in trophic interactions (Soukup et al., in prep.).

More generally, current theory posits that higher HC should modify predator search efficiency and encounter rates (Gotceitas & Colgan, 1989; Hauzy et al., 2010; Hossie & Murray, 2010). Half of the previous studies confirm this theory, with 3 out of 32 predator–prey pairs with relevant data showing an increase as in our study, 13 pairs exhibiting a decrease, and 16 pairs showing no significant change in attack rates with HC, sometimes possibly due to few replicates. Magnitude of the effect across studies was usually comparable to or smaller than our result (increase in *a* with HC: $\Delta a = 0.14$–1.67, mean = 0.77; decrease: $\Delta a = -2.20$ to -0.45, mean = -1.15; no change: $\Delta a = -2.14$ to 2.49, mean = -0.10; Figure 5). Like us, most studies including three or more HC levels found a stepwise change in attack rate in line with the 'threshold hypothesis' (8 out of 15 predator–prey pairs; e.g. Barrios-O'Neill et al., 2015; Wasserman et al., 2016). Other results suggest HC-independent attack rates (e.g. Barbosa et al., 2019; Hoddle, 2003) or a monotone relationship (Alexander et al., 2012; Table S1).

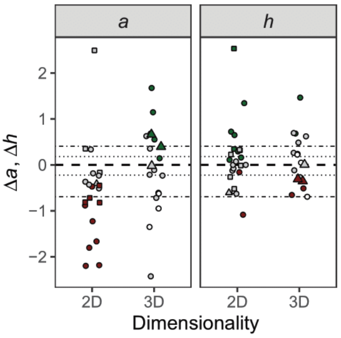


FIGURE 5 Magnitudes of the HC effect on attack rate *a* (Δa) and on handling time *h* (Δh) found in previous population-level experiments (circles, squares and small triangles; data in Table S1) and in the three plausible models of our data (large triangles). Predator–prey encounter mode: circles = active mobile, squares = active static, triangles = sit-and-pursue; symbol fill: white = effect was not tested, grey = no significant change, red = decline and green = increase with increasing HC. Dotted horizontal lines show ± 20% change (as in *h* in Figure 1) and the dash-dotted lines are ±50% change (as in *a* in Figure 1). See Text S1 and Table S1 for details

Results from our behavioural experiment provide further insights into the mechanisms by which HC can modulate foraging behaviour of predators. In the structurally simple environment, *Aeshna* larvae attacked least often and had the lowest foraging success, resulting in the lowest attack rates and prey mortality. The increasing probability of a successful attack was leveraged by fewer attacks in high HC relative to low HC, most likely as the predator's hunger level decreased (Jeschke et al., 2002). This leads to constant prey mortality and attack rates across all positive HC levels.

The relationship between HC and attack rate may further be context-dependent and, for example, vary with temperature (Wasserman et al., 2016) or the choice of the functional response formula (Barrios-O'Neill et al., 2015). Encounter rates also depend on the dimensionality of predator–prey interactions and predator–prey encounter mode (Barrios-O'Neill et al., 2016, 2019; Pawar et al., 2012). Data from our experiment and previous studies imply that attack rates decrease and increase in more complex habitats when the interactions occur in 2D and 3D, respectively (Figure 5). This suggests that HC tends to impede predators in 2D predator–prey interactions irrespective of the encounter mode. More data, especially from 3D contexts in terrestrial and marine environments, could help disentangle the relative importance of these putative drivers on changes in functional responses along HC gradients.

4.3 | Dependence of handling time on HC

Current evidence of possible links between HC and the maximum feeding capacity of predators, characterized by the handling time parameter of functional responses, is equivocal. We found strongest support for a concave-up response with the shortest handling times at intermediate levels of HC in the population-level experiment. This contrasted with HC-independent estimates of handling time, defined as the time needed to subdue and process the prey, in our and most other behavioural studies (4 out of 5 predator–prey pairs; e.g. Hauzy et al., 2010; Hossie & Murray, 2010; Table S1). We conclude that HC may directly interfere with handling behaviour only in special cases such as wading birds probing the mud for hiding molluscs (de Fouw et al., 2016).

Population-level studies (Table S1) usually reported no change (22 out of 34 predator–prey pairs with relevant data) or longer handling times (8 predator–prey pairs) in more complex environments. Magnitude of the effect was mostly comparable to or larger than in our study (increase of *h* with HC: $\Delta h = 0.11$–2.53, mean = 0.83; decrease: $\Delta h = -1.08$ to -0.16, mean = -0.51; no change: $\Delta h = -0.63$ to 0.69, mean = 0.002; Figure 5). Among the studies including three or more HC levels, *c.* half of them found constant handling time (9 out of 16 predator–prey pairs; e.g. Hauzy et al., 2010). The remaining ones reported a concave-down relationship with the longest handling time at intermediate levels of HC (Hoddle, 2003), stepwise or monotone decline (Kalinkat, Brose, et al., 2013; Wasserman et al., 2016), or stepwise or monotone increase with HC (Alexander et al., 2012; Cuthbert et al., 2020; Long et al., 2012; Table S1). As with the attack rate, some of the results depended on the experimental or modelling context (Barrios-O'Neill et al., 2015; Wasserman et al., 2016). Interestingly, handling times tend to, respectively, decrease and increase in more complex habitats for trophic interactions in 3D and 2D (Figure 5).

Given that digestion should be independent of HC, the reported variation of the handling time parameter of the functional response could stem from HC-driven changes in foraging activity and other predator and prey behaviour (Jeschke, 2007; Li et al., 2018). Our study implies that the relative importance of the mechanisms affecting maximum foraging rates varies with HC such that the largest positive or negative effect on handling time typically occurs at the transition from a structurally simple to more complex habitat. In our study, *Aeshna* larvae attacked the prey more often and were more successful in the structurally complex environments, thereby supporting the ‘threshold hypothesis’ (Gotceitas & Colgan, 1989). This pattern was likely driven by increased access to the prey in the water column and improved perching of the predators, which increased their strike accuracy. These mechanisms may also explain the stepwise decrease in handling time found in one experiment by Wasserman et al. (2016).

On the other hand, highly complex habitats can increase the time predators spend to orientate to and pursuit prey (Anderson, 1984), which may lead to the commonly observed increases in handling time parameter with HC as discussed above. In our experiment, *Chaoborus* larvae likely aggregated in pockets of free space created by the convoluted ‘leaves’ of the artificial plants at the highest HC level, and spatial aggregation of the prey is known to affect functional responses (Uiterwaal et al., 2019). *Chaoborus* larvae can also detect and avoid predators (Berendonk & O'Brien, 1996), which could have forced *Aeshna* to relocate and prolong pursuit. Taken together, these mechanisms could generate a nonlinear, unimodal dependence of handling time on HC as in our population-level experiment.

Another reason for the commonly reported HC-dependent handling times in the population-level experiments could be the non-independency of attack rate and handling time estimates and the ability of different parameter combinations to fit the same functional response curve (Uszko et al., 2020). We thus recommend using additional evidence to inform the population-level models and resolve the inherent uncertainty in parameter estimates and in the identification of (most) parsimonious models of the population-level data. In our study, results from Experiment 2 align best with models (10) and (12) from Experiment 1 assuming a stepwise increase in attack rate and a constant or varying handling time. Model (10) assuming constant handling time, despite its lower BIC ranking, may thus appropriately describe the changes in functional response along a HC gradient in our data.

4.3.1 | Implications for predator–prey dynamics, habitat restoration and regime shifts

In sum, our results and some of the previous studies show that functional responses can change nonlinearly along HC gradients. This will have important implications for predator–prey and community dynamics (Barrios-O'Neill et al., 2015; Williams & Martinez, 2004). Current evidence suggests that the functional response shape is usually independent of HC (but see Barrios-O'Neill et al., 2015), which means that predator–prey and community responses to HC alterations will be mostly driven by changes in attack rates and handling time. The combination of a stepwise increase in attack rate and a concave-up dependence of handling time (Figure 1a) found in our Experiment 1 has not been reported before. Together with this result, the reported changes cover all scenarios defined in Figure 1a–i and include cases that can both stabilize and destabilize predator–prey dynamics (Table S1). Observed relative changes of attack rate or handling time due to HC alteration vary substantially across studies; their magnitude would determine the strength of this (de)stabilizing effect. Overall, increased HC appears to, respectively, weaken and strengthen trophic links in 2D and 3D predator–prey interactions.

Human-driven changes in HC are a pervasive issue in aquatic ecology (Kovalenko et al., 2012). These changes can have negative or positive effects on the biota, such as the removal of coarse wood debris from rivers or management practices aiming to restore or conserve elements of complexity in degraded rivers (Foote et al., 2020). Other examples include shallow lake eutrophication and the loss of submerged macrophytes versus re-oligotrophication aiming to restore the original lake status (Perrow et al., 1999), and coral- or oyster-based reef flattening versus creation of artificial reefs in marine habitats (Newman et al., 2015). Nonlinear changes in functional responses may amplify or dampen other mechanisms by which these changes in HC alter local communities, especially if the communities are relatively simple and the changes of HC affect trophic interactions of top predators or other keystone species (Kalinkat, Brose, et al., 2013).

Future studies of trophic interactions across HC gradients should thus go beyond the commonly used presence–absence binary scale, combine different experimental approaches to disentangle the underlying mechanisms and involve multiple predator–prey pairs to investigate how gradual changes in HC alter food web dynamics and community structure.

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AUTHORS' CONTRIBUTIONS

J.M., P.R.S. and D.S.B. designed the experiment 1; P.R.S., J.N. and D.S.B. designed the experiment 2; J.M. and P.R.S. conducted the experiments; J.M., P.R.S. and D.S.B. analysed the data with additional input from J.N.; J.M. and P.R.S. wrote the first draft and all authors contributed significantly to revisions.

DATA AVAILABILITY STATEMENT

All experimental data are available from the Dryad Digital Repository https://doi.org/10.5061/dryad.931zcrjjr (Mocq et al., 2021).

ORCID

Julien Mocq https://orcid.org/0000-0003-4492-8815
Pavel R. Soukup https://orcid.org/0000-0001-8864-9530
Joacim Näslund https://orcid.org/0000-0003-1091-2225
David S. Boukal https://orcid.org/0000-0001-8181-7458

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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Chapter III

Invasive crayfish predation risk and habitat complexity effects on community assembly in small standing waters

[Manuscript prepared for Biological Invasions]

Chapter III

Invasive crayfish predation risk and habitat complexity effects on community assembly in small standing waters

Pavel R. Soukup[1,2*], Vojtěch Kolář[1,2], David S. Boukal[1,2]

[1]*University of South Bohemia, Faculty of Science, Department of Ecosystem Biology, 370 05 České Budějovice, Czech Republic*

[2]*Czech Academy of Sciences, Biology Centre, Institute of Entomology, 370 05 České Budějovice, Czech Republic*

*Corresponding author: Pavel R. Soukup. University of South Bohemia, Faculty of Science, Department of Ecosystem Biology, 370 05 České Budějovice, Czech Republic. E-mail: pavelsoukup@protonmail.com

ORCID:
Pavel R. Soukup: 0000-0002-9930-2388
David S. Boukal: 0000-0001-8181-7458
Vojtěch Kolář: 0000-0001-6144-317X

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Abstract

Invasive crayfish have a strong potential to alter the structure and functioning of freshwater communities. Habitat complexity is a key environmental characteristic shaping these communities, but its ability to modify the effects of invasive crayfish on lower trophic levels is little understood.

We focused on the effects of habitat complexity and the consumptive and non-consumptive effects of predation risk by the invasive crayfish Orconectes limosus on community assembly in a full factorial outdoor mesocosm experiment that ran for 29 days. Habitat complexity was increased by added plastic plant models, which allowed us to focus on the habitat provisioning effect of complexity.

We observed no effects of habitat complexity or crayfish presence on water quality including turbidity and chlorophyll-a concentrations. Habitat complexity and predation risk also did not alter the abundance of the colonizing macroinvertebrates, and their effects on the biomass were additive. More complex habitats had a higher biomass of ephemeropteran larvae and lower biomasses of gastropods and culicid larvae. Both consumptive and non-consumptive predation risk only lead to lower gastropod biomass. Finally, the size spectrum of chironomid larvae was significantly shallower in the structurally simple treatment without crayfish.

Our results show that habitat complexity can be at least as important as the biotic effects of invasive crayfish during initial stages of community assembly in small standing waters, and highlight the need for future studies of invasive species effects across multiple time scales.

Introduction

Invasive crayfish are on their way to replacing indigenous species in Europe (Holdich *et al.*, 2009), with potentially widespread consequences for the structure and functioning of the local freshwater communities (Rodríguez *et al.*, 2005; Correia & Anastácio, 2008; Lodge *et al.*, 2012; Watanabe & Ohba, 2022). Although the role of crayfish in structuring the community can be small in some systems (Arce *et al.*, 2019), the effects of invasive crayfish species on community structure can also be dramatic and persistent (Twardochleb, Olden & Larson, 2013; Mathers *et al.*, 2016). Some invading species appear to serve a similar ecological function and alter the community similarly to native crayfish taxa (*Orconectes rusticus* native, *O. propinquus* invader, Kuhlmann, 2016). Other replacements lead to major decreases in benthic taxon richness and density, as seen in sublittoral lake assemblages in which the *Pacifastacus leniusculus* replaced *Astacus astacus* (Ercoli *et al.*, 2015).

As omnivores, crayfish directly interact with multiple trophic levels. They can efficiently predate on benthic fauna (Nyström, Brönmark & Granéli, 1996; Correia & Anastácio, 2008), especially on slow-moving taxa such as molluscs (Nyström & Perez, 1998; Kreps, Baldridge & Lodge, 2012; Ruokonen, Karjalainen & Hämäläinen, 2014). *Orconectes virilis* can even negatively impact fish recruitment by feeding on fish eggs in ponds (Dorn & Wojdak, 2004). Crayfish also consume and/or destroy macrophytes (Lodge *et al.*, 1994; Chandler, Gorman & Haas, 2016; Roessink *et al.*, 2017). For example, *Procambarus clarkii* can eliminate macrophytes (Matsuzaki *et al.*, 2009; Rodríguez-Pérez, Hilaire & Mesléard, 2016), although it prefers certain species (Carreira, Dias & Rebelo, 2014). This can lead to indirect cascading effects on macrophyte-associated taxa (e.g., decapods > gastropods > periphyton, Rosewarne *et al.*, 2016).

Crayfish behaviour underpins further indirect effects of their presence on local communities. Burrowing increases substrate heterogeneity that can in turn enhance macroinvertebrate abundance in streams (Brown & Lawson, 2010). *Orconectes rusticus* can indirectly increase periphyton and phytoplankton densities due to perturbation of sediment, however, since it also reduces macrophyte density, the total biomass of primary producers could decrease due to the reduction of surface area available for periphyton growth (Lodge *et al.*, 1994). Cascading trophic effects of crayfish are therefore mostly obscured, owing to the omnivorous nature of crayfish (Wootton, 2017). Theory and empirical evidence in other taxa further imply that indirect, non-consumptive effects of predation risk by invasive crayfish should accompany the direct, consumptive effects. For example, predation risk can deter adult insects from oviposition (mosquitoes with hemipteran predator: Eitam, Blaustein & Mangel, 2002). Individuals of many aquatic vertebrate and invertebrate taxa reduce their activity under predation risk, which leads to slower growth and development (Relyea, 2003; Davis, Purrenhage & Boone, 2012; Stahr & Shoup, 2015).

Habitat complexity, representing the distribution of structural elements in space (Kovalenko, Thomaz & Warfe, 2012), interacts with individual, interaction and community level processes in aquatic environments (Soukup *et al.*, 2022). In particular, habitat complexity and predation risk have been widely recognized to influence community assembly in small water bodies. Habitat complexity provides substrate for periphyton growth (Warfe & Barmuta, 2006) and refuges from predation (e.g., Grutters *et al.*, 2015). It could therefore modify the direct consumptive effects of crayfish (Nyström & Perez, 1998). Potential indirect non-consumptive effects (see above) should however manifest regardless of habitat complexity (Davis *et al.*, 2012).

Habitat complexity can therefore alter the effects of invasive species on the local community (Garvey *et al.*, 2003), but empirical evidence for its potential to mediate the effects of invasive crayfish species in standing waters is limited and equivocal. Ruokonen *et al.* (2014) showed that *Pacifastacus leniusculus* caused a decrease in snail density and taxon richness in rocky habitats but not in vegetated habitats in lakes, likely due to decreased mobility and lower density of crayfish in vegetated habitats. Crayfish can also alter the impact of habitat complexity on lower trophic levels as demonstrated in a whole-lake crayfish removal experiment with *Orconectes rusticus* (Hansen *et al.*, 2017). Crayfish removal did not alter the community but lead to the rewiring of the food web, because its removal lead to a regrowth of submerged plants, which in turn provided refuge for fish predators and increased their feeding pressure on macroinvertebrates. This increase in fish predation compensated for decreased predation by crayfish (Hansen *et al.*, 2017). These studies suggest that habitat complexity can mediate the effects of invasive crayfish on local communities in multiple ways, but we are not aware of any studies examining the joint effects of crayfish presence and habitat complexity on the early stages of community assembly in small standing waters.

To fill these gaps, we conducted a colonisation experiment using the spiny-cheek crayfish *Orconectes limosus* as a predator and artificial plant models as added habitat complexity. *Orconectes limosus* is one of the 'Old non-indigenous invasive species' (old NICS) in Europe (Holdich *et al.*, 2009). It is highly omnivorous (Vojkovská, Horká & Ďuriš, 2014) with strong potential to alter small standing water communities (Mathers *et al.*, 2020). Individual *O. limosus* can travel large distances, especially during mating season (Buřič, Kouba & Kozák, 2009), and may colonize relatively new water bodies and interfere with local community assembly. We combined crayfish presence and habitat complexity (1) to identify direct and indirect effects of predation and predation risk by *O. limosus* on macroinvertebrate community composition including functional traits, and (2) to investigate how habitat complexity modifies these direct and indirect crayfish effects on community assembly.

Based on the current theory and empirical evidence, we expected that *O. limosus* would predate on slow-moving benthic taxa such as gastropods and chironomid larvae (direct effects). Furthermore, we hypothesized that the indirect effects of *O. limosus* would be compensated by its interactions with multiple trophic levels (Dorn & Wojdak, 2004), and that non-lethal effects of *O. limosus* would be weak or absent (Lodge *et al.*, 1994). We also expected that habitat complexity would alter the community assembly by taxon-specific preferences for more or less complex habitats

(Holzer & Lawler, 2015; Wulf & Pearson, 2017; Donadi *et al.*, 2019) and by modulating the direct effects of *O. limosus* on its prey (Nyström & Perez, 1998).

Methods

Experimental protocol

We conducted an outdoor mesocosm experiment at the main campus of the University of South Bohemia in České Budějovice (Czech Republic, GPS: N 48°58'31", E 14°26'48"). We used a 2×3 full factorial design with two levels of habitat complexity represented by the presence (N=17) or absence (N=17) of artificial plant models and three levels of predation risk with a free-ranging (N=12), caged (N=12) or absent *O. limosus* (N=10); each treatment was replicated 5–6 times. We used round plastic containers (45 cm diameter, water depth 25 cm, holding about 45 L of water, with a mesh-covered overflow to drain excess water from rain showers). This corresponded to a relatively high effective crayfish density of 6.3 inds.m^{-2} (as compared to, e.g., Roessink *et al.*, 2017). Three artificial plant models, made by tying three 50 cm long and 5 cm wide strips of green plastic mesh folded in half to a small stone, were placed in the high complexity treatments. One dome-shaped metal cage (mouse trap, 8 cm height, 14 cm diameter) was put in each container; the cage held the crayfish in the ‘caged predator’ treatments. The containers were arranged in four double rows. All treatments were distributed evenly across the double rows and randomly within each row.

The containers were filled with tap water a day before the experiment and the bottom of each container was covered with fine crystalline gravel. The experiment began in the morning of 5 August 2014 by adding the artificial vegetation, predators (where appropriate), and 0.5-L aliquotes of a well-mixed inoculum of phyto- and zooplankton in each pool to mimic a small, early-stage body of standing water. The inoculum was obtained with a plankton net (20 cm in diameter, mesh size 40 µm) from the nearby Dubenský rybník pond (N 48°58'48", E 14°22'36"). The containers were then left for spontaneous colonization by aquatic macroinvertebrates from nearby source populations (several permanent small ponds and pools and a seasonally flooded meadow within a 2 km radius).

The crayfish were obtained from experimental populations maintained at the Faculty of Fisheries and Protection of waters of the University of South Bohemia (carapace length: 17–24 mm, fresh weight: 0.94–3.58 g) and randomized across treatments. They were monitored every other day and dead or moulted individuals were replaced to maintain comparable predation potential. We did not observe temperature stress signals in the crayfish (based on fish stress signals, Nakata *et al.*, 2002) during monitoring, and hence assume that the effects on the community assembly in our experimental system could be extrapolated to natural conditions. Crayfish received no additional food in the containers to prevent the input of external nutrients into the environment. Free-ranging crayfish had ingested food visible when we inspected their abdomen. We therefore presume that they fed readily on colonizers, although we have no data on the composition of their diet. Caged crayfish fed very rarely, presumably on organisms that swam or crawled into their cages.

Water temperature was monitored continuously 5 cm above the bottom in 15 randomly chosen containers using HOBO® Pendant® Temperature dataloggers (Onset Computer Corporation, Massachusetts, USA) during the experiment (range: 11.6–28.2 °C, mean ± SD: 18.0 ± 2.9 °C, daily amplitude: 5.6 ± 2.3 °C). The conditions changed dramatically after the first 8 days (21.9 ± 2.5 °C), when it got cold for the rest of the experiment (16.8 ± 1.7 °C; Appendix S3).

We terminated the experiment after 29 days on 4 September 2014. Water temperature (°C), conductivity (µS.cm^{-1}), pH, turbidity (NTU), chl-a (mg.L^{-1}), and dissolved oxygen (mg.L^{-1})were taken by a YSI 6600V2 field probe (YSI, Yellow Springs, Ohio, USA) and water samples from all replicates were collected, frozen and analysed in laboratory to determine

$N\text{-}NO_3^-$, $P\text{-}PO_4^-$, TN, TP and POC ($mg.L^{-1}$) content in an accredited laboratory to quantify total nutrient content in the replicates. Macroinvertebrate communities were sampled destructively by filtering the entire content of each container through a net with 200 µm mesh size. Predator cages and artificial vegetation were washed in the container prior to sampling and taken out. Gravel was washed thoroughly in the container using the initial volume of water and then added tap water. No more macroinvertebrates were observed in the gravel after this procedure. The samples were stored in 80% ethanol and all aquatic macroinvertebrates (N=7918) were identified to one of the five present taxonomic groups that essentially corresponded to different trophic levels and habitat domains: aquatic beetles (Coleoptera; predatory, benthic), mosquito larvae (Diptera: Culicidae; primarily detritivorous, occupying water column), chironomid larvae (Diptera: Chironomidae; primarily detritivorous, benthic, as in Burdett & Watts, 2009; Walker, Wijnhoven & van der Velde, 2013; Lagrue *et al.*, 2014), mayfly larvae (Ephemeroptera; primarily herbivorous, benthic/phytophilous), and snails (Gastropoda; herbivorous, benthic). We further split the Coleoptera into adults and larvae to account for their differences in size and colonization mode. Larvae rear from eggs and remain in the same environment until they mature, while adult beetles can enter and leave at any stage of community assembly (Nilsson, 1996). We identified the beetles, mayfly larvae and snails to the species level (Galewski, 1998; Ložek, 1956; Rozkošný, 1980). We did not attempt to identify the dipteran larvae because many of them belonged to early instars that often cannot be keyed. Overall biomass and abundance were calculated separately for each of the six groups (adult Coleoptera, Coleoptera larvae, Culicidae, Chironomidae, Ephemeroptera, and Gastropoda) in every container.

Measurements of body size

Body length (without antennae and abdominal appendages) of each individual was measured either by hand (adult Coleoptera, Ephemeroptera, *N*=674) or using a semi-automated procedure (Diptera, *N*=5749) by analysing pictures taken with computer assisted stereomicroscope Olympus SZX10 (magnification 3.15×) in Quick Photo Camera 2.3 (PROMICRA, s.r.o., Czech Republic) software. The resulting binary image was then processed in the NIS-Elements software (Laboratory Imaging, Ltd., Czech Republic) to identify individuals in the photographs and FIJI plugin “analyse skeleton” (Polder *et al.*, 2010) was used to measure their length. Shell diameter was measured as a proxy for body size in Gastropoda (*N*=313).

To correct for possible errors of the semi-automated procedure, we re-measured by hand a subset of individuals spanning the minimum-maximum length interval (Chironomidae: *N*=103, range 0.6–17.3 mm; Culicidae: *N*=107, range 1.2–8.6 mm). We approximated the error of the automated measurement, expressed as a function of measured length, with polynomial regression and compared polynomials of increasing degree and identified the best model based on the smallest AIC value. We then corrected the automated measurements by the estimated length-dependent measurement error (Text S1).

We used published length-mass equations to estimate the dry mass of each individual. When multiple equations were available, we chose one according to criteria established by Benke et al. (2010). We did not find published equations for some taxa. In that case, we chose equations for the morphologically and taxonomically closest taxa (Table 1 and Table S1). Coleoptera larvae (*Hydroglyphus geminus*, *N*=1495) changed shape due to their preservation in ethanol. Instead of measuring them, we classified them into three size categories corresponding with larval instars, dried 10 individuals of each instar at 60 °C for 8 hours, weighed them to the nearest 0.001 mg, and assigned the average weight to all individuals of the same instar.

Statistical analyses

We first used redundancy analysis (RDA) to evaluate the differences in environmental conditions and in the abundances and biomasses of the main taxa among the treatments. In the first RDA, we used only NTU, chl-a, $N\text{-}NO_3^-$, $P\text{-}PO_4^-$, TN, TP and POC; other environmental characteristics were excluded because of their low variability (see Table S2). The treatments were included as a categorical explanatory variable and the response data were centred, and log(x+1) transformed prior to each RDA analysis. Moreover, we used analyses of species functional traits found in our experiment. The traits were obtained from the 'freshwaterecology.info' database (Schmidt-Kloiber & Hering, 2015). Locomotion type of *Hydroglyphus geminus* (not scored in the database) was inferred from values common in the Dytiscidae. We used the community-weighted mean (CWM) approach for the analyses, i.e. we averaged the trait values across species in the community weighted by the species abundance. The final CWM values were then related to each treatment by an RDA analysis with centred CWM values as the response variable and the treatment as the categorical explanatory variable. These analyses were run in CANOCO 5.12 (ter Braak & Šmilauer, 2012). Statistical significance of each ordination analysis was tested by a Monte Carlo permutation test (4999 unrestricted permutations).

We used generalized linear models (GLMs) and a model selection approach (Burnham & Anderson, 2002) to analyse the univariate data on the total abundance and biomass of individual taxonomic groups. The data contained zero values; preliminary analyses showed that zero-inflated Gamma GLMs with a constant zero-inflation term were appropriate for the biomass data. Negative binomial GLMs were appropriate to model the abundance data; to meet the model requirements (integer responses), we rounded the weight data to the nearest µg. One type of negative binomial GLM did not satisfactorily fit the abundance data of all groups. We thus proceeded in two steps: we first identified an appropriate model structure by selecting the model with the lowest value of the Akaike information criterion corrected for small sample size (AICc) in full models (i.e., with habitat structure, predation risk and their statistical interaction as predictors) with a linear or quadratic parameterization linking the variance to the mean (Hardin & Hilbe 2007) and with or without a constant zero-inflation term (results not shown). We then fixed the most parsimonious model structure for each response variable and compared the full model and all four possible simpler models using AICc (see Tables S1 and S2 for details). We report the model parameters with the treatment without predation risk and habitat complexity as a baseline. We do not use any post-hoc tests after the model selection. Instead, we deem the treatment effect 'insignificant' if the 95% confidence interval of its parameter estimate overlaps zero and the difference between the treatments with caged and free-ranging predators as 'insignificant' if their 95% confidence intervals of parameter estimates overlap.

We used standardized major axis (SMA) regression to analyse the size spectra because both the dependent and independent variables were measured with error (Warton *et al.*, 2006). We focused on the size ranges in which abundance declined with body mass. To identify this range, we first binned the weight data and plotted a histogram for each combination of taxonomic group and treatment and used only the size range above the body weight at which the maximum frequency was reached. The size spectra were not fully continuous as they contained gaps, especially towards the largest individuals. Bin size for each taxon was set at the smallest value that yielded zeroes, i.e. no individuals in the size bin, in at most 40% of final size bins across all treatments and in at most 50% of the bins in any individual treatment. We replaced the zeroes with the value of 0.01 (other similar values did not qualitatively change the results; details not shown). We then took the mean size of each size class used in the histogram and its frequency and log-transformed their values prior to analysis. We used the package 'smatr-3' to fit the allometries linking body size and abundance and to compare the slopes of the resulting size spectra between individual treatments (Warton *et al.*, 2012). We are not aware of a method that could compare size spectra as a function of two independent factors, and we thus considered each of the six treatments as independent. SMA regression of the Coleoptera and Ephemeroptera data did not produce meaningful results due to low numbers of individuals (not shown).

All univariate analyses were carried out in R version 4.1.2 (R Core Team, 2021) using the packages ‘glmmTMB’ (Brooks *et al.*, 2017) to analyse the models, ‘DHARMa’ (Hartig, 2018) to inspect model residuals and ‘sjPlot’ (Lüdecke, 2014) to tabulate the model parameters.

Results

Water chemistry, turbidity and chl-a concentrations did not differ significantly among the treatments (RDA: pseudo-*F* = 0.30, *P* = 0.92, Fig. S2). Macroivertebrate diversity in our samples was low (Table 1). The small predatory dytiscid *Hydroglyphus geminus* was the most common beetle colonizer found in the containers, along with its larvae. Other aquatic beetles were found only rarely. Mayfly larvae were represented only by *Cloeon dipterum*, a grazer that mainly feeds on periphyton (Zahrádková *et al.*, 2009). Only one species of snail appeared in the samples, the herbivorous *Gyraulus albus*, was most likely introduced with the zooplankton inoculum. All mosquito larvae most probably belonged to *Culex*. Its larvae are highly mobile suspension feeders that filter the water column for microalgae and fine detritus (Merritt, Dadd & Walker, 1992). Chironomids were represented by at least six species, some of which were predatory (P. Soukup, unpublished data), but the majority of individuals belonged to the tribe Chironomini. We treated all chironomids for simplicity as one group of benthic detritivores in the analyses.

Effect of habitat complexity and predation risk on macroinvertebrate abundance and traits composition

We found no significant differences in the macroinvertebrate community composition at the end of the experiment (RDA, abundance: pseudo-*F* = 0.6, *P* = 0.94; functional trait composition: pseudo-*F* = 0.7, *P* = 0.78; Fig. S3AC). Similarly, the most parsimonious models found no effect of predation risk and habitat complexity on the abundance of any group (Fig. S1, Tables 2 and S3). Other plausible models suggested that adult beetles and chironomid and mayfly larvae tended to be more abundant in the complex than in the simple habitat (i.e., without the added artificial plants), while culicid larvae tended to avoid the complex habitat with artificial plants and adult beetles tended to avoid tanks with both free-ranging and caged crayfish (Table S4). However, the effect of habitat complexity and predation risk as well as the differences between the free-ranging and caged predator were always insignificant based on the overlapping 95% confidence intervals. The full model corresponding to complexity-specific effects of predation risk was never included among the plausible models (Table S4).

Effect of habitat complexity and predation risk on macroinvertebrate biomass

We found no significant differences in the biomass-based macroinvertebrate community composition at the end of the experiment (RDA, pseudo-F = 1.0, P = 0.48; Fig. S3). However, the more detailed univariate models identified several patterns that could not be identified in the multivariate analysis. Total biomass of culicid and mayfly larvae and gastropods depended on habitat complexity, and the biomass of the latter group also varied with predation risk, while the biomass of chironomid larvae and larval and adult beetles did not differ among treatments (Tables 3 and S5). Simple habitats had significantly lower total biomasses of the culicid larvae and gastropods and higher total biomass of the mayfly larvae. Gastropod biomass was also significantly lowered by predation risk and the impact of both caged and free-ranging predator was comparable based on the overlapping 95% confidence intervals (Fig. 1 and Table 3). Other plausible models suggested that the biomass of chironomid and mayfly larvae tended to decrease under predation risk, with comparable effects of caged and free-ranging predators based on the overlapping 95% confidence intervals. Similar to the abundances, the full model corresponding to complexity-specific effects of predation risk on the biomass was never included among the plausible models (Table S6).

Effect of habitat complexity and predation risk on macroinvertebrate size spectra

Only the chironomid and mosquito larvae and the gastropod data yielded meaningful size spectra (Fig. 2). Mean slopes estimated by the SMA regression ranged between -1.00 and -0.26 for the chironomid larvae, between -1.85 and -1.08 for the mosquito larvae and between -1.06 and -0.74 for the gastropods. That is, the size spectrum of mosquito larvae was on average steeper than those of chironomids and gastropods (Table 4).

The slopes of size spectra varied significantly with habitat complexity and predation risk only in the chironomid larvae (Fig. 2, Tables 4 and S7). Size spectrum of the chironomid larvae was significantly shallower in the structurally simple environment without a predator, mainly due to the relative absence of large individuals in the other treatments. Moreover, post-hoc test identified a significantly shallower size spectrum in the predator-free treatment with added artificial plants than in the treatment with free-ranging predator in the structurally simple environment (Fig. 2, Tables 4 and S7).

Discussion

Habitat structure can mediate biotic interactions and hence the impact of top predators on local communities (Kovalenko *et al.*, 2012; Soukup *et al.*, 2022). This can be particularly important for emerging invasive taxa such as various crayfish with a high potential to disrupt local communities persistent (Twardochleb *et al.*, 2013; Mathers *et al.*, 2016), but comparative data on the impacts of invasive species along gradients of habitat complexity are all but lacking (but see Nyström & Pérez, 1998; Corkum & Cronin, 2004). Previous studies dealt separately with habitat complexity (Taniguchi & Tokeshi, 2004; Burdett & Watts, 2009; Walker *et al.*, 2013) or predation risk (Stav, Blaustein & Margalit, 2000; Dorn & Wojdak, 2004; Usio *et al.*, 2009; Vonesh *et al.*, 2009) as a determining factor for community assembly in small water bodies. Research on community assembly combining these two factors is, however, scarce and mostly focuses on underlying mechanisms such as predation effectivity (Jordan & McCreary, 1996; Flynn & Ritz, 1999; Warfe & Barmuta, 2004) as opposed to overall patterns in community assembly. Moreover, few studies have investigated the impact of invasive species such as crayfish on community assembly. This limits our understanding of the impacts of invasive species on community structure along environmental gradients (but see Nyström & Pérez, 1998). Our manipulative experiment therefore focused on the joint role of habitat complexity and both consumptive and non-consumptive effects of predation risk by the invasive crayfish *O. limosus* on the early stages of macroinvertebrate community assembly in small standing waters.

As trophic interactions change with body size (Rudolf & Rasmussen, 2013; Rudolf *et al.*, 2014), we characterized the resulting community structure not only by total abundance but also by total biomass and size spectra of the main colonizing macroinvertebrate taxa. Most importantly, while the experimental treatments did not significantly affect macroinvertebrate abundance, we found multiple effects of habitat complexity and predation risk on the total biomass and size spectra. This shows that abundance estimates, and biodiversity inventories can miss important information on the processes structuring natural communities (Gilljam *et al.*, 2011) and may not provide reliable signals of more subtle effects of invasive species on local communities (Woodward & Hildrew, 2002). We also found no evidence of non-additive effects of habitat complexity and predation risk except on the chironomid size spectra, and we therefore discuss their effects separately.

Effect of habitat complexity

Environmental conditions including the chlorophyll-a concentrations as a measure of primary production did not differ between the structurally simple and complex habitats. This implies that all observed effects of habitat complexity can be attributed to the physical modification of habitat structure provided by the added plant models such as increased surface available for colonization (reviewed in Smokorowski & Pratt, 2007; Kovalenko *et al.*, 2012; Soukup *et al.*, 2022). Indirect effects of increased habitat complexity such as increased primary production (Ferreiro *et al.*, 2014; Wolters *et al.*, 2019) likely played only minor role in our experiment.

We found no significant effect of habitat complexity on macroinvertebrate abundance, although detailed analyses of individual taxa identified possible trends towards higher abundance of chironomid and mayfly larvae and adult beetles in treatments with added plant models. The effect of habitat complexity on total biomass and size spectra of macroinvertebrate taxa differed among groups and did not follow the same patterns as the responses in abundance. In the presence of habitat complexity, the biomass of mayfly larvae (*C. dipterum*) increased, while the biomass of gastropods (*G. albus*) and mosquito larvae (*Culex* sp.) decreased. Finally, the size spectrum of chironomid larvae was significantly shallower in the treatment without predation risk in a structurally simple habitat.

Presence of submerged macrophytes is typical for more permanent pools (Boven *et al.*, 2008) with more predators (Resetarits, 1996; Wellborn, Skelly & Werner, 1996). Nevertheless, many grazers and detritivores such as *C. dipterum* but also small predators such as the diving beetle *H. geminus* prefer vegetated water bodies (Bauernfeind & Soldan, 2012) because the increased habitat provisioning and food availability likely offsets an increase in predation risk in such habitats. Long-term colonization experiment found more abundant *C. dipterum* populations in sandpit ponds with the same artificial plant models as used in our experiment than in ponds without them (Sroka, Klečka & Boukal, 2016). The observed higher biomass but the same abundance of *C. dipterum* in the more complex habitat in our experiment could have been caused by preferential (i.e., earlier) oviposition by adult female *C. dipterum* and faster growth of the larvae in containers with artificial plants that get gradually overgrown with periphyton (Walker *et al.*, 2013; Sroka *et al.*, 2016). Similar mechanisms may explain the shallower size spectrum of chironomid larvae in containers without artificial plants: some chironomid taxa are typical ‘pioneer’ species that can quickly colonize new habitats (Frouz, Matěna & Ali, 2003; Vebrová *et al.*, 2018) and the ovipositing females may recognize them by the lack of submerged vegetation.

We attribute the observed lower gastropod biomass in complex habitats to a random seeding event, given that they feed on decaying biomass as well as periphyton and hence should prefer complex habitats with macrophytes (e. g. Walker *et al.*, 2013). The higher biomass of mosquito larvae in containers without artificial plants could be due to slightly higher abundance (compare Figs. 1 and S2), earlier oviposition or faster growth. Finally, mosquitoes may avoid oviposition to structurally complex microhabitats because they often host more predators (salamanders: Sadeh, Mangel & Blaustein, 2009).

These results suggest that the primary mechanism driving the differences in community assembly between simple and complex habitats in our experiment was the habitat provisioning and possibly increased periphyton availability in the complex habitat. However, we focused purely on the role of habitat complexity and therefore did not use live plants in the experiment, which could have affected our results. Macrophytes serve other functions beyond increasing the complexity that make habitats with aquatic plants more suitable for various groups of macroinvertebrates (Grutters *et al.*, 2015). For example, Burdett & Watts (2009) observed no effect of plastic models of vegetation on the abundance of mosquito and chironomid larvae but found more of them in complex habitats with live plants, indicating that plant-animal interactions determine the suitability of vegetated water bodies for these groups. Walker *et al.* (2013) observed no preference of chironomid larvae for any specific plant, suggesting that this interaction is general rather than species specific. Both taxa can also benefit from fine detritus produced by plant decay (Merritt *et al.*, 1992). Finally, yet importantly, we decided to use artificial plant models because they cannot be eaten and destroyed by the omnivorous crayfish (reviewed in e.g., Twardochleb *et al.*, 2013).

Effect of predation risk

Similar to habitat complexity, environmental conditions including the chl-a concentrations as a measure of primary production did not vary significantly with the crayfish presence and predation risk unlike in (Doherty-Bone *et al.*, 2019). This implies that all observed effects of predation risk in our experiment can be attributed to the consumptive and non-consumptive effects of *O. limosus* on lower trophic levels and not to other indirect effects such as increased nutrient cycling by the crayfish (Stav *et al.*, 2000).

Predation risk had negligible impact on abundance and a limited impact on total biomass and size spectra. We detected no positive effects of predation risk. Biomass of gastropods (*G. albus*) decreased significantly and adult beetle abundance and chironomid and mayfly larval biomass tended to be lower in habitats with predation risk. The shallower size spectrum of chironomid larvae in the treatment without predation risk in a structurally simple habitat (mentioned above under the effects of habitat complexity) was driven primarily by the presence of larger individuals.

Moreover, the differences between caged and free-ranging predators were at most minor, suggesting that the responses of taxa to the top predator *Orconectes limosus* were dominated by non-lethal and indirect effects of predation risk and that any lethal effects were either negligible or compensated by bottom-up facilitation (Stav *et al.*, 2000). This contrasts with our expectations and observations of crayfish with full guts during the experiment.

Four different processes could have led to these results: (1) all treatments were colonized at similar rates irrespective of predation risk but the individuals grew more slowly when exposed to predators (Nyström *et al.*, 2001); (2) colonization rates were higher in habitats with free-ranging predators due to positive cues (Albeny-Simões *et al.*, 2014) but the abundances were subsequently decreased by predation, and individual growth in habitats with predators was slower due to competition or predation risk; (3) habitats with predators were colonized later when the costs of perceived predation risk became similar to the costs of competition (Arav & Blaustein, 2006; Albeny-Simões *et al.*, 2014); or (4) colonizers and ovipositing females might have avoided certain habitats, e.g. those without added habitat structure or with predators, but our results lack statistical power due to the relatively small number of replicates.

Prey exposed to predation risk cues can become less active (Resetarits, 2001), attempt to hide (Gotceitas & Colgan, 1989; Oram & Spitze, 2013; Klecka & Boukal, 2014) or change energy allocation in favour of development as opposed to growth (Werner & Gilliam, 1984; Werner & Anholt, 1993), which typically results in slower growth and smaller size-at-age as in the first two processes outlined above. Predation risk cues released by actively feeding predators can be evaluated as undesirable due to increased risk of predation (Eitam, Blaustein & Mangel, 2002; Eitam & Blaustein, 2004; Blaustein *et al.*, 2004) but also as desirable indicating a habitat suitable for conspecifics to colonize in numbers (Albeny-Simões *et al.*, 2014). Moreover, predators can promote nutrient regeneration and cause trophic cascade favourable for quickly developing grazers (Stav *et al.*, 2000). The latter effects can lead to higher colonization rates compensated by the consumptive effects of predation on larger prey individuals, which can result in a community with equal abundance, lower biomass and steeper size spectra of individual prey taxa as in the second process outlined above. Under the third process, some colonizers can simultaneously assess the presence or relative magnitude of both predation risk and competition and maximize their fitness by taking both into account simultaneously (Albeny-Simões *et al.*, 2014). Below we discuss the relevance of these processes for the main groups found in our study.

Crayfish including *O. limosus* prey on snails (Nyström & Perez, 1998; Vojkovská *et al.*, 2014) and can control their populations (Nyström *et al.*, 2001; Dorn & Wojdak, 2004). However, gastropod abundance remained comparable across treatments in our experiment. We most likely introduced the snails randomly with plankton inoculum (ruling out the second and third processes outlined above), and our results imply that the direct effect of predation by *O. limosus* was negligible. This contrasts with the reduced gastropod density found in another mesocosm experiment with a similar duration (Doherty-Bone *et al.*, 2019) and with an experiment using a different crayfish (*Pacifastacus leniusculus*) and a larger snail species (*Lymnaea stagnalis*, shell size 10–47 mm; Nyström & Pérez, 1998). We assume that most of the *G. albus* used in the experiment (shell size ca. 0.6–6.2 mm) were too small for *O. limosus*. Given that the total gastropod biomass in both caged and free-ranging predator treatments decreased similarly, we conclude that the lower biomass was caused by predator avoidance behaviour that led to slower growth (i.e., the first process outlined above). Indeed, gastropod activity and growth can decrease dramatically in the presence of predator cues (*Physa acuta* predated by fish; Turner & Montgomery (2003)), although a direct evidence for gastropod behavioural responses to predation risk by invasive crayfish is lacking.

Water beetles are known to respond to nonlethal predation risk by fish: Resetarits (2001) observed fewer adults and egg cases in the presence of fish. Although we found fewer adults, we detected no effect on the larvae and cannot infer how predation risk affected oviposition site selection. It is possible that adult beetles moved between containers and stayed more often in habitats without predator cues released by both caged and free-ranging predator. Total biomass of beetles did not vary with predation risk, possibly because larger species were less alarmed by predator cues, which would compensate for predator avoidance by smaller beetles. However, our sample sizes were too small for a robust analysis of these patterns.

Our results on chironomid and mayfly larvae broadly agree with Usio *et al.* (2009), who reported no effect of crayfish predation on chironomid abundance except for fewer Tanytarsini. On the other hand, Creed & Reed (2004) found fewer chironomids, especially large ones, in river enclosures with crayfish. The lack of difference in abundance combined with the trend towards lower biomass under predation risk in the chironomid and mayfly larvae in our experiment could be attributed to the first process outlined above, i.e. similar oviposition rates and subsequent slower growth under predation risk as in the gastropods.

The size spectra comparison suggests that at least some chironomids preferred the habitat without added artificial plants and without predation risk in line with the fourth process suggested above; see the section ‘Effects of habitat complexity’ for a detailed explanation. Crayfish in our experiment (body length: 34–53 mm) were large enough to prefer the largest chironomid larvae (body length > 3.15 mm, which represents the 75th percentile in our data), since they commonly feed on larger prey (e.g. Trichoptera larvae: Usio *et al.*, 2009). Free-ranging crayfish, unlike caged ones, could also disturb the sediment and help release nutrients from detritus (Creed & Reed, 2004). This could hide the impact of selective predation on the slope of the size spectrum by increasing the growth rate of surviving individuals, but should also lead to decreased abundance, which we did not observe. Finally, a late colonization of containers with free-ranging *O. limosus* (the third process listed above) could have also lead to lower biomass compared to other treatments. However, this would most likely translate into a shift along a common slope in the size spectra analysis, which we did not observe. Alternatively, our sample sizes might have been insufficient to detect the effects of predation risk on the abundance and biomass in individual containers, which only became apparent when we pooled the data in the comparison of the size spectra.

Concluding remarks

Our study demonstrated that habitat complexity can alter early stages of community assembly, while the consumptive and non-consumptive effects of predation risk by an invasive crayfish species were relatively minor (as in, e.g., (Arce *et al.*, 2019)). These effects were not evident in the comparison of taxon abundance and only became observable when we compared total biomass and size spectra across treatments. This highlights the need for future studies to link community assembly to research on size-structured communities and to identify conditions under which differences in size spectra and biomass composition provide reliable signals of the effects of invasive species on community assembly and structure.

Our results corroborate earlier findings that the impacts of invasive crayfish on local communities are context-dependent, although we did not find strong negative effects reported by the majority of studies (Twardochleb *et al.*, 2013) including another mesocosm experiment over a comparable time period (Doherty-Bone *et al.*, 2019). Community assembly in our study might have been influenced strongly by stochastic processes (Chase, 2010). After 8 days of the experiment, temperature dropped substantially, and it rained every other day (P. Soukup, personal observation). These weather conditions could have decreased colonization rates. It is possible that some of the trends identified by the plausible but not by the most parsimonious models, e.g., those of habitat complexity, would become more apparent if the experiment ran longer or in a warmer period. Due to unfavourable weather conditions, crayfish activity might also have decreased and hence decreased their predation rates and the magnitude of predation risk perceived by the colonizing macroinvertebrates. These results indicate that the community-level effects of invasive crayfish and top predators in general can vary with seasonality and temporal scales, and future work may thus compare these effects across different time points and between seasons (Freeland-Riggert *et al.*, 2016). Such studies may also provide much needed guidance on the timing of any containment and eradication programmes targeting invasive crayfish (Krieg, King & Zenker, 2021).

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Tables

Table 1: Abundances, size ranges and length-mass relationships for the taxa observed in the experiment.

Order/Class and stage	Family	Species	*N*	Body length		Length-mass equation
				range (mm)	mean ± SD (mm)	
Coleoptera, adults	Dytiscidae	*Agabus bipustulatus*	1	10.5	-	(2)
		Rhantus suturalis	3	10.5–11.9	11.41 ± 0.79	(2)
		Hydroglyphus geminus	92	2.1–2.9	2.45 ± 0.14	(2)
		Graptodytes pictus	1	2.7	-	(2)
		Hydroporus angustatus	1	3.0	-	(2)
	Haliplidae	*Haliplus* sp.	3	2.9–3.3	3.01 ± 0.23	(3)
	Helophoridae	*Helophorus* sp.	21	2.4–3.6	2.86 ± 0.26	(1)
	Hydrophilidae	*Enochrus melanocephalus*	1	4.3	-	(4)
		Hydrobius fuscipes	5	3.3–8.0	6.63 ± 1.92	(4)
		Helochares obscurus	2	3.2–5.6	4.39 ± 1.73	(4)
		Anacaena lutescens	7	2.1–3.4	2.77 ± 0.42	(4)
	Hydraenidae	*Limnebius truncatellus*	2	2.4–2.8	2.61 ± 0.24	(1)
Coleoptera, larvae	Dytiscidae	*Hydroglyphus geminus*	1495	0.0028–0.077*	0.04 ± 0.13*	-
Diptera, larvae	Chironomidae	NA	2240	0.6–15.8	2.65 ± 1.67	(6)
	Culicidae	*Culex pipiens*	3509	1.2–8.1	2.92 ± 0.62	(8)
Ephemeroptera, larvae	Baetidae	*Cloeon dipterum*	222	0.5–3.2	1.41 ± 0.76	(9)
Gastropoda	Planorbidae	*Gyraulus albus*	313	0.7–6.2	1.61 ± 0.57	(13)

N = number of individuals. NA = not identified to species level; * = weight data (mg dry weight) instead of lengths, based on mean weights for each instar. Equation numbers as in Table S1.

Table 2: Summary of the most parsimonious negative binomial GLMs describing the effect of predation risk by *Orconectes limosus* and habitat complexity on the abundance of the main macroinvertebrate taxa. Parameter estimates given as mean with 95% confidence intervals on the predictor scale. Intercept = constant term of the nonzero part model; ZI = intercept of the zero-inflated model.

Parameter	**Chironomidae larvae** [a]	**Culicidae larvae** [b]	**Coleoptera adults** [b]	**Coleoptera larvae** [c]	**Ephemeroptera larvae** [b]	**Gastropoda** [a]
Intercept	4.19 (3.82 – 4.56)	4.64 (4.18 – 5.09)	1.41 (1.08 – 1.73)	3.88 (3.66 – 4.09)	1.88 (1.41 – 2.34)	2.22 (1.96 – 2.48)
ZI intercept	-	-	-	-2.34 (-3.53 to -1.15)	-	-

[a] = model with linear parameterization (see Table S3)

[b] = model with quadratic parameterization (see Table S3)

[c] = zero-inflated model with linear parameterization (see Table S3)

Table 3: Summary of the most parsimonious zero-inflated Gamma GLMs describing the effect of predation risk by *Orconectes limosus* and habitat complexity on the biomass of the main macroinvertebrate taxa. Parameter estimates given as mean with 95% confidence intervals on the predictor scale. Intercept = constant term of the nonzero part model (or term describing the biomass in the simple habitat without predation risk); HC = effect of habitat complexity; predator = effects of predation risk; ZI intercept = intercept of the zero-inflated model.

Parameter	**Chironomidae larvae**	**Culicidae larvae**	**Coleoptera adults**	**Coleoptera larvae**	**Ephemeroptera larvae**	**Gastropoda**
Intercept	1.16 (0.68 – 1.64)	2.28 (1.72 – 2.84)	1.88 (1.44 – 2.32)	2.96 (2.75 – 3.16)	-3.46 (-4.36 to -2.55)	1.11 (0.45 – 1.77)
HC (complex vs. simple habitat)	-	-0.92 (-1.70 to -0.14)	-	-	2.43 (1.22 – 3.65)	-0.62 (-1.23 – 0.00)
predator (caged vs. none)	-	-	-	-	-	-1.22 (-1.97 to -0.47)
predator (free vs. none)	-	-	-	-	-	-1.14 (-1.89 to -0.39)
ZI intercept	-3.50 (-5.49 to -1.51)	-2.34 (-3.52 to -1.15)	-2.02 (-3.06 to -0.97)	-2.34 (-3.52 to -1.15)	-1.35 (-2.18 to -0.52)	-3.50 (-5.49 to -1.51)

Table 4: The effect of habitat complexity and predation risk by *Orconectes limosus* on the size spectra of the most abundant macroinvertebrate taxa in the experiment.

Taxonomic group	**Habitat complexity**	**Predation risk**	**c_1 (95% CI)**	**c_2 (95% CI)**
Chironomidae, larvae	no	none	0.18 (0.04, 0.33)	-0.26 (-0.32, -0.22) ^{a}
	no	caged	-2.31 (-2.71, -1.91)	-0.83 (-0.97, -0.71) ^{bc}
	no	free	-1.96 (-2.27, -1.66)	-0.73 (-0.84, -0.64) ^{b}
	yes	none	-1.75 (-2.09, -1.40)	-1.00 (-1.16, -0.86) ^{c}
	yes	caged	-1.67 (-2.02, -1.33)	-0.87 (-0.98, -0.78) ^{bc}
	yes	free	-1.54 (-1.89, -1.20)	-0.76 (-0.86, -0.67) ^{bc}
Culicidae, larvae	no	none	-3.04 (-3.76, -2.32)	-1.82 (-2.22, -1.49) $^{\text{n.s.}}$
	no	caged	-2.14 (-3.26, -1.02)	-1.55 (-2.29, -1.05) $^{\text{n.s.}}$
	no	free	-1.10 (-1.96, -0.25)	-1.08 (-1.66, -0.70) $^{\text{n.s.}}$
	yes	none	-2.79 (-3.27, -2.31)	-1.39 (-1.64, -1.17) $^{\text{n.s.}}$
	yes	caged	-2.74 (-3.34, -2.14)	-1.60 (-1.92, -1.34) $^{\text{n.s.}}$
	yes	free	-2.81 (-3.43, -2.18)	-1.60 (-1.98, -1.30) $^{\text{n.s.}}$
Gastropoda	no	none	-1.57 (-2.87, -0.28)	-1.06 (-1.93, -0.59) $^{\text{n.s.}}$
	no	caged	-0.86 (-1.52, -0.20)	-0.74 (-1.02, -0.54) $^{\text{n.s.}}$
	no	free	-1.26 (-2.12, -1.19)	-0.77 (-1.19, -0.49) $^{\text{n.s.}}$
	yes	none	-0.79 (-1.58, -0.001)	-0.86 (-1.26, -0.58) $^{\text{n.s.}}$
	yes	caged	-1.61 (-2.26, -0.97)	-0.80 (-1.12, -0.57) $^{\text{n.s.}}$
	yes	free	-1.28 (-1.85, -0.70)	-0.80 (-1.05, -0.61) $^{\text{n.s.}}$

Results based on SMA regression with treatments as one factor. Coefficients: c_1 = elevation, c_2 = slope; 95% confidence intervals given in parentheses. Estimates of c_2 with different letters differ significantly ($P < 0.05$) within each taxon; n.s. = no significant differences.

Figures

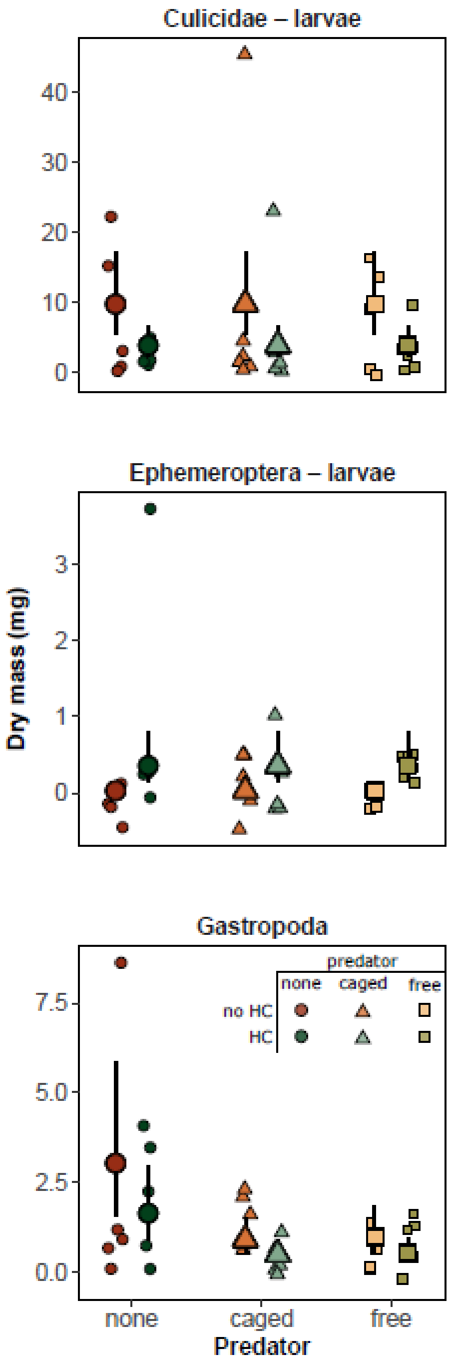


Figure 1: Description continues the next page.

Figure 1: Predictions of the most parsimonious models describing the effect of predation risk by *Orconectes limosus* and habitat complexity on the biomass of Culicidae, Ephemeroptera and Gastropoda (see Fig. S2 for Chironomidae and Coleoptera adults and larvae). Small symbols = individual replicates; large symbols = model fit; error bars = 95% confidence intervals. Predation risk: circles = none, triangles = caged predator, square = free-ranging predator; habitat complexity: red = without artificial plants, green = with artificial vegetation.

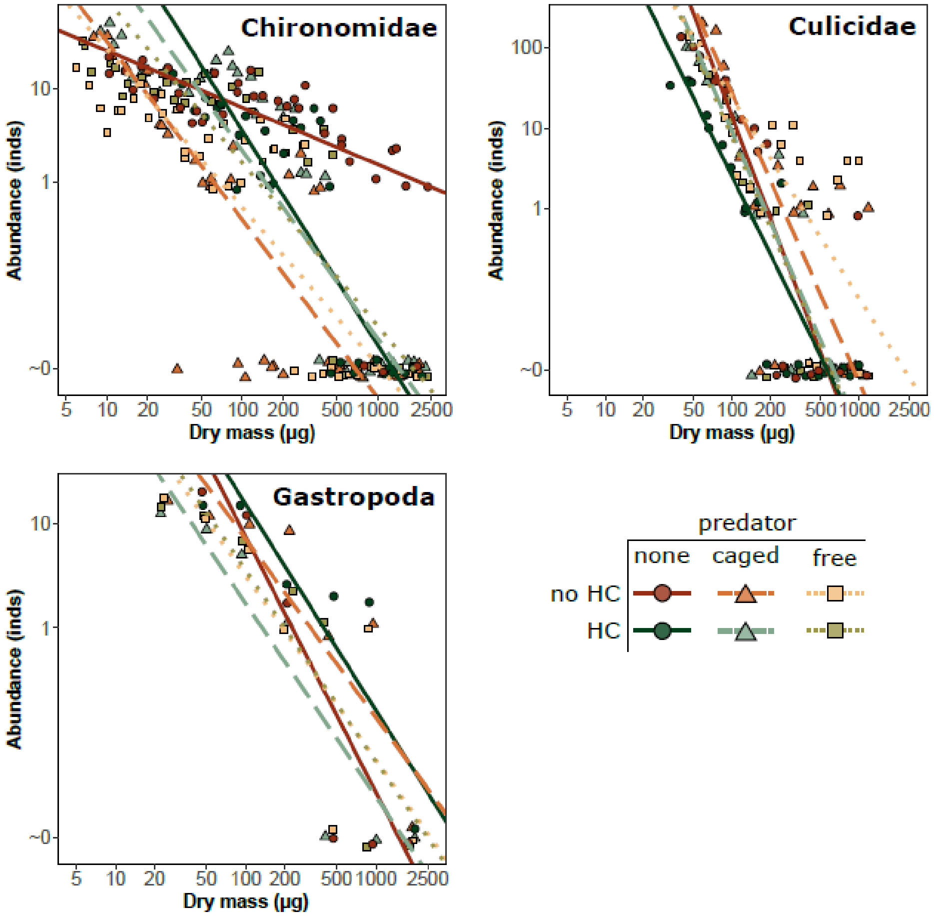


Figure 2: Effect of experimental treatments on the size spectra of Chironomidae, Culicidae and Gastropoda. Filled symbols represent individual data and lines the results of the SMA regression. Habitat complexity: light to dark green symbols and lines = added artificial plants, orange to dark red symbols and lines = no artificial plants. Predation risk: dark hue colour and solid lines = no predator, medium hue colour and dashed lines = caged predator, light hue colour and dotted lines = free-ranging predator. Zero abundance values set arbitrarily at 0.01.

Supplementary material for "Invasive crayfish predation risk and habitat complexity effects on community assembly in small standing waters"

Pavel R. Soukup[1,2*], Vojtěch Kolář[1,2], David S. Boukal[1,2]

[1]University of South Bohemia, Faculty of Science, Department of Ecosystem Biology, 370 05 České Budějovice, Czech Republic
[2]Czech Academy of Sciences, Biology Centre, Institute of Entomology, 370 05 České Budějovice, Czech Republic
*Corresponding author: Pavel R. Soukup. University of South Bohemia, Faculty of Science, Department of Ecosystem Biology, 370 05 České Budějovice, Czech Republic. E-mail: pavelsoukup@protonmail.com

Appendices

Figure S4: RDA diagrams of the effects of experimental treatments on macroinvertebrate community composition, functional trait composition, and biomass-based community composition.

Table S3: Model comparison: Effect of habitat complexity and predation risk on the abundance of the main macroinvertebrate taxa.

Table S4: Other plausible models of the effect of predation risk by *Orconectes limosus* and habitat complexity on the total abundance of the major macroinvertebrate taxa.

Table S5: Model comparison: Effect of habitat complexity and predation risk on the biomass of the main macroinvertebrate taxa.

Table S6: Other plausible zero-inflated Gamma GLM models with log-link function describing the effect of predation risk by *Orconectes limosus* and habitat complexity on the total biomass of the major macroinvertebrate taxa.

Table S7: Pairwise comparisons of treatment-specific size spectra of chironomid larvae, culicid larvae and gastropods based on the SMA analysis.

Figure S5: Abundance of the main invertebrate groups in buckets with no predator, a caged predator, and a free predator with or without added habitat complexity.

Figure S6: Dry mass of the main invertebrate groups.

Figure S7: Treatment-specific size spectra of chironomid larvae.

Figure S8: Treatment-specific size spectra of culicid larvae.

Figure S9: Treatment-specific size spectra of gastropods.

Table S1: Overview of published length-mass relationship with details.

Eq	Order/Class	Family	Species	Stage	N	Range (mm)	a	b	R^2	Source
(1)	Coleoptera	all	all	Ad	-	0.6–17.2*	0.0077	2.910	–	Benke et al. 2010
(2)		Dytiscidae	*Hydroporus* spp.	Ad	42	3.1–6.5	0.6180	2.502	0.71	Smock 1980
(3)		Haliplidae	*Peltodytes sexmaculatus*	Ad	17	4.4–6.0	0.0271	2.744	0.76	Smock 1980
(4)		Hydrophilidae	*Enochrus bicolor*	Ad	150	2.8–4.0	0.0150	3.012	0.89	Heydarnejad 2010
(5)	Diptera	Chironomidae	all	L	-	2.0–19.0	0.0011	2.730	0.96	Johnston & Cunjak 1999
(6)		Chironomidae	all	L	-	1.0–13.7*	0.0018	2.617	–	Benke et al. 2010
(7)		Chironomidae	NA	L	41	2.0–14.0	0.0047	1.820	0.50	Baumgärtner & Rothhaupt 2003
(8)		Culicidae	*Culex* sp.	L	36	1.4–7.1	0.0017	3.168	0.98	Quintana 1995
(9)	Ephemeroptera	Baetidae	all	L	-	1.8–8.5*	0.0053	2.875	–	Benke et al. 2010
(10)		Baetidae	*Cloeon dipterum*	L	1096	2.0–8.4	0.0010	3.680	0.95	Johnston & Cunjak 1999
(11)	Gastropoda	Pleuroceridae	*Elimia clavaeformis*	Ad	50	-	0.0123	3.984	0.96	Benke et al. 2010
(12)		Lymnaeidae	*Radix peregra/ovata*	Ad	8	2.0–12.2	0.0265	3.150	0.96	Baumgärtner & Rothhaupt 2003
(13)		Bithyniidae	*Bithynia tentaculata*	Ad	10	1.6–6.6	0.0106	3.660	0.95	Baumgärtner & Rothhaupt 2003

“all” = result based on multiple equations for multiple taxa at the family or species level, NA = species not determined. Coefficients a, b are given for allometric equation $M = a \cdot L^b$, where M = dry mass and L = body length. Stage: Ad = adults, L = larvae. N = sample size, R^2 = coefficient of determination. Missing values (‘-‘) could not be acquired from source materials. * = values not explicitly given but inferred from the published material.

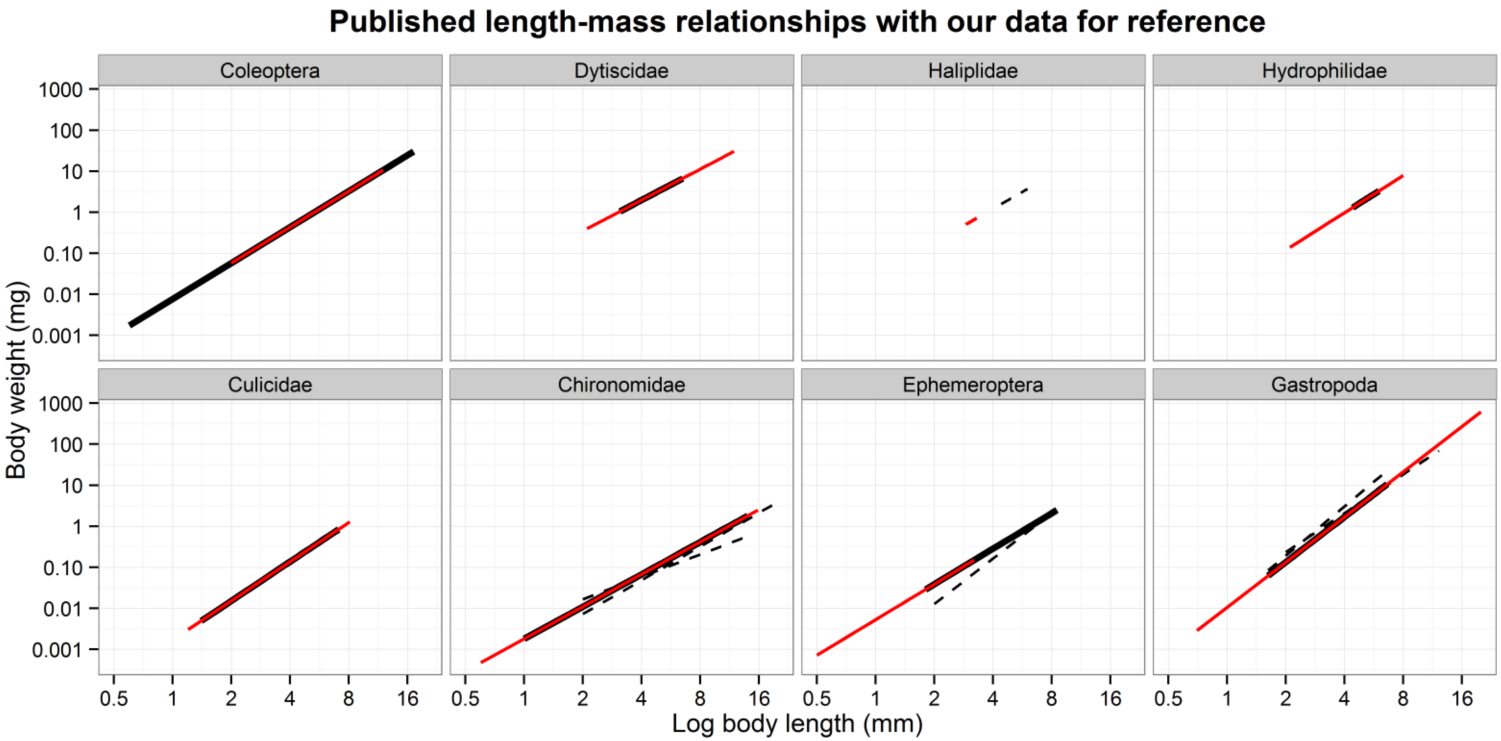


Figure S1: Comparison of length-mass allometries from Table S1 with our data. Each black line corresponds to one equation. Dashed lines were not used in our study; thick black lines represent equations used in our study. Red lines depict the chosen allometry over the size range observed in our study. No thick black line in a panel = equation for a higher taxon was used instead.

Text S1: Automatic measurement error analysis and correction of the individual length data

Automatic measurement error ranged from -12.3% to +14.7% in the Chironomidae and from -12.3% to +15.5% in the Culicidae. The fitted polynomial (Table S2) provided a good fit for the data (Figure S2) with no obvious biases (diagnostic plots not shown). Equation (1) corresponds to the correction for automated length measurement (m), where l is the manually measured length for the Culicidae and equation (2) to the correction for the Chironomidae:

$$l = -3 \cdot 10^{-13} m^5 + 6 \cdot 10^{-10} m^4 - 4 \cdot 10^{-7} m^3 - 1 \cdot 10^{-4} m^2 + 221 \cdot 10^{-5} m - 1.258 \tag{1}$$

$$l = -3 \cdot 10^{-12} m^4 + 6 \cdot 10^{-9} m^3 - 5 \cdot 10^{-6} m^2 + 15 \cdot 10^{-4} m - 0.146 \tag{2}$$

Table S2: Comparison of different polynomial models correcting the automatic measurement error as a function of measured length for the Chironomidae and Culicidae. Chosen model for each taxon in bold. A simpler model was preferred over the most parsimonious one in the Chironomidae to avoid clear overfitting.

Taxon	**Polynomial**	**AIC**
Culicidae	~const	-745.51
	~a	-750.46
	~a+a^2	-753.24
	~a+a^2+a^3	-754.92
	~a+a^2+a^3+a^4	-755.99
	~a+a^2+a^3+a^4+a^5	**-756.39**
	~a+a^2+a^3+a^4+a^5+a^6	-755.41
Chironomidae	~const	-669.26
	~a	-680.46
	~a+a^2	-685.16
	~a+a^2+a^3	-688.19
	~a+a^2+a^3+a^4	**-690.44**
	~a+a^2+a^3+a^4+a^5	-701.50
	~a+a^2+a^3+a^4+a^5+a^6	-702.05

Figure S2: Automatic measurement error as a function of length (left) for the Chironomidae (top) and Culicidae (bottom) and residuals as a function of fitted values (right). Black dots = measured individuals, black line = model prediction, grey interval = 95% confidence interval.

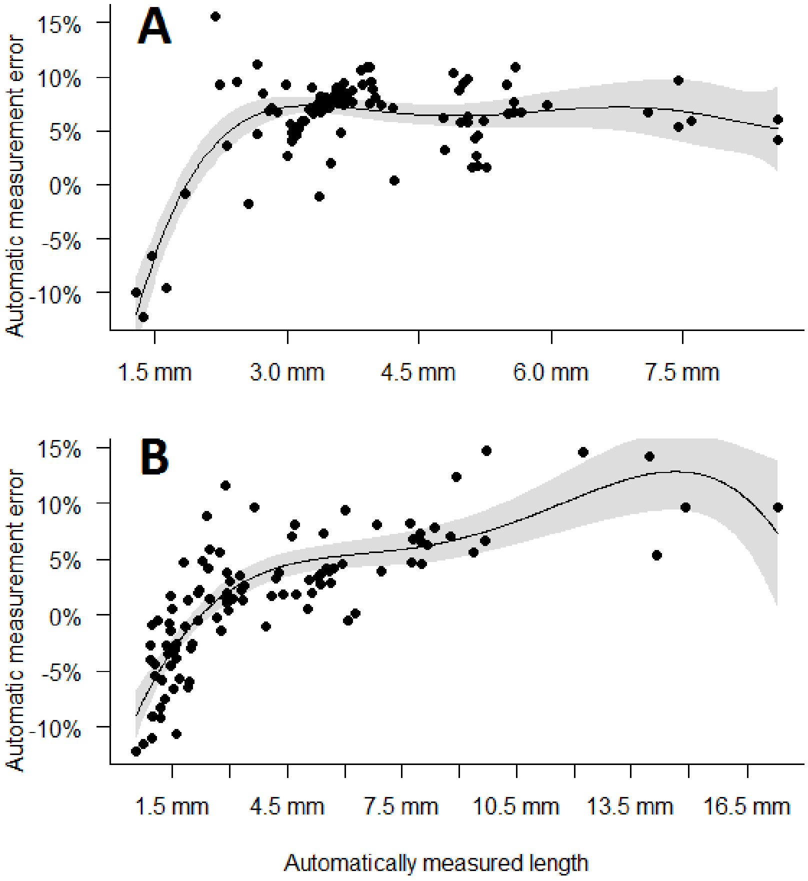


Table S2: Water parameters and chemistry. Temperature was measured at the end of the experiment in samples taken for water measurements (^{1}) and continuously during the entire experiment (^{2}, 15 HOBO® Pendant® Temperature dataloggers), each placed permanently in a randomly selected replicate 5 cm above the bottom, with 15-minute measuring intervals, *N* = 34320 individual readings). Other parameters were measured on the last day of the experiment with YSI 6600V2 multimeter (September 4th, 2014). Water samples were collected, frozen and later analyzed in a laboratory to determine N-NO_3, P-PO_4, TN, TP and POC concentrations.

Parameter	**Range**	**Mean ± SD**
Temperature [°C]	15.2–15.8^1 11.6–28.3^2	15.11 ± 0.15^1 18.95 ± 2.86^2
Conductivity [µS.cm^{-1}]	194–214	197.4 ± 5.3
pH	8.7–9.9	9.2 ± 0.4
Turbidity [NTU]	14.5–21.9	17.1 ± 2.2
Chlorophyll a [mg.L^{-1}]	2.9–78.5	19.6 ± 14.9
Oxygen [mg.L^{-1}]	9.6–12.3	9.8 ± 0.4
N-NO_3 [mg.L^{-1}]	<1.3–687.7	177.64 ± 202.38
P-PO_4 [mg.L^{-1}]	0.11–16.2	1.86 ± 2.77
Total N [mg.L^{-1}]	217.5–854.7	444.43 ± 201.68
Total P [mg.L^{-1}]	13.0–67.5	21.54 ± 10.08
Particulate organic P [mg/L]	3.8–8.9	5.04 ± 1.12

Figure S3. RDA diagram of the effect of experimental treatments (symbols; see Figure 1 for shapes and colours) on environmental conditions.

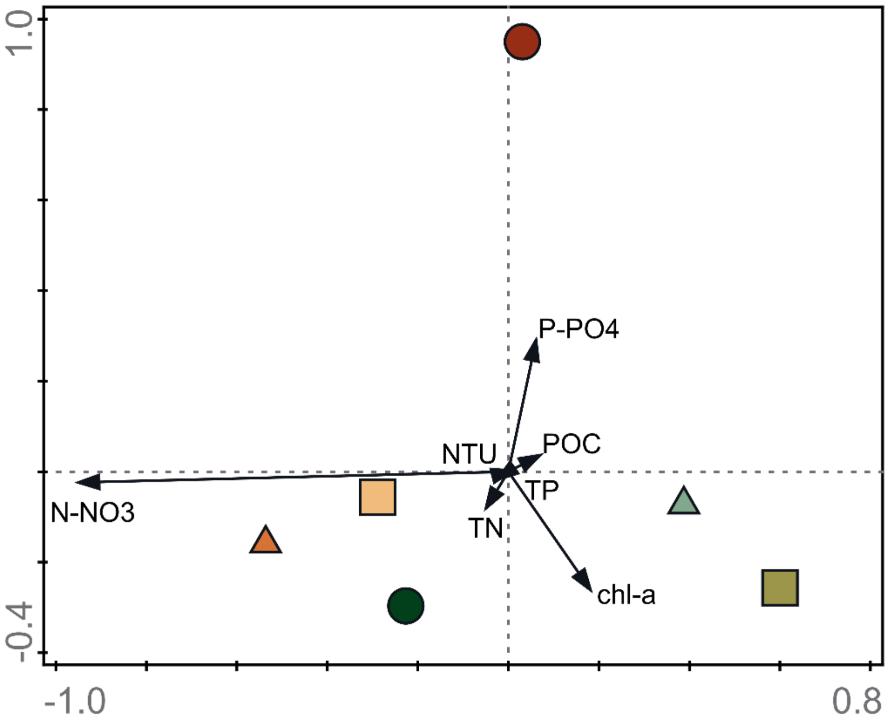
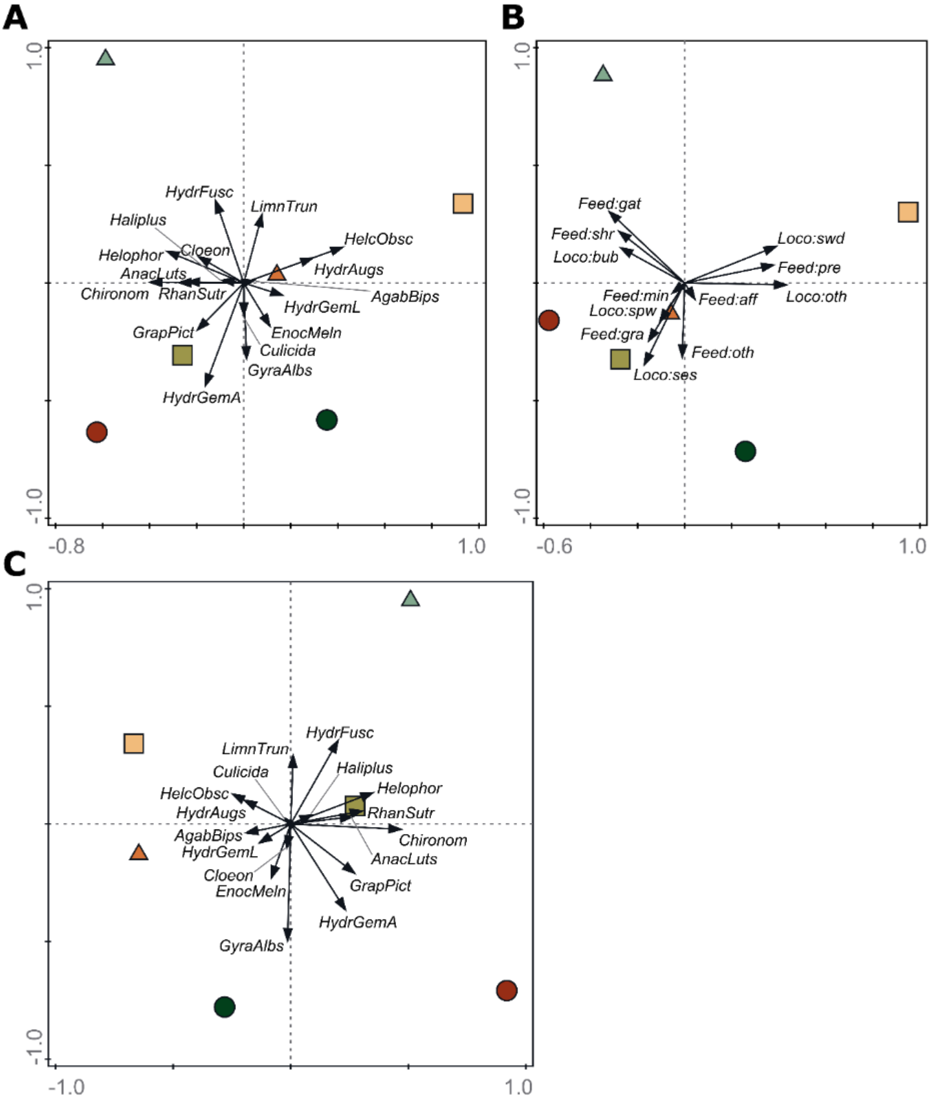


Figure S4. RDA diagrams of the effects of experimental treatments (symbols; see Figure 1 for shapes and colours) on macroinvertebrate community composition (A), functional trait composition (B), and biomass-based community composition (C). Species names (A, C): *Agabus bipustulatus* – AgabBips; *Anacaena lutescens* – AnacLuts; Chironomidae – Chironom; *Cloeon dipterum* – Cloeon; Culicidae – Culicida; *Enochrus melanocephalus* – EnocMeln; *Graptodytes pictus* – GrapPict; *Gyraulus albus* – GyraAlbs; *Haliplus* sp. – Haliplus; *Helochares obscurus* – HelcObsc; *Helophorus* sp. – Helophor; *Hydrobius fuscipes* – HydrFusc; *Hydroporus angustatus* – HydrAugs; *Limnebius truncatellus* – LimnTrun; *Rhantus suturalis* – RhanSutr; *Hydroglyphus geminus* adults – HydrGemA; *Hydroglyphus geminus* larvae – HydrGemL. Functional traits (B): Feeding modes, Feed:gra – grazer/scraper; Feed:min – miner; Feed:shr – shredder; Feed:gat – gatherer/collector; Feed:aff – active filter feeder; Feed:pff – passive filter feeder; Feed:pre – predator; Feed:par – parasite; Feed:oth – other; locomotion types, Loco:sws – swimming/scating; Loco:swd – swimming/diving; Loco:bub – burrowing/boring; Loco:spw – sprawling/walking; Loco:ses – (semi)sessil; Loco:oth – other. See main text for details.



(For description see previous page.)

Table S3: Model comparison: Effect of habitat complexity (‘HC’) and predation risk (‘predator’) on the abundance of the main macroinvertebrate taxa. df = degrees of freedom; ln(*L*) = model log-likelihood; ΔAICc = difference in AICc from the most parsimonious model; *w* = Akaike weight based on AICc. Most parsimonious model for each taxon in bold; other plausible models with ΔAICc ≤ 2 in italics. Models for each taxon ranked by the level of parsimony. Model structure: const = constant model. Families: nbinom1 = negative binomial GLM with linear parameterization (Hardin & Hilbe 2007); nbinom2 = negative binomial GLM with quadratic parameterization (Hardin & Hilbe 2007); zi-nbinom1 = zero-inflated negative binomial GLM with linear parameterization (Hardin & Hilbe 2007) and a constant zero inflation term.

Taxon	**Family**	**Model structure**	**df**	**Ln(*L*)**	**ΔAICc**	***w***
Chironomidae, larvae	nbinom1	**~ const**	**2**	**-176.3**	**0**	**0.622**
		~ HC	*3*	*-176.0*	*1.8*	*0.255*
		~ predator	4	-175.8	3.9	0.086
		~ HC + predator	5	-175.6	6.2	0.028
		~ HC × predator	7	-173.7	8.6	0.008
Culicidae, larvae	nbinom2	**~ const**	**2**	**-187.5**	**0**	**0.516**
		~ HC	*3*	*-186.6*	*0.6*	*0.389*
		~ predator	4	-187.3	4.5	0.053
		~ HC + predator	5	-186.2	5.1	0.039
		~ HC × predator	7	-185.9	10.7	0.002
Coleoptera, adults	nbinom2	**~ const**	**2**	**-85.1**	**0**	**0.425**
		~ HC	*3*	*-84.4*	*1.0*	*0.258*
		~ predator	*4*	*-83.6*	*1.8*	*0.170*
		~ HC + predator	5	-82.5	2.4	0.126
		~ HC × predator	7	-81.2	6.0	0.021

Coleoptera, larvae	zi-nbinom1	**~ const**	**3**	**-155.2**	**0**	**0.648**
		~ HC	4	-155.0	2.1	0.230
		~ predator	5	-154.5	3.9	0.092
		~ HC + predator	6	-154.2	6.3	0.028
		~ HC × predator	8	-153.8	12.1	0.002
Ephemeroptera, larvae	nbinom2	**~ const**	**2**	**-97.9**	**0**	**0.583**
		~ *HC*	*3*	*-97.3*	*1.2*	*0.316*
		~ predator	4	-97.5	4.2	0.071
		~ HC + predator	5	-97.1	6.1	0.027
		~ HC × predator	7	-96.1	10.2	0.003
Gastropoda	nbinom1	**~ const**	**2**	**-108.7**	**0**	**0.642**
		~ HC	3	-108.5	2.2	0.216
		~ predator	4	-108.0	3.6	0.104
		~ HC + predator	5	-107.9	6.2	0.029
		~ HC × predator	7	-106.0	8.5	0.009

Table S4: Other plausible models of the effect of predation risk by *Orconectes limosus* and habitat complexity on the total abundance of the major macroinvertebrate taxa. Parameters given as mean with 95% confidence intervals in parentheses. Intercept = parameter estimate for the treatment without predator and without added habitat structure; HC = habitat complexity. See main text for details.

Parameter	**Chironomidae, larvae** [a]	**Culicidae, larvae** [b]	**Coleoptera, adults** [b]	**Coleoptera, adults** [b]	**Ephemeroptera, larvae** [b]
(Intercept)	4.07 (3.59 – 4.55)	4.90 (4.27 – 5.53)	1.19 (0.73 – 1.66)	1.76 (1.21 – 2.30)	1.59 (0.93 – 2.24)
HC (complex vs. simple habitat)	0.23 (-0.33 – 0.79)	-0.63 (-1.52 – 0.26)	0.39 (-0.25 – 1.03)	-	0.52 (-0.40 – 1.43)
predator (caged vs. none)	-	-	-	-0.72 (-1.49 – 0.06)	-
predator (free vs. none)	-	-	-	-0.39 (-1.15 – 0.36)	-

[a] = negative binomial GLM model with linear parameterization (see Table S3)

[b] = negative binomial GLM model with quadratic parameterization (see Table S3)

Table S5: Model comparison: Effect of habitat complexity (‘HC’) and predation risk (‘predator’) on the biomass of the main macroinvertebrate taxa. Most parsimonious model for each taxon in bold; other plausible models with ΔAICc ≤ 2 in italics. All symbols and model ranking criterion as in Table S1. All taxa modelled with zero-inflated Gamma GLMs with a log-link function and a constant zero inflation term.

Taxon	Model structure	df	Ln(*L*)	ΔAICc	*w*
Chironomidae, larvae	**~ const**	**3**	**-69.1**	**0**	**0.533**
	~ predator	*5*	*-67.4*	*1.9*	*0.211*
	~ HC	4	-69.1	2.5	0.150
	~ HC + predator	6	-67.0	4.0	0.072
	~ HC × predator	8	-64.4	5.5	0.034
Culicidae, larvae	**~ HC**	**4**	**-96.7**	**0**	**0.662**
	~ const	3	-99.1	2.3	0.207
	~ HC + predator	6	-95.7	3.7	0.103
	~ predator	5	-98.7	6.7	0.023
	~ HC × predator	8	-95.3	9.5	0.006
Coleoptera, adults	**~ const**	**3**	**-96.8**	**0**	**0.602**
	~ HC	4	-96.5	2.0	0.220
	~ predator	5	-96.0	3.7	0.095
	~ HC + predator	6	-95.2	5.2	0.045
	~ HC × predator	8	-92.1	5.5	0.038
Coleoptera, larvae	**~ const**	**3**	**-125.4**	**0**	**0.667**
	~ HC	4	-125.1	2.1	0.239
	~ predator	5	-125.0	4.5	0.070
	~ HC + predator	6	-124.6	6.8	0.023
	~ HC × predator	8	-124.1	12.3	0.001
Ephemeroptera, larvae	**~ HC**	**4**	**24.8**	**0**	**0.603**
	~ HC + predator	*6*	*26.9*	*1.7*	*0.264*
	~ HC × predator	8	29.3	3.5	0.107
	~ predator	5	22.4	7.6	0.014
	~ const	3	19.6	7.8	0.012
Gastropoda	**~ HC + predator**	**6**	**-35.7**	**0**	**0.504**
	~ predator	*5*	*-37.5*	*0.7*	*0.362*
	~ HC × predator	8	-34.2	3.7	0.079
	~ const	3	-42.6	5.5	0.033
	~ HC	4	-41.7	6.3	0.022

Table S6: Other plausible zero-inflated Gamma GLM models with log-link function describing the effect of predation risk by *Orconectes limosus* and habitat complexity on the total biomass of the major macroinvertebrate taxa. Parameters given as mean with 95% confidence intervals on the predictor scale. Intercept = constant term of the nonzero part model (or term describing the biomass in the simple habitat without predation risk); HC = habitat complexity; ZI intercept = intercept of the zero-inflated model. See main text for details.

Parameter	**Chironomidae, larvae**	**Ephemeroptera, larvae**	**Gastropoda**
Intercept	1.71 (0.87 – 2.54)	-2.85 (-4.40 to -1.30)	0.79 (0.22 – 1.35)
HC (complex vs. simple habitat)	-	2.23 (0.93 – 3.54)	-
predator (caged vs. none)	-0.89 (-2.03 – 0.24)	-1.46 (-2.91 – 0.004)	-1.06 (-1.83 to -0.30)
predator (free vs. none)	-0.97 (-2.12 – 1.90)	-0.29 (-1.97 – 1.39)	-1.16 (-1.94 to -0.38)
ZI intercept	-3.50 (-5.49 to -1.51)	-1.35 (-2.18 to -0.52)	-3.50 (-5.49 to -1.51)

Table S7: Pairwise comparisons of treatment-specific size spectra of chironomid larvae, culicid larvae and gastropods based on the SMA analysis. HC = added habitat complexity; P = predator. Significantly different pairs (P < 0.05; values corrected for multiple comparisons with Sidak correction) in bold. See main text for details and Table 4 for the slope and intercept values.

Taxon	**Treatment 1**	**Treatment 2**	X^2	P
Chironomidae	no P, no HC	no P, HC	74.7	**$< 10^{-3}$**
	no P, no HC	caged P, no HC	60.2	**$< 10^{-3}$**
	no P, no HC	caged P, HC	70.8	**$< 10^{-3}$**
	no P, no HC	free P, no HC	54.7	**$< 10^{-3}$**
	no P, no HC	free P, HC	58.6	**$< 10^{-3}$**
	no P, HC	caged P, no HC	2.88	0.76
	no P, HC	caged P, HC	1.90	0.94
	no P, HC	free P, no HC	9.08	**0.038**
	no P, HC	free P, HC	7.41	0.093
	caged P, no HC	caged P, HC	0.31	1.00
	caged P, no HC	free P, no HC	1.36	0.99
	caged P, no HC	free P, HC	0.72	1.00
	caged P, HC	free P, no HC	3.91	0.52
	caged P, HC	free P, HC	2.58	0.82
	free P, no HC	free P, HC	0.13	1.00
Culicidae	no P, no HC	no P, HC	4.33	0.44
	no P, no HC	caged P, no HC	0.55	1.00
	no P, no HC	caged P, HC	0.91	1.00
	no P, no HC	free P, no HC	4.78	0.36
	no P, no HC	free P, HC	0.81	1.00
	no P, HC	caged P, no HC	0.29	1.00
	no P, HC	caged P, HC	1.42	0.98
	no P, HC	free P, no HC	1.18	0.99

	no P, HC	free P, HC	1.22	0.99
	caged P, no HC	caged P, HC	0.02	1.00
	caged P, no HC	free P, no HC	1.61	0.97
	caged P, no HC	free P, HC	0.02	1.00
	caged P, HC	free P, no HC	2.91	0.75
	caged P, HC	free P, HC	0.00	1.00
	free P, no HC	free P, HC	2.84	0.76
Gastropoda	no P, no HC	no P, HC	0.48	1.00
	no P, no HC	caged P, no HC	1.40	0.98
	no P, no HC	caged P, HC	0.85	1.00
	no P, no HC	free P, no HC	0.99	1.00
	no P, no HC	free P, HC	0.99	1.00
	no P, HC	caged P, no HC	0.44	1.00
	no P, HC	caged P, HC	0.09	1.00
	no P, HC	free P, no HC	0.20	1.00
	no P, HC	free P, HC	0.14	1.00
	caged P, no HC	caged P, HC	0.15	1.00
	caged P, no HC	free P, no HC	0.02	1.00
	caged P, no HC	free P, HC	0.14	1.00
	caged P, HC	free P, no HC	0.04	1.00
	caged P, HC	free P, HC	0.00	1.00
	free P, no HC	free P, HC	0.03	1.00

Figure S2: Abundance of the main invertebrate groups in buckets with no predator (circles), a caged predator (triangles), and a free predator (squares) with added habitat structure (green tones, shifted right) or without (orange tones, shifted left). N = 5 for treatments with no predator; N = 6 other treatments. Model prediction (thick line) and confidence intervals (in between dashed lines) for the best model (abundance ~ const).

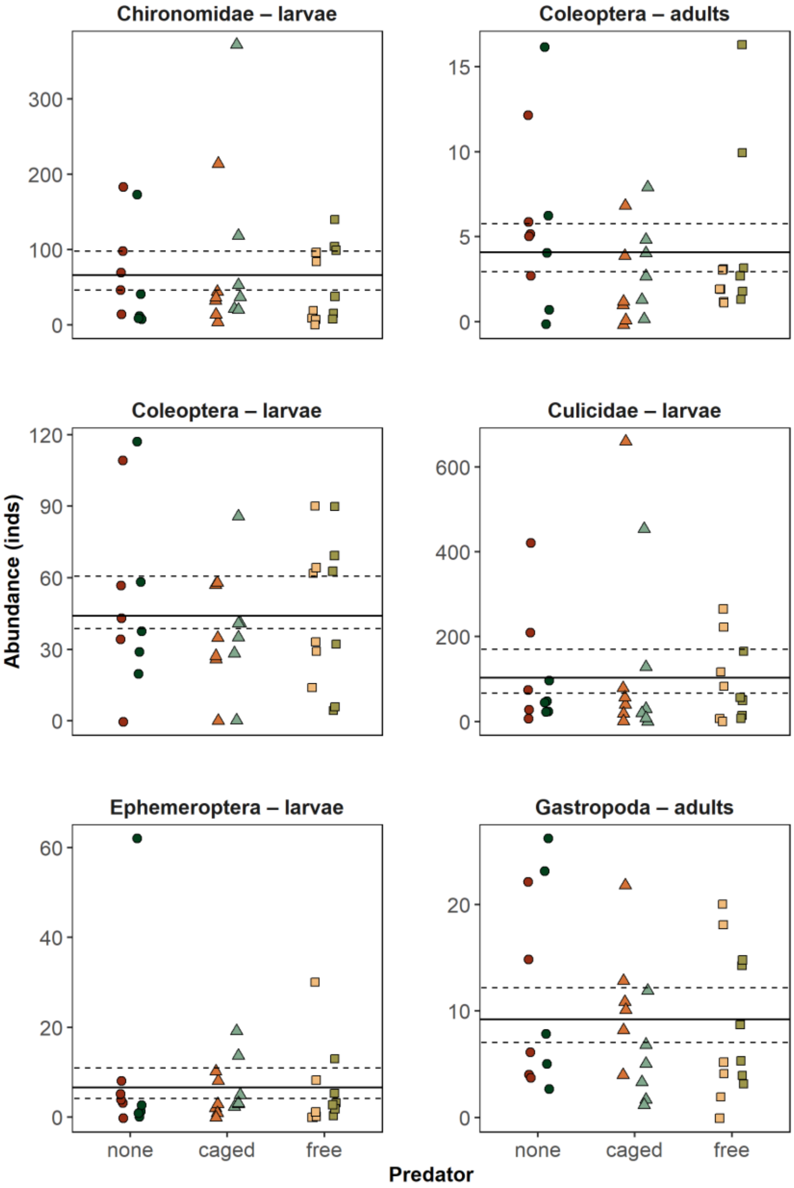


Figure S3: Dry mass of the main invertebrate groups. Symbols as in Figure S1.

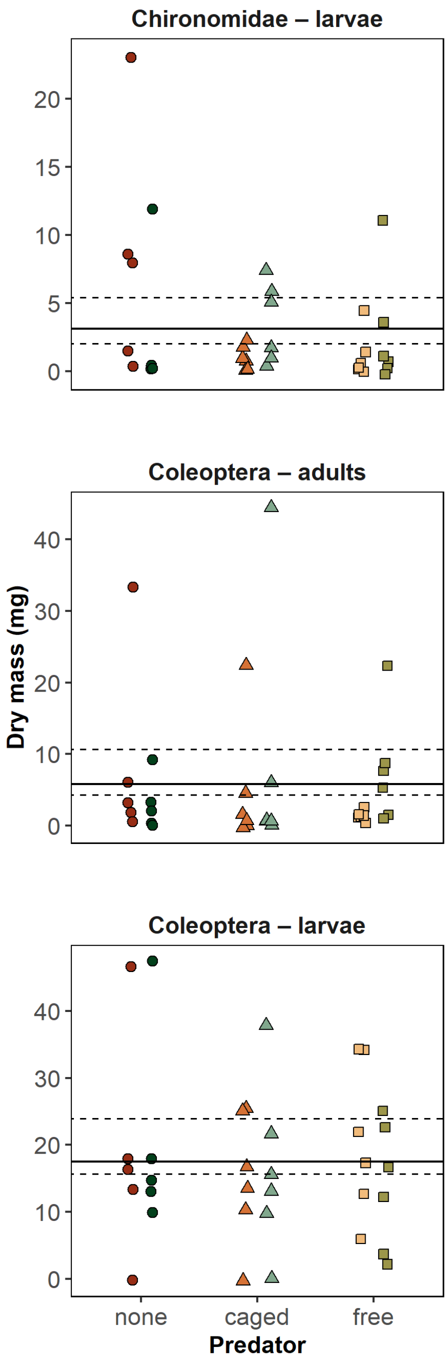


Figure S4: Treatment-specific size spectra of chironomid larvae. Each size spectrum is pooled across all replicates of the given treatment. See main text for details.

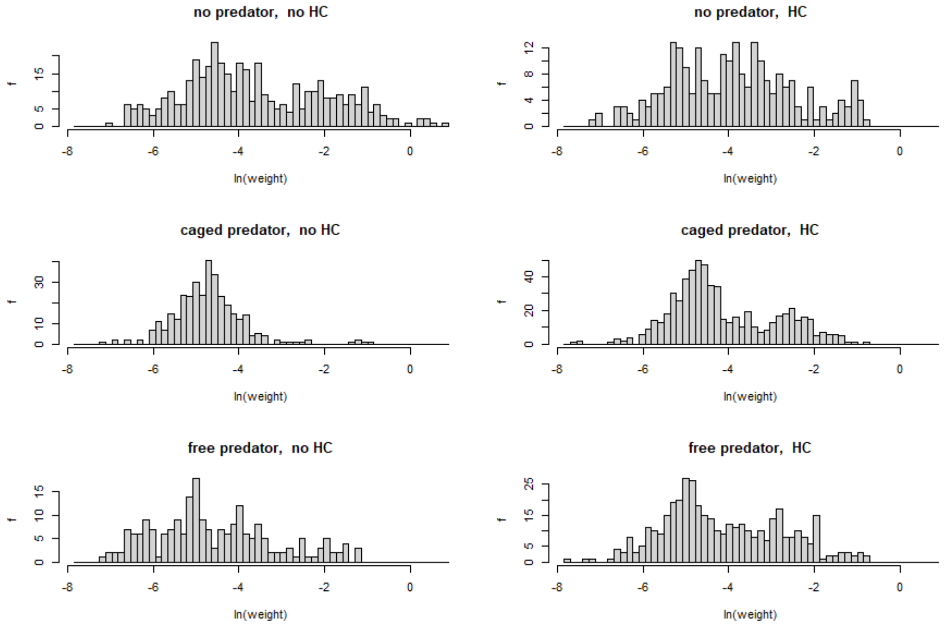


Figure S5: Treatment-specific size spectra of culicid larvae. Each size spectrum is pooled across all replicates of the given treatment. See main text for details.

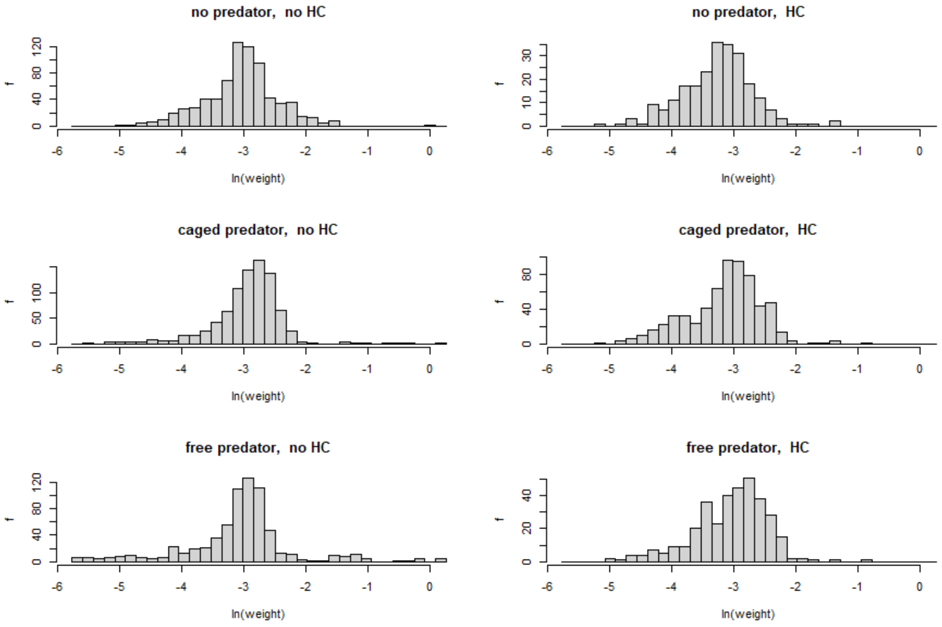
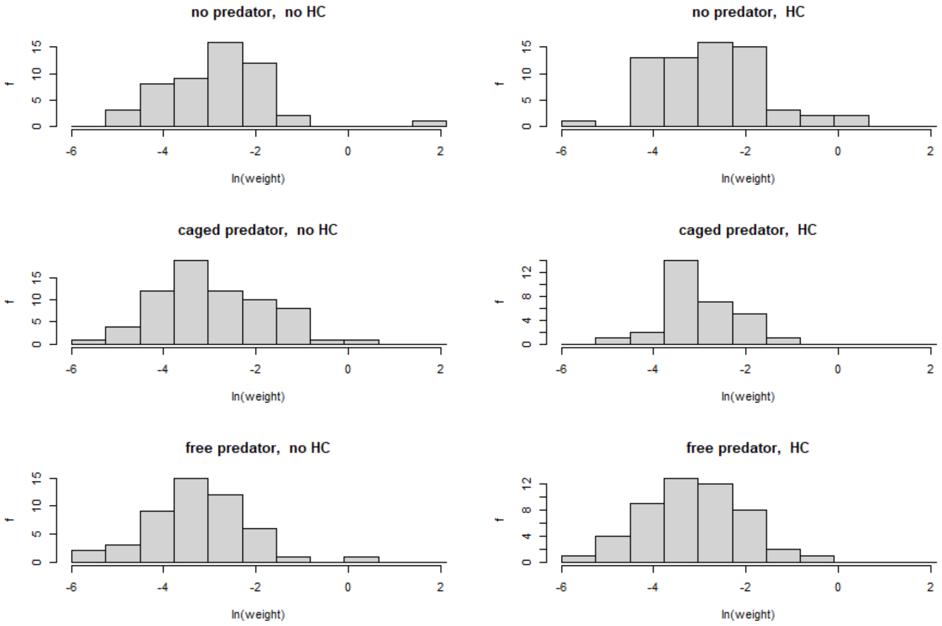


Figure S6: Treatment-specific size spectra of gastropods. Each size spectrum is pooled across all replicates of the given treatment. See main text for details.



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Summary

Habitat complexity and predation risk are important factors for the structure and assembly of aquatic communities.

Chapter I of my thesis reviewed how habitat complexity affects the structure and assembly of aquatic communities. Habitat complexity interacts with all levels of organization, as it effects individuals, their interactions, and entire communities. This review has demonstrated that current knowledge of these interactions is uneven, although no complete gaps exist. Ecological feedbacks resulting in secondary changes to individuals and their interactions in habitat complexity altered communities, or to habitat complexity itself are among the least understood mechanisms underpinning the role of habitat complexity in aquatic ecosystems. Interestingly, most researchers are studying habitat complexity effects on a binary scale, which is detrimental to discovering potential nonlinear effects. Working with a gradient of complexities could help uncover and quantify saturating, unimodal or stepwise relationships, which are common in nature.

Chapter II dealt with this knowledge gap and estimated functional responses of *Aeshna cyanea* preying on *Chaoborus obscuripes* larvae using the traditional population level approach and compared the results with direct behavioural observations and measurement of functional response parameters. Despite some evidence to the contrary, habitat complexity did not influence functional response shape in this experiment. Differences in handling time are sometimes reported when fitting a functional response on population level data. Behavioural observations on the other hand yield no such increase. This fundamental discrepancy can be attributed to predator behaviours that are not directly linked to the consumption and digestion of prey. Additional review of existing data showed that the dependence of handling time and attack rate, two key parameters of the functional response, on habitat complexity varies widely across studies; the

differences can be attributed to weakening and strengthening predator-prey interactions with habitat complexity in 2D and 3D habitats.

Chapter III examined the effects of habitat complexity and predation risk by an invasive omnivorous crayfish *Orconectes limosus* in a controlled outdoor mesocosm experiment. It showed that both factors can measurably impact freshwater macroinvertebrate communities over relatively short timescales during the early phases of community assembly. The observed effects of the crayfish on the community were commensurate with published data on its diet, and could be attributed mainly to indirect, non-consumptive effects on the prey. The effects of habitat complexity were taxon specific and in line with previous studies, and overall, more important than the effects of predation risk. Finally, the experimental data illustrated the importance of size-based approaches in community-level studies as the effects of habitat complexity and predation risk were more apparent when using prey biomass and size spectra rather than abundance.

Taken together, this thesis provides novel insights into the role of habitat complexity and predation risk on community structure in small standing waters. It shows that habitat complexity may (or may not) modify trophic interactions in complex and sometimes non-intuitive ways. I was able to demonstrate the effects of habitat complexity on the *Aeshna* – *Chaoborus* predator-prey system in multiple levels of focus: on the population level, examining functional responses in habitats of various habitat complexity and on an individual level by analysing video-recordings of predators' behaviour and hunting success. Using the same model of habitat complexity (submerged plant mimic from identical materials), I also examined the effects of *Orconectes limosus* on community assembly in structurally simple and complex habitats, showing that both predation risk and habitat complexity are relevant in a more natural, community-level perspective. These results agree with current consensus outlined in the review article: different scales of interactions provide valuable insights and can be used to make more realistic predictions about the way habitat complexity alters predator-prey interactions.

Take-home messages and future directions

Going forward, several points should be noted. Studies included in this thesis reiterate the common observation that simple experiments may not always provide reliable or complete results. Gradients of habitat complexity should be used wherever possible to paint a more holistic image of its effect on the structuring of aquatic communities. Moreover, various ecological feedbacks can mediate or amplify short-term effects. Further inquiry into such feedbacks could help reconcile predictions based on short-term experiments under controlled conditions with long-term field observations.

Concerning the community level consequences of predation and habitat complexity, the role of omnivorous predators requires further study. Using living macrophytes in place of plastic models and extending the experiment by several months could reveal more distinct effects. Such experiments could also shed more light on the differences between the community-level effects of ‘true’ top predators such as the dragonfly larvae used in Chapter II and top-level omnivores such the invasive crayfish used in Chapter III.

Curriculum vitae

Author's curriculum vitae

Name: **Mgr. Pavel R. Soukup**
Date of Birth: December 21st, 1990
Nationality: Czech
Address: Na Zlaté stoce 1862/9c,
370 05 České Budějovice,
Czech Republic
Tel.: +420 728 846 748
E-mail: pavelsoukup@protonmail.com

Education

2015 – present	Ph.D. in Hydrobiology, University of South Bohemia in České Budějovice, Faculty of Science *Dissertation: Role of habitat complexity and predation in the structuring of aquatic communities* Supervisor: David Boukal
2013 – 2015	M.Sc. in Secondary School Teacher Training in Biology and Informatics, University of South Bohemia in České Budějovice, Faculty of Science *Thesis: Habitat complexity and predation risk effects on community assembly in small standing waters* Supervisor: David Boukal
2010 – 2013	B.Sc. in Biology and Informatics for Secondary School Education, University of South Bohemia in České Budějovice, Faculty of Science *Thesis: Role of species interactions in colonization of small standing water bodies.* Supervisor: David Boukal, Consultant: Jan Klečka

Work experience

2016 – present	Secondary School Teacher at Česko-anglické gymnázium, s.r.o. (‘Anglo-Czech high school’), Information Technology
2011 – 2015	Technician/research assistant involved in various projects (supervised by David Boukal)

Fellowship

2019	University of Gothenburg, Sweden, prof. J. Höjesjö (6 weeks)

Teaching

2018 – 2021	External lecturer, University of South Bohemia, Faculty of Pedagogy, Invertebrate Zoology (seminars for future primary school biology teachers)
2018	Teacher’s assistant, University of South Bohemia, Faculty of Science, Introduction to R modelling for Ecologists
2018 – 2019	Various popular science seminars for children with the Biological Centre of the Czech Academy of Sciences

Students

Mentorship of high school students participating in scientific competitions

Štěpánka Jakubcová (2018) Mentorship for a high school science fair project (SOČ), Topic: Caught red-handed: How dragonflies really hunt their prey (Přistižen při činu: jak vážky doopravdy loví svou kořist)

Martina Hřebeková (2017) Mentorship for a high school science fair project (SOČ) and Association for Youth, Science and Technology competition (AMAVET), Topic: The impact of global climate change on the intensity of predation in small standing waters (Vliv globálních změn klimatu na intenzitu predace v malých stojatých vodách)

Nam Ha Nguyen (2016) Mentorship for a high school science fair project (SOČ), Topic: Ecotoxicity of common drugs (Ekotoxicita běžných léčiv)

Author details based on Scopus

Number of publications in peer-reviewed journals with IF: 2
Total citations / with self-citations excluded: 2/2
h-index: 1

Online presence

https://www.researchgate.net/profile/Pavel-Soukup
https://scholar.google.com/citations?user=jmUxS28AAAAJ

Peer-reviewed publications with impact factor (IF)

Published or accepted:

Soukup P. R., J. Näslund, J. Höjesjö & Boukal D. S. (2022) From individuals to communities: habitat complexity affects all levels of organization in aquatic environments. *WIREs Water*, DOI: 10.1002/wat2.1575

Mocq J., Soukup P. R., Näslund J. & Boukal D. S. (2021). Disentangling the nonlinear effects of habitat complexity on functional responses. *Journal of Animal Ecology*, 1–13. https://doi.org/10.1111/1365-2656.13473

In preparation:

Soukup P. R., V. Kolář, Boukal D. S. Invasive crayfish predation risk and habitat complexity effects on community assembly in small standing waters. (Manuscript)

International conferences

Soukup, P. R., Šorf, M., Lepšová, O., Boukal D. S. (2017) Habitat complexity and predation risk effects on community assembly in small standing waters, June 2-7, 2017, Olomouc, Czech Republic

Soukup, P. R., Šorf, M., Klečka, J., Boukal D. S. (2016) The effect of predation risk and habitat complexity on community assembly in small standing waters, 2nd Central European Symposium for Aquatic Macroinvertebrate Research, June 3-8, 2016, Pécs, Hungary

Awards

2019	2nd place for best student presentation, PhD student's conference of the Department of Ecosystem Biology, University of South Bohemia in České Budějovice, Vodňany
2017 & 2018	3rd place for best student presentation, PhD student's conference of the Department of Ecosystem Biology, University of South Bohemia in České Budějovice, Vodňany
2016	Best Young Speaker Award, 2nd Central European Symposium for Aquatic Macroinvertebrate Research, June 3-8, 2016, Pécs, Hungary
2015	Dean's Award for excellent study and research results, awarded by the dean of the Faculty of Science, University of South Bohemia
2015	Rector's Award for excellent study results, awarded by the rector of the University of South Bohemia

pavelsoukup@protonmail.com

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University of South Bohemia in České Budějovice
Faculty of Science
Branišovská 1760
CZ-37005 České Budějovice, Czech Republic

Phone: +420 387 776 201
www.prf.jcu.cz, e-mail: sekret-fpr@prf.jcu.cz