








ARTICLE

Freshwater Ecology

Integrative analysis of stressor gradients reveals multiple discrete trait-defined axes underlie community assembly

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Abstract

The generalizable functional attributes of organisms (traits) relate strongly to their environment across multiple levels of biological organization, making trait-based approaches a powerful mechanistic framework to understand species distributions and community composition in relation to environmental change. To investigate how a wide range of stressor types shape stream macroinvertebrate communities, we conducted an integrative analysis using community and taxon trait information across drying, flooding, eutrophication, fine sediment, and acid mine drainage (AMD) gradients. Each gradient spanned relatively unimpacted to severely impacted sites. To characterize community change in response to stressors, we incorporated abundance-based trait information from all stressor gradients in a single trait-based ordination (non-metric multidimensional scaling), defining the trait space within which each stressor gradient acted. We hypothesized that different stressors would apply different environmental filters, moving communities along distinct axes in trait space and resulting in communities with definable trait combinations. Particularly strong relationships were associated with anthropogenically derived stressors (fine sediment, eutrophication, and AMD) compared to natural stressors (drying and flooding). Anthropogenic stressors instigated significant movement of communities along multiple axes in trait space, likely driven by limited adaptation to these novel stressors. We demonstrate that trait-based analysis of communities across multiple stressor gradients can support a more comprehensive understanding of how community composition changes than taxonomic methods or investigation of a single stressor type, and could underpin community-focused management actions.

KEYWORDS

acid mine drainage, community assembly, community dynamics, disturbance, drying, environmental filter, eutrophication, flooding, traits

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INTRODUCTION

Understanding community responses to abiotic stress requires characterization of community composition across multiple environmental gradients (Keddy, 1991; McGill et al., 2006). Functional perspectives based on taxon traits facilitate those comparisons, offering additional insights into communities' abiotic responses beyond taxonomic methods (Brown et al., 2014; Kuzmanovic et al., 2017). The abiotic drivers of community composition act as environmental filters, which only allow taxa with particular traits to persist (Keddy, 1991; Kraft et al., 2014). This idea underpins a key concept in ecology: That important aspects of community composition are determined by the physicochemical environment, driven by intrinsic tolerances of taxa to abiotic conditions (Craine et al., 2012; Lee et al., 2009; Sheth & Angert, 2014). Similar ideas underlie the habitat templet hypothesis, which proposes that evolution acts based on abiotic habitat characteristics (Scarsbrook & Townsend, 1993; Southwood, 1977; Townsend et al., 2003). Thus, focusing on traits (such as body size and feeding method), which reflect organisms' resource use, habitat requirements, and stress tolerance, and that influence both organismal responses to the environment and their effects on ecosystem function, will provide additional insights into the effects of abiotic stressors (Díaz & Cabido, 2001; Lavorel & Garnier, 2002; McGill et al., 2006).

Trait-based analysis facilitates comparisons of communities, which may be spatially and thus taxonomically distant, but with comparable functional attributes, thereby enabling identification of general patterns in community composition (Mouillot et al., 2012; Usseglio-Polatera et al., 2000). This functional perspective can also suggest potential mechanisms behind community change along an abiotic stressor gradient (Cadotte, 2017; Sebastián-González et al., 2017). Mechanisms can involve constraints on function, whereby specific traits facilitate or hinder survival (Poff, 1997). Although some behavioral plasticity is possible (e.g., active drift in response to flow disturbance; Gjerløv et al., 2003), the ability to alter morphology or other functional traits in response to stress is limited in stream macroinvertebrates and indeed most organism types (Auld et al., 2010; van Kleunen & Fischer, 2005). Therefore, traits constitute evolutionary constraints, which are often defined by trade-offs between traits representing adaptations to different stressors (Agrawal et al., 2010; Townsend et al., 1997); for example, caddisfly cases offer protection against predation but increase susceptibility to flood mortality (Wootton et al., 1996). Hence, trait information will likely offer deeper insights into taxon–environment patterns, by

providing a functional perspective of community structure.

The responses of taxa, and thus niche-driven community composition, are likely to vary among stressor types. Mechanistically, stressor types acting as different environmental filters will result in communities of taxa with unique trait combinations (Kraft et al., 2014), such as fewer cased and more mobile macroinvertebrates in a flood-disturbed system (Wootton et al., 1996), or taxa with greater egg protection in pesticide-impacted streams (Kuzmanovic et al., 2017). Equally, some stressors may shape communities in similar ways, with some traits conferring either sensitivity to, or tolerance of, multiple different stressors. For example, generalist traits might increase survival under multiple stressor types (Büchi & Vuilleumier, 2015).

Characterization of stressors may help to predict the nature and magnitude of community change; for example, stressor duration or whether stressors are natural or anthropogenic. Some stressors are anthropogenically derived or typically only reach problematic levels under human influence (e.g., acid mine drainage [AMD], eutrophication, and fine sediment) and are therefore more novel; other stressors are natural and occur more ubiquitously (e.g., drying and flooding). Furthermore, some stressors, in particular, flooding and drying, are relatively short-term events that last days to months. By contrast, anthropogenic stressors (including AMD, eutrophication, and fine sediment) can persist indefinitely. Survival under shorter-term floods and drought is enabled by traits promoting resistance (i.e., the capacity to persist during a perturbation) and resilience (i.e., the capacity to recolonize after a perturbation ends; Bogan et al., 2017), whereas exposure to long-term stressors typically leads to depauperate communities dominated by taxa with traits promoting stress tolerance.

Advancing understanding of niche-driven community composition could inform management actions that address ongoing degradation associated with multiple abiotic stressors (Wilson, 1999). Trait-based methods may be used to identify the most important stressors in impacted habitats, helping to target management measures (Menezes et al., 2010). Furthermore, focusing on one type of degraded community may neglect important factors associated with other degraded community types; while anthropogenic stressors shaping communities in comparable ways may warrant similar management strategies, stressors leading to contrasting community responses, and thus different functional compositions, will likely require different actions to facilitate community recovery (Wohl et al., 2015). Therefore, concurrent examination of multiple, independent stressor gradients

and how they shape communities can underpin effective management decisions.

Here, we analyzed stream macroinvertebrate communities across stressor gradients, including relatively unimpacted sites and sites severely degraded by anthropogenic stress, to reveal the role of different stressors in community assembly. By incorporating multiple stressor types into a single analysis, we aimed to define a trait space within which each stressor gradient acted. Our first hypothesis was that different stressors would typically have functionally distinct effects and would therefore move communities along different axes of change. Our second hypothesis was that magnitude of community change would depend on stressor intensity, with communities becoming more functionally distinct across each stressor gradient. Finally, we hypothesized that community composition would also depend on stressor novelty: Organisms are less likely to be adapted to novel stressors, resulting in greater community change (Eveleens et al., 2019). Therefore, novel anthropogenically derived stressors (e.g., low pH and high metal concentrations associated with AMD) will likely have greater effects on community composition than stressors, which have existed naturally for longer.

METHODS

We analyzed data from published studies showing macroinvertebrate community responses to stressors. These studies were conducted in temperate streams on the South Island of New Zealand, covering five spatially independent systems with associated stressor gradients common in lotic environments: drying, flooding, eutrophication, fine sediment, and AMD (Appendix S1: Table S1). These studies originated from the same research group, and methodologies were consistent: Samples were collected using a Surber sampler and sieved with either 250- or 500- μ m mesh. Macroinvertebrates were identified to the lowest practical level, usually genus. Where the taxonomic resolution differed between datasets, data were standardized to the highest level. Counts of macroinvertebrates were averaged across 3–5 replicate samples (Appendix S1: Table S1) and standardized per square meter. Abundance data rather than presence–absence data were used to better represent trait occurrence within communities (Lengyel et al., 2021).

All stressor gradients covered abiotic conditions ranging from unimpacted to extremely impacted, defined by physicochemical measurements. Drying intensity was measured using wetted cross-sectional area, with smaller cross-sectional areas indicating higher drying intensity when comparing sites across a single stream (McHugh

et al., 2015). Flooding intensity (McHugh et al., 2010) was measured with the Pfankuch River Disturbance Index, a channel stability scoring system based on stream bed, bank, and valley characteristics (Pfankuch, 1975), that reliably reflects the effects of high flow events on stream bed habitats (Jellyman et al., 2013; Peckarsky et al., 2014). A eutrophication gradient was defined using a principal component analysis (PCA) axis associated with productivity-related variables including nitrate and phosphate concentrations, gross primary productivity, macrophyte cover, and shade (Graham et al., 2015). A gradient of fine sediment was defined by visually assessed reach scale (30 m) estimates of fine (<2 mm) inorganic particle cover (Burdon et al., 2013). Finally, an AMD gradient was defined by a PCA axis associated with pH, specific conductance, and concentrations of dissolved metals (Pomeranz, Warburton, et al., 2019; Pomeranz, Wesner, et al., 2020).

Traits for all macroinvertebrate taxa were derived from a National Institute of Water and Atmospheric research database (NIWA, 2018; https://niwa.co.nz/sites/niwa.co.nz/files/nz_trait_database_v19_2_18.xlsx). In this database, trait scores for each taxon are fuzzy-coded, with an affinity between 0 (no affinity) and 3 (high affinity) determined for each trait modality, enabling relation of taxa to more than one modality within a single trait (Chevenet et al., 1994). From the database, 37 modalities within 10 traits were selected, chosen to reflect morphology, life history, mobility, and resource acquisition (Table 1), excluding variables for which trait data were incomplete. Where traits described similar functional attributes (e.g., oviposition site and egg mass attachment), a single trait was selected for which trait data were more complete. Where trait data were at a higher taxonomic resolution than our data, a mean trait affinity was calculated from all lower delineations.

To investigate community change across multiple stressor gradients simultaneously, we used nonmetric multidimensional scaling (NMDS) ordination of traits using the package *vegan* in R (Oksanen et al., 2019). Since all trait data were quantitative, Euclidean distances were used to infer compositional differences between communities (Mouchet et al., 2008). To account for taxa with affinities for multiple modalities within a trait, the fuzzy-coded trait matrix was converted to proportions using the package *ade4* (Dray & Dufour, 2007). The trait-by-site matrix was obtained by multiplying a site-by-taxa abundance matrix and a fuzzy-coded taxa-by-traits matrix; therefore, the trait-by-site matrix gives an affinity-weighted trait abundance measure for each site. We used three NMDS axes because this produced a low-stress, interpretable solution (Appendix S2).

TABLE 1 Macroinvertebrate traits and trait modalities (NIWA, 2018).

| Trait | ID | Trait modality |
|--|----|--------------------------------------|
| Maximum potential body size (mm) | 1 | ≤5 |
| | 2 | >5–10 |
| | 3 | >10–20 |
| | 4 | >20–40 |
| | 5 | >40 |
| Maximum no. reproductive cycles per year | 6 | Semivoltine |
| | 7 | Univoltine |
| | 8 | Plurivoltine |
| Reproductive technique | 9 | Single individual |
| | 10 | Hermaphroditism |
| | 11 | Male and female |
| Egg/egg mass attachment | 12 | Free |
| | 13 | Cemented |
| | 14 | Female bears eggs in/on body |
| Dispersal (all stages) | 15 | Low (10 m) |
| | 16 | Medium (1 km) |
| | 17 | High (>1 km) |
| Attachment to substrate of aquatic stages (excluding eggs) | 18 | Swimmers |
| | 19 | Crawlers |
| | 20 | Burrowers |
| | 21 | Attached |
| Body flexibility | 22 | None (<10°) |
| | 23 | Low (>10–45°) |
| | 24 | High (>45°) |
| Body form | 25 | Streamlined |
| | 26 | Flattened (dorso-ventral or lateral) |
| | 27 | Cylindrical |
| | 28 | Spherical |
| Feeding habits | 29 | Shredders |
| | 30 | Scrapers |
| | 31 | Deposit-feeders |
| | 32 | Filter-feeders |
| | 33 | Predator |
| | 34 | Algal piercer |
| Dietary preferences | 35 | Strong (specialist) |
| | 36 | Moderate |
| | 37 | Weak (generalist) |

To analyze and visualize community shifts in trait space along stressor gradients, we extracted NMDS axis scores for each trait assemblage. For all stressors except

drying, we ran separate linear models for each NMDS axis as a response variable representing trait assemblages and used the stressor gradient as a continuous independent variable. The variability explained by stressor gradients was evaluated with R^2 values. For the drying gradient, to account for multiple sampling points along each of 14 streams, linear mixed-effects models were fitted using the package *nlme* (Pinheiro et al., 2022) with cross-sectional area as a continuous independent variable and stream as a random effect. For these models, marginal and conditional R^2 values were obtained using the package *MuMin* (Bartoń, 2020; Nakagawa & Schielzeth, 2013). For all gradients, ANOVA was run to determine significance of relationships. The integrative analysis required to address our hypotheses also required an integrative approach to visualization: To interpret relationships between stressor gradients and shifts in trait combinations represented by NMDS axes, the positioning of individual traits along axes was plotted in relation to significant community movement along NMDS axes as a result of each stressor gradient. These trait combinations and the positioning of individual traits are the equivalent of sites and species, respectively, in a typical community ordination. These trait–stressor patterns were then compared against the results of more traditional fourth corner analyses of each separate stressor gradient to support this novel, multigradient approach (Appendix S3). All statistical analyses were conducted in R (R Core Team, 2018).

RESULTS

Plots of axis pairs from the 3D NMDS solution showed that relatively unimpacted sites (i.e., at low end of stressor gradients) plotted toward the center of the ordination, indicating a greater range of traits. Stressed communities spread outward from the ordination center in different directions depending on the stressor type, indicating different trait compositions and supporting our hypothesis of stressor-driven community change along multiple axes (Figure 1).

Significant community shifts along axes in trait space were identified across all stressor gradients (Figure 2). In particular, AMD was associated with large community shifts in trait space along all three axes ($R^2 = 0.46–0.65$; $p < 0.001$), indicating extreme compositional change. Sediment was also linked to community change along all three axes ($R^2 = 0.26–0.58$; $p < 0.01$), but the relationships were weaker than for AMD, spanning smaller ranges within trait space, and indicating less extreme compositional change (Figure 2). In general, anthropogenic stressors (AMD, fine sediment, and

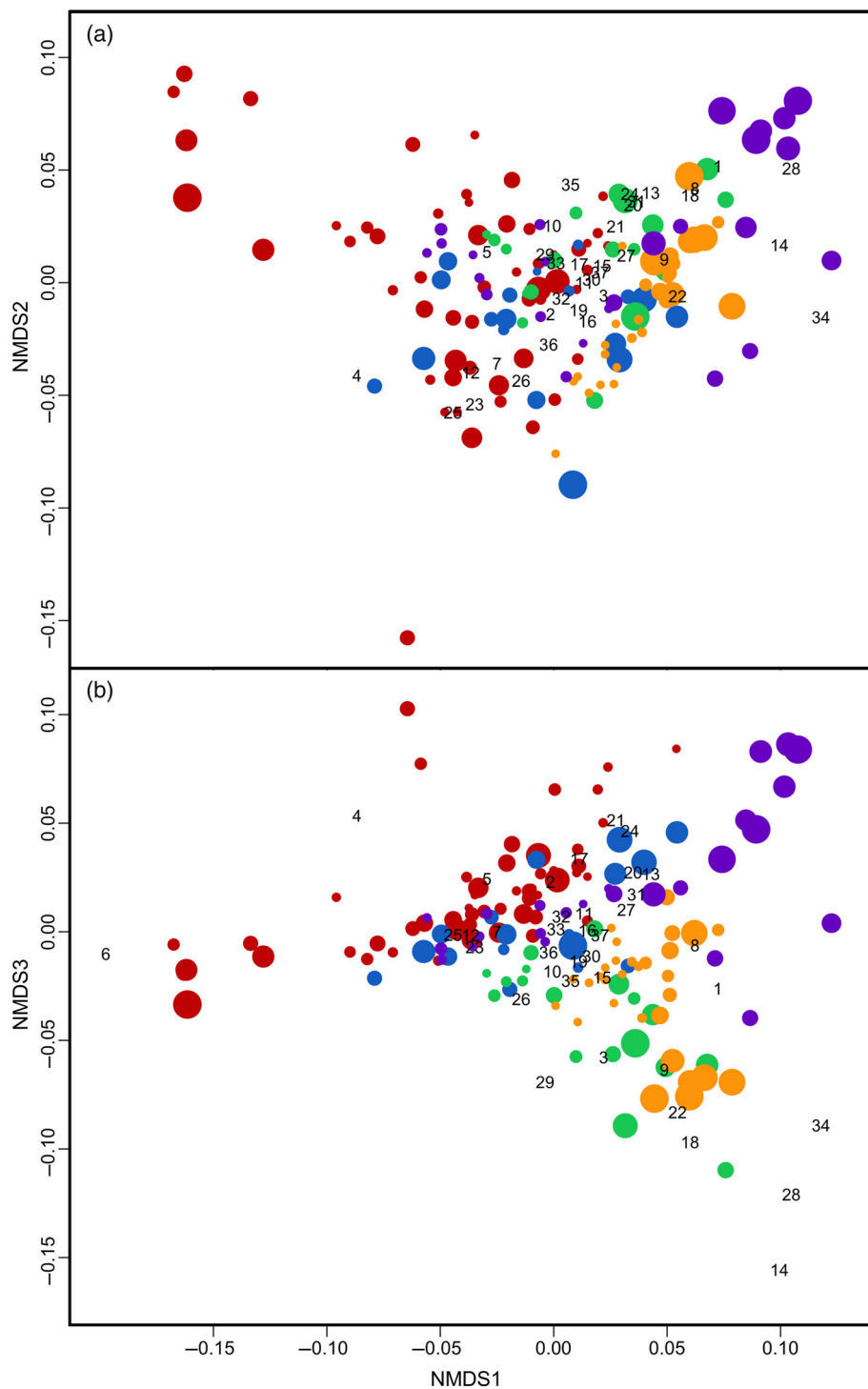


FIGURE 1 Nonmetric multidimensional scaling (NMDS) ordination of stream macroinvertebrate community composition based on taxon traits (numbers) at sites (points) across five stressor gradients. Point size is proportional to stressor intensity, and point color indicates stressor type: drying (red), flooding (blue), eutrophication (green), fine sediment (yellow), and acid mine drainage (purple). Numbers indicate traits as described in Table 1.

eutrophication) triggered greater community shifts in trait space along more axes than natural stressors (Figure 2; R^2 ranged from <0.01 to 0.41 for natural stressors and from -0.04 to 0.65 for anthropogenic

stressors), indicating more comprehensive changes in trait composition between unimpacted and most impacted sites. Community responses to fine sediment and eutrophication were characterized by similar

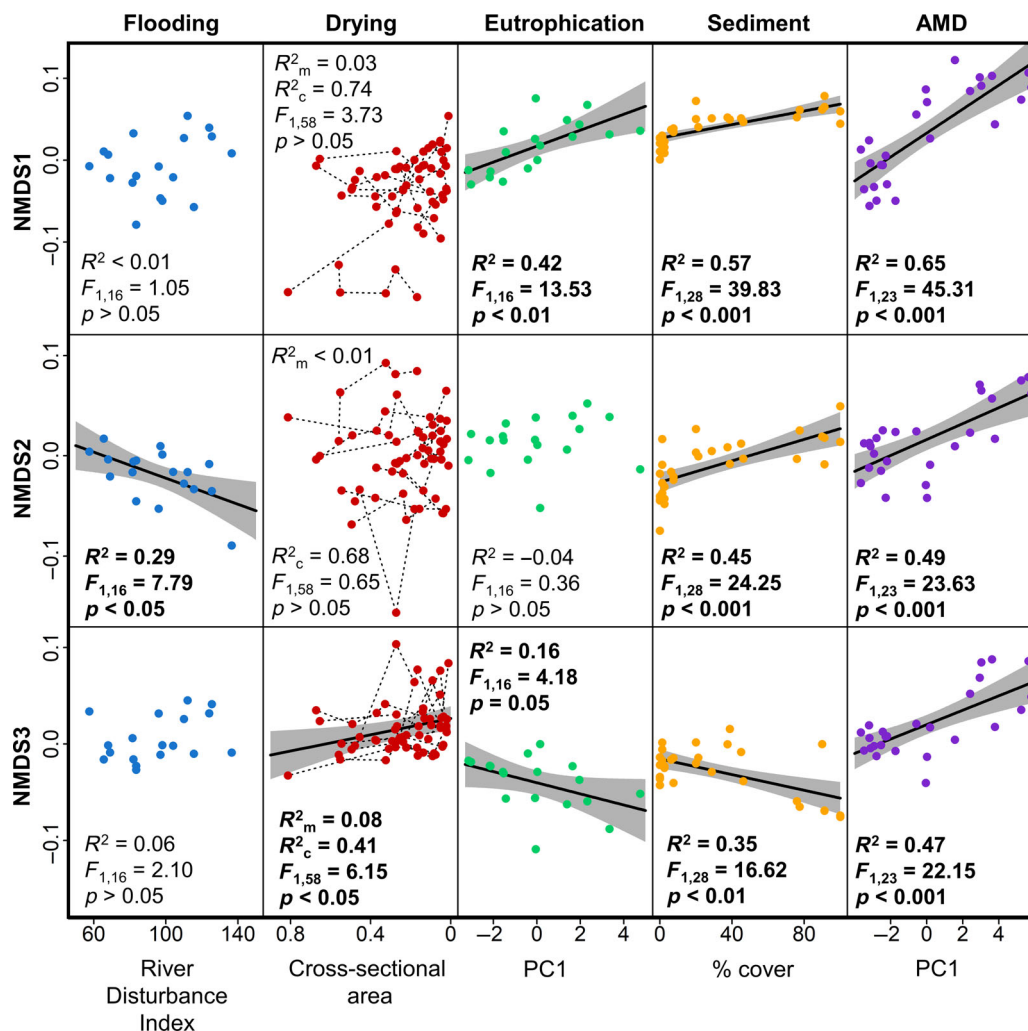


FIGURE 2 Axis scores from nonmetric multidimensional scaling (NMDS) ordination of macroinvertebrate communities at sites spanning five stressor gradients, with stressor intensity increasing from left to right and colors as in Figure 1. Characterization of each stressor gradient is described in the *Methods*. For all stressors except drying, solid lines indicate significant linear regressions ($p < 0.05$). For drying, solid lines indicate significant linear mixed-effects models with stream (dashed lines) as a random effect. Shading shows 95% CI for each significant model.

movement along Axes 1 (Figure 3) and 3 (Figure 5), suggesting that these different stressors result in similar communities.

The anthropogenic stressors, eutrophication, fine sediment, and AMD shifted functional communities along NMDS Axis 1 toward dominance of organisms with smaller body size, more generations per year and greater egg protection (Figure 3). Dominance of spherical organisms also increased along Axis 1, indicating their persistence under increased anthropogenic stress, replacing streamlined organisms, which were associated with unimpacted conditions (Figure 3). This pattern was echoed along Axis 2, which suggested that the anthropogenic stressors fine sediment and AMD shifted communities toward dominance of spherical and swimming organisms (Figure 4). Flooding shifted communities in the opposite

direction along Axis 2, toward dominance of streamlined and crawling organisms (Figure 4). While Axes 1 and 2 indicated similarities in the way the anthropogenic stressors affect community functional composition, community movement along NMDS Axis 3 helped to tease apart trait-based community responses to these stressors (Figure 5). Eutrophication and fine sediment shifted communities in the same direction along Axis 3, toward dominance of taxa with lower body flexibility and swimming organisms. Conversely, AMD shifted communities toward dominance of cylindrical and flexible organisms, and those which attach to substrate. Drying also shifted communities along Axis 3 in the same direction as AMD; however, the distance moved by communities in trait space was smaller for drying, with variation predominantly explained by the random factor (stream;

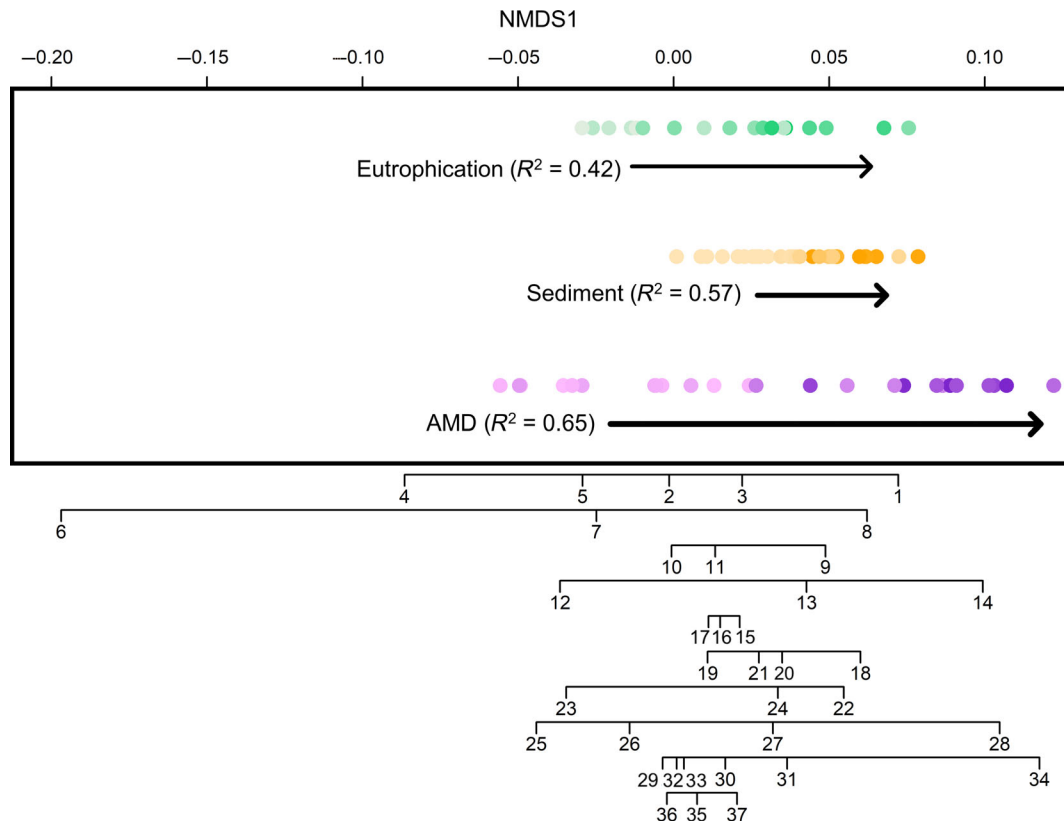


FIGURE 3 Movement of functional communities in trait space (nonmetric multidimensional scaling [NMDS] Axis 1 from a three-dimensional NMDS ordination) across three stressor gradients (eutrophication, fine sediment, and acid mine drainage [AMD]). Axis-associated trait modalities are indicated by numbers listed in Table 1. Points represent communities, with colors as in Figure 1, becoming darker as the stressors intensify. Arrows represent linear models for which $p < 0.05$, with line length determined from model predictions using the minimum and maximum values from each stressor gradient, and line width representing R^2 values.

$R_m^2 = 0.08$ and $R_c^2 = 0.41$). Overall, our results show that different stressors altered communities along different, independent axes of trait composition, each associated with different combinations of traits.

DISCUSSION

Abiotic environments can determine which organisms exist in a community based on their functional traits (Kraft et al., 2014), driven by environmental filtering (Poff, 1997). Through an integrative analysis of abundance-weighted traits of invertebrate taxa across multiple stressor gradients (drying, flooding, fine sediment, eutrophication, and AMD), we have described an exemplar trait space, which can be used to define functional drivers of community change. Our analysis visualized community changes along different stressor gradients in relation to each other. In line with our first hypothesis, different stressors moved functional communities in different directions in trait space. Magnitude of

community change depended on stressor intensity, supporting hypothesis two. Weak trait–environment relationships for flooding and drying compared to the other stressors support hypothesis three: The greatest changes to community composition were associated with novel, anthropogenic stressors (eutrophication, fine sediment, and AMD). Below we summarize additional insights from this analysis and outline how development of integrative, functional approaches such as this could help to inform restoration and conservation actions.

Overall, our integrative approach, which included multiple stressor gradients in one analysis, enabled characterization of the relative influences of different stressors and the possible mechanisms determining community composition. In an ordination of all five stressor gradients, relatively unimpacted sites plotted toward the ordination center and were generally associated with greater trait diversity. This concurs with the observation of higher functional diversity at unimpacted sites (Weijters et al., 2008). By comparison, communities at stressed sites were more dispersed in trait space,

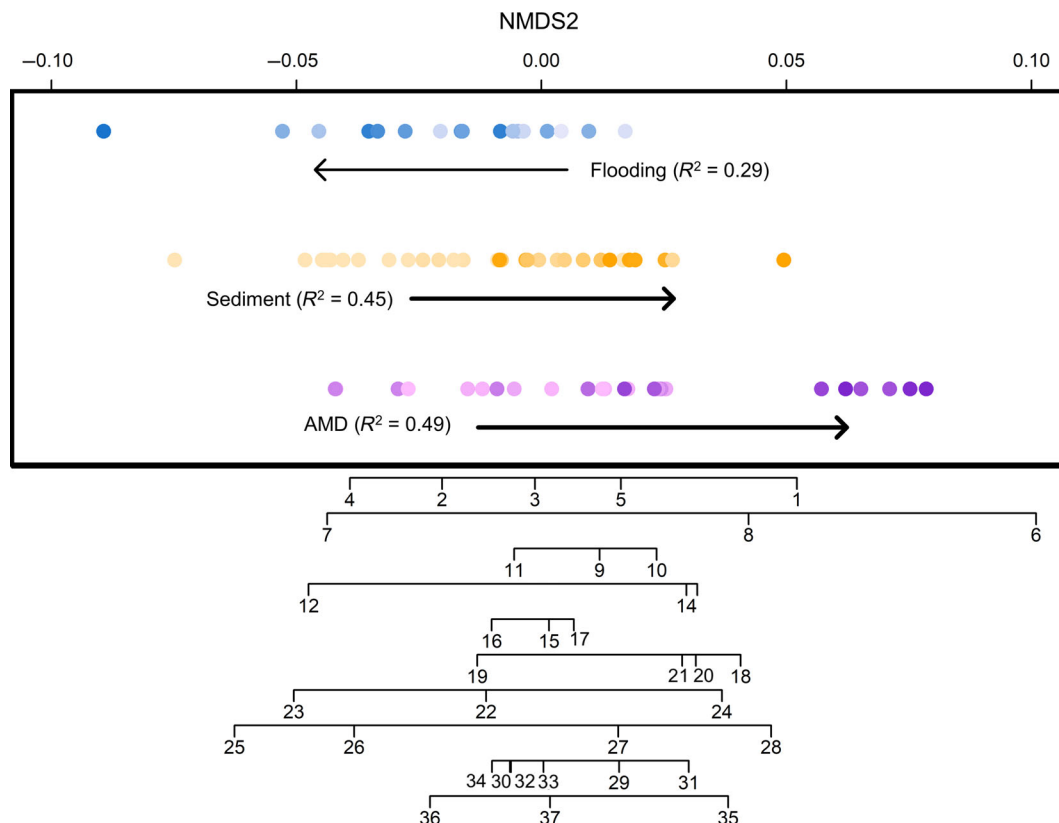


FIGURE 4 Movement of functional communities in trait space (nonmetric multidimensional scaling [NMDS] Axis 2 from a three-dimensional NMDS ordination) across three stressor gradients (flooding, fine sediment, and acid mine drainage [AMD]). Axis-associated trait modalities are indicated by numbers listed in Table 1. Points represent communities, with colors as in Figure 1, becoming darker as the stressors intensify. Arrows represent linear models for which $p < 0.05$, with line length determined from model predictions using the minimum and maximum values from each stressor gradient, and line width representing R^2 values.

supporting our second hypothesis and indicating trait-driven change associated with increasing stressor intensity.

Theoretically, different environments apply different abiotic environmental filters (Kraft et al., 2014). Thus, different stressors likely impose different filters, and across a particular stressor gradient, the filter will intensify, altering community trait composition. We saw this in the stressor-driven movement of communities along axes in trait space. Traits associated with these axes can be used to infer function-related mechanisms driving community responses.

For example, we linked fine sediment to the dominance of taxa in which females carry eggs on the body as opposed to cementing eggs to substrate, likely driven by lack of clean substrate (i.e., habitat loss; Burdon et al., 2013; Niyogi et al., 2007). Such mechanistic insights are valuable, and comparison among stressor gradients can further advance understanding of community responses. For example, as well as fine sediment, we also linked eutrophication to females carrying eggs on the

body, likely driven by similar mechanisms but with benthic algae smothering substrate rather than fine sediment (Niyogi et al., 2007). Moreover, fine sediment, eutrophication, and AMD were linked to organisms with spherical body shapes, perhaps due to the buffer provided by a small surface area to volume ratio in these stressed environments (Dolédec & Statzner, 2008). Conversely, flooding was associated with more streamlined organisms, enabling survival under higher flows (Townsend & Hildrew, 1994), thus pushing functional communities in an opposing direction to that linked to fine sediment, eutrophication, and AMD stressors. This supports our first hypothesis that different stressors elicit movement of communities in different directions in trait space associated with different functional compositions, but also highlights the potential for stressors to produce communities with some comparable functional attributes.

Differences in how stressor gradients drove functional community composition were evident across multiple trait-space axes, and the magnitude of community change varied among different stressor gradients. For

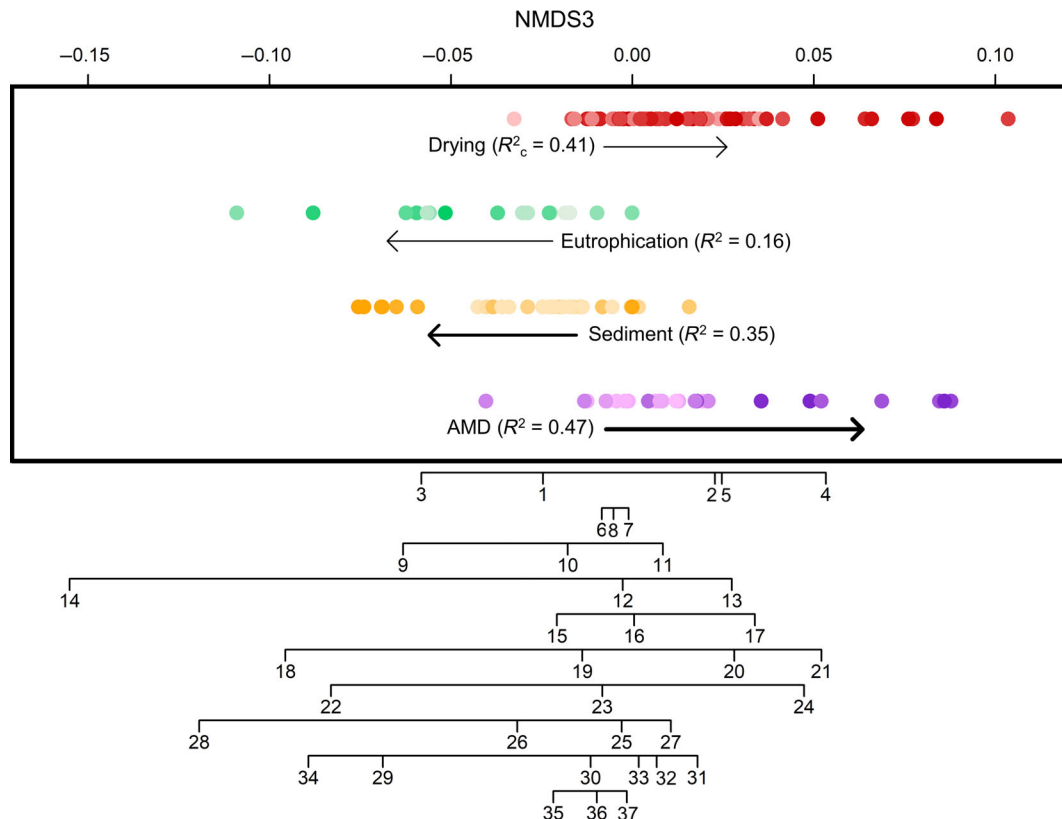


FIGURE 5 Movement of functional communities in trait space (nonmetric multidimensional scaling [NMDS] Axis 3 from a three-dimensional NMDS ordination) across three stressor gradients (drying, eutrophication, fine sediment, and acid mine drainage [AMD]). Axis-associated trait modalities are indicated by numbers listed in Table 1. Points represent communities, with colors as in Figure 1, becoming darker as the stressors intensify. Arrows represent linear models for which $p < 0.05$, with line length determined from model predictions using the minimum and maximum values from each stressor gradient, and line width representing R^2 values.

example, the fine sediment and AMD gradients resulted in significant community shifts along all three axes, indicating comprehensive changes in multiple traits. Acid mine drainage had a particularly strong effect, pushing communities further in trait space than other stressors, indicating more substantial functional changes. By comparison, flooding and drying caused less community change, with each working across a single axis in trait space. These differences may reflect the novelty of these stressors, both regarding stressor type and duration. Our analyses suggest that novel, anthropogenic stressors act as stronger environmental filters. Antecedent conditions and associated taxon adaptations can influence community response to subsequent stress (Eveleens et al., 2019), so there are likely to be fewer taxa, which have adaptations to novel stressors. For example, the intermittent streams included in the drying gradient have been intermittent for long timescales, promoting evolution of adaptations (e.g., the ability to burrow into the hyporheic zone for refuge during drying; Stubbington, 2012; Vander Vorste et al., 2016), which may help to explain the lack of a strong community response seen here. Alternatively,

the lack of functional community change along the drying gradient may reflect the need for flexible phenology under changing flow regimes for which functional traits may not be good predictors (Carey et al., 2021). For the anthropogenic stressors, the line between taxon persistence and taxon loss as determined by their traits is less ambiguous; for example, most stream macroinvertebrates are ill-equipped to survive the low pH and heavy metals associated with AMD (Hogsden & Harding, 2012), so observing extreme community change was not surprising, supporting the hypothesized greater effects of anthropogenic stressors. In response to such novel stressors, communities moved further in trait space, necessitating more extensive restoration to return to a trait composition associated with unimpacted conditions (Gunn et al., 2010).

Our findings demonstrate that trait-based analysis of communities across multiple stressor gradients simultaneously can support a more comprehensive understanding of community composition. Single stressor studies (e.g., Crabot et al., 2021; Rabení et al., 2005) and multiple stressor experiments (typically in mesocosms under

controlled conditions, e.g., Elbrecht et al., 2016; Matthaei et al., 2010) provide useful observations, but understanding the relative effects of different stressors on in situ community composition using the common currency of traits can yield more broadly applicable insights. Unfortunately, integrative analyses based on in situ field data across multiple stressor gradients are often limited by a lack of comparable, concurrent measurements of physicochemical variables. Measuring a standard set of physicochemical variables associated with communities across multiple stressor gradients would facilitate use of more conventional trait-based analyses (e.g., fourth corner analysis; Brown et al., 2014). This would facilitate clearer visualization of relative changes in community composition between stressors and would therefore be hugely valuable.

Acknowledging the relative roles of different stressors in shaping communities could guide evidence-based management and restoration practices. Recognizing similarities in community change associated with different stressor types could inform community-focused management measures, which work across a variety of stressors by promoting recolonization by taxa with lost traits, thus promoting trait diversity and ecosystem functioning. For example, degradation by eutrophication and fine sediment showed strong similarities in trait–environment relationships; therefore, comparable methods could be used to restore communities degraded by these stressors. By contrast, stressor types such as AMD, which lead to more distinct trait compositions, might require tailored restoration strategies for community recovery. Integrative studies of multiple, independent stressor gradients may also help to identify potential restoration methods. That different stressors move communities along different axes of change in trait space suggests the potential for communities to be altered by changing stressor regimes and that these changes may be predictable. Therefore, manipulating stressors, which push communities in opposing directions in trait space, could enable community recovery, particularly in cases where recovery is lacking despite successful abiotic restoration (Barrett et al., 2021).

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Barrett et al., 2022) are available from the National Science Challenge for New Zealand's Biological Heritage repository: <https://doi.org/10.34721/8Y4R-V714>.

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