



PRIMARY RESEARCH PAPER

Biotic interactions enhance survival and fitness in the caddisfly *Micropterna sequax* (Trichoptera: Limnephilidae)

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Abstract Patches of coarse particulate organic matter in lowland streams are inhabited by many different macroinvertebrate species, yet knowledge of interactions among the members of these assemblages is scarce. In a mesocosm experiment we aimed to determine the effect of interspecific interactions on species survival and fitness of two caddisfly species. It was hypothesized that, as a result of positive interactions, mixed species populations would yield higher survival and fitness than single species populations. Larvae of two caddisfly species, *Micropterna sequax* and *Potamophylax rotundipennis*, were reared in single species and mixed species populations. Emergence rate was recorded and adult fitness was measured in terms of wingspan and biomass. We found that in mixed populations, emergence rate, wing length and biomass of *M. sequax* were higher than in single species populations. *P. rotundipennis* was only significantly, yet negatively, affected in terms of biomass of the male individuals. This study showed

that occurring together with other species holds advantages for *M. sequax*, and emphasizes the importance of species diversity in streams. Furthermore, the observed positive effects on survival and fecundity might influence population sizes of the interacting species, in turn affecting macroinvertebrate-mediated ecosystem processes such as leaf litter decomposition.

Keywords Macroinvertebrates · Interspecific facilitation · Niche complementarity · Ecosystem functioning · Biodiversity

Introduction

High-flow-induced within-stream habitat fragmentation results in isolated patches of preferred substrate for many macroinvertebrate species (Tolkamp, 1980; Lake, 2000; Jähnig et al., 2009; Schröder et al., 2013). In lowland streams these patches consist of coarse particulate organic material (leaves, leaf fragments, twigs) embedded in a matrix of sand, and are an important resource in terms of, amongst others, food and shelter (Egglishaw, 1964; Lancaster & Hildrew, 1993). As consumers of leaf material aggregated in these patches, shredders play an important role in the decomposition process (Anderson et al., 1978; Malmqvist & Oberle, 1995; Mermillod-Blondin et al., 2002). With many different species inhabiting these

Handling editor: Nicholas R. Bond

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patches, intra- and interspecific interactions are expected to be frequent. Nonetheless, knowledge on biotic interactions among macroinvertebrates performing the same functional role is scarce.

Biotic interactions can be positive (mutualism and commensalism; Milbrink, 1993; Tokeshi, 1993) and/or negative (competition, parasitism, amensalism; Burkholder, 1952; Connel, 1983; Didham et al., 1996) for one or both species. The positive effect of an interaction, also known as facilitation, is seen as a key mechanism in which species diversity positively affects ecosystem processes and functioning (Mulder et al., 2001; Stachowicz & Byrnes, 2006; Bulleri et al., 2016). A study by Cardinale et al. (2002) showed that multiple species from the same functional feeding guild (aquatic suspension-feeders) enhanced each other's feeding success by decelerating the flow from upstream to downstream neighbours. This example shows that it is well possible that changes in species assemblages alter the likelihood of positive species interactions. While Cardinale et al.'s study is valuable for a better understanding of biotic interactions and resource partitioning, it remains unknown how biotic interactions affect species survival and development, and with that the long-term effect on future populations.

Species belonging to the same functional guild within a community could hypothetically become functionally redundant, with several species occupying the same ecological niche and consequently competing for resources (Walker, 1992; Duffy et al., 2001; Dolédec & Bonada, 2013). However, studies across terrestrial, marine and freshwater ecosystems suggest that species within the same functional guild often have niches that do not overlap, causing functional complementarity instead of redundancy (Fargione et al., 2007; Rudolf et al., 2014; Kelly et al., 2016). Functional or niche complementarity results in greater resource uptake efficiency and faster ecosystem process rates (Loreau, 2000; Loreau & Hector, 2001; Fox, 2005; Leibold et al., 2016). Considering the organic patches as rather isolated streambed microhabitats, inhabited by a set of species with similar feeding strategies, it is probable that these species have adapted to cope with frequent biotic interactions, and may even benefit from them. In other words, the high organic patch species diversity observed in lowland streams might be the result of niche complementarity.

In this study we investigated the effects of interspecific interactions in leaf-shredding caddisfly (Trichoptera) larvae. Caddisflies were selected as model organisms because of their abundance and species richness in lowland streams (Giller & Malmqvist, 1998), and their vital role as shredders within the macroinvertebrate community involved in decomposition of leaf litter (Malmqvist & Oberle, 1995). *Micropterna sequax* McLachlan, 1875 and *Potamophylax rotundipennis* (Brauer, 1857) belong to the shredder functional feeding guild and are characteristic of and abundant in northwestern European low-gradient streams with a streambed dominated by sand and patches of organic material. Both species belong to the family Limnephilidae, subfamily Limnephilinae. Studying two almost taxonomically and functionally similar species will stress the importance of biotic interactions when differences are found.

Biologically, *M. sequax* differs from *P. rotundipennis* in terms of a longer period of emergence and a larger wing span (Higler, 2008; Graf et al., 2015). Ecologically, *M. sequax* displays more sedentary behaviour when positioned at its preferred substratum than *P. rotundipennis*, which is more ubiquitous (Verdonschot et al., 2012). It is known that both species occur on similar habitat patches spatially and temporally, but differ slightly in their preferred microhabitat within the patch (Westveer et al., 2017). This behaviour could be a consequence of interspecific interaction, which caused us to use these two species for this experiment.

We tested the effects of their interaction on adult fitness correlates related to emergence, growth and fecundity, by studying single species and mixed populations in leaf patches differing in the degree of patchiness. In a mesocosm experiment we tested: (1) if habitat isolation increases interspecific interactions among species, and (2) how these interactions affected emergence and fitness in the individual species. We hypothesized that mixed species populations yielded a higher emergence rate and fitness as a result of adaptations to living in dense multi-species aggregations and that this effect was more evident under increased interaction pressure resulting from patch isolation.

Materials and methods

Collection of specimens

The fifth-instar larvae were hand-collected from natural streams in the first half of March. *P. rotundipennis* was collected at Rode Beek near Roermond, while *M. sequax* was collected at Seelbeek near Heveadorp, the Netherlands. While both species have similar distribution patterns throughout the Netherlands, each species occurred in largest abundance at different locations within the watershed. This provided the opportunity to efficiently collect many individuals from the same instar at the same time. All individuals were acclimatized before being released in the mesocosms. Fifth-instar larvae were used because the larvae spend the largest part of developmental time in this life stage (Hickin, 1967). Resources are acquired during this stage for the remainder of their lifespan (Boggs, 2009; Jannot, 2009). Adults may take up some additional food after emergence but individuals will not continue their growth and nutrients required for adult body parts (e.g. wings, abdomen, eggs and sperm) must derive from feeding during larval stage (Boggs, 1981).

Stream mesocosm setup

Tests were carried out between March and November 2015. In the experiment we used six indoor stream mesocosms, each consisting of four artificial recirculating channels. Each channel was divided into two compartments, from now on referred to as 'experimental units' (Fig. 1A). Each experimental unit contained 20 individuals of either *Micropterna sequax* or *Potamophylax rotundipennis* (single species population) or ten individuals of both species (mixed species population). This setup allowed us to incorporate both species, while population pressure was kept similar across all experimental units. Larvae were similar sized (fifth instar, $n = 28$), with a mean head width of 1.737 mm for *M. sequax* and 1.834 mm for *P. rotundipennis*.

Each experimental unit contained a 5-cm-thick stream bottom consisting of sand (grain size 1–3 mm) and patches of leaves (abscised oak; *Quercus robur*). Water depth was 10 cm. Leaf patches were offered in three different spatial arrangements, differing in the number of patches and individual patch size (Fig. 1B).

Total patch size and biomass of leaves were kept constant in all experimental units. Per unit 10 g of leaf material was distributed equally across all leaf patches. To keep patch configuration intact during the experiment and especially to prevent mixing of the substrates, PVC slots were placed between the patches of sand and leaves. To prevent downstream transport of the leaves by the current, patches were covered by a 1×2.2 cm mesh (Fig. 1C). Each unit was covered with a perspex plate to prevent the escape of emerged caddisflies.

With three population composition types and three spatial leaf patch configurations, this resulted in nine different treatments. Each treatment was replicated five times and randomly distributed across 45 experimental units.

Current velocity was kept constant at 10 cm/s in all units and fell within the preferred flow preference range described for both species (Dolédec et al., 2007; de Brouwer et al., 2017). The water inside the units was constantly aerated and recirculated from a 600-L reservoir and consisted of preconditioned water (preconditioning time was 2 weeks, water consisted of a mixture of 550 L of tap water and 50 L of filtered water from a nearby stream). Light regime followed natural seasonal conditions. Water temperature was kept constant at 12 °C, air temperature at 16 °C.

To prevent food availability to become a limiting factor, 5 g of extra leaf material was added per unit halfway through the experiment. This resource addition mimics a natural situation in which *Q. robur* leaves, a very slow decomposing litter type (Swift et al., 1979), are occasionally distributed across the stream bottom in forested areas throughout the year (Minshall, 1967). Furthermore, additional food in the form of one cube (2 g) of frozen *Tubifex* oligochaetes (Dutch Select Food Tubifex; crude protein 6.2%, crude fat 2.6%, crude fibre 0.6%, ash 0.5%) was supplied every 2 weeks in each compartment to prevent cannibalism or predation in species which supplement their diet with (dead) invertebrates (Wisinger et al., 2004). These extra food sources were added to ensure that all potential components of the caddisflies diet were available and, therefore, would not limit survival and growth during the experiment.

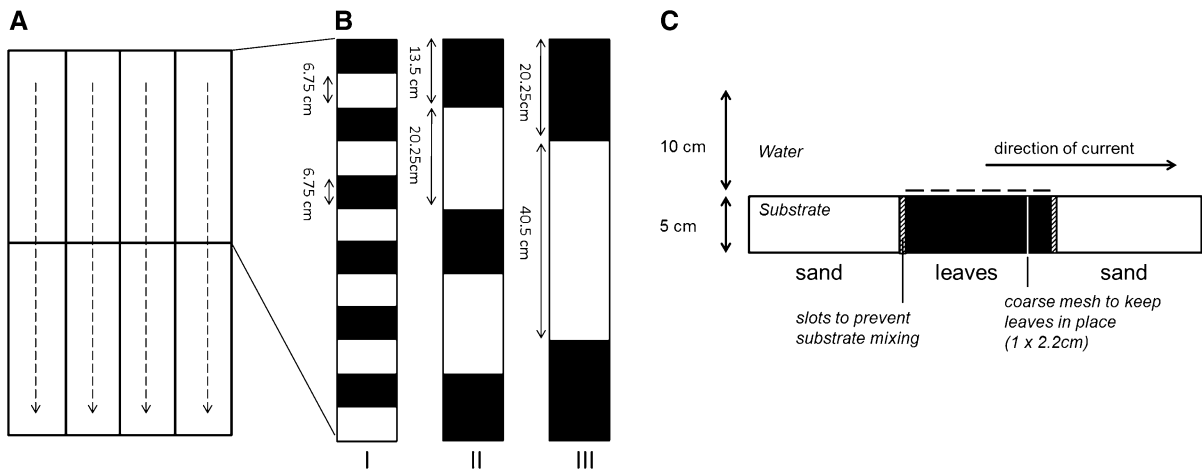


Fig. 1 **A** Outline of a mesocosm with four stream channels. Each channel was divided into two compartments with mesh (1×1 mm) to keep water flowing (direction of arrow) but prevent exchange between compartments. Six identical stream mesocosms were used, with a total of 48 compartments/experimental units. **B** Top-down view of three different patch

configurations. One configuration per experimental unit, with increasing patch isolation and subsequent biotic interaction frequency potential. I = low-frequency interaction, II = intermediate-frequency interaction, III = high-frequency interaction. **C** Side view of bottom substrate of the experimental compartments

Data collection and statistical analyses

After emergence, adults were collected within 48 h and frozen at -18 °C until further processing. Number of emerged males and females (sex ratio) was identified and counted (Malicky, 2004). Left forewing length was measured using a microscope with an eyepiece micrometre to the nearest 0.1 mm. To determine adult abdomen dry mass, the caddisflies were dried to a constant weight at 60 °C for 48 h and weighted on a microbalance to the nearest 0.0001 g (minimum measured weight = 0.0020 g). Wing span and biomass were used as fitness correlates because of their effect on, respectively, dispersal capacity (Hoffsten, 2004) and fecundity (Honěk, 1993).

Results regarding fitness do not include drowned, nor deformed individuals (Table 1). Drowned individuals were regarded as dead, while deformed individuals were regarded as alive and counted for emergence rate, yet their deformities were so severe that it potentially compromised their reproductive success. Therefore, these individuals were disregarded in the fitness analysis. Since male and female caddisflies differ in wing span and body weight, they were analysed separately.

The number of emerged individuals per experimental unit was expressed as ratios, where 1 equals emergence of 20 individuals in the single species populations and 10 individuals in the mixed species populations. All individuals were considered

Table 1 Overview of species' overall development time and emergence rate

Species	Adult emergence		Development time (days)			
	Total	Drowned	Deformed	Male:female	Mean	Min–max
<i>M. sequax</i>	310 (68.9%)	1 (0.3%)	20 (6.4%)	1:1.7	111.3	55–221
<i>P. rotundipennis</i>	415 (92.2%)	41 (9.9%)	37 (8.9%)	1:0.63	131.7	63–195

Percentage of total emerged adults is calculated by number of fully developed adults that were found in the experimental units divided by 450 individuals that were introduced into the experiment as larvae (Corbet, 1964). Percentages of drowned and deformed adults are calculated by dividing the observed number of drowned/deformed adults by the amount of emerged adults. It is unknown what caused drowning or the development of deformations

pseudoreplicates within their experimental unit. Therefore, mean values and standard deviations for emergence rate and fitness correlates were calculated per experimental unit ($n = 5$) and subsequently tested for mesocosm effects (mesocosm number as independent factor). No significant effects of mesocosm were found (Independent t test, $n = 6$, $P = 0.715$ (*M. sequax*), $P = 0.116$ (*P. rotundipennis*)). All data were tested for normal distribution (Shapiro–Wilk). All normally distributed data were analysed with one-way ANOVAs to test for the effect of population type (single or mixed species) on fitness, and two-way ANOVAs with spatial configuration (I, II, III) and population type as fixed factors, followed by Tukey's HSD post hoc procedures. Non-normal data were analysed using Kruskal–Wallis non-parametric ANOVAs. Statistical tests were conducted in IBM SPSS Statistics (version 22.0/IBM Corp, Armonk, NY, USA).

Results

The emergence rate of the species differed, with a higher emergence rate in *P. rotundipennis* in comparison to *M. sequax*. The mean development time (post-winter larval development till emerged adult) of *M. sequax* was shorter than that of *P. rotundipennis* (respectively, 111.3 and 131.7 days). However, variation in development time was larger in *M. sequax*, with individuals emerging over a period of 166 days (Table 1). Treatments with mixed species populations had interspecific interaction potential throughout the vast majority (87%) of the experiment. On average, both species were present together in the experimental unit for 146.2 days before emergence, after which an average of 18.7 days remained with only one species in the unit. Thus, in the final stages of the experiment some mixed population units had low interaction potential; however, this stage was spent while pupating and, therefore, no biotic interactions would have been expected.

Effects of patch configuration on biotic interactions

All responses, in terms of emergence rate, effects of biotic interactions and of spatial configuration, appeared to be species specific. *M. sequax* showed a

higher emergence rate in mixed populations in all spatial configurations (Fig. 2A, two-way ANOVA $F(1, 2) = 12.05$, $P = 0.002$). Additionally, *M. sequax* showed a significant decrease in emergence rate in the habitat with a high patch isolation ($F(1, 2) = 9.087$, $P = 0.001$). However, a two-way ANOVA showed that combining both factors (interaction population type and spatial configuration) did not cause an additional effect ($F(2, 24) = 0.707$, $P = 0.503$), indicating *M. sequax* did not respond differently to patch configuration when reared with *P. rotundipennis*. This means that patch configuration influences emergence, but the uniform direction of change from single to

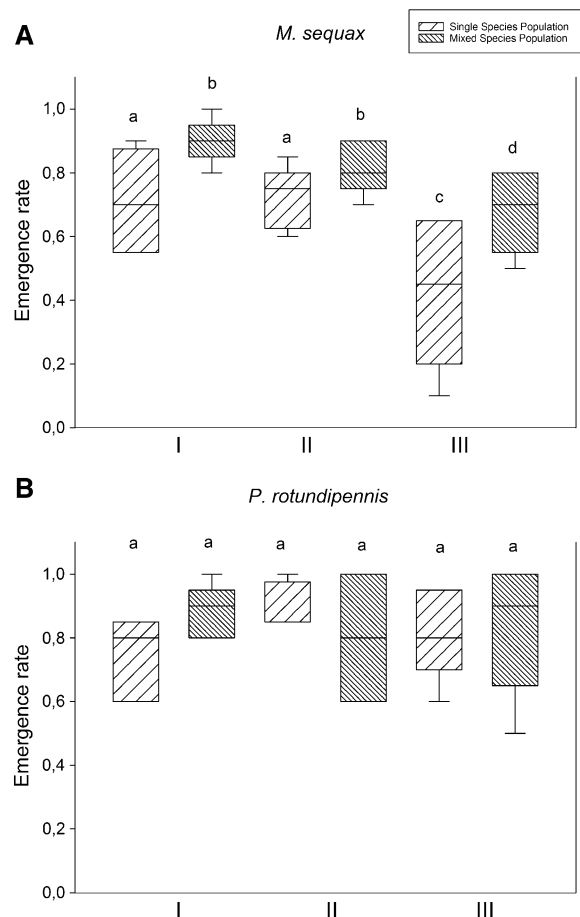


Fig. 2 Boxplots of the emergence rates of **A** *M. sequax* and **B** *P. rotundipennis* with median, 25–75th percentiles in box, 10–90th percentiles as error bars and dots indicating outliers, in single and mixed populations across three spatial configurations range from low patch isolation and low interaction potential (I) to high patch isolation and high interaction potential (III). Different letters indicate significant differences between groups. (Two-way ANOVA, Tukey post hoc test $P < 0.05$)

mixed populations indicate the effect of an interspecific interaction.

Potamophylax rotundipennis was unaffected by both biotic interactions with *M. sequax* (two-way ANOVA: $F(1, 2) = 0.136$, $P = 0.716$) and spatial configuration ($F(1, 2) = 0.181$, $P = 0.835$) in terms of survival rate (Fig. 2B). This species showed overall high emergence rates, regardless of the population in which the larvae developed or the level of patch isolation and subsequent interaction frequency potential. Once more, no interaction effect was found between the two independent factors ($F(2, 24) = 1.630$, $P = 0.217$).

Due to the non-significant interaction effect of spatial configuration and population type, all spatial configurations were pooled and data were grouped into either single species population or mixed species population for analysis of biotic interaction effects on emergence and fitness rates.

Effects of biotic interactions on survival and fitness

In *M. sequax* more individuals emerged from the experimental units with a mixed species population ((Fig. 3A; independent samples t test, $t(28) = -2.78$, $P = 0.010$). *Potamophylax rotundipennis* showed overall high emergence rates, while no significant difference was found between single species- and

mixed populations (independent samples t test, $t(28) = -0.3$, $P = 0.731$) (Fig. 3B).

M. sequax females developed larger forewings in mixed populations ($F(1, 182) = 14.4$, $P < 0.001$) and had higher abdomen dry weights (Kruskal–Wallis $X^2(1) = 20.28$, $P = 0.000$, Fig. 4, panel A and B). Similar results were found for *M. sequax* males (Fig. 4, panel C and D) with larger forewings ($F(1, 103) = 25.5$, $P < 0.001$) and abdomen dry weight ($F(1, 103) = 34.5$, $P < 0.001$).

Potamophylax rotundipennis females did not show any significant responses to biotic interactions during developmental stages in terms of wing length ($F(1, 135) = 1.01$, $P = 0.3$) and abdomen dry weight ($F(1, 135) = 1.43$, $P = 0.2$) (Fig. 5, panels A and B). *Potamophylax rotundipennis* males showed no significant response for wing length ($F(1, 197) = 3.15$, $P = 0.078$), but did show significantly lower abdomen weight (Kruskal–Wallis $X^2(1) = 11.4$, $P = 0.001$) in the mixed populations (Fig. 5, panels C and D).

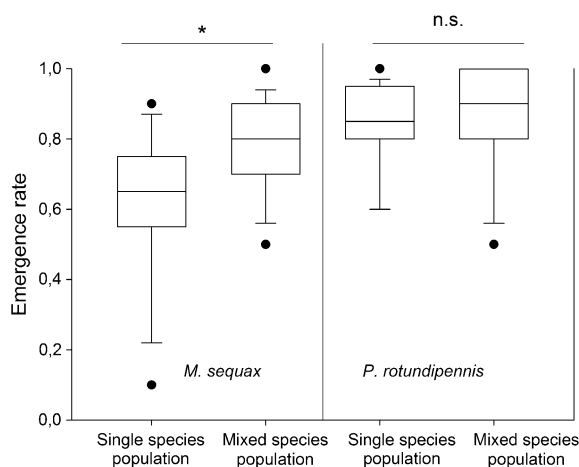


Fig. 3 Boxplots of the emergence rates of single and mixed *M. sequax* and *P. rotundipennis* populations with median, 25–75th percentiles in box, 10–90th percentiles as error bars and dots indicating outliers (independent t tests $P < 0.05$). Asterisk indicates significant difference

Discussion

Effects of patch configuration on biotic interactions

Patch configuration did not affect the outcome of the biotic interactions among *M. sequax* and *P. rotundipennis*. A positive effect of occurring in mixed populations in the leaf patches was observed in each of the three spatial configurations offered to the larvae. The observed negative effects on *M. sequax* in the least patchy most isolated configuration where comparable in both single and mixed populations, and might be related to the species' microhabitat preference and/or behaviour: being an inhabitant of the edge of organic substrate patches (organic–sand interface) and displaying relatively sedentary behaviour, this configuration might have been less suitable for this species (Higler, 1975; Schmera, 2002; Urbanič et al., 2005; Verdonschot et al. 2012), resulting in a decreased emergence rate regardless of interspecific interaction occurrence.

Positive effects of biotic interactions

Our study showed that *M. sequax* performed better in the presence of *P. rotundipennis* in the leaf patches

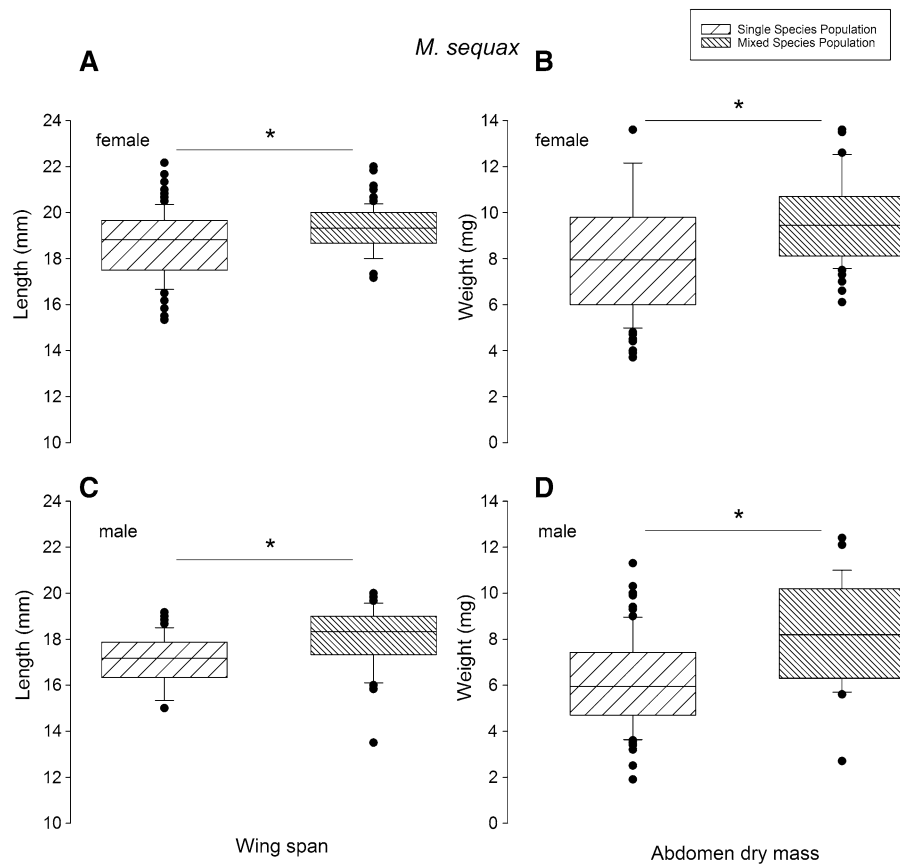


Fig. 4 Boxplots of the fitness correlates of *M. sequax* in single species and mixed populations. **A** Forewing length (mm) of females, **B** abdomen dry mass (mg) of females ($n = 113$ for single species population, $n = 71$ for mixed population), **C** forewing length (mm) of males, **D** abdomen dry mass (mg)

of males ($n = 73$ for single species population, $n = 32$ for mixed species population) with median, 25–75th percentiles in box, 10–90th percentiles as error bars and dots indicating outliers. Asterisk indicates significant differences (Tukey post hoc tests $P < 0.05$)

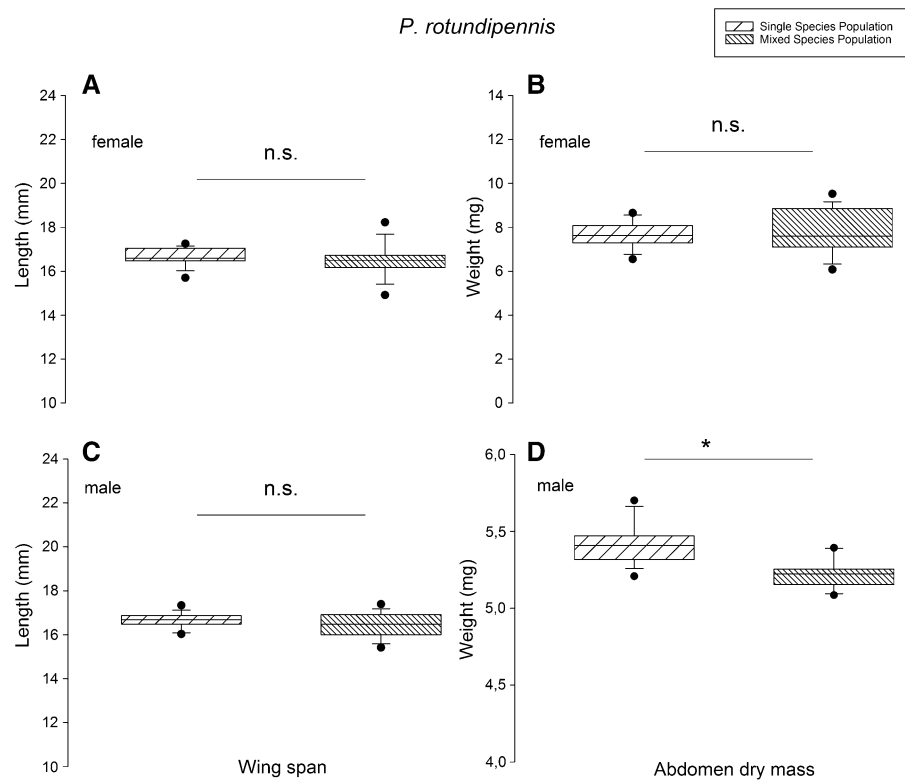
than in the presence of conspecifics. On the contrary, *P. rotundipennis* did not appear to be affected by the presence of *M. sequax* in a different way than the presence of its conspecifics. Differences in the fitness of *M. sequax* arising from these altered biotic interactions included a larger wingspan and a higher abdomen biomass. With wing size being an important determinant for dispersal capacity in caddisflies (Hoffsten, 2004), and abdomen biomass being directly correlated to adult fecundity (Honěk, 1993), it is well possible that in our mixed species populations the fitness of *M. sequax* was increased by the presence of *P. rotundipennis*.

Our experimental setup allowed us to unravel the influence of increased inter- and intraspecific interactions. By limiting the number of favourable habitat patches (patch figuration III, Fig. 1B) we increased the

number of potential encounters between individuals. This was done for single species populations and mixed species populations. The results show that *M. sequax* has a lower emergence rate and fitness with increased number of interactions, but has a significantly higher emergence rate when this interaction is interspecific instead of intraspecific. However, a future experimental treatment which includes a lower density of conspecifics and no additional individuals of other species to differentiate positive effects from reduced negative effects would be valuable to elucidate this effect even more.

One of the mechanisms through which one of these species might enhance the other's realized niche could be their foraging strategy. It is possible that both species prefer different food particle size ranges, in this case leaf fragments colonized by microorganisms.

Fig. 5 Boxplots of the fitness correlates of *P. rotundipennis* in single species and mixed populations. **A** Forewing length (mm) of females, **B** abdomen dry mass (mg) of females ($n = 101$ for single species population, $n = 37$ for mixed species population), **C** forewing length (mm) of males, **D** abdomen dry mass (mg) of males ($n = 135$ for single species population, $n = 64$ for mixed species population). Asterisk indicates significant differences (Tukey post hoc tests $P < 0.05$)



This concept has also been described as ‘selective feeding’ by Cummins & Klug (1979). Selective feeding is defined as the ingestion of only certain particles from a range of those that are equally available to the feeding insect. This feeding strategy involves no mechanical interference and, therefore, excludes some of the materials that need a morphological–behavioural specialization of the insect (Cummins, 1973). Thus, insects do not have to invest in specialized ways to make food available for ingestion, but selectively feed on appropriate food particles due to food partitioning with a similar species. In this case, *P. rotundipennis* potentially cuts leaf fragments into its preferred particle size, after which *M. sequax* forages on the smaller sized remains.

An alternative explanation could be that *M. sequax* feeds on the faeces of *P. rotundipennis*. A study by Milbrink (1993) showed a mutualistic interaction in freshwater oligochaete communities, where two species of oligochaetes feed on the bacteria that colonize each other’s faecal pallets. Even though both species appear to be very similar in their functional traits (Higler, 2005; Graf et al., 2015) they showed species-specific responses. It is known that *M. sequax*

is a specialized species when it comes to substrate preference (Rumbos et al., 2010) but unfortunately there is no literature on preferred food particle size.

It has been hypothesized that a shift in feeding ecology from omnivorous shredding to epilithic grazing, and corresponding mandible adaptations to do so, has caused the diversification within the Limmephilidae (Pauls et al., 2008; Waringer et al., 2013). Within this family, evolutionary adaptations have led to spoon-shaped mandibles, toothed mandible edges and mandibles lacking any type of serration. Both *M. sequax* and *P. rotundipennis* have mandibles with teeth which they use for shredding as well as grazing, yet there can be subtle differences in the morphology of the mandibles that lead to a difference in food processing. Future research on food preference and mandible morphology could elucidate this issue.

Neutral and negative effects of biotic interactions

The presence of *M. sequax* did not affect the measured fitness correlates in *P. rotundipennis* females and the wing length in *P. rotundipennis* males. In line with this finding, Cardinale et al. (2002) showed that one out of

three species of suspension feeding Trichoptera did not show significant differences in resource uptake in a mixed population, while the other two species did. This demonstrates the one-way facilitating direction, termed ‘commensalism’, that an interspecific interaction can have (Connell, 1983). It has been found that Chironomidae often display commensalistic interactions to increase their feeding opportunity, mobility, protection from disturbance and reduce predation risk (Tokeshi, 1993; Callisto et al., 2006), but this entails interactions with other orders of aquatic invertebrates. Within-class commensalism has not been found or described for many aquatic invertebrates, yet could have a large explanatory value when it comes to niche expansion and range shifts (Bulleri et al., 2016).

A negative effect of being reared in mixed populations was found for the abdomen biomass of *P. rotundipennis* males. Biotic interactions in which one species benefits at the expense of the other are referred to as antagonistic interactions. Negative effects on fitness correlates could be explained with developmental trade-offs arising under specific conditions (Stevens et al., 1999, 2000). For example, while larvae develop into pupae, strategic allocation of resources could favour wing span, and thereby dispersal capacity, over fecundity. However, the lower abdomen biomass did not cause an increased wing span for the males of *P. rotundipennis*, it merely developed equal wing lengths compared to individuals from the single species population. Allocating resources at the expense of fecundity could also be a response to the difference in intraspecific population density. In the mixed species populations both species were present with 10 individuals, while in the single species populations 20 individuals of one of the species was present. Lower sperm competition risk in populations with fewer females of their own species (Gage, 1995; McNamara et al., 2010) could lead to a decreased investment of resources in fecundity. Without measuring the precise allocation of energy, we cannot conclude that a developmental trade-off is apparent in this case, neither is it clear why only *P. rotundipennis* males were affected.

Conclusion

In our study we demonstrated that biotic interactions take place between caddisfly species inhabiting

patches of coarse organic material, resulting in positive effects on *M. sequax* and neutral to negative effects on fitness correlates in *P. rotundipennis*. Whether these reflect synergistic interactions, or simply a reduction of negative intraspecific interactions at lowered population densities of *M. sequax* cannot be determined. Changes in fitness of individual members of macroinvertebrate assemblages resulting from interspecific interactions could affect future population sizes and species distributions, and with that are an important determinant of stream macroinvertebrate community composition. By linking the enhanced survival and fitness of members of the community to the ecosystem processes performed by these species, the presence of positive interactions is likely to influence ecosystem processes. In this case, decomposition rates in patches of organic material, an essential process in temperate lowland streams. We show that biotic interactions have an impact on population level and thereby, when viewed at a larger scale, might influence stream ecosystem functioning. It is likely that biotic interactions comparable to those we observed occur in lowland stream ecosystems more generally. Gaining a greater understanding of the extent of such interactions should be a theme in future research.

Acknowledgements We would like to thank Dorine Dekkers for her help during all stages of the practical work as well as Sandy Hofland and Jacob Ferrús Muñoz, who have helped out tremendously with setting up all mesocosms. Additionally, Hanneke Keizer-Vlek and Marielle van Riel are acknowledged for their help in capturing the emerging caddisflies and Emiel van Loon for his suggestions regarding the statistical analyses. This work was funded by the Foundation for Applied Water Research STOWA.

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References

- Anderson, N., J. R. Sedell, L. M. Roberts & F. J. Triska, 1978. The role of aquatic invertebrates in processing of wood debris in coniferous forest streams. *American Midland Naturalist* 100: 64–82.

- Boggs, C. L., 1981. Nutritional and life-history determinants of resource allocation in holometabolous insects. *American Naturalist* 117: 692–709.
- Boggs, C. L., 2009. Understanding insect life histories and senescence through a resource allocation lens. *Functional Ecology* 23: 27–37.
- Bulleri, F., J. F. Bruno, B. R. Silliman & J. J. Stachowicz, 2016. Facilitation and the niche: implications for coexistence, range shifts and ecosystem functioning. *Functional Ecology* 30: 70–78.
- Burkholder, P. R., 1952. Cooperation and conflict among primitive organisms. *American Scientist* 40: 601–631.
- Callisto, M., M. D. C. Goulart, P. Moreno & R. P. Martins, 2006. Does predator benefits prey? Commensalism between *Corynoneura* Winnertz (Diptera, Chironomidae) and *Corydalus* Latreille (Megaloptera, Corydalidae) in Southeastern Brazil. *Revista Brasileira de Zoologia* 23: 569–572.
- Cardinale, B. J., M. A. Palmer & S. L. Collins, 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415: 4–7.
- Connell, J. H., 1983. On the prevalence and relative importance of interspecific competition; evidence from field experiments. *American Naturalist* 122: 661–696.
- Corbet, P. S., 1964. Temporal patterns of emergence in aquatic insects. *The Canadian Entomologist* 96: 264–279.
- Cummins, K. W. & M. J. Klug, 1979. Feeding ecology of stream invertebrates. *Annual Review of Ecology and Systematics* 10: 147–172.
- Cummins, K. W., 1973. Trophic relations of aquatic insects. *Annual Review of Entomology* 18: 183–206.
- De Brouwer, J. H. F., A. A. Besse-Lototskaya, C. J. F. ter Braak, M. H. S. Kraak & P. F. M. Verdonshot, 2017. Flow velocity tolerance of lowland stream caddisfly larvae (Trichoptera). *Aquatic Sciences* 79: 419–425.
- Didham, R. K., J. Ghazoul, N. E. Stork & A. J. Davis, 1996. Insects in fragmented forests: a functional approach. *Trends in Ecology and Evolution* 11: 255–260.
- Dolédec, S. & N. Bonada, 2013. So What? Implications of Loss of Biodiversity for Ecosystem Functioning. In Sabater, S. & A. Elosegi (eds), *River Conservation Challenges and Opportunities*. Fundacion BBVA, Madrid: 169–192.
- Dolédec, S., N. Lamouroux, U. Fuchs & S. Merigoux, 2007. Modelling the hydraulic preferences of benthic macroinvertebrates in small European streams. *Freshwater Biology* 52: 145–164.
- Duffy, J. E., K. S. Macdonald, J. M. Rhode & J. D. Parker, 2001. Grazer diversity, functional redundancy, and productivity in seagrass beds: an experimental test. *Ecology* 82: 2417–2434.
- Egglishaw, H. J., 1964. The distributional relationship between the bottom fauna and plant detritus in streams. *Journal of Animal Ecology* 33: 463–476.
- Fargione, J., D. Tilman, R. Dybzinski, J. HilleRisLambers, C. Clark, W. S. Harpole, J. M. H. Knops, P. B. Reich & M. Loreau, 2007. From selection to complementarity: shifts in the causes of biodiversity-productivity relationships in a long-term biodiversity experiment. *Proceedings of the Royal Society B* 274: 871–876.
- Fox, J. W., 2005. Interpreting the ‘selection effect’ of biodiversity on ecosystem function. *Ecology Letters* 8: 846–856.
- Gage, M. J. G., 1995. Continuous variation in reproductive strategy as an adaptive response to population density in the moth *Plodia interpunctella*. *Proceedings of the Royal Society B: Biological Sciences* 261: 25–30.
- Giller, P. S. & B. Malmqvist, 1998. *The biology of streams and rivers*. Oxford University Press, Oxford, UK.
- Graf, W., J. Murphy, J. Dahl, C. Zamora-Muñoz, M.J. López-Rodríguez & A. Schmidt-Kloiber, 2015. Dataset “Trichoptera: <http://www.freshwaterecology.info>” – the taxa and autecology database for freshwater organisms.
- Hickin, N. E., 1967. *Caddis Larvae, larvae of the British Trichoptera*. Hutchinson & Co publishers, London.
- Higler, L. G. W., 1975. Reaction of some caddis larvae (Trichoptera) to different types of substrate in an experimental stream. *Freshwater Biology* 5: 151–158.
- Higler, L. G. W., 2005. *De Nederlandse kokerjufferlarven, determinatie en ecologie*. KNNV uitgeverij, Zeist.
- Higler, L. G. W., 2008. *Verspreidingsatlas Nederlandse kokerjuffers (Trichoptera)*. EIS Nederland, Leiden.
- Hoffsten, P. O., 2004. Site-occupancy in relation to flight-morphology in caddisflies. *Freshwater Biology* 49: 810–817.
- Honěk, A., 1993. Intraspecific variation in body size and fecundity in insects. *Oikos* 66: 483–492.
- Jähnig, S. C., A. Lorenz & D. Hering, 2009. Restoration effort, habitat mosaics, and macroinvertebrates – does channel form determine community composition? *Aquatic Conservation of Marine and Freshwater Ecosystems* 19: 157–169.
- Jannot, J. E., 2009. Life history plasticity and fitness in a caddisfly in response to proximate cues of pond-drying. *Oecologia* 161: 267–277.
- Kelly, E. L. A., Y. Eynaud, S. M. Clements, M. Gleason, R. T. Sparks, I. D. Williams & J. E. Smith, 2016. Investigating functional redundancy versus complementarity in Hawaiian herbivorous coral reef fishes. *Oecologia* 182: 1151–1163.
- Lake, P. S., 2000. Disturbance, patchiness, and diversity in streams. *Journal of the North American Benthological Society* 19: 573–592.
- Lancaster, J. & A. G. Hildrew, 1993. Flow refugia and the microdistribution of lotic macroinvertebrates. *Journal of North American Benthological Society* 12: 385–393.
- Leibold, M. A., J. M. Chase & S. K. M. Ernest, 2016. Community assembly and the functioning of ecosystems: how metacommunity processes alter ecosystems attributes. *Ecology* 98: 909–919.
- Loreau, M. & A. Hector, 2001. Partitioning selection and complementarity in biodiversity experiments. *Nature* 412: 72–76.
- Loreau, M., 2000. Biodiversity and ecosystem functioning: recent theoretical advances. *Oikos* 91: 3–17.
- Malicky, H., 2004. *Atlas of European Trichoptera*. Springer, Dordrecht.
- Malmqvist, B. & D. Oberle, 1995. Macroinvertebrate effects on leaf pack decomposition in a stream in Northern Sweden. *Nordic Journal of Freshwater Research* 70: 12–20.
- McNamara, K. B., M. A. Elgar & T. M. Jones, 2010. Adult responses to larval population size in the almond moth, *Cadra cautella*. *Ethology* 116: 39–46.

- Mermillod-Blondin, F., M. Gérino, M. Creuzé des Châtelliers & V. Degrange, 2002. Functional diversity among 3 detritivorous hyporheic invertebrates: an experimental study in microcosms. *Journal of the North American Benthological Society* 21: 132–149.
- Milbrink, G., 1993. Evidence for mutualistic interactions in freshwater oligochaete communities. *Oikos* 68: 317–322.
- Minshall, G. W., 1967. Role of allochthonous detritus in the trophic structure of a woodland springbrook. *Ecology* 48: 139–149.
- Mulder, C. P. H., D. D. Uliassi & D. F. Doak, 2001. Physical stress and diversity-productivity relationships: the role of positive interactions. *PNAS* 98: 6704–6708.
- Pauls, S. U., W. Graf, P. Haase, H. T. Lumbsch & J. Waringer, 2008. Grazers, shredders and filtering carnivores – the evolution of feeding ecology in Drusinae (Trichoptera: Limnephilidae): insights from a molecular phylogeny. *Molecular Phylogenetics and Evolution* 46: 776–791.
- Rudolf, V. H. W., N. L. Rasmussen, C. J. Dibble & B. G. V. Allen, 2014. Resolving the roles of body size and species identity in driving functional diversity. *Proceedings of the Royal Society B: Biological Sciences* 281: 20133203.
- Rumbos, C., D. Stampoulos, G. Georgoulas & E. Nikolopoulou, 2010. Factors affecting leaf litter decomposition by micropterna sequax (Trichoptera: Limnephilidae). *International Review of Hydrobiology* 95: 383–394.
- Schmera, D., 2002. Notes on the larval habitat preference and microdistribution of *Potamophylax rotundipennis* (Insecta:Trichoptera) in a stream reach of the Börzsöny Mountains (Northern Hungary). *Folia Historico-Naturalia Musei Matraensis* 26: 241–243.
- Schröder, M., J. Kiesel, A. Schattmann, S. C. Jähnig, A. W. Lorenz, S. Kramm, H. Keizer-Vlek, P. Rolauffs, W. Graf, P. Leitner & D. Hering, 2013. Substratum associations of benthic invertebrates in lowland and mountain streams. *Ecological Indicators* 30: 178–189.
- Stachowicz, J. J. & J. E. Byrnes, 2006. Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. *Marine Ecology Progress Series* 311: 251–262.
- Stevens, D. J., M. H. Hansell & P. Monaghan, 2000. Developmental trade-offs and life histories: strategic allocation of resources in caddis flies. *Proceedings of the Royal Society of London B* 267: 1511–1515.
- Stevens, D. J., M. H. Hansell, J. A. Freel & P. Monaghan, 1999. Developmental trade-offs in caddis flies: increased investment in larval defence alters adult resource allocation. *Proceedings of the Royal Society B: Biological Sciences* 266: 1049–1054.
- Swift, M. J., O. W. Heal & J. M. Anderson, 1979. *Decomposition in Terrestrial Ecosystems*. Blackwell Scientific Publications, Oxford.
- Tokeshi, M., 1993. On the evolution of commensalism in the chironomidae. *Freshwater Biology* 29: 481–484.
- Tolkamp H, 1980. *Organism–substrate relationships in lowland streams*. Wageningen (NL): Agricultural University Agricultural Research. Report 907: 211 p.
- Urbanič, G., M. J. Toman & C. Krušnik, 2005. Microhabitat type selection of caddisfly larvae (Insecta: Trichoptera) in a shallow lowland stream. *Hydrobiologia* 541: 1–12.
- Verdonschot, P. F. M., B. M. Spears, C. K. Feld, S. Brucet, H. Keizer-Vlek, A. Borja, M. Elliott, M. Kernan & R. K. Johnson, 2012. A comparative review of recovery processes in rivers, lakes, estuarine and coastal waters. *Hydrobiologia* 704: 453–474.
- Walker, B. H., 1992. Biodiversity and ecological redundancy. *Conservation Biology* 6: 18–23.
- Waringer, J., W. Graf, M. Bálint, M. Ku Ini, S. U. Pauls, A. Previsi, L. Keresztes & S. Vitecek, 2013. The larvae of *Drusus franzressli* Malicky 1974 and *Drusus spelaeus* (Ulmer 1920) (Trichoptera: Limnephilidae: *Drusinae*) with notes on ecology and zoogeography. *Zootaxa* 3637: 1–16.
- Westveer, J. J., P. F. M. Verdonschot & R. C. M. Verdonschot, 2017. Substrate homogenization affects survival and fitness in the lowland stream caddisflies *Micropterna sequax* and *Potamophylax rotundipennis*: a mesocosm experiment. *Freshwater Science* 36(June): 585–594. <https://doi.org/10.1086/692940>.
- Wissinger, S., J. Steinmetz, J. S. Alexander & W. Brown, 2004. Larval cannibalism, time constraints, and adult fitness in caddisflies that inhabit temporary wetlands. *Oecologia* 138: 39–47.