

Biotic interactions could control colonization success during stream restoration

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Abstract: Biotic interactions involved in colonization are likely important if tolerant aquatic taxa, which have settled first, prevent desired taxa from colonizing when conditions improve. These interactions could be particularly influential during restoration but are poorly understood in streams. We investigated the interactions between 3 stream macroinvertebrate taxa, the snail *Potamopyrgus antipodarum* (Gray, 1843), mayfly nymphs in the genus *Deleatidium*, and caddisfly larvae in the family Conoesucidae, to assess whether order of arrival and competitor identity influence colonization success. In a replicated ($n = 5$) mesocosm experiment, we added an early colonist—either snails, mayflies, or caddisflies—then added 1 of the other 2 invertebrates and measured colonization success. Snails were competitively dominant over mayflies, reducing their colonization regardless of arrival order. Caddisflies, in comparison, had an inhibitory priority effect on both mayflies and snails, whereas mayflies had an inhibitory priority effect on caddisfly colonization. Last, snails had a facilitative priority effect on caddisfly colonization. These results indicate that competitive dominance and multiple types of priority effects could shape freshwater macroinvertebrate assemblages and, therefore, could inhibit desired taxa from colonizing during restoration efforts. Thus, stream restoration strategies should consider the effects of biotic interactions, including priority effects, on restoration outcomes.

Key words: stream, competition, restoration, priority effect, biotic interactions, colonization, New Zealand mud snails, macroinvertebrates

The order of species arrival in an ecosystem can substantially influence their interactions with other species, a process involving priority effects (Fukami 2015). Through habitat modification, or niche pre-emption, early arriving species can have negative or positive effects on colonization of later arriving species and influence community assembly via species-sorting mechanisms (Chase 2003, Fukami 2015). Alternatively, some species will always competitively exclude other species from colonizing, regardless of arrival order, which occurs when there is a strong competitive hierarchy (Fukami 2015). Competitive superiority may arise because of feeding rate efficiency (McAuliffe 1984, Hart 1992), density-dependent effects (Hall et al. 2006), or morphological traits (Vinson and Baker 2008). However, determinations of the drivers of stream community structure have often disregarded such biotic interactions, especially competition, while focusing on large-scale disturbance events and

stochastic colonization effects (Townsend 1989, Death 2010, Tonkin et al. 2018b). The prevalence of this view has meant that strong biotic interactions have often not been given the prominence they potentially deserve (but see Hart 1981, McAuliffe 1984, Chesson and Huntly 1997, Ledger et al. 2006, Little and Altermatt 2018). Because most stream recolonization is not from a de novo state, the effects of an existing community could be particularly important in understanding community assembly outcomes.

Biotic interactions, including competitive exclusion and inhibitory or facilitative priority effects, have been well studied in a range of ecosystems (Louette and De Meester 2007, Loureiro et al. 2013, Waters et al. 2013, Geange et al. 2017) and have important influences on succession (Dickson et al. 2012, Halpern et al. 2016, Filibeck et al. 2020), invasion (Schreiber et al. 2002, Chadwell and Engelhardt 2008, Riley and Dybdahl 2015), and restoration (Yannelli et al. 2020,

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Weidlich et al. 2021). These interactions are also an important part of the species-sorting mechanisms involved in meta-community dynamics (Chase 2003, Leibold et al. 2004). In a metacommunity, the relative importance of species-sorting mechanisms, like priority effects and competitive dominance, will depend on whether these mechanisms are overwhelmed by the mass effects of colonist availability or other stochastic drivers (Chase 2007, Chase et al. 2009). Despite this dependence, investigating the potential for priority effects to occur will improve understanding of a fundamental aspect of stream community assembly (Thompson and Townsend 2006, Datry et al. 2016, Little and Altermatt 2018).

Where recolonization of a community by desired colonists is an objective, such as macroinvertebrate colonization in stream restoration, priority effects could influence whether biological recovery is successful. Many stream restoration actions prioritize improvement of abiotic conditions (Lake et al. 2007, Palmer et al. 2010, Haase et al. 2013) in the hope that biodiversity will follow. There are countless examples of restoration efforts that have successfully improved abiotic parameters but failed to improve macroinvertebrate biodiversity (Lepori et al. 2005, Louhi et al. 2011, Haase et al. 2013, Lorenz et al. 2018). This lack of success may be because abiotic improvements are only influential when paired with other restorative actions because multiple assembly processes are involved in community assembly (Patrick et al. 2021). Along with the physical conditions of an environment, the return of macroinvertebrate biodiversity is positively correlated to the number of colonists available and their respective dispersal distance from the desired site (Tonkin et al. 2014, Patrick et al. 2021). However, even if abiotic conditions are restored and an adequate number of colonists are available, priority effects influencing colonization could still be important if their effect on the return of sensitive taxa is inhibitory or facilitative.

One example of inhibitory effects on colonization under restored abiotic conditions is provided by degraded communities that become highly resistant to change and, consequently, prevent desired taxa from colonizing. A degraded community is an established community composed of tolerant organisms that persisted in the degraded environment, such as those dominated by the pollution-tolerant snail *Potamopyrgus antipodarum* (Gray, 1843) that can prevent desired mayflies and caddisflies from colonizing restored streams (Barrett et al. 2021). Additionally, high densities of *P. antipodarum* can cause mayflies to spend less time foraging, potentially decreasing mayfly fitness and further perpetuating negative resistance and resilience (White et al. 2021). Thus, biotic interactions, like priority effects and competitive dominance, may play an important role in the colonization success of sensitive macroinvertebrates in the presence of an established tolerant fauna. Such interactions are well known and common in plant communities and introduce important contingencies into restoration plans (Weidlich et al. 2021), but these interactions are poorly understood in aquatic macroinvertebrate assemblages. Know-

ing how species respond to the presence of other species and how order of arrival might affect their colonization ability will help develop knowledge of how to successfully re-introduce sensitive taxa to abiotically restored streams.

We investigated species interactions occurring during the colonization of 3 common and key macroinvertebrate taxa in New Zealand streams: *P. antipodarum* snails, *Deleatidium* mayflies, and Conoesucidae caddisflies. We used stream mesocosms to test how their colonization success changed in the presence of one another and how order of arrival affected those interactions as a 1st step in evaluating whether such interactions could be important in the restoration of previously degraded streams. More specifically, we assessed whether high numbers of *P. antipodarum* snails, a characteristic component of many degraded New Zealand streams (Greenwood et al. 2012, Graham et al. 2015), dominate once established and, if so, whether dominance is attributable to either priority effects or competitive dominance. We expected that the snail, if established first, might have an advantage because of the general antipredator benefits of their protective shell (e.g., by facilitating daytime foraging), and that those effects would be stronger on *Deleatidium* mayflies than the caddisflies because caddisflies also have a protective case.

METHODS

Study design

To investigate the colonization success of the 3 taxa, we mimicked a stable, healthy stream environment with 30 flow-through mesocosms. By closely imitating the natural environment and allowing control of environmental variables, such experiments offer an ideal environment for untangling complex interactions that are difficult to detect in larger-scale studies (Lamberti and Steinman 1993, Spivak et al. 2011). To compare snail, mayfly, and caddisfly colonization success and to evaluate the effect of order of arrival on colonization success, we used a 6-treatment design with 5 replicates each. Each treatment consisted of 1 of the 6 possible combinations, with mesocosms initially colonized by either snails, mayflies, or caddisflies, after which 1 of the other 2 invertebrate types was added to the same tank (Table 1). We then measured the proportion of biomass that drifted out of the mesocosms at 12-h intervals as well as the biomass remaining at the end of the experiment and used analysis of variance (ANOVA) to assess differences between treatments for each species individually.

MESOCOSM SETUP

The 0.226-m² mesocosms (described by White et al. 2021) were located at University of Canterbury's Cass field station, New Zealand. We fed mesocosms with filtered stream water pumped from Grasmere Stream (lat -43.034954, long 171.757896), home to all 3 focal macroinvertebrates as well as various fish (Nyström et al. 2003). Flow entered from 2 small, opposite-facing jets, creating a clockwise current

Table 1. The experimental design of 6 different treatments, each with an early arriving colonist of either *Potamopyrgus antipodarum* snails (S), *Deleatidium* mayflies (M), or Conoesucidae caddisflies (C) and a late arriving colonist consisting of 1 of the other 2 taxa.

Late colonists (added 2 nd)	Early colonists (added 1 st)		
	S	M	C
S	–	M + S	C + S
M	S + M	–	C + M
C	S + C	M + C	–

(velocity: mean \pm SE: 0.04 ± 0.0005 m/s). A central standpipe maintained mesocosm water depth (12.5 cm) and allowed invertebrates to leave, a key component of our design. The bottom of this standpipe outlet was covered by a net to collect invertebrates drifting out, allowing unsuccessful colonists to be counted. We covered the mesocosm bases with nontoxic paint mixed with sand, creating a rough surface suitable for macroinvertebrates to cling to, and we created microhabitats by adding gravel and periphyton-covered rocks (2 large, 12-cm diameter; 5 medium, 8-cm diameter). Prior to the experiment, we also grew periphyton by soaking terracotta tiles in fertilized stream water (see Hornblow 2021). Tiles had consistent algal growth made up of green algae (6.14 ± 0.19 μg Chlorophyll *a* [Chl *a*]/cm²), cyanobacteria (2.03 ± 0.17 μg Chl *a*/cm²), and diatoms (1.83 ± 0.44 μg Chl *a*/cm²; Hornblow 2021). We placed 4 tiles in each tank as a source of food and replaced the tiles once during the experiment when algae were depleted. During tile replacement we put caps on the standpipes so that organisms could not drift out, and we gently washed off any organisms on the tiles being replaced. We set the lighting 15D:9N to imitate summer daylight outside. Natural stream flow throughflow ensured abiotic conditions (13.7°C, pH 7.07, 6.7 mg/L dissolved O₂, and 70.4 $\mu\text{S}/\text{cm}$ conductivity) were excellent for macroinvertebrates and reflected natural diel changes in Grasmere Stream.

ANIMAL COUNTING AND STOCKING

We grouped study animals at different taxonomic levels for practicality: species level for snails, genus level for mayflies, and family level for caddisflies. The different species of mayfly nymph are difficult to distinguish, and the different caddisfly taxa have qualitatively similar characteristics (a small, stony case). Thus, the taxonomic variation between animals in our experiment was relatively unimportant given the large differences in the characteristics of the 3 groups of animals compared.

We collected snails from streams by carefully shaking small nets under stream macrophytes. We collected mayflies via electric fishing methods to avoid physical damage

to their appendages (Taylor et al. 2001), and we only used *Deleatidium* with undeveloped wing pads in the experiment to avoid their possible emergence. We collected stony-cased Conoesucidae caddisflies, mostly *Pycnocentria* spp and *Pycnocentroides* spp, via D-nets. All 3 groups of macroinvertebrates were carefully transferred into oxygenated containers once collected and placed into the mesocosms as soon as possible, typically within 4 h.

Before adding macroinvertebrates to mesocosms, we determined the number of each taxon that should be added. *Potamopyrgus antipodarum* snails, *Deleatidium* mayflies, and Conoesucidae caddisflies differ substantially in body size, with *Deleatidium* roughly 5 \times larger than *P. antipodarum*. To enable easy comparison between the 3 focal macroinvertebrate types, we added them at equal total biomass. This strategy meant we added a different number of each macroinvertebrate to the mesocosms, as determined using length–dry mass regressions (Towers et al. 1994 [caddisfly and mayfly], Baumgärtner and Rothhaupt 2003 [snail]):

$$\text{Ln}(DM) = (\text{Ln}[a + b]) (\text{Ln}[L]), \quad (\text{Eq. 1})$$

where *DM* is dry mass (mg) of the taxon, *L* is body length (mm), and *a* and *b* are fitted regression coefficients (*P. antipodarum*: *a* = -4.74 , *b* = 3.21 ; *Deleatidium*: *a* = -5.38 , *b* = 3.06 ; and Conoesucidae: *a* = -4.87 , *b* = 2.50). Using this equation, we calculated 1000 snails, 200 mayflies, or 340 caddisflies to equate to a mean dry mass of 0.6 g/tank. We arrived at this stocking density because previous work in these tanks with similar resource indicated 0.6 g/tank was around the carrying capacity of the mesocosms (i.e., over this density and drift out of the tanks increased substantially; Hornblow 2021). We counted snails into mesocosms using teaspoons, rather than individually, for time management reasons. Five level teaspoons of *P. antipodarum* counted prior to the experiment contained a mean of 496 snails/tsp, and snails were spooned into all mesocosms by the same person. We used turkey basters to count both *Deleatidium* and caddisflies individually into mesocosms to avoid damage.

Experimental protocol

We added 1st colonists to mesocosms with the standpipe covered for 30 min to allow macroinvertebrates to settle and avoid premature drift. After the standpipe cover was removed, we left these 1st colonists for 12 h of daylight. After 12 h, we collected the 1st drift sample, which we stored in ethanol for later counting. We then added the 2nd colonists to their respective tanks just before nightfall, and we took 3 additional drift samples (4 drift samples in total) every 12 h (total experiment duration of ~ 48 h). We also collected and counted every individual remaining in the tank after 48 h. We then applied Eq. 1 to calculate biomass estimates for both drift and number remaining. We analyzed both because animals emigrated at different rates and times, so there are

mechanistic insights to be gleaned from the drift data that are not apparent from end-of-experiment totals.

End-of-experiment biomass analysis

To assess colonization success of macroinvertebrates based on biomass remaining at the end of the experiment, we used `aov` in base R (version 4.05; R Project for Statistical Computing, Vienna, Austria) to run separate 2-way ANOVAs for each taxon. We compared differences in biomass between 2 fixed treatments: competitor identity (other species present) and order (1st or 2nd). We examined parametric assumptions of all models and applied logit transformations to the snail and caddisfly drift data to correct for nonnormal residuals and to improve homogeneity of variances. We used `ggplot2` (version 3.4; Wickham 2009) to plot means and the `effects` package (version 4.2-2; Fox and Weisberg 2018) to calculate 95% CIs.

Drift biomass over time analysis

To assess colonization success of macroinvertebrates based on drift biomass as a proportion of biomass available to drift at each time period, we used the `aov` function with the `+Error` argument in base R to run separate repeated measure ANOVAs for each taxon. Each model included 3 fixed effects, competitor identity (other taxa present), order (1st or 2nd), and period (the 12-h period during which drift occurred), and we included mesocosm as a random effect to account for the repeated drift measurements. We classified period as the within-subject factor and competitor identity

and order as between-subject factors, with the proportion of drift biomass of the focal species as the response. We examined the models for parametric assumptions as above and used `ezANOVA` in the `ez` package (version 4.4.0; Lawrence 2016) to run Mauchly's test to test the sphericity assumption for the repeated measures analyses. For the caddisfly drift data that did not meet the sphericity assumption, we report Greenhouse–Geisser-corrected *p*-values for the within-subjects effect. As above, we used `ggplot2` to plot the means with 95% CIs based on the repeated measures analyses, which we calculated with the R package `emmeans` (version 1.8.8; Lenth et al. 2023).

RESULTS

Snail responses

Snail biomass remaining within mesocosms at the end of the experiment depended on competitor type and order of addition, indicated by a moderate competitor \times order interaction (Table S1). Remaining snail biomass was lower when snails were added to an established assemblage of caddisflies compared with when they were added first, illustrating that the effect of caddisflies on snail biomass depended on the order of arrival (Fig. 1A). In contrast, in the presence of mayflies, remaining snail biomass was always higher, regardless of order, illustrating that mayflies had little effect on remaining snail biomass (Fig. 1A). Thus, snail colonization was only affected by caddisflies and not by mayflies, and then only when caddisflies were added first.

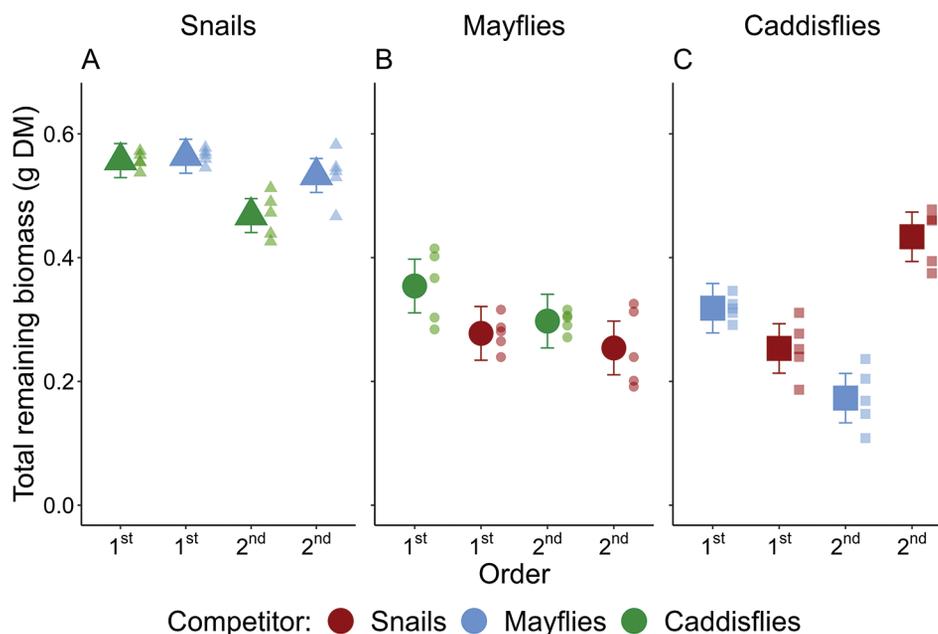


Figure 1. Mean biomass (g dry mass; DM) and 95% CI of *Potamopyrgus antipodarum* snails (A; triangles), *Deleatidium* mayflies (B; circles), and Conoesucidae caddisflies (C; squares) remaining in mesocosms at experiment end depending on order of arrival (either 1st or 2nd) and competitor identity (snails = red, mayflies = blue, and caddisflies = green). Raw data points (smaller icons) sit to the right of their respective means (larger icons).

Patterns in snail colonization were further explained by drift patterns. There was no 3-way interaction between competitor, order, and period, but there was a moderate order \times period interaction and a strong competitor effect (Table S2). The interaction between period and order was driven by a higher proportion of snail drift at night when snails were added to the tanks 2nd, whereas there were no changes in drift with period when they were added 1st (Fig. 2A, D). Snails drifted more when they were in mesocosms with caddisflies compared with mesocosms with mayflies, explaining the competitor effect (Fig. 2D). However, the magnitudes of snail responses were small, especially compared with both mayfly and caddisfly drift (Fig. 2B–F). Despite these small differences in drift, the consistently higher snail drift at night when added 2nd to caddisflies culminated in the observed decrease in total snail colonization. Overall, these results indicate that there was a priority effect of caddisflies on snail colonization but no priority effect of mayflies on snails.

Mayfly responses

Mayfly biomass remaining at the end of the experiment was $\sim 1/2$ that of snails, indicating the mayflies had much higher emigration from the mesocosms than the snails (Fig. 1A, B). Remaining mayfly biomass depended on competitor identity only and, unlike that of snails, was not dependent on the order of introduction (Table S1). The strong competitor effect occurred because the presence of snails always reduced mayfly biomass, regardless of order, more than the presence of caddisflies did (Fig. 1B). These results indicate that the presence of an established assemblage, made up of either snails or caddisflies, influenced remaining mayfly biomass, but with snails reducing mayfly colonization more than caddisflies.

The drift results also explain further aspects of mayfly colonization. The proportion of mayflies drifting was driven by a strong competitor \times period interaction (Table S2). Mayflies tended to drift less when in the presence of caddisflies and more in the presence of snails. This effect was

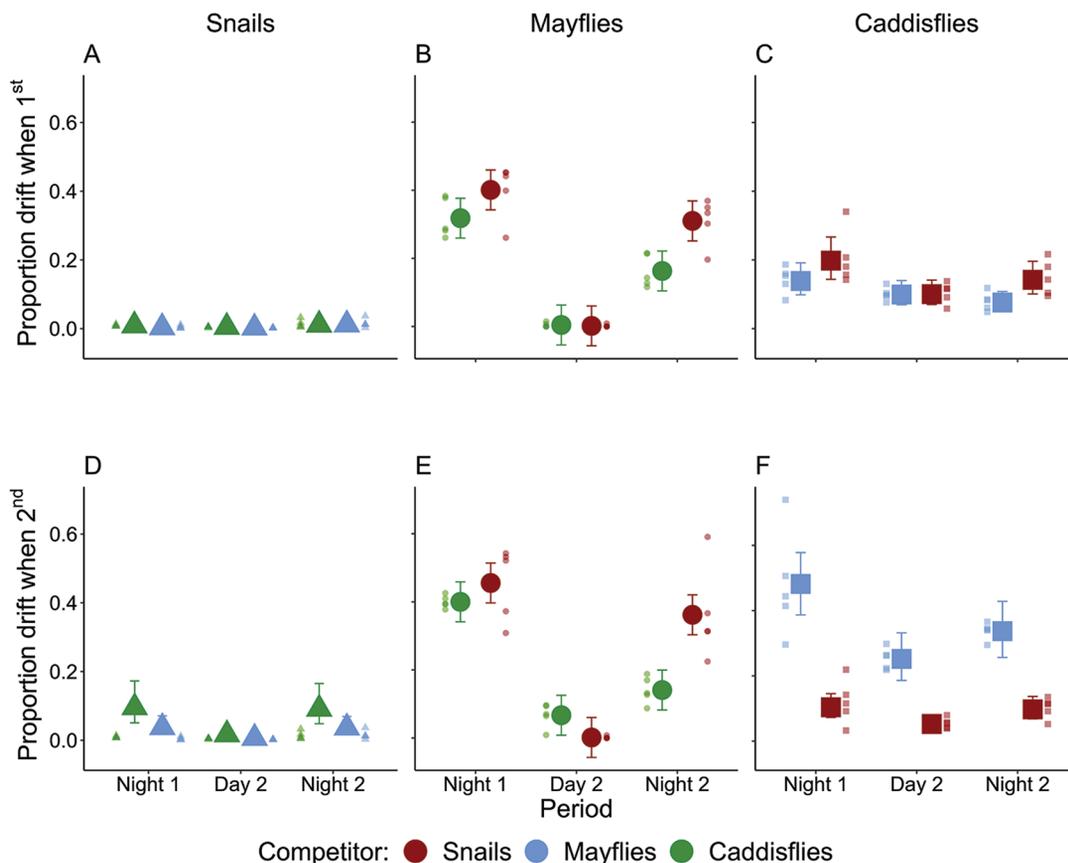


Figure 2. Biomass drift out of mesocosms as a proportion of available biomass to drift for each 12-h period (night 1, day 2, or night 2) and 95% CI for *Potamopyrgus antipodarum* (A, D; triangles), *Deleatidium* mayflies (B, E; circles), and Conoesucidae caddisflies (C, F; triangles) split by order of arrival (added 1st, top panels; added 2nd, bottom panels) and competitor identity (snails = red, mayflies = blue, and caddisflies = green). Raw data points (smaller icons) sit to the side of their respective means (larger icons).

more pronounced during the night but occurred regardless of order (Fig. 2B, E). Thus, the strong effect of snails on mayfly colonization occurred regardless of order of addition.

Caddisfly responses

Caddisfly biomass remaining within mesocosms at the end of the experiment depended on competitor type and order of addition, shown by the very strong competitor \times order interaction (Table S1). When caddisflies were added to mesocosms 1st, their remaining biomass was similar in the presence of both snails and mayflies (Fig. 1C). However, when caddisflies were added after snails, remaining caddisfly biomass increased compared with when they were added 1st. In comparison, when caddisflies were added after mayflies, remaining caddisfly biomass decreased compared with when they were added 1st. These results indicate that snails facilitated caddisfly colonization, whereas mayflies inhibited caddisfly colonization.

Drift patterns again explained the different effects of snails and mayflies on caddisfly colonization success. There was a very strong period effect driven by, on average, a higher proportion of caddisflies drifting during the 1st night (Table S2, Fig. 2C, F). However, more importantly, and as with the remaining biomass results, the proportion of caddisflies drifting was driven by a very strong competitor \times order interaction (Table S2). A higher proportion of caddisflies drifted when added 2nd to tanks containing mayflies compared with tanks containing snails. However, when caddisflies were added 1st, a smaller proportion drifted in tanks containing mayflies, and a larger proportion drifted in tanks containing snails (Fig. 2C, F). When mayflies already occupied an area, they had an immediate negative effect on caddisfly colonization, causing caddisflies to drift more, whereas caddisflies were consistently more tolerant to areas already occupied by snails. Thus, when mayflies were added 1st, they had an inhibitory priority effect on caddisfly colonization, whereas when snails were 1st, they had a facilitative effect on caddisfly colonization.

DISCUSSION

Knowledge of the role of species interactions during colonization could be integral to explaining variations in stream restoration success and is an under-researched aspect of stream community assembly (Barrett et al. 2021). We tested 3 different macroinvertebrates to assess how order of arrival and competitor identity affected their colonization success. Our findings show that, depending on taxon identity, order of arrival affects macroinvertebrate colonization success and alters the impact that other taxa have on them (Fig. 3A–F). More specifically, consistently fewer *Deleatidium* mayflies colonized when in the presence of *P. antipodarum* snails compared with the presence of Conoesucidae caddisflies regardless of the arrival order, indicating competitive dominance of *P. antipodarum* snails over *Deleatidium* mayflies

(Fig. 3A, B). Snail colonization was reduced when added 2nd to an established caddisfly assemblage (Fig. 3C vs F), whereas caddisfly colonization was reduced when added after mayflies (Fig. 3D vs B), indicating inhibitory priority effects. Finally, more caddisfly biomass remained when added 2nd to tanks already colonized by snails (Fig. 3F vs C), indicating that snails had a facilitative priority effect on caddisfly colonization. Overall, these findings indicate that competitive dominance and priority effects have the potential to shape assemblages in streams more than has been appreciated, and these influences could be especially important during restoration.

Competitive dominance

Priority-effect interactions only occur when the effect of 1 species on another depends on arrival order, meaning that colonization outcomes can only be predicted when the arrival order is known (Fukami 2015). In comparison, competitive dominance occurs when there is a strong competitive hierarchy, meaning that the more competitive species will always dominate regardless of the arrival order or stage of succession (Fukami 2015). Because the effect of snails on mayfly biomass did not depend on the order of arrival, patterns in mayfly colonization in the presence of snails were driven by competitive dominance rather than priority effects. Given that *Potamopyrgus* snails, although native to New Zealand, are also a worldwide invader (da Silva et al. 2019), this finding suggests that competitive interactions like this could play an underappreciated role in structuring many freshwater communities undergoing restoration.

There are several possible mechanisms, including resource competition, space monopolization, and drift behavior, that could drive *P. antipodarum* dominance over *Deleatidium*. *Potamopyrgus* snails are strong competitors (Riley and Dybdahl 2015), a characteristic that has aided their worldwide invasion. When mayflies were added 1st, they were introduced to the tank during the morning, meaning that the 12-h period before the arrival of snails was during the day. However, *Deleatidium* feed mostly at night (McIntosh and Townsend 1995), meaning that it is unlikely they depleted resources before the arrival of the snails. Additionally, because mayfly drift differed between caddisfly and snail mesocosms, it is improbable that snails dominated just because mayflies have a higher drift propensity than snails. Alternatively, the success of the snails over the mayflies may have been influenced by traits related to their tolerance of degradation (Barrett et al. 2022). *Potamopyrgus antipodarum* snails effectively monopolize space in freshwater ecosystems (Schreiber et al. 2002), likely aided by their lack of mobility and hard exterior. If the snails successfully dominated the space surrounding available resources and other desirable areas, they may have prevented the mayflies from settling and obtaining food. Moreover, Holomuzki and Biggs (2006) found that food limitation affected *Deleatidium*

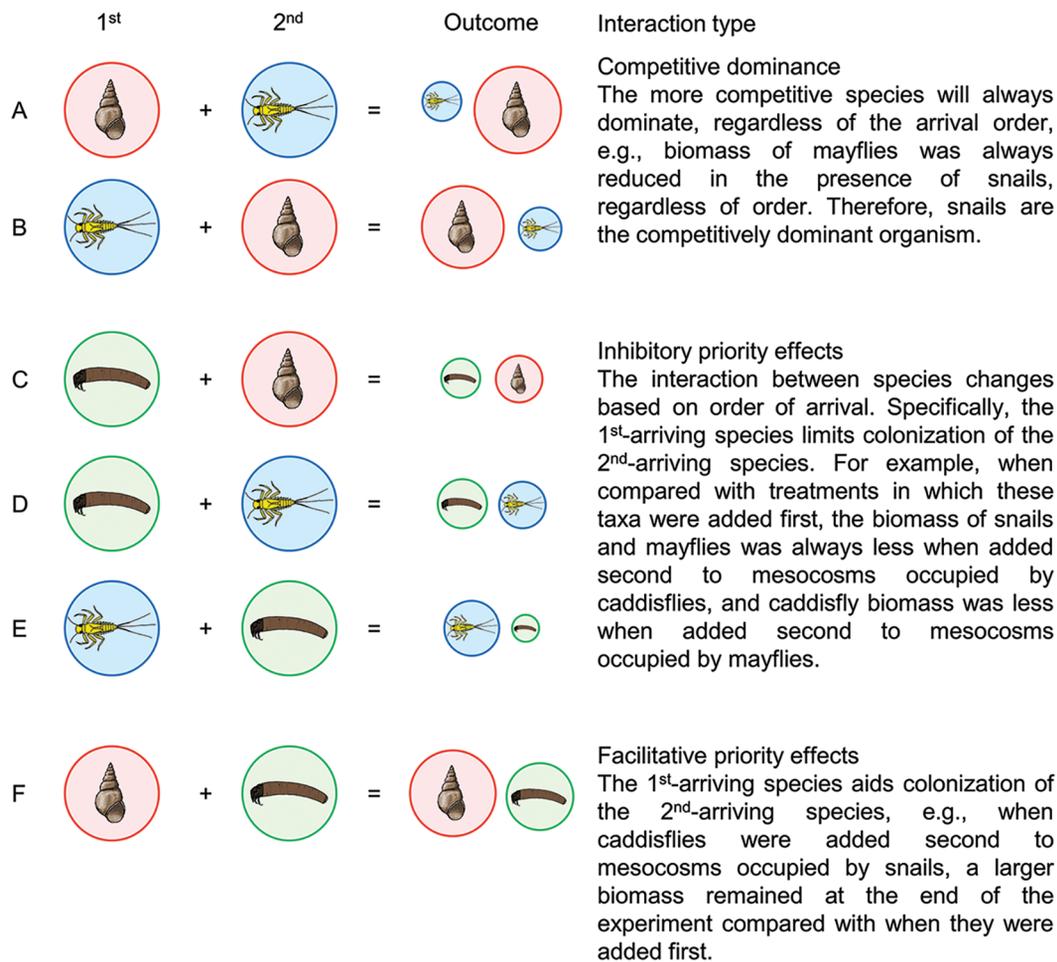


Figure 3. Summary of interaction outcomes detected in the experiments manipulating the order (1st or 2nd) in which 3 consumers (*Potamopyrgus antipodarum* snails, *Deleatidium* mayflies, and Conoesucidae caddisflies) were added to mesocosms. Interaction outcomes included competitive dominance (A, B), inhibitory priority effects (C–E), and facilitative priority effects (F). Circle sizes are proportional to the biomass of the organism at the various stages of the experiment (initial dry mass was 0.6 g/mesocosm).

more than it affected *P. antipodarum*, likely explaining why mayfly drift increased more than snail drift as the experiment progressed. Thus, during restoration, decreasing densities of competitively dominant established species, like *P. antipodarum*, are likely to enhance colonization success of taxa like mayflies that may otherwise have difficulty establishing.

Inhibitory priority effects

Competitive exclusion occurs when 1 species dominates over the other, regardless of order, whereas when priority effects occur, the interaction between species changes based on order of arrival (Fukami 2015). Both snail and mayfly colonization were lower when added to an established assemblage of caddisflies compared with being added first. Likewise, caddisfly colonization was lower when added to an established assemblage of mayflies compared with being added 1st. These results suggest that there was an inhibitory

priority effect of caddisflies on both mayfly and snail colonization and an inhibitory priority effect of mayflies on caddisfly colonization. Such influences are common in terrestrial systems but are poorly known from stream systems (Weidlich et al. 2021). However, Little and Altermatt (2018) observed that priority effects linked to niche pre-emption likely explained a long-standing conundrum in the distribution of gammarid amphipods, arguing that directional colonization likely enhances the occurrence of such pre-emption effects in streams.

Several mechanisms linked to grazing efficiency and related morphological traits potentially underly these inhibitory effects. Snails, mayflies, and caddisflies all effectively graze periphyton in streams, and in the wild, they tend to avoid foraging in the same area (Holomuzki and Biggs 2006, Kerans et al. 2010). Therefore, it is likely that interspecific competition for algal food resources increased as our experiment progressed. Holomuzki and Biggs (2006)

found the conoesucid caddisfly *Pycnocentroides* was a more effective grazer than either *Deleatidium* or *P. antipodarum* because of its large body size, higher foraging rate, and tough exterior. If caddisflies are efficient algal grazers, it is likely that resources within the mesocosms would have been substantially depleted before the arrival of mayflies or snails, therefore creating an unfavorable habitat that, in turn, induced the higher drift rates we observed for both taxa. Additionally, caddisflies have similar traits to *P. antipodarum*, such as hard exteriors and lower levels of mobility (Mackay and Wiggins 1979, Johansson 1991), which likely protect them from predation (Wootton et al. 1996) and may have aided their resource acquisition or blocked other taxa from gaining resources. Using experimental algae-covered tiles, Kerans et al. (2010) found *Brachycentrus occidentalis* caddisflies caused *P. antipodarum* to seek resources elsewhere. Thus, caddisflies could have spatially blocked later-arriving species from colonizing our mesocosms.

Caddisflies inhibited the colonization of mayflies, but mayflies also inhibited caddisfly colonization. Caddisflies and *Deleatidium* mayflies graze similar areas and have similar niche requirements in streams (Holomuzki and Biggs 2006), so niche pre-emption may have driven this priority effect. Niche pre-emption occurs when an early arriving species reduces available resources, such as food or space, thereby inhibiting later species from colonizing (Fukami 2015). However, when mayflies were added to mesocosms 1st, they were added early in the morning, and because *Deleatidium* mayflies are nocturnal (McIntosh and Townsend 1995), it is unlikely that resources were suppressed substantially before the addition of caddisflies. Thus, it is improbable that caddisfly drift was solely caused by a depletion of food resources prior to their arrival but rather by spatial blocking of substrate surfaces. Mayflies, with their long filamentous cerci (or tails), are larger and more mobile than caddisflies (Holomuzki and Biggs 2006). They may have disturbed caddisflies with their tail movement or taken up a large amount of space within the mesocosms, thereby spatially blocking caddisflies from accessing resources. Although the exact causes of these interactions are still unclear, overall, these inhibitory effects indicate that the order of species arrival could influence the outcome of colonization success, whereby initial residents or 1st colonists could inhibit colonization of later arriving species.

Facilitative priority effects

Although some species inhibit the colonization of later-arriving taxa, it is also possible for species to aid the colonization of later-arriving taxa; better understanding of these interactions would be very useful in restoration. Facilitative priority effects occur when an early colonist modifies the environment in ways that aid further species (Gosling 2005). The outcome that caddisflies colonized more successfully when added 2nd to an established snail assemblage com-

pared with when they were added 1st, indicates that snails had a facilitative priority effect on caddisfly colonization. Many facilitative interactions have been described in terrestrial environments, such as the creation of unique microhabitats (Arroyo et al. 2003), increased nutrient availability (Gosling 2005), soil oxygenation (Callaway and King 1996), and altered light (Meira-Neto et al. 2017). Facilitation is important in recovery of macroinvertebrate assemblages from disturbance in streams (Ledger et al. 2006), and although potentially widespread (Silknetter et al. 2020), its role in other circumstances is probably underappreciated in freshwater ecosystems.

Habitat modification or nutrient excretion could have been involved in the facilitative interactions we observed. First, flow-driven microhabitats greatly influence macroinvertebrate foraging and movement (Hoffman et al. 2006, Hintz and Wellnitz 2013), and the characteristics of those microhabitats could be altered by other taxa. For example, Cardinale et al. (2002) found that topographical roughness in a flume increased with net-spinning caddisfly species richness and enhanced collective caddisfly feeding. In our case, large numbers of *P. antipodarum* snails may have altered habitats in a way that enhanced caddisfly colonization, such as by introducing stable flow microhabitats. An alternative mechanism could involve the feeding activities of *P. antipodarum*. Schreiber et al. (2002) suggested that feces associated with high *P. antipodarum* densities enhance detrital resources. However, in both cases, there is no obvious reason why caddisflies would benefit but mayflies would not. Thus, although any facilitative interactions would be very useful for restoration, especially of streams dominated by *P. antipodarum*, the underlying drivers of such interactions need more investigation. Future research is needed to improve understanding of the effects of such facilitative priority effects on macroinvertebrate assemblages.

Implications for community assembly

Overall, our results indicate that order of addition, depending on taxon identity, can influence colonization success, suggesting that order of colonization could have important implications for stream community assembly. Nevertheless, there has been a prevailing view that disturbance and stochastic drivers are the dominant mechanisms influencing benthic community structure (Minshall and Minshall 1977, Death 2010). Even as understanding of stream community assembly has matured, with the incorporation of metacommunity perspectives, the roles of dispersal-driven stochastic processes have been to the fore (Tonkin et al. 2018a). Our findings here, together with others (Little and Altermatt 2018, Barrett et al. 2021, White et al. 2021), highlight the potential relevance of these biotic interactions to community assembly.

There are, of course, limitations to transferring our results to wider community assembly contexts because we

used small-scale experiments with a limited number of focal macroinvertebrates. However, the scale of the experiments was necessary to identify and characterize the interactions, and the short duration allowed temporal patterns in drift to be assessed, facilitating further insights about the processes involved in such biotic interactions. We designed our experiments to approximate stream restoration contexts where there is a pre-existing community of organisms, which provides proof of concept. Future research could incorporate additional designs, such as restoration of severely degraded systems where no organisms are present. Field experiments, especially those involving restoration scenarios, are a next step for testing the importance of priority effects and competitive dominance on colonization success in situ. Indeed, the influence of priority effects and other biotic interactions on colonization success must work in concert with larger-scale stream metacommunity influences like dispersal. Nevertheless, even in the early 1980s, McAuliffe (1984) suggested that many studies investigate biotic interactions at too large a scale, meaning their significance is lost behind more conspicuous processes, such as environmental filtering, a sentiment recently echoed by Little and Altermatt (2018). Thus, until restoration is attempted, these interactions may not be particularly obvious, which could help explain some aspects of restoration failure. We hope our findings will stimulate a rethinking of the current, and mostly unsuccessful, approaches commonly used in stream restoration (Palmer et al. 2010, Bernhardt and Palmer 2011, Wohl et al. 2015, Lorenz et al. 2018).

Implications for stream restoration

Improving abiotic conditions is an essential part of restoration, but it may not be sufficient if biotic interactions underly the resistance and resilience of established assemblages (Lake et al. 2007). This lingering negative resistance and resilience could explain why restoring biodiversity is often much more difficult than improving abiotic conditions (Lepori et al. 2005, Lake et al. 2007, Palmer et al. 2010, Haase et al. 2013). Therefore, future restoration efforts may need to move towards considering all the factors that underpin colonization success, including biotic interactions such as priority effects and competitive dominance. Natural colonization may be insufficient to reestablish aquatic communities when there are priority effects operating, and reassembly of a community may require some further disruption (e.g., to remove competitive dominants) and seeding with colonists.

Our findings suggest that understanding the hierarchies of interactions could help with improving restoration success. For example, because snails facilitated caddisfly colonization, it is possible that caddisflies can more successfully colonize previously degraded streams dominated by *P. antipodarum*. In turn, finding ways to suppress strong competitors may make subsequent colonization by species with pollution-sensitive traits, such as *Deleatidium*, easier. Similar

ideas surrounding the manipulation of biotic interactions are often enacted in terrestrial restoration (Weidlich et al. 2021). For example, priority effects have already been deemed important in shaping terrestrial communities, are commonly studied with a restoration perspective (Dickson et al. 2012, Delory et al. 2019, Ploughe et al. 2020), and put an emphasis on the removal of hardy invasive weeds through manual intervention or biocontrol methods to enhance restoration success (Hill et al. 2008, Broadfield and McHenry 2019, Lam et al. 2021). These types of restoration methods are relatively uncommon in freshwater environments, and their absence could explain some of the lack of stream restoration success thus far. Manipulating specific patterns of trait-environment relationships could be used to help restore stream environments that are dominated by hardy taxa and currently difficult to restore (Barrett et al. 2022).

Most importantly, our findings indicate that a suite of influences likely needs to be considered when designing restoration to reverse the effects of degradation in streams. Our findings also suggest that successful restoration will need to consider biotic interactions along with improving the physical conditions of the environment and provide colonist populations. By translocating partially pollution-tolerant species, like caddisflies, to streams dominated by hardy taxa, we may be able to break the negative resilient and resistant cycles that currently dominate previously degraded environments. White et al. (2021) highlighted that many colonists would need to be added during restoration to overcome the effects of predation, and, consequently, any predator species should be added last to the system. Although macroinvertebrate translocation is thought to be time consuming and relatively unsuccessful (Jourdan et al. 2019), recent evidence suggests it can be accomplished (Haase and Pilotto 2019, Dumeier et al. 2020) and is likely to be more successful with adoption of best-practice protocols (Clinton et al. 2022). Moreover, by knowing the order of addition that allows organisms to successfully colonize, the rate of failure will likely decrease. Therefore, by determining how species respond to the presence of one another and how order of arrival affects colonization success, we can develop the restoration tools needed to successfully introduce sensitive taxa back into abiotically restored streams.

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LITERATURE CITED

- da Silva, M. V. A., J. V. Nunes Souza, J. R. B. de Souza, and L. M. Vieira. 2019. Modelling species distributions to predict areas at risk of invasion by the exotic aquatic New Zealand mudsnail *Potamopyrgus antipodarum* (Gray 1843). *Freshwater Biology* 64:1504–1518.
- Arroyo, M. T. K., L. A. Cavieres, A. Peñaloza, and M. A. Arroyo-Kalin. 2003. Positive associations between the cushion plant *Azorella monantha* (Apiaceae) and alpine plant species in the Chilean Patagonian Andes. *Plant Ecology* 169:121–129.
- Barrett, I. C., A. R. McIntosh, C. M. Febria, S. E. Graham, F. J. Burdon, J. P. F. Pomeranz, and H. J. Warburton. 2022. Integrative analysis of stressor gradients reveals multiple discrete trait-defined axes underlie community assembly. *Ecosphere* 13:e4164.
- Barrett, I. C., A. R. McIntosh, C. M. Febria, and H. J. Warburton. 2021. Negative resistance and resilience: Biotic mechanisms underpin delayed biological recovery in stream restoration. *Proceedings of the Royal Society B: Biological Sciences* 288:20210354.
- Baumgärtner, D., and K.-O. Rothhaupt. 2003. Predictive length-dry mass regressions for freshwater invertebrates in a pre-alpine lake littoral. *International Review of Hydrobiology* 88:453–463.
- Bernhardt, E. S., and M. A. Palmer. 2011. River restoration: The fuzzy logic of repairing reaches to reverse catchment scale degradation. *Ecological Applications* 21:1926–1931.
- Broadfield, N., and M. T. McHenry. 2019. A world of gorse: Persistence of *Ulex europaeus* in managed landscapes. *Plants* 8:523.
- Callaway, R. M., and L. King. 1996. Temperature-driven variation in substrate oxygenation and the balance of competition and facilitation. *Ecology* 77:1189–1195.
- Cardinale, B. J., M. A. Palmer, and S. L. Collins. 2002. Species diversity enhances ecosystem functioning through interspecific facilitation. *Nature* 415:426–429.
- Chadwell, T. B., and K. A. M. Engelhardt. 2008. Effects of pre-existing submersed vegetation and propagule pressure on the invasion success of *Hydrilla verticillata*. *Journal of Applied Ecology* 45:515–523.
- Chase, J. M. 2003. Community assembly: When should history matter? *Oecologia* 136:489–498.
- Chase, J. M. 2007. Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences* 104:17,430–17,434.
- Chase, J. M., E. G. Biro, W. A. Ryberg, and K. G. Smith. 2009. Predators temper the relative importance of stochastic processes in the assembly of prey metacommunities. *Ecology Letters* 12:1210–1218.
- Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist* 150:519–553.
- Clinton, S., J. Hartman, K. Macneale, and A. Roy. 2022. Stream macroinvertebrate reintroductions: A cautionary approach for restored urban streams. *Freshwater Science* 41:507–520.
- Datry, T., N. Bonada, and J. Heino. 2016. Towards understanding the organisation of metacommunities in highly dynamic ecological systems. *Oikos* 125:149–159.
- Death, R. G. 2010. Disturbance and riverine benthic communities: What has it contributed to general ecological theory? *River Research and Applications* 26:15–25.
- Delory, B. M., E. W. A. Weidlich, M. Kunz, J. Neitzel, and V. M. Temperton. 2019. The exotic species *Senecio inaequidens* pays the price for arriving late in temperate European grassland communities. *Oecologia* 191:657–671.
- Dickson, T. L., J. L. Hopwood, and B. J. Wilsey. 2012. Do priority effects benefit invasive plants more than native plants? An experiment with six grassland species. *Biological Invasions* 14:2617–2624.
- Dumeier, A. C., A. W. Lorenz, and E. Kiel. 2020. Active reintroduction of benthic invertebrates to increase stream biodiversity. *Limnologia* 80:125726.
- Filibeck, G., M. G. Sperandii, L. Bragazza, A. Bricca, S. Chelli, S. Maccherini, C. Wellstein, A. L. Conte, M. Di Donatantonio, T. G. W. Forte, L. Lazzaro, T. Macchiavelli, S. Maestri, R. Marchesini, M. Marignani, G. Midolo, L. Oddi, L. Rosati, G. Silan, and L. Cancellieri. 2020. Competitive dominance mediates the effects of topography on plant richness in a mountain grassland. *Basic and Applied Ecology* 48:112–123.
- Fox, J., and S. Weisberg. 2018. Visualizing fit and lack of fit in complex regression models with predictor effect plots and partial residuals. *Journal of Statistical Software* 87:1–27.
- Fukami, T. 2015. Historical contingency in community assembly: Integrating niches, species pools, and priority effects. *Annual Review of Ecology, Evolution, and Systematics* 46:1–23.
- Geange, S. W., D. E. Poulos, A. C. Stier, and M. I. McCormick. 2017. The relative influence of abundance and priority effects on colonization success in a coral-reef fish. *Coral Reefs* 36:151–155.
- Gosling, P. 2005. Facilitation of *Urtica dioica* colonisation by *Lupinus arboreus* on a nutrient-poor mining spoil. *Plant Ecology* 178:141–148.
- Graham, S. E., J. M. O'Brien, T. K. Burrell, and A. R. McIntosh. 2015. Aquatic macrophytes alter productivity-richness relationships in eutrophic stream food webs. *Ecosphere* 6:89.
- Greenwood, M. J., J. S. Harding, D. K. Niyogi, and A. R. McIntosh. 2012. Improving the effectiveness of riparian management for aquatic invertebrates in a degraded agricultural landscape: Stream size and land-use legacies. *Journal of Applied Ecology* 49:213–222.
- Haase, P., D. Hering, S. C. Jähnig, A. W. Lorenz, and A. Sundermann. 2013. The impact of hydromorphological restoration on river ecological status: A comparison of fish, benthic invertebrates, and macrophytes. *Hydrobiologia* 704:475–488.
- Haase, P., and F. Pilotto. 2019. A method for the reintroduction of entire benthic invertebrate communities in formerly degraded streams. *Limnologia* 77:125689.

- Hall Jr, R. O., M. F. Dybdahl, and M. C. VanderLoop. 2006. Extremely high secondary production of introduced snails in rivers. *Ecological Applications* 16:1121–1131.
- Halpern, C. B., J. A. Antos, D. McKenzie, A. M. Olson, and L. Souza. 2016. Past tree influence and prescribed fire mediate biotic interactions and community reassembly in a grassland-restoration experiment. *Journal of Applied Ecology* 53:264–273.
- Hart, D. D. 1981. Foraging and resource patchiness: Field experiments with a grazing stream insect. *Oikos* 37:46–52.
- Hart, D. D. 1992. Community organization in streams: The importance of species interactions, physical factors, and chance. *Oecologia* 91:220–228.
- Hill, R. L., J. Ireson, A. W. Sheppard, A. H. Gourlay, H. Norambuena, G. P. Markin, R. Kwong, and E. M. Coombs. 2008. A global view of the future for biological control of gorse, *Ulex europaeus* L. Pages 680–686 in B. G. Rector, R. Sforza, M. C. Bon, H. C. Evans, M. H. Julien, H. L. Hinz, and P. E. Hatcher (editors). *Proceedings of the XII international symposium on biological control of weeds*. CAB International, Wallingford, United Kingdom.
- Hintz, W. D., and T. Wellnitz. 2013. Current velocity influences the facilitation and removal of algae by stream grazers. *Aquatic Ecology* 47:235–244.
- Hoffman, A. L., J. D. Olden, J. B. Monroe, N. LeRoy Poff, T. Wellnitz, and J. A. Wiens. 2006. Current velocity and habitat patchiness shape stream herbivore movement. *Oikos* 115:358–368.
- Holomuzki, J. R., and B. J. F. Biggs. 2006. Food limitation affects algalivory and grazer performance for New Zealand stream macroinvertebrates. *Hydrobiologia* 561:83–94.
- Hornblow, K. J. 2021. How many snails are too many? Sustained densities of tolerant taxa in post-restoration waterways may be a barrier to ecological recovery. MS Thesis, University of Canterbury, Christchurch, New Zealand.
- Johansson, A. 1991. Caddis larvae cases (Trichoptera, Limnephilidae) as anti-predatory devices against Brown Trout and sculpin. *Hydrobiologia* 211:185–194.
- Jourdan, J., M. Plath, J. D. Tonkin, M. Ceylan, A. C. Dumeier, G. Gellert, W. Graf, C. P. Hawkins, E. Kiel, A. W. Lorenz, C. D. Matthaei, P. F. M. Verdonschot, R. C. M. Verdonschot, and P. Haase. 2019. Reintroduction of freshwater macroinvertebrates: Challenges and opportunities. *Biological Reviews* 94:368–387.
- Kerans, B. L., C. A. Cada, and J. Zickovich. 2010. Asymmetrical behavioral interactions between the New Zealand mud snail, *Potamopyrgus antipodarum*, and scraping, collector-gathering and collector-filtering macroinvertebrates. *Journal of Freshwater Ecology* 25:657–666.
- Lake, P. S., N. Bond, and P. Reich. 2007. Linking ecological theory with stream restoration. *Freshwater Biology* 52:597–615.
- Lam, W., Q. Paynter, and Z.-Q. Zhang. 2021. Functional response of *Amblyseius herbicolus* (Acari: Phytoseiidae) on *Sericothrips staphylinus* (Thysanoptera: Thripidae), an ineffective biocontrol agent of gorse. *Biological Control* 152:104468.
- Lamberti, G. A., and A. D. Steinman. 1993. Research in artificial streams: Applications, uses, and abuses. *Journal of the North American Benthological Society* 12:313–384.
- Lawrence, M. A. 2016. *_ez*: Easy analysis and visualization of factorial experiments. (Available from: <https://CRAN.R-project.org/package=eZ>)
- Ledger, M. E., R. M. L. Harris, A. M. Milner, and P. D. Armitage. 2006. Disturbance, biological legacies and community development in stream ecosystems. *Oecologia* 148:682–691.
- Leibold, M. A., M. Holyoak, N. Mouquet, P. Amarasekare, J. Chase, M. Hoopes, R. Holt, J. Shurin, R. Law, and D. Tilman. 2004. The metacommunity concept: A framework for multi-scale community ecology. *Ecology Letters* 7:601–613.
- Lenth, R.V., B. Bolker, B. Buerkner, I. Giné-Vázquez, M. Herve, M. Jung, J. Love, F. Miguez, H. Riebl, H. Singmann. 2023. *emmeans*: Estimated marginal means, aka least-squares means. (Available from: <https://cran.r-project.org/web/packages/emmeans/index.html>)
- Lepori, F., D. Palm, E. Brännäs, and B. Malmqvist. 2005. Does restoration of structural heterogeneity in streams enhance fish and macroinvertebrate diversity? *Ecological Applications* 15:2060–2071.
- Little, C. J., and F. Altermatt. 2018. Do priority effects outweigh environmental filtering in a guild of dominant freshwater macroinvertebrates? *Proceedings of the Royal Society B: Biological Sciences* 285:20180205.
- Lorenz, A. W., P. Haase, K. Januschke, A. Sundermann, and D. Hering. 2018. Revisiting restored river reaches—Assessing change of aquatic and riparian communities after five years. *Science of the Total Environment* 613–614:1185–1195.
- Louette, G., and L. De Meester. 2007. Predation and priority effects in experimental zooplankton communities. *Oikos* 116:419–426.
- Louhi, P., H. Mykrä, R. Paavola, A. Huusko, T. Vehanen, A. Mäkipetäys, and T. Muotka. 2011. Twenty years of stream restoration in Finland: Little response by benthic macroinvertebrate communities. *Ecological Applications* 21:1950–1961.
- Loureiro, C., M. A. Pedrosa, F. Gonçalves, and B. B. Castro. 2013. Competitive outcome of *Daphnia-simocephalus* experimental microcosms: Salinity versus priority effects. *PLoS ONE* 8:e70572.
- Mackay, R. J., and G. B. Wiggins. 1979. Ecological diversity in Trichoptera. *Annual Review of Entomology* 24:185–208.
- McAuliffe, J. R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. *Ecology* 65:894–908.
- McIntosh, A. R., and C. R. Townsend. 1995. Impacts of an introduced predatory fish on mayfly grazing in New Zealand streams. *Limnology and Oceanography* 40:1508–1512.
- Meira-Neto, J. A. A., M. C. N. A. da Silva, G. S. Tolentino, M. Gastauer, T. Buttschardt, F. Ulm, and C. Máguas. 2017. Early *Acacia* invasion in a sandy ecosystem enables shading mediated by soil, leaf nitrogen and facilitation. *Biological Invasions* 20:1567–1575.
- Minshall, G. W., and J. N. Minshall. 1977. Microdistribution of benthic invertebrates in a rocky mountain (U.S.A.) stream. *Hydrobiologia* 55:231–249.
- Nyström, P., A. R. McIntosh, and M. J. Winterbourn. 2003. Top-down and bottom-up processes in grassland and forested streams. *Oecologia* 136:596–608.
- Palmer, M. A., H. L. Menninger, and E. Bernhardt. 2010. River restoration, habitat heterogeneity and biodiversity: A failure of theory or practice. *Freshwater Biology* 55:205–222.
- Patrick, C. J., K. E. Anderson, B. L. Brown, C. P. Hawkins, A. Metcalfe, P. Saffarinia, T. Siqueira, C. M. Swan, J. D. Tonkin, and L. L. Yuan. 2021. The application of metacommunity theory to the management of riverine ecosystems. *Wiley Interdisciplinary Reviews: Water* 8:e1557.

- Ploughe, L. W., C. N. Carlyle, and L. H. Fraser. 2020. Priority effects: How the order of arrival of an invasive grass, *Bromus tectorum*, alters productivity and plant community structure when grown with native grass species. *Ecology and Evolution* 10:13,173–13,181.
- Riley, L. A., and M. F. Dybdahl. 2015. The roles of resource availability and competition in mediating growth rates of invasive and native freshwater snails. *Freshwater Biology* 60:1308–1315.
- Schreiber, E. S. G., P. S. Lake, and G. P. Quinn. 2002. Facilitation of native stream fauna by an invading species? Experimental investigations of the interaction of the snail, *Potamopyrgus antipodarum* (Hydrobiidae) with native benthic fauna. *Biological Invasions* 4:317–325.
- Silknetter, S., R. P. Creed, B. L. Brown, E. A. Frimpong, J. Skelton, and B. K. Peoples. 2020. Positive biotic interactions in freshwaters: A review and research directive. *Freshwater Biology* 65:811–832.
- Spivak, A. C., M. J. Vanni, and E. M. Mette. 2011. Moving on up: Can results from simple aquatic mesocosm experiments be applied across broad spatial scales? *Freshwater Biology* 56:279–291.
- Taylor, B. W., A. R. McIntosh, and B. L. Peckarsky. 2001. Sampling stream invertebrates using electroshocking techniques: Implications for basic and applied research. *Canadian Journal of Fisheries and Aquatic Sciences* 58:437–445.
- Thompson, R. M., and C. R. Townsend. 2006. A truce with neutral theory: Local deterministic factors, species traits and dispersal limitation together determine patterns of diversity in stream invertebrates. *Journal of Animal Ecology* 75:476–484.
- Tonkin, J. D., F. Altermatt, D. S. Finn, J. Heino, J. D. Olden, S. U. Pauls, and D. A. Lytle. 2018a. The role of dispersal in river network metacommunities: Patterns, processes, and pathways. *Freshwater Biology* 63:141–163.
- Tonkin, J. D., J. Heino, and F. Altermatt. 2018b. Metacommunities in river networks: The importance of network structure and connectivity on patterns and processes. *Freshwater Biology* 63: 1–5.
- Tonkin, J. D., S. Stoll, A. Sundermann, and P. Haase. 2014. Dispersal distance and the pool of taxa, but not barriers, determine the colonisation of restored river reaches by benthic invertebrates. *Freshwater Biology* 59:1843–1855.
- Towers, D. J., I. M. Henderson, and C. J. Veltman. 1994. Predicting dry weight of New Zealand aquatic macroinvertebrates from linear dimensions. *New Zealand Journal of Marine and Freshwater Research* 28:159–166.
- Townsend, C. R. 1989. The patch dynamics concept of stream community ecology. *Journal of the North American Benthological Society* 8:36–50.
- Vinson, M. R., and M. A. Baker. 2008. Poor growth of Rainbow Trout fed New Zealand mud snails *Potamopyrgus antipodarum*. *North American Journal of Fisheries Management* 28: 701–709.
- Waters, J. M., C. I. Fraser, and G. M. Hewitt. 2013. Founder takes all: density-dependent processes structure biodiversity. *Trends in Ecology & Evolution* 28:78–85.
- Weidlich, E. W. A., C. R. Nelson, J. L. Maron, R. M. Callaway, B. M. Delory, and V. M. Temperton. 2021. Priority effects and ecological restoration. *Restoration Ecology* 29:e13317.
- White, B. E., A. R. McIntosh, C. M. Febria, and H. J. Warburton. 2021. The potential role of biotic interactions in stream restoration. *Restoration Ecology* 29:e13396.
- Wickham, H. 2009. *ggplot2: elegant graphics for data analysis*. Springer, Berlin, Germany.
- Wohl, E., S. N. Lane, and A. C. Wilcox. 2015. The science and practice of river restoration. *Water Resources Research* 51: 5974–5997.
- Wootton, J. T., M. S. Parker, and M. E. Power. 1996. Effects of disturbance on river food webs. *Science* 273:1558–1560.
- Yannelli, F. A., C. MacLaren, and J. Kollmann. 2020. Moving away from limiting similarity during restoration: Timing of arrival and native biomass are better proxies of invasion suppression in grassland communities. *Frontiers in Ecology and Evolution* 8:238.