Community Ecology (2023) 24:257–269
https://doi.org/10.1007/s42974-023-00149-3

ORIGINAL ARTICLE

Community type and disturbance type interact to determine disturbance response: implications for extending the environmental filter metaphor

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Received: 29 January 2023 / Accepted: 2 June 2023 / Published online: 25 June 2023

Abstract

Ecological disturbances act as environmental filters by removing species with particular characteristics, resulting in community types associated with different disturbance histories. However, studies to date on community responses to disturbance have neglected the potential for different community assemblages to display different responses. Using lotic invertebrate communities as a study system, this study investigated the influence of community composition on disturbance response. We undertook a 26-h stream channel experiment to test how distinct invertebrate community types (an undisturbed spring community, flood-disturbed community, and agriculture-disturbed community), shaped by specific disturbance histories and characterised by different species with particular functional groups, responded to additional disturbance of varying types and combinations (an undisturbed control, high-flow, nutrients, sediment, and a combined sediment and nutrients treatment). Invertebrate drift was used as a diagnostic tool to assess community responses. Significant three-way interactions were identified for total invertebrate drift, drift of typically sensitive taxa (Ephemeroptera, Plecoptera and Trichoptera) and drift of cased organisms between community type, disturbance type and time, indicating that disturbance history and corresponding community type influenced community response to disturbance. Differing responses to disturbance between community types were often characterised by specific taxa, likely driven by adaptive traits, but also by phenotypic plasticity and altered biotic interactions. Community responses to the multiple disturbance scenario suggested potential for interactive effects, with differing responses potentially driven by species co-tolerance mechanisms. When determining the impacts of disturbance, our results suggest there is insight to be gained from a broader perspective incorporating multiple community types into future research. This approach could also improve management outcomes, facilitating tailored restoration and conservation strategies.

Keywords Community assembly · Community composition · Disturbance history · Environmental filtering · Mesocosm

Introduction

The abiotic environment has long been acknowledged as a key driver of community composition (Southwood, 1977), and the process of selecting for species with characteristics that facilitate survival is often referred to as environmental filtering (Keddy, 1991; Kraft et al., 2014). Ecological disturbances act as environmental filters by removing species lacking the physical characteristics or behavioural traits required for survival (Poff, 1997; Southwood, 1977). From this disturbance-influenced species pool, communities may then be subject to other assembly processes, including biotic interactions (Chase, 2007). Under these pressures, different disturbance regimes lead to different community types, characterised by species with specific trait combinations (Poff, 1997). It is likely that community composition and associated combinations of species traits affect responses to disturbance, for example differing responses to disturbance of plant communities at different stages of succession (Sousa, 1980). Basic community responses to disturbance are well documented (Dornelas, 2010), for example, reduced diversity with increased disturbance intensity (Death &

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Winterbourn, 1995). There is also extensive information available regarding specific effects of different disturbance types, and potential for interactive effects in multi-stressor scenarios (Brooks, 2019; Orr et al., 2020). However, the priming effect of the antecedent community composition on responses to disturbance, and how this will vary between different communities, is often neglected. When determining community response to disturbance, and forecasting potential future impacts, a mechanistic approach considering the influence of disturbance history on the starting community will be essential. This will be especially important for anticipating the influence of changing disturbance regimes associated with global change.

Disturbance includes both anthropogenic and natural phenomena, which vary in both type and magnitude (Newman, 2019), and play a key role in shaping communities (Connell, 1978; Ricklefs, 2004). The influences of disturbance on a community may include loss of species, proliferation of other species, and alteration of biotic interactions, all leading to community change (Kneitel & Perrault, 2006). However, specific disturbances drive change via different mechanisms, influencing species according to their intrinsic tolerances to abiotic conditions (Craine et al., 2012; Lee et al., 2009; Sheth & Angert, 2014). Within any particular assemblage, species will likely be best adapted to antecedent conditions; the disturbance they have historically been exposed to (Eveleens et al., 2019). Thus, since disturbance history effectively defines the local species pool, antecedent conditions will influence the susceptibility of a community to subsequent disturbances.

Adaptation to one disturbance type does not necessarily confer resistance to another disturbance type, though it is likely that communities subjected to disturbance that echoes their disturbance history will experience less change (Eveleens et al., 2019; Fukami, 2001), likely due to presence of species with traits which facilitate survival. A similar disturbance or a mild disturbance would impose a similar or weaker filter, which the community has already demonstrated an ability to endure, thus leading to minimal community change. On the other hand, different subsequent disturbance to previous, antecedent disturbances would likely be more novel and act as a more intense filter (Fig. 1), inciting more community change due to lack of adaptation. Therefore, the impacts of a disturbance should be relative to disturbance history, which will determine the combination of species present. Antecedent disturbances also likely play a role in community responses to multiple-stressor scenarios, which are notoriously unpredictable (Crain et al., 2008; Holmstrup et al., 2010; Jackson et al., 2015). In these cases, disturbance history and associated adaptations of taxa in the community should be considered in relation to multiple simultaneous subsequent disturbances, with the additional complication of potential interactive effects of these multiple disturbances (Breitburg et al., 1998). Recognition of

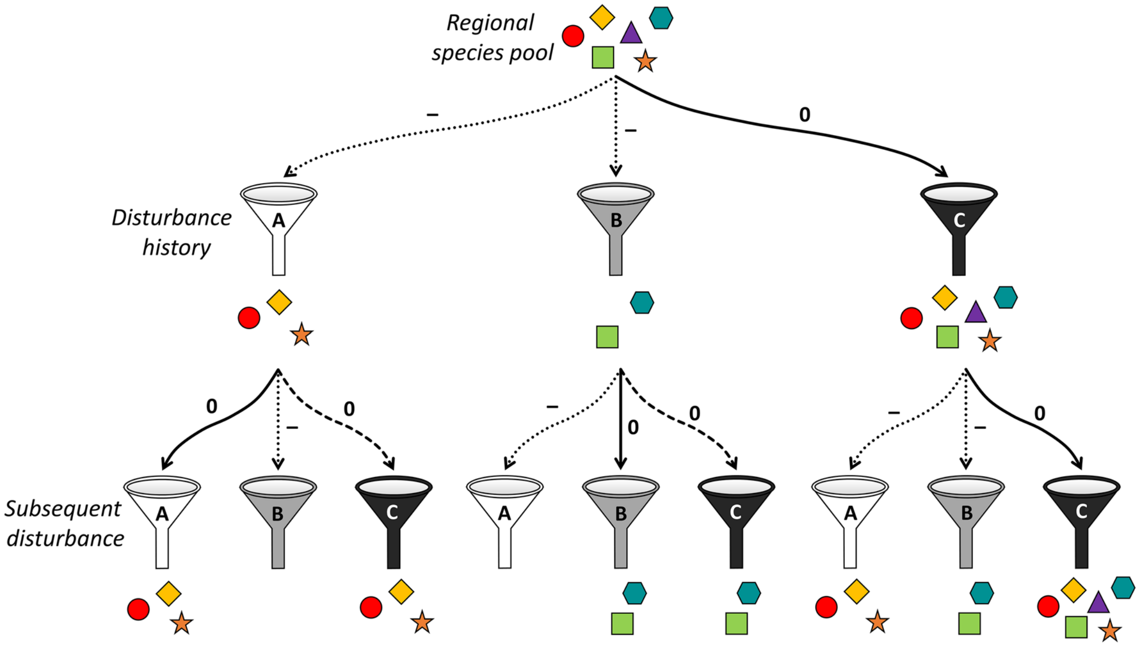

Fig. 1 The potential role of disturbance history in shaping the species (shapes) that make up communities (upper arrows) and thus influencing response to subsequent disturbance (lower arrows). Solid or dashed lines indicate the subsequent disturbance is a similar or weaker environmental filter than the historical disturbance, therefore having minimal impact on the community (0). Dotted lines indicate the subsequent disturbance is a functionally different filter to historical disturbance; thus, the community is more severely affected characterised by species loss (-)

antecedent conditions and their effects on community composition will likely be essential to appreciate the influences of subsequent disturbance, especially in multiple-stressor scenarios.

Here, we focus on lotic ecosystems in New Zealand, where rivers are subject to a range of disturbance types, across which invertebrate communities can be found. We undertook a stream channel experiment to test how distinct invertebrate community types, shaped by different disturbance histories and characterised by different taxa, responded to additional disturbance of varying types and combinations. This short-term assay was used to invoke predominantly behavioural responses, which may lead to longer-term community change. We hypothesised that community response to disturbance depends on the disturbance type and on community type as defined by disturbance history, predicting that more similar disturbance to historical disturbance will invoke less species loss via downstream drift, and therefore indicate less community change. Invertebrate drift occurs naturally in all lotic systems (Brittain & Eikeland, 1988), and altered drift patterns are a common response of invertebrates to unfavourable conditions, driven by behavioural modifications or physical responses to changing flow conditions (Brittain & Eikeland, 1988; Naman et al., 2015). Therefore, drift patterns over a short time can give insight into responses, which could considerably impact community composition over much longer periods. We also expected the impacts of a combined disturbance scenario to be more severe than disturbances applied alone, especially when communities lack previous exposure to these disturbances, with greater potential for additive or multiplicative interactive effects when species lack adaptation.

Materials and methods

We used a stream channel experiment to test the effects of community type and disturbance type on invertebrate communities, with invertebrate drift measurements used as a diagnostic tool to assess community impacts. Three community types (undisturbed spring, flood-disturbed and agriculture-disturbed) were each established in a recirculating colonist header tank. Each tank fed five stream channels, randomly assigned to disturbance treatments: an undisturbed control, high-flow, nutrients, sediment, and a combined sediment and nutrients treatment. The experiment ran for 26 h, which was sufficient to assess invertebrate drift over time, and was repeated over multiple days for a total of seven replicate trials for each community and disturbance type combination. Channel disturbance types were re-randomised for each run, and any legacy effects were removed by fully cleaning the mesocosm system between runs. The undisturbed spring and agriculture-disturbed community trials were run between March and April 2018. Intense flooding in early 2018 meant collection of flood-disturbed communities was not possible, so the flood-disturbed community trials were run in January 2019.

Each channel was through-flowing, 3 m long and 0.1 m wide (Appendix 1). To improve similarity to the natural environment, the channel interiors were painted with non-toxic pond paint mixed with sediment (<3 mm), providing a rough surface for crawling invertebrates. Ten cobbles and five unglazed terracotta tiles were positioned evenly along the channel to provide habitat, refugia and flow variation. Cobbles were sourced from a local stream with an established biofilm, an important food source for many invertebrates (Guo et al., 2016; Winterbourn, 1990). Water pumped from Grasmere Stream, flowing through the University of Canterbury Cass Field Station bordering Arthur's Pass National Park, New Zealand (43°02′07.4"S 171°45′28.2"E), provided a consistent source of cool, oxygenated water and fine particulate organic matter (Nyström & McIntosh, 2003). A velocity of $0.01 \pm$ SE 0.0003 m s^{-1} was established in the channels, with water flow-through maintaining temperature ($8.7 \pm$ SE 0.1 °C), dissolved oxygen ($10.9 \pm$ SE 0.3 mg L^{-1}) and organic matter inputs.

Three community types shaped by three common stream disturbances of the Canterbury region were chosen: an undisturbed spring community, a flood-disturbed community, and an agriculture-disturbed community, and these had notably different compositions (Appendix 2). Invertebrates were collected from local streams (Appendix 3) with macroinvertebrate faunas typical of the three chosen community types. A variety of methods were used to target different fauna for collection. Mobile invertebrates were collected using 'electrobugging' (Taylor et al., 2001); we used a NIWA EFM300 electric fishing machine with a small, 19-cm electrode to produce a focussed electric field, enabling us to catch large numbers of invertebrates with minimal physical damage to their bodies. More sessile invertebrates, mainly caddisflies, snails, and Diptera larvae, were collected using gentle agitation of the benthos and kick nets. Invertebrates were transferred to the field station in aerated buckets.

The three community types were characterised by different compositions of taxa. Biodiversity was highest in the spring communities and lower in the flood-disturbed and agricultural communities, which, despite having very different compositions, had similar species richness. The spring and flood-disturbed communities were dominated by Ephemeroptera (E, mayflies), Plecoptera (P, stoneflies) and Trichoptera (T, caddisflies), which are typically sensitive to organic pollution and poor water quality (Resh & Jackson, 1993), with a mean of 92.0% EPT (Ephemeroptera, Plecoptera and Trichoptera collectively) by abundance in spring communities and 98.6% EPT in the flood-disturbed communities (Appendix 2). In comparison, the agricultural community contained 0.6% EPT by abundance and was instead dominated by highly pollution-tolerant taxa such as *Potamopyrgus antipodarum* snails, ostracods, platyhelminths and oligochaete worms. These taxa, particularly *P. antipodarum*, thrive where sediment and nutrient build-up lead to proliferation of algae (Alonso & Castro-Díez, 2008). They benefit from additional habitat provided by invasive macrophyte growth, and the slower flows that often occur in such agriculture-disturbed systems (Richards et al., 2001).

Prior to the experiment beginning, stream channels were switched on for 24 h to enable some organic matter to settle. Two hours prior to the experiment beginning, invertebrate communities were added to the colonist header tanks. Water pumped into these header tanks was recirculated around a baffle, before flowing down the five disturbance treatment channels (Appendix 1). Recirculation in the header tanks slowed drift of invertebrates into the channels, providing a colonist source for the duration of the experiment. Colonist tanks were then emptied and replenished prior to subsequent replicates.

At the start of the experiment, five disturbance treatments were applied: an undisturbed control, high-flow, nutrients, fine sediment, and a combined sediment and nutrients treatment. The high-flow treatment aimed to turn over substrate and flush out any settled organic matter. This involved increasing the flow with additional water also from Grasmere stream via a hose for 20 min at the start of the experiment and again after 8 and 22 h. For the sediment treatment, fine sediment collected from the Waimakariri riverbed was sieved to remove particles above 650 µm and distributed throughout the channel to form a 2-cm layer covering all in-stream substrate. A dissolved nutrient solution (nitrate and phosphate as $NaNO_3$ and KH_2PO_4) and gravity-fed irrigation system were used to drip nutrients into the top of nutrient treatment channels, achieving a concentration of $5.0 \pm$ SE 0.3 mg L^{-1} nitrate and $0.4 \pm$ SE 0.02 mg L^{-1} phosphate in the nutrient-enriched channels, consistent with agricultural streams in the Canterbury region of New Zealand (Collins et al., 2012). By comparison, non-nutrient channels reached levels of $0.6 \pm$ SE 0.02 mg L^{-1} nitrate and undetectable phosphate. The singular and combined sediment and nutrient treatments were included to help detangle the potential effects of these disturbances on invertebrate communities, acknowledging that elevated levels of fine sediment and nutrients are often found in tandem, particularly in agricultural systems.

Community responses were assessed using counts of invertebrates leaving the channels over time. Alongside cumulative invertebrate drift, we also investigated more specific groups of invertebrates, to gain greater insight into drift patterns. We calculated cumulative EPT drift, since these aforementioned taxa are notably sensitive to poor water quality (for example low dissolved oxygen or presence of pollutants; (Resh & Jackson, 1993) and may be weaker competitors (Holomuzki et al., 2010). We also calculated cumulative drift count of cased organisms. Presence of a case or shell is an easily defined trait, which is typically associated with tolerance of slower flows and poor water quality (Graham et al., 2015) as well as resistance to increased predation pressure (Wootton et al., 1996). Invertebrate drift samples were collected from mesh bags attached to the end of each channel. Bags were emptied and replaced 2, 4, 6, 24 and 26 h into the experiment. These samples (preserved in 70% ethanol) were sorted and counted at 10–63 × magnification, and identified based on Winterbourn et al. (2006).

To test whether cumulative invertebrate drift over time was dependent on community type and disturbance type, we used a repeated-measures general linear model. Community type, disturbance type and time (the repeated measure) were fixed effects, experimental run number was a random effect, and experimental runs were replicates. The model was run in base R (R Core Team, 2018) using the *aov* function and the '+error' argument to account for the hierarchical nature of a repeated-measures design. We extracted 95% confidence intervals for significant three-way interactions using the *effects* package (Fox et al., 2020). To investigate which characteristics of the different community types may underlie general response patterns, the same model structure was used substituting cumulative invertebrate drift for cumulative drift of EPT, large organisms, cased organisms, mobile organisms, shredders and grazers.

Results

All three community types were visually observed to have successfully colonise the channels in the two hours prior to the experiment beginning. Following disturbance application, mixed effects modelling identified that community response to disturbance, measured as cumulative invertebrate drift, depended on an interaction between community type, disturbance type and time (three-way ANOVA $_{RM}$: $F_{40,345} = 2.01$, $p < 0.05$; Fig. 2A–C). This result is consistent with our hypothesis that different disturbances incite different levels of drift in a community depending on community type and associated taxa present as determined by antecedent conditions. Mixed effects modelling also identified significant impacts of community type and disturbance type over time on more specific taxa within communities: cumulative EPT drift (three-way ANOVA $_{RM}$: $F_{40,345} = 1.94$, $p = 0.05$; Fig. 2D–F) and cumulative drift of cased organisms (three-way ANOVA $_{RM}$: $F_{40,345} = 2.11$, $p < 0.05$; Fig. 2G–I). Below, we examine the patterns underpinning the three-way interactions identified between disturbance type, community type and time for cumulative invertebrate drift, EPT drift and cased drift, using differences between the models to identify

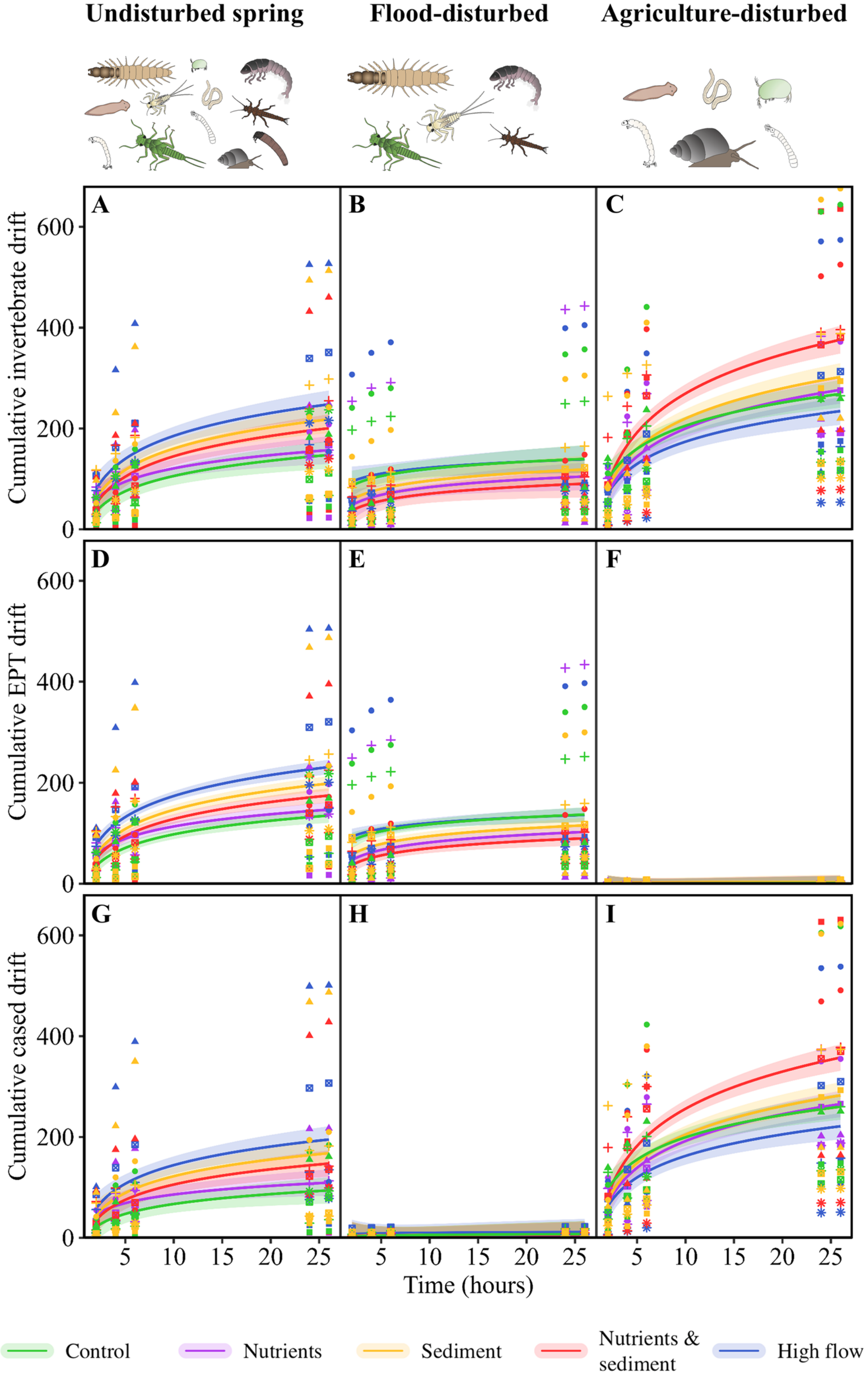

Fig. 2 Results of generalised linear mixed effects modelling (lines) showing the interaction between community type (columns) and disturbance type (colours) across three invertebrate drift metrics: cumulative drift of all invertebrates (top row), cumulative drift of individuals from orders Ephemeroptera, Trichoptera and Plecoptera (EPT; middle row), and cumulative drift of cased organisms (bottom row). Colours indicate disturbance treatments: an undisturbed control (green), nutrients (purple), sediment (yellow), sediment and nutrients (red) and high-flow (blue). Lines are model fits, and shaded areas indicate 95% confidence intervals. Points show raw data, with symbols indicating different experimental runs

likely drivers of invertebrate drift. We use invertebrate loss from the experimental communities to represent likely trajectories for community change.

Our prediction that disturbances that echo antecedent conditions will invoke less invertebrate drift, and therefore indicate less community change, was supported in the spring community. Here, the control treatment was associated with the lowest drift, and drift patterns were similar for cumulative total drift, EPT drift and drift of cased organisms (Fig. 2A, D, G), indicating that responses were driven primarily by the cased caddisflies which dominated the spring community. Nutrients increased initial total drift compared to the control; however, cumulative drift levelled off beyond 6 h, bringing cumulative drift closer to the control treatment. Between the control and nutrient treatment, 95% confidence intervals mostly overlap (Fig. 2A, D, G), indicating that nutrients were a reasonably benign disturbance to the spring community. The combination of sediment and nutrients raised drift from the control, with minimal overlap of confidence intervals, indicating a substantial effect. The sediment and the high-flow treatments were also influential disturbances for the undisturbed spring community, both increasing cumulative drift relative to the control treatment, indicated by no overlap of confidence intervals with the control beyond 6 h (Fig. 2A, D, G). These patterns indicate that the undisturbed control, which matches the historical conditions of the spring system from which this community was sourced, provided the least stress on invertebrates, inciting the least drift, while all other disturbances imposed a more intense driving force for invertebrate drift. Therefore, in this case, disturbance history predictably determined response to disturbances.

Drift responses to the high-flow disturbance treatment differed markedly between community types, indicating the importance of community type in determining response to disturbance. Compared to other disturbance treatments, the high-flow treatment instigated the highest drift in both the spring community and flood-disturbed community, but the lowest drift in the agriculture-disturbed community. For the flood-disturbed community, this appears contrary to our prediction that a community formed in a flood-disturbed system would be adapted to higher flows and thus drift less under high-flow relative to other disturbances. However, while the high-flow disturbance incited slightly elevated drift initially, beyond 6 h invertebrate drift in the control matched the high-flow disturbance almost exactly, with full overlap of 95% confidence intervals. This suggests that invertebrates in the flood-disturbed community responded similarly regardless of flow level. Therefore, adaptation to historical disturbance may be an explanatory mechanism, and the lower drift in the remaining treatments was the more surprising result.

Lower drift from the flood-disturbed community under the sediment, nutrients and the combination treatments was unexpected for a community dominated by EPT taxa. The similarity between total drift (Fig. 2B) and EPT drift (Fig. 2E) patterns for this source community, and the smaller 95% confidence intervals associated with EPT drift than total drift, indicate the observed response was driven by uncased EPT taxa. Unlike drift patterns for the other community types where initial drift (at 2 h) was similar for all disturbance treatments, under nutrients, sediment and the combination treatments, the flood-disturbed community had lower initial drift than the control or high-flow treatments, with minimal overlap of confidence intervals for total drift and no overlap for EPT drift between these two groups of treatments. This suggests that drift into the channels may have been reduced, or invertebrates left the channels by other means, for example by emergence which was observed but not measured. Therefore, the responses of the flood-disturbed community point to more complex behavioural or development-related responses of flood-disturbed community taxa to subsequent disturbance.

Responses of the agricultural community to disturbance were also contrary to our prediction that a community formed under agricultural disturbance, such as sediment build-up, nutrient pollution and slower flows, would be least affected by the sediment and nutrients typical of their source environment and would be least adapted to and therefore most impacted by the high-flow treatment. We observed the opposite. The high-flow treatment incited the lowest invertebrate drift, with minimal overlap of confidence intervals with the control or nutrients treatment beyond 6 h (Fig. 2C, I), and the combination of sediment and nutrients caused the highest drift with no overlap of confidence intervals beyond 4 h (Fig. 2C, I). Similar patterns were evident in cumulative invertebrate drift (Fig. 2C) and cumulative cased drift (Fig. 2I), indicating that community responses were driven predominantly by the snails which dominated these communities. As with the spring community, the nutrients and control treatments provoked similar responses with 95% confidence intervals mostly overlapping, suggesting that nutrients were also a relatively benign disturbance to the agriculture-disturbed community (Fig. 2C, I). Sediment incited slightly more drift than the control; however, 95% confidence intervals overlapped substantially with the control, suggesting sediment alone did not have a large influence on this community.

While the effects of the nutrients treatment and the sediment treatment on drift in the agriculture-disturbed community were minimal, the combination of both sediment and nutrients increased drift substantially in this community. Beyond initial drift samples at 2 h, there was no overlap of confidence intervals between the control and the sediment and nutrients combination treatment (Fig. 2C, I), indicating an interactive effect of sediment and nutrients which was not evident for other community types (Fig. 2). However, contrary to our prediction, the impacts of the combination treatment did not relate to the previous exposure of the agriculture-disturbed community. The flood-disturbed community also displayed the opposite of expectation, with the least drift under the sediment and nutrients combination treatment. For the spring community, invertebrate drift was raised in the sediment and sediment and nutrients combination treatment, but nutrients alone did not increase drift much beyond the control treatment. This suggests sediment was driving increased invertebrate drift in the spring community. Despite our predictions not matching experimental observations for the multi-stressor scenario, patterns in drift responses to the combination of sediment and nutrients did differ considerably between communities. Therefore, community type plays an unpredictable but important role in determining drift responses to multi-stressor scenarios.

Discussion

Across systems, disturbance history has been linked to differences in community composition (Graham et al., 2014; Gunderson, 1994; Zelikova & Breed, 2008), with communities often defined by specific, predictable species traits associated with survival ability (Poff, 1997). While most experimental research into the ecological impacts of disturbance focuses on a single starting community (Ledger et al., 2011; Lugthart & Wallace, 1992), it is likely that differing combinations of species (i.e., starting position) and therefore different adaptive characteristics and biotic interactions impact response to subsequent disturbances. The specific responses of each community were difficult to predict; however, the interactive effects of disturbance type and community type identified here suggest responses to disturbance depend on the composition of the starting community. Therefore, our results suggest that assessments of community change under disturbance should carefully acknowledge starting points. Here, we discuss potential mechanisms behind the interactive effects of disturbance type and community type on community responses, and outline how these ideas can be used to extend the environmental filter analogy, taking into account starting communities and multi-stressor scenarios. Finally, we propose how these ideas might be applied in a management and restoration context.

Communities that lack a specific disturbance history and have therefore assembled under a lenient environmental filter often retain high diversity in both taxa and traits (Hughes et al., 2007). The presence of taxa with different susceptibilities means that under any kind of pressure, there are likely to be some taxa that lack adaptation and are therefore lost. This was demonstrated in our experiment by greater drift in all disturbance treatments compared to the control for the spring community, even under the nutrient treatment whose effects were likely reduced in this experiment due to the short time frame, reflecting effects of toxicity rather than long-term nutrient-related stress and eutrophication. Conceptually, this suggests all disturbance types imposed a stronger environmental filter than this community's neutral disturbance history. Where communities have been subject to historical disturbance, like the flood- and agriculture-disturbed community types in our experiment, it is likely that organisms have adaptations to suit their disturbance history, leading to communities with a specific set of traits (Poff, 1997). For example, one might expect more mobile and fewer cased organisms in a flood-disturbed system (Death, 2008; Eveleens et al., 2019). In these cases, conditions similar to the disturbance history are likely to illicit a smaller response, as demonstrated by the equivalent responses of the flood-disturbed community to the control and high-flow treatments, indicating a negligible impact of flood-like conditions on taxa from historically flood-disturbed communities. Interestingly, reduced drift for the flood-disturbed community in the other disturbance treatments could demonstrate a phenotypically plastic response in which drifting in reaction to disturbance is unfavourable; a phenomenon also associated with predation cues in aquatic invertebrates (Douglas et al., 1994; Peckarsky et al., 1993). Such behavioural responses to disturbance may have been adapted to specific types or intensities of disturbance, resulting in outcomes which may appear maladaptive. For example, in our experiment, less drift in the flood-disturbed community may be a response to reduce exposure to unfavourable conditions, or may be an attempt to survive increased predation pressure which this community associates with similar stress based on antecedent events. Unexpected responses could also be underpinned by indirect mechanisms such as changes in abundance or activity of predators or competitors, or subsequent impacts on resource availability (Fleeger et al., 2003). Therefore, to understand community responses to disturbance we need to understand how disturbance history has shaped that community, how characteristics of that community might make it either vulnerable or tolerant to specific subsequent disturbances, and how behaviours associated with antecedent conditions might manifest in the face of novel disturbances.

Novel disturbance usually refers to more recent, anthropogenic impacts such as acid mine drainage or other pollution events (Newman, 2019). However, our results suggest novelty may be a matter of perspective. Severity of a disturbance is likely relative to the community type experiencing it; for example, acid mine drainage might be less novel for a community inhabiting a naturally acidic stream (Gray & Harding, 2011). Likewise, the flood-disturbed community in our experiment contained species likely adapted to higher flows, so the high-flow treatment was less novel and therefore elicited a less extreme drift response. Meanwhile, the spring community contained organisms accustomed to stable flows which likely lacked adaptation and therefore found high flows to be more extreme, eliciting higher drift. Poff and Ward (1990) posited that historical disturbance and habitat characteristics influence biotic recovery from subsequent disturbance. Our results suggest this may be driven by differing community types associated with disturbance history, whereby novelty and therefore severity of a disturbance are likely dependent on the composition of the community experiencing it, and the adaptations of taxa present as a result of their disturbance history (Lugo, 2020). The hypothesis that more novel disturbances will likely trigger more extreme community change must therefore be investigated within the context of disturbance history.

Adaptation of species to disturbance based on disturbance history is a likely mechanism driving community responses; however, the ability to survive does not necessarily correspond to preference for disturbed conditions. The *P. antipodarum* snails which dominated the agriculture-disturbed community in our study are extremely resistant to poor water quality, fine sediment and slow flows (Alonso & Castro-Díez, 2008); however, the combined sediment and nutrients treatment incited the highest drift, with snails observed lifting up and using surface tension to drift on the underside of the water surface. This avoidance behaviour suggests a preference for finding more favourable conditions before resorting to tolerance and incidentally may contribute to the rapid spread of *P. antipodarum* (Levri et al., 2019), actually assisting its proliferation under unfavourable, highly disturbed conditions. Thus, while adaptation may dictate survival ability, actual proliferation under disturbance may be driven by other factors, such as species' abiotic preferences (Richardson et al., 1994). It is also likely that biotic interactions play a key role in determining community response to disturbance. Loss of maladapted species under disturbance may have repercussions by alleviating competition or altering predation pressures, or by disrupting mutualistic, commensalistic or parasitic interactions (Vandvik et al., 2020). Consequently, loss of the same species from two different communities under the same disturbance may have differing knock-on effects based on its position within the community's network of biotic interactions. Therefore, just as abiotic conditions determine a species' fundamental niche and biotic interactions determine its realised niche (Soberón and Arroyo-Peña 2017), species characteristics (i.e., traits) likely determine survival ability under different disturbances, but altered biotic interactions may determine the actual, realised community response.

The synchronous influence of community type and disturbance type on community response to disturbance is likely to be complicated further by multiple disturbance scenarios; however, these are often a better reflection of reality (Breitburg et al., 1998; Ormerod et al., 2010). Extending the environmental filter analogy, when communities are subjected to multiple concurrent disturbances we might expect filters to overlap and become more intense; however, previous work has consistently demonstrated the irregularity of responses to multi-stressor scenarios (Crain et al., 2008; Holmstrup et al., 2010; Jackson et al., 2015). Our results echoed some of this contingency, but also identified clear differences in how different communities responded, for example potentially multiplicative effects of sediment and nutrients in the agriculture-disturbed community, but no clear interaction in the flood-disturbed or spring communities. It is likely that disturbance history and resulting community types play a key role in community response to multi-stressor scenarios, driven by multiple factors including species adaptations and altered biotic interactions. In particular, differences in response may be driven by species co-tolerance mechanisms, whereby correlations between species sensitivities to multiple disturbances determine whether interactive effects occur (Vinebrooke et al., 2004). Therefore, to fully appreciate the influence of subsequent disturbance, we may need to acknowledge the impacts of multiple historical disturbance types on community composition.

Community ecology is inherently complex; thus, simplified mechanisms to explain community responses, such as the environmental filter metaphor, are critical. However, simplifications, such as using data based on responses of a single community type to disturbance, may neglect important co-dependent mechanisms, resulting in misleading conclusions and ineffective application to management. For example, in disturbed stream ecosystems, habitat addition (e.g., woody debris) as a singular management tool may be limited by a pre-existing community assemblage that is poorly suited and therefore non-responsive to introduced management measures. When determining the impacts of disturbance, our results suggest there is considerable insight to be gained from a broader perspective incorporating multiple community types into future research. Such knowledge and improved predictive capacity may help to inform management and improve restoration outcomes, for example helping to identify communities that could be most severely impacted by future disturbance, especially under intensifying anthropogenic impacts, climate change and more frequent and severe natural phenomena (Vandvik et al., 2020). Beyond the short-term responses investigated here, there are also likely to be impacts of community type and disturbance type on community recovery following disturbance (Death, 1996; Johnstone et al., 2016; Wolff et al., 2019). Initial responses of communities to disturbance will also impact metacommunity dynamics through altered drift patterns, with potential cascading effects on a landscape scale, which may influence community recovery and responses to future disturbance. Therefore, identifying the characteristics of a community which affect its ability to withstand and recover from disturbance will have important management implications. The ability to reverse an environmental filter depends on more than just the start and endpoint community compositions. The antecedent community and expression of traits therein may instead be a better indicator of disturbances and mechanisms to overcome, rather than a predictor of the final community structure. A deeper understanding of such mechanisms is a far more powerful tool when applied to management and restoration.

Appendix 1: Experimental setup

See Fig. 3.

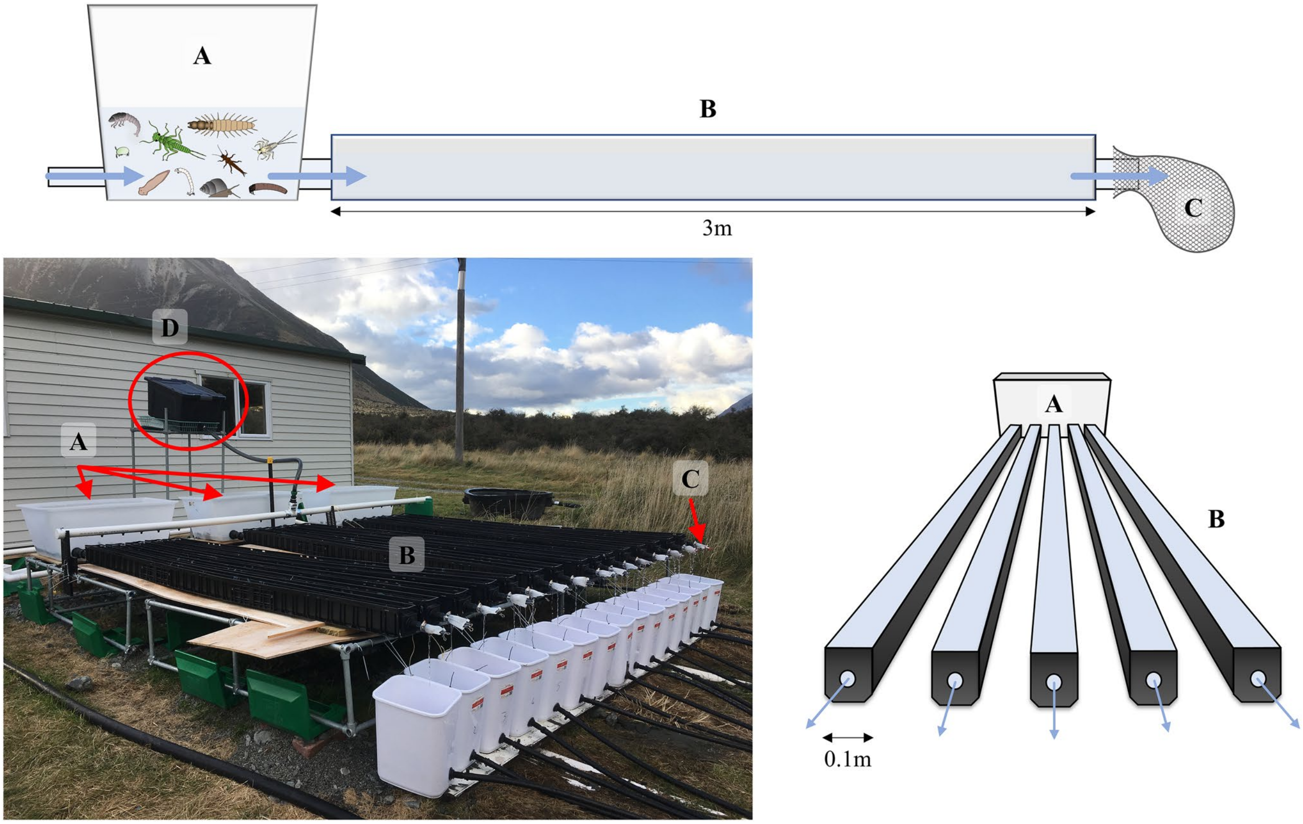

Fig. 3 Design of stream channel channels situated at the Cass field station in the Canterbury High Country, New Zealand showing colonist header tanks (A), 3 m disturbance treatment channels (B), drift collection nets (C) and nutrient dripping system for application of a nutrient disturbance treatment (D). Flow direction is indicated by blue arrows

Appendix 2: Community analysis

Here we detail methods used to describe the three invertebrate community types used in our experiment, and report on the differences.

Methods

Community types were described using summed abundances of invertebrate drift from each channel and invertebrates remaining in each channel at the end of the experiment. Non-metric multidimensional scaling ordination based on community abundance data was used to identify similarities between the communities. To test whether communities differed significantly between community types, permutational multivariate analysis of variance (PERMANOVA) was conducted on Bray–Curtis distances from ordinations of community data.

Basic community metrics were calculated from community data to further describe communities. Number of taxa (genus level) was used as a measure of richness, and an abundance weighted percentage of the sensitive taxa Ephemeroptera, Plecoptera and Trichoptera (EPT%) was calculated for each community. General linear modelling was used to visualise how each of these metrics (dependent variable) differed with community type (independent variable), with channels across all experimental runs used as replicates.

Results

NMDS ordination of communities from each channel showed community types were different (PERMANOVA: $F_{2,89} = 133.93$, $p < 0.001$; Fig. 4). Richness was also different between community types (ANOVA: $F_{2,87} = 30.83$, $p < 0.001$; Fig. 5A); however, a post hoc Tukey test showed there were only significant differences between the undisturbed spring and agriculture-disturbed pair ($p < 0.001$) and the undisturbed spring and flood-disturbed pair ($p < 0.001$) and, however, not between the flood-disturbed and agriculture disturbed communities ($p > 0.05$). EPT% differed between all pairs of community types (ANOVA: $F_{2,87} = 12{,}901$, $p < 0.001$; Tukey test: all pairs $p < 0.001$; Fig. 5B).

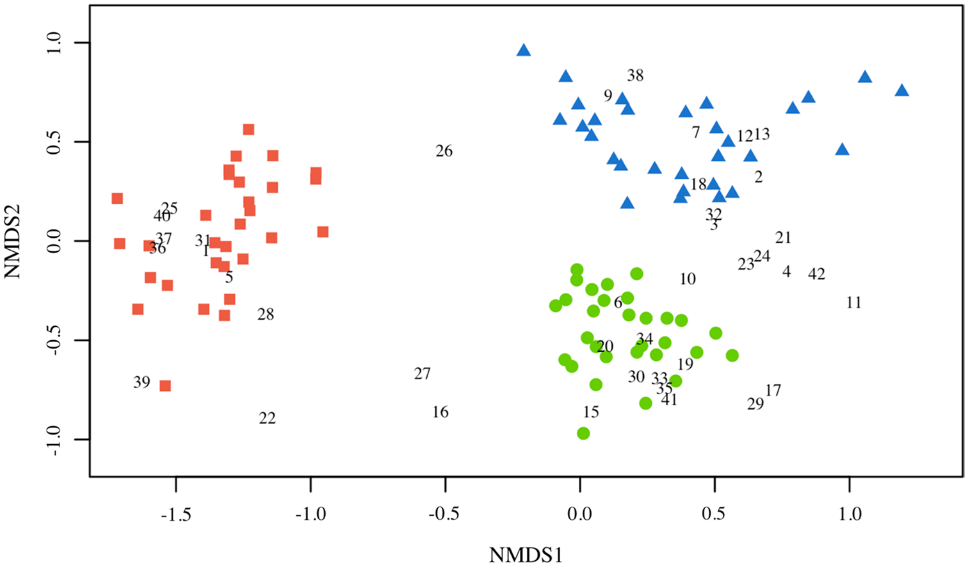

Fig. 4 Non-metric multidimensional scaling (NMDS) ordination of communities based on taxon abundances from stream channel channels (points) across three community types (undisturbed spring = green circles; flood-disturbed = blue triangles; agriculture-disturbed = red squares). Each point represents a macroinvertebrate community from a channel, determined by summing invertebrate drift from each channel and invertebrates remaining in each channel at the end of the experiment. Numbers represent the ordination of different taxa: Acari (1), *Aoteapsyche* (2), *Aphrophila* (3), *Archichauliodes* (4), *Austropeplea* (5), *Austrosimulium* (6), *Beraeoptera* (7), Ceratopogonidae (8), Chironomidae (9), *Coloburiscus* (10), *Confluens* (11), *Deleatidium* (12), Elmidae (13), Eriopterini (14), *Helicopsyche* (15), *Hudsonema* (16), *Hydrobiosella* (17), *Hydrobiosis* (18), *Megaleptoperla* (19), *Microvelia* (20), *Nesameletus* (21), Oligochaeta (22), *Olinga* (23), *Oniscigaster* (24), Ostracoda (25), *Oxyethira* (26), *Physa* (27), Platyhelminthes (28), *Plectrocnemia* (29), *Polyplectropus* (30), *Potamopyrgus* (31), *Psilochorema* (32), *Pycnocentria* (33), *Pycnocentrodes* (34), Scirtidae (35), *Sigara* (36), *Sphaerium* (37), *Stenoperla* (38), *Triplectides* (39), *Xanthocnemis* (40), *Zelandobius* (41), *Zelandoperla* (42)

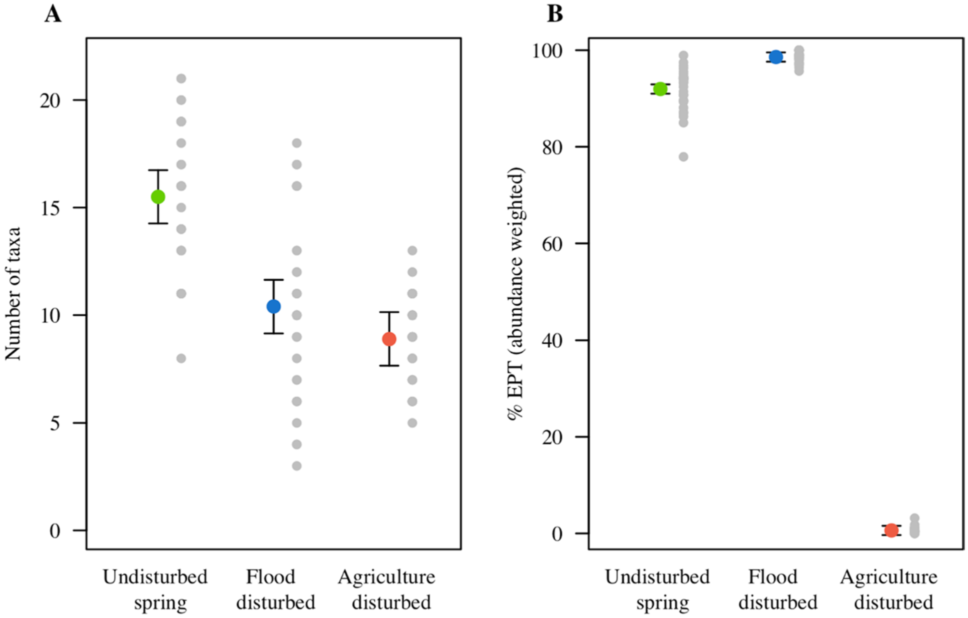

Fig. 5 Community metrics (**A**–**B**) for three community types added to experimental stream channel channels. Number of taxa (**A**) is a measure of species richness. Abundance weighted percentage of sensitive orders Ephemeroptera, Plecoptera and Trichoptera (EPT) indicates proportion of pollution-sensitive invertebrates (**B**). Coloured points indicate modelled metrics for each community type: undisturbed spring (green), flood-disturbed (blue) and agriculture-disturbed (red). Error bars indicate modelled 95% confidence intervals. Grey points indicate raw data for each stream channel

Appendix 3: Physicochemical data

See Tables 1 and 2

Table 1 Physicochemical measurements at invertebrate collection sites (Table 2) corresponding to three invertebrate community types

Community type	Temperature (°C)		Dissolved oxygen (mg L^{-1})		pH		Conductivity (μS_{25} cm^{-1})		Flow ($m\ s^{-1}$)	
	Mean	Range	Mean	Range	Mean	Range	Mean	Range	Mean	Range
Undisturbed spring	12.5	10.9–13.5	10.4	9.2–11.1	6.4	6.2–6.9	58	42–73	0.35	0.28–0.42
Flood-disturbed	11.6	10.5–13.4	10.9	9.8–11.5	7.4	6.9–8.1	55	38–68	0.48	0.36–0.61
Agriculture-disturbed	13.9	11.5–15.1	9.3	8.9–10.7	7.2	6.8–7.8	231	69–313	0.19	0.12–0.34

Table 2 Coordinates of sites used for invertebrate collection, corresponding to three community types

Community type	Undisturbed spring	Flood-disturbed	Agriculture-disturbed
Site coordinates	43°02′07.4"S 171°45′28.2"E 43°00′07.0"S 171°48′30.3"E	43°14′36.4"S 171°43′47.7"E 42°59′34.9"S 171°47′34.5"E	43°02′07.4"S 171°45′28.2"E 43°41′38.1"S 172°26′10.3"E

Acknowledgements We are grateful to Linda Morris for technical support, Ben McGinlay for assisting mesocosm design and construction, the University of Canterbury (UC) and Jenny Ladley for field station access, and UC's Freshwater Ecology Research Group for field help and feedback. In particular, we thank Katie Collins, Christopher Meijer, Alex Barclay, Tim Green, Lily Brailsford and Hayley Devlin for field assistance. Discussions with or comments from Jon Harding, Kristy Hogsden, Elizabeth Graham, Simon Howard, Jonathan Tonkin, Marc Schallenberg, William Clements and two anonymous reviewers greatly improved the manuscript.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. Our work, including support for ICB and HJW, was funded by New Zealand's Ministry of Business, Innovation and Employment (through New Zealand's Biological Heritage National Science Challenge, C09X1501, Project 3.4, 'Reigniting Healthy Resilience'). AM was also supported by a grant from the Mackenzie Charitable Foundation as part of the Canterbury Waterway Rehabilitation Experiment (CAREX).

Data availability The dataset supporting this article will be made available on the BioHeritage National Science Challenge repository once accepted for publication (https://data.bioheritage.nz/).

Declarations

Conflicts of interest All authors consent to submission of this manuscript for publication. It is not being considered for publication elsewhere, and the authors have no conflicts of interest to declare.

References

Alonso, A., & Castro-Díez, P. (2008). What explains the invading success of the aquatic mud snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca)? *Hydrobiologia, 614*, 107–116.

Breitburg, D. L., Baxter, J. W., Hatfield, C. A., Howarth, R. W., Jones, C. G., Lovett, G. M., & Wigand, C. (1998). Understanding effects of multiple stressors: Ideas and challenges. In M. L. Pace & P. M. Groffman (Eds.), *Successes, Limitations, and Frontiers in Ecosystem Science* (pp. 416–431). Springer.

Brittain, J. E., & Eikeland, T. J. (1988). Invertebrate drift: A review. *Hydrobiologia, 166*, 77–93.

Brooks, P. R. (2019). Combined effects of multiple stressors: New insights into the influence of timing and sequence. *Frontiers in Ecology and Evolution, 7*, 387.

Chase, J. M. (2007). Drought mediates the importance of stochastic community assembly. *Proceedings of the National Academy of Sciences, 104*, 17430–17434.

Collins, K. E., Doscher, C., Rennie, H. G., & Ross, J. G. (2012). The effectiveness of riparian 'restoration' on water quality: A case study of lowland streams in Canterbury, New Zealand. *Restoration Ecology, 21*, 40–48.

Connell, J. H. (1978). Diversity in tropical rain forests and coral reefs. *Science, 199*, 1302–1310.

Crain, C. M., Kroeker, K. J., & Halpern, B. S. (2008). Interactive and cumulative effects of multiple human stressors in marine systems. *Ecology Letters, 11*, 1304–1315.

Craine, J. M., Engelbrecht, B. M. J., Lusk, C. H., McDowell, N. G., & Poorter, H. (2012). Resource limitation, tolerance, and the future of ecological plant classification. *Frontiers in Plant Science, 3*, 1–10.

Death, R. G. (1996). The effect of patch disturbance on stream invertebrate community structure: The influence of disturbance history. *Oecologia, 108*, 567–576.

Death, R. G. (2008). The effect of floods on aquatic invertebrate communities. In J. Lancaster & R. A. Briers (Eds.), *Aquatic Insects: Challenges to Populations* (pp. 103–121). CAB International.

Death, R. G., & Winterbourn, M. (1995). Diversity patterns in stream benthic invertebrate communities: The influence of habitat stability. *Ecology, 76*, 1446–1460.

Dornelas, M. (2010). Disturbance and change in biodiversity. *Philosophical Transactions of the Royal Society of London Series b, Biological Sciences, 365*, 3719–3727.

Douglas, P. L., Forrester, G. E., & Cooper, S. D. (1994). Effects of trout on the diel periodicity of drifting in baetid mayflies. *Oecologia, 98*, 48–56.

Eveleens, R. A., McIntosh, A. R., & Warburton, H. J. (2019). Interactive community responses to disturbance in streams: Disturbance history moderates the influence of disturbance types. *Oikos, 128*, 1170–1181.

Fleeger, J. W., Carman, K. R., & Nisbet, R. M. (2003). Indirect effects of contaminants in aquatic ecosystems. *Science of the Total Environment, 317*, 207–233.

Fox, J., S. Weisberg, B. Price, M. Friendly, J. Hong, R. Andersen, D. Firth, S. Taylor, and R. C. Team. (2020) Effect displays for linear, generalized linear, and other models. https://cran.r-project.org/web/packages/effects/effects.pdf, R package version 4.2–0.

Fukami, T. (2001). Sequence effects of disturbance on community structure. *Oikos, 92*, 215–224.

Graham, N. A. J., Chong-Seng, K. M., Huchery, C., Januchowki-Hartley, F. A., & Nash, J. L. (2014). Coral reef community composition in the context of disturbance history on the Great Barrier Reef, Australia. *Plos ONE, 9*, e101204.

Graham, S. E., O'Brien, J. M., Burrell, T. K., & McIntosh, A. R. (2015). Aquatic macrophytes alter productivity-richness relationships in eutrophic stream food webs. *Ecosphere, 6*, art89.

Gray, D. P., & Harding, J. S. (2011). Acid mine drainage index (AMDI): A benthic invertebrate biotic index for assessing coal mining impacts in New Zealand streams. *New Zealand Journal of Marine and Freshwater Research, 46*, 335–352.

Gunderson, L. H. (1994). Vegetation of the Everglades: Determinants of community composition. In S. Davis & J. C. Ogden (Eds.), *Everglades: The ecosystem and its restoration* (pp. 323–340). CRC Press.

Guo, F., Kainz, M. J., Sheldon, F., & Bunn, S. E. (2016). The importance of high-quality algal food sources in stream food webs–current status and future perspectives. *Freshwater Biology, 61*, 815–831.

Holmstrup, M., Bindesbøl, A.-M., Oostingh, G. J., Duschl, A., Scheil, V., Köhler, H.-R., Loureiro, S., Soares, A. M. V. M., Ferreira, A. L. G., Kienle, C., Gerhardt, A., Laskowski, R., Kramarz, P. E., Bayley, M., Svendsen, C., & Spurgeon, D. J. (2010). Interactions between effects of environmental chemicals and natural stressors: A review. *Science of the Total Environment, 408*, 3746–3762.

Holomuzki, J. R., Feminella, J. W., & Power, M. E. (2010). Biotic interactions in freshwater benthic habitats. *Journal of the North American Benthological Society, 29*, 220–224.

Hughes, A. R., Byrnes, J. E., Kimbro, D. L., & Stachowicz, J. J. (2007). Reciprocal relationships and potential feedbacks between biodiversity and disturbance. *Ecology Letters, 10*, 849–864.

Jackson, M. C., Loewen, C. J. G., Vinebrooke, R. D., & Chimimba, C. T. (2015). Net effects of multiple stressors in freshwater ecosystems: A meta-analysis. *Global Change Biology, 22*, 180–189.

Johnstone, J. F., Allen, C. D., Franklin, J. F., Frelich, L. E., Harvey, B. J., Higuera, P. E., Mack, M. C., Meentemeyer, R. K., Metz, M. R., Perry, G. L. W., Schoennagel, T., & Turner, M. G. (2016). Changing disturbance regimes, ecological memory, and forest resilience. *Frontiers in Ecology and the Environment, 14*, 369–378.

Keddy, P. A. (1991). Working with heterogeneity: An operator's guide to environmental gradients. In J. Kolasa & S. T. A. Pickett (Eds.), *Ecological Heterogeneity* (pp. 181–201). Springer.

Kneitel, J. M., & Perrault, D. (2006). Disturbance-induced changes in community composition increase species invasion success. *Community Ecology, 7*, 245–252.

Kraft, N. J. B., Adler, P. B., Godoy, O., James, E. C., Fuller, S., & Levine, J. M. (2014). Community assembly, coexistence and the environmental filtering metaphor. *Community Phylogenetics and Ecosystem Functioning, 29*, 592–599.

Ledger, M. E., Edwards, F. K., Brown, L. E., Milner, A. M., & Woodward, G. (2011). Impact of simulated drought on ecosystem biomass production: An experimental test in stream mesocosms. *Global Change Biology, 17*, 2288–2297.

Lee, J. E., Janion, C., Marais, E., van Vuuren, B. J., & Chown, S. L. (2009). Physiological tolerances account for range limits and abundance structure in an invasive slug. *Proceedings of the Royal Society B, 276*, 1459–1468.

Levri, E. P., R. Luft, & X. Li. (2019). Predator detection and a possible dispersal behavior of the invasive New Zealand mud snail, Potamopyrgus antipodarum (Gray, 1843). *Aquatic Invasions, 14*, 417–432.

Lugo, A. E. (2020). Effects of extreme disturbance events: from ecesis to social-ecological-technological systems. *Ecosystems, 23*, 1726.

Lugthart, G. J., & Wallace, J. B. (1992). Effects of disturbance on benthic functional structure and production in mountain streams. *Journal of the North American Benthological Society, 11*, 138–164.

Naman, S. M., Rosenfeld, J. S., & Richardson, J. S. (2015). Causes and consequences of invertebrate drift in running waters: From individuals to populations and trophic fluxes. *Canadian Journal of Fisheries and Aquatic Sciences, 73*, 1292–1305.

Newman, E. A. (2019). Disturbance ecology in the Anthropocene. *Frontiers in Ecology and Evolution, 7*, 147.

Nyström, P., & McIntosh, A. R. (2003). Are impacts of an exotic predator on a stream food web influenced by disturbance history? *Oecologia, 136*, 279–288.

Ormerod, S. J., Dobson, M., Hildrew, A. G., & Townsend, C. (2010). Multiple stressors in freshwater systems. *Freshwater Biology, 55*, 1–4.

Orr, J. A., Vinebrooke, R. D., Jackson, M. C., Kroeker, K. J., Kordas, R. L., Mantyka-Pringle, C., Van den Brink, P. J., De Laender, F., Stoks, R., Holmstrup, M., Matthaei, C. D., Monk, W. A., Penk, M. R., Leuzinger, S., Schäfer, R. B., & Piggott, J. J. (2020). Towards a unified study of multiple stressors: Divisions and common goals across research disciplines. *Proceedings of the Royal Society B, 287*, 20200421.

Peckarsky, B. L., Cowan, C. A., Penton, M. A., & Anderson, C. (1993). Sublethal consequences of stream-dwelling predatory stoneflies on mayfly growth and fecundity. *Ecology, 74*, 1836–1846.

Poff, N. L. (1997). Landscape filters and species traits: Towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society, 16*, 391–409.

Poff, N. L., & Ward, J. V. (1990). Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. *Environmental Management, 14*, 629.

R Core Team. 2018. R: A language and environment for statistical computing., R Foundation for Statistical Computing, Vienna, Austria. http://cran.univ-paris1.fr/web/packages/dplR/vignettes/intro-dplR.pdf.

Resh, V. H., & Jackson, J. K. (1993). Rapid assessment approaches to biomonitoring using benthic macroinvertebrates. In D. M. Rosenberg & V. H. Resh (Eds.), *Freshwater Biomonitoring and Benthic Macroinvertebrates* (pp. 195–233). Chapman & Hall.

Richards, D. C., Cazier, L. D., & Lester, G. T. (2001). Spatial distribution of three snail species, including the invader *Potamopyrgus antipodarum*, in a freshwater spring. *Western North American Naturalist, 61*, 375–380.

Richardson, J., J. A. T. Boubée, & D. W. West. (1994). Thermal tolerance and preference of some native New Zealand freshwater fish. *New Zealand Journal of Marine and Freshwater Research, 28*, 399–407.

Ricklefs, R. E. (2004). A comprehensive framework for global patterns in biodiversity. *Ecology Letters, 7*, 1–15.

Sheth, S. N., & Angert, A. L. (2014). The evolution of environmental tolerance and range size: A comparison of geographically restoricted and widespread *Mimilus*. *Evolution, 68*, 2917–2931.

Soberón, J., & B. Arroyo-Peña. (2017). Are fundamental niches larger than the realized? Testing a 50-year-old prediction by Hutchinson. *PLoS ONE, 12* e0175138.

Sousa, W. P. (1980). The response of a community to disturbance: The importance of successional age and species' life histories. *Oecologia, 45*, 72–81.

Southwood, T. R. E. (1977). Habitat, the templet for ecological strategies? *Journal of Animal Ecology, 46*, 337–365.

Taylor, B. W., McIntosh, A. R., & Peckarsky, B. L. (2001). Sampling stream invertebrates using electroshocking techniques: Implications for basic and applied research. *Canadian Journal of Fisheries and Aquatic Sciences, 58*, 437–445.

Vandvik, V., Skarpaas, O., Klanderud, K., Telford, R. J., Halbritter, A. H., & Goldberg, D. E. (2020). Biotic rescaling reveals importance of species interactions for variation in biodiversity responses to climate change. *Proceedings of the National Academy of Sciences, 117*, 22858–22865.

Vinebrooke, R. D., Cottingham, K. I., Norberg, J., Scheffer, M., Dodson, S. I., Maberly, S. C., & Sommer, U. (2004). Impacts of multiple stressors on biodiversity and ecosystem functioning: The role of species co-tolerance. *Oikos, 104*, 451–457.

Winterbourn, M. (1990). Interactions among nutrients, algae and invertebrates in a New Zealand mountain stream. *Freshwater Biology, 23*, 463–474.

Winterbourn, M. J., Gregson, K. L. D., & Dolphin, C. H. (2006). *Guide to the aquatic insects of New Zealand*. Entomological Society of New Zealand.

Wolff, B. A., Duggan, S. B., & Clements, W. H. (2019). Resilience and regime shifts: Do novel communities impede ecological recovery in a historically metal-contaminated stream? *Journal of Applied Ecology, 56*, 2698–2709.

Wootton, J. T., Parker, M. S., & Power, M. E. (1996). Effects of disturbance on river food webs. *Science, 273*, 1558–1561.

Zelikova, T. J., & Breed, M. D. (2008). Effects of habitat disturbance on ant community composition and seed dispersal by ants in a tropical dry forest in Costa Rica. *Journal of Tropical Ecology, 24*, 309–316.