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Special Feature

Extreme flood disturbance effects on multiple dimensions of river invertebrate community stability

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Abstract

1. Multidimensional analysis of community stability has recently emerged as an overarching approach to evaluating ecosystem response to disturbance. However, the approach has previously been applied only in experimental and modelling studies.
2. We applied this concept to an 18-year time series (2000–2017) of macroinvertebrate community dynamics from a southeast Alaskan river to further develop and test the approach in relation to the effects of two extreme flood events occurring in 2005 (event 1) and 2014 (event 2).
3. Five components of stability were calculated for pairs of pre- or post-event years. Individual components were tested for differences between pre- and post-event time periods. Stability components' pairwise correlations were assessed and ellipsoids of stability were developed for each time period and compared to a null model derived from the permuted dataset.
4. Only one stability component demonstrated a significant difference between time periods. In contrast, 80% of moderate and significant correlations between stability components were degraded post-disturbance and significant changes to the form of stability ellipsoids were observed. Ellipsoids of stability for all periods after the initial disturbance (2005) were not different to the null model.
5. Our results illustrate that the dimensionality of stability approach can be applied to natural ecosystem time-series data. The major increase in dimensionality of stability observed following disturbance potentially indicates significant shifts in the processes which drive stability following disturbance. This evidence improves our understanding of community response beyond what is possible through analysis of individual stability components.

KEYWORDS

colonisation, deterministic community assembly, dimensionality of stability, ecological stability, extinction, stochastic community assembly, temporal variability, time series

1 | INTRODUCTION

Changing land use, pollutants and climate change are driving declines in biodiversity (Tickner et al., 2020) with associated effects on ecosystem and community stability (Fussmann et al., 2014). Ecosystem and community responses to environmental disturbance have recently been shown to be complex (Lemm et al., 2020; Polazzo & Rico, 2021) such that multiple components, or 'dimensions', of ecological stability should be measured (Donohue et al., 2013; Hillebrand et al., 2018; White et al., 2020; Yang et al., 2019). Dimensional components of stability include variability of biomass, abundance or percentage cover; resistance to change; rate of recovery following change; turnover of community composition; and rates of colonisations and extinctions (Clark et al., 2021; Donohue et al., 2016). Evidence is now available to indicate that using individual stability components alone may risk over or underestimating stability when interpreting community response to disturbance, providing unreliable evidence for ecosystem management (Donohue et al., 2013).

Understanding of the dimensionality of ecological stability has developed rapidly in recent years. In undisturbed experimental controls, strong intercorrelations (low effective dimensionality) have been demonstrated between stability components (Donohue et al., 2013). These correlations suggest that stability can be a relatively simple property, with all components responding to environmental or biodiversity change in a consistent manner. However, the decoupling of relationships between components (increasing dimensionality) has been proposed to occur when ecosystems are under stress (Donohue et al., 2013). This decoupling is significant because it may be indicative of alterations to the influence and form of deterministic and/or stochastic processes which govern the response of individual components and, therefore, overall community stability.

The multidimensional stability approach has to date been evaluated in small-scale aquatic microcosms (250 ml; Pennekamp et al., 2018), mesocosms (500 L; Hillebrand et al., 2018) and exclosure (0.12 m^2) experiments on rocky shores (0.12 m^2; Donohue et al., 2013; White et al., 2020), for meta-analysis of experimental press disturbances (Hillebrand & Kunze, 2020) and for simulated community dynamics in empirically or process-based models (Domínguez-García et al., 2019; Radchuk et al., 2019; Yang et al., 2019; Zelnik et al., 2019). However, concepts developed in experimental and modelling studies remain to be tested in natural ecosystems.

Modelling evidence suggests that disturbance form (pulse, repeat, press, random etc.), as opposed to magnitude, may affect how dimensionality is altered (Radchuk et al., 2019). This finding is important given the changing timings, frequencies and durations of extreme events now being observed globally (Berg et al., 2013; Berghuijs et al., 2017; Trenberth, 2011). In natural ecosystem studies, data are typically collected as long time series involving sampling before and after disturbance. Consequently, the multidimensional stability approach which was developed for experimental systems comparing disturbed and undisturbed replicates requires adaptation and testing (Kéfi et al., 2019), particularly because ecosystems and associated communities following a disturbance may not return to a predisturbance state (Petersen et al., 2008). The failure to return to a previous state could occur for two reasons: (a) the potential for multiple stable states in ecosystems (Ramstack et al., 2016; Sayer et al., 2010; Sutherland, 1974) or (b) periodic/continued disturbance of the system (Matthews et al., 2013; Paine, 1977), potentially complicating interpretations of stability dynamics.

Floods have a major influence in structuring river ecosystems, with high-magnitude rainfall events expected to increase with climate change (Berg et al., 2013), and major flooding disturbances already occurring more frequently in many regions (Berghuijs et al., 2017). However, there is uncertainty about the capability of different flood regimes, with varied duration, magnitude and timing, to (re-)structure biotic communities (Milner et al., 2018). Altered river flow regimes (Brown et al., 2015) can reduce community robustness (local extinctions) as a result of differences in resistance traits, facilitate colonisation due to differences in resilience traits (Poff et al., 2018), alter productivity (Wright et al., 2015), govern resource utilisation (Larson et al., 2018) and ultimately restructure food webs (Fell et al., 2018; McHugh et al., 2010). Long-term studies of floods have typically measured multiple components of community stability but treated them independently (Milner et al., 2018; Robinson et al., 2018; Woodward et al., 2015). Nevertheless, these kinds of time-series data offer significant potential for evaluation and development of the multidimensional stability approach.

Here, the dimensionality of macroinvertebrate community compositional stability was assessed in response to two extreme flood disturbances at different time periods (a single high-magnitude flood in November 2005 following a rain on snow event, and recurrent summer floods in 2014 due to prolonged rainfall events) in a well-studied wilderness small river system (Wolf Point Creek, Alaska) with one of the most extensive temporal records of river invertebrate community composition available globally (Milner et al., 2018). The overall aim was to generalise the concept and methods of multidimensional stability to long-term community data, thereby testing this approach for evaluating macroinvertebrate community stability responses to extreme flood disturbances using the available extensive dataset. Three hypotheses were tested:

H_1: Stability will show low dimensionality during the period prior to the first extreme flood in 2005 (event 1) due to strong directional relationships between stability components (Donohue et al., 2013). The components of community stability included in this study have theoretical and mathematical relationships with one another, based on the variability of populations within the community caused by density-dependent effects and to a lesser extent environmental/resource variability (Johnson et al., 2017) which can drive low dimensionality of stability (Radchuk et al., 2019).

H_2: Post-event 1 dimensionality of stability will be higher than pre-event 1 because post-disturbance declines in resource availability and total community density can release taxa from predisturbance taxa interactions (Chanut et al., 2019). In addition, the

response of individual aquatic macroinvertebrate stability components to disturbance can vary, total density often recovers rapidly (Woodward et al., 2015) whereas community structure response is less predictable (Hillebrand & Kunze, 2020; Milner et al., 2018). These varied rates and extents of response will disrupt the correlations between stability components, thereby increasing dimensionality.

H_3: A compound disturbance effect of the 2005 and 2014 (event 2) floods will be observed on dimensionality of stability (Buma & Wessman, 2011), potentially due to the homogenisation of the habitat template during and post-event 1 (Milner et al., 2013). This habitat modification will alter biotic processes and density-dependent effects (Punttila et al., 1996) present within the community, weakening the correlations which underpin low dimensionality (Radchuk et al., 2019) which can then be further disrupted by subsequent floods.

2 | MATERIALS AND METHODS

2.1 | Study site

Rapid deglaciation in Glacier Bay National Park and Preserve, southeast Alaska, United States, has exposed proglacial landscapes that are in a transient geomorphological state (cf. Carrivick & Heckmann, 2017), and large numbers of ponds, lakes and rivers have formed (Fritz et al., 2004; Klaar et al., 2009; Milner et al., 2008). Wolf Point Creek (WPC; approximately 2.5 km in length averaging 10 m in width with a catchment area of 29.8 km^2) is a well-studied river dominated by pool/run—riffle morphologies (Milner et al., 2008). The catchment is predomiantly covered by cottonwood *Populus trichocarpa* and some Sitka spruce *Picea sitchensis*, with extensive alder *Alnus sinuata* along the river margins (Klaar et al., 2015). The benthic macroinvertebrate community has been studied since the late 1970s (Milner, 1987) with near annual sampling since 1986 (Milner et al., 2018).

Benthic macroinvertebrate samples used in this study were collected from 2000 to 2017. Macroinvertebrate samples (10 replicates) were collected annually in August or early September, in all years except 2003 and 2009, using a Surber sampler (330 μm mesh) from a long-standing 15-m survey reach (58°59′43.3″N, 136°11′16.3″W) approximately 1 km upstream from the tidal limit, and representative of the wider river network. Samples were preserved in 70% ethanol. Individual specimens were identified under a binocular microscope to the lowest possible taxonomic level using North American keys (e.g. Merritt & Cummins, 1996; Thorp & Covich, 2009). Oligochaeta were identified to class. Chironomidae larvae were identified using Andersen et al. (2017); Brooks et al. (2008).

Due to the protected wilderness location, long-term installations including river gauges are not permitted, and thus, no long-term WPC flow records were available, although inferences about flood disturbances can be made from local rainfall measurements (Milner et al., 2013). Prior to 2005, WPC mostly experienced limited hydrological disturbances compared to the scale of the extreme high-magnitude event (est. >1 in 100-year recurrence interval) in the winter of 2005 (Milner et al., 2013) except for the summer of 2002 which was the wettest in the 30-year record until 2014. In 2014, the wettest summer on record occurred in southeast Alaska creating high-frequency floods throughout the summer and early autumn. In Glacier Bay National Park, June (total 133 mm precipitation) and July (total 211 mm) were the second wettest on record, with 12th July (51 mm) the wettest July day on record. August (222 mm) was the fifth wettest summer month on record (Figure S1; Eagle et al., 2021). These precipitation events resulted in extensive and repeated flooding across the region with peak discharge eight times greater than the median at Lemon Creek, a gauged stream proximal to the study area (Figure S2).

This dataset provides a unique opportunity to compare the response of multidimensional community stability following extreme disturbance to an extended pre-flood dataset. The wilderness location of the study catchment also enables an assessment of stability responses to disturbance in the complete absence of direct anthropogenic stressors.

2.2 | Data analysis

Adjustments to the quantification of stability components are needed for time-series data compared to previous experimental approaches (Donohue et al., 2013) as it is typically not possible to compare 'end points' to an external control particularly for landscape-scale disturbances such as flooding, and time-series replication among similar ecosystems is often lacking. Rather, when using time-series data, a flexible approach has been called for to encourage the opportunistic exploration of unexpected environmental change (Jassby & Powell, 1990; Turner et al., 2003). Establishing ecological change relative to a predisturbance time period has long been used to explore individual components of community stability, such as resilience, resistance and productivity (Müller et al., 2016; Turner et al., 2003), and here is used to explore variation in multiple community stability components within distinct time periods pre- and post-disturbance.

Four time periods were established in which components of stability were calculated: 2000 to 2005 (excluding 2004–2005—not included in the analyses, pre-event 1, $n = 9$), 2006 to 2011 (excluding 2010–2011—included in the 2010–2013 period, post-event 1, $n = 9$), 2010 to 2013 (including 2010–2011, pre-event 2, $n = 6$) and 2014 to 2017 (post-event 2, $n = 6$, Figure S3). Sample sizes (n) refer to the total number of pairwise year comparisons in each time period. These time periods were defined based on the availability of data and the need for consistent sample sizes pre and post each event. Post-event 2 sample size (i.e. n years following event 2) governed the size of the pre-event 2 period. Similarly, the pre-event 1 time period sample size was governed by the availability of data following the 2005 flood but not included in the pre-event 2 time period. To balance sample sizes in pre- and post-event 1 time periods, the final

data point (2004–2005) was removed from the pre-event 1 time period to be consistent with the removal of the final data point from the post-event 1 time period (2010–2011). Through this selection process, the inclusion of repeated data points within each time period was avoided and the largest possible sample sizes were maintained. The two flood events were analysed separately considering only the pre- to post-event response for each flood/flood sequence. Non-metric multidimensional scaling (NMDS) was undertaken using a Bray–Curtis dissimilarity matrix of $\log_{10}$ (original taxa density data + 1) for all year samples included in this study, using metaMDS in the vegan package (Oksanen et al., 2018) to provide contextual community compositional information.

Five components of stability were calculated: proportional *temporal variability* of community density, number of *extinctions*, number of *colonisations*, compositional *dissimilarity* and density-*weighted* community *turnover* (Table 1). Mean density per taxon was calculated from replicate Surber sample data for each individual year for the calculation of *temporal variability* of density and density-*weighted* community *turnover*. Presence/absence data were derived from density data to allow for the calculation of the remaining stability components. Stability components were calculated using all pairwise comparisons between years within each of the four time periods. Testing for differences was completed for each individual component for each pre- to post-event time period. Mann–Whitney tests were used to test for differences between time periods due to heterogeneity of variances and non-normal population distributions. *p* Values were adjusted for multiple testing using the Bonferroni adjustment.

Pairwise Pearson's correlation coefficients were calculated for components in each time period to assess relationships between individual pairs of components. Relationships between components were assessed for linearity visually prior to ellipsoid calculation. Ellipsoids of stability were produced from the covariance matrices of each time periods' standardised stability components data using the prcomp function in R (v 3.5.1). The current framework requires equal and consistent datasets between time periods to allow the covariance matrices comparison and extra work would likely be required if data are more varied.

Ellipsoids describe the relationships between stability components in multidimensional stability space. The volume and shape of ellipsoids for each time period were compared to a null distribution (sensu Donohue et al., 2013) using permutation analyses and associated permutation tests. Permutation analyses (×10,000) reassigned stability components from year pairs randomly without replacement. Due to the presence of multiple testing between time periods, *p* values were adjusted using the Bonferroni correction. The form of a given ellipsoid was then used to calculate the dimensionality of stability during both pre- and post-flood time periods. Semi axis lengths were calculated for all ellipsoids based on their axis eigenvalues by:

$$\text{Semi axis length} = (\lambda_i)^{0.5}, \quad (1)$$

TABLE 1 Components of stability used in this study and their method of quantification

Component of stability	Description	Quantification method	Formula
Number of *extinctions*	Follows the concept of community robustness, in which a robust community demonstrates limited extinctions as a result of environmental disturbance or biotic interactions (Cai & Liu, 2016; Pimm, 1991; Solé & Montoya, 2001)	Quantified as the sum of the number of taxa identified in the earliest year of each pair of years, but not present in the later year	$\text{ext} = \sum \text{sp}_n(\text{yr1} \geq 0) \,\&\, \text{sp}_n(\text{yr2} = 0)$ where sp_n is the *n*th taxa in the matrix, yr is year within each pairwise comparison
Number of *colonisations*	Follows from the concept of community persistence, in which persistent communities are hard to invade (Roopnarine et al., 2019) and demonstrate limited new colonisations (Pimm, 1984)	Quantified as the number of individual taxa identified in the most recent year of each pair of years, but not present in the earlier year	$\text{col} = \sum \text{sp}_n(\text{yr1} = 0) \,\&\, \text{sp}_n(\text{yr2} \geq 0)$ where sp_n is the *n*th taxa in the matrix, yr is year within each pairwise comparison
Proportional *Temporal variability* of density	Variability of community abundance, density or biomass through time (Clark et al., 2021). A community demonstrating higher levels of variability is less stable than a community where variability through time is low (Ives & Carpenter, 2007)	Quantified as the absolute proportional variation of total macroinvertebrate density from the earlier to later year in each pair of years	$\text{temp}\,v = \left\lvert \frac{n_{\text{yr1}} - n_{\text{yr2}}}{n_{\text{yr1}}} \right\rvert$ where *n* is the total community density, yr is year within each pairwise comparison
Compositional *dissimilarity*	Change in the taxonomic composition of a community through time. A stable community demonstrates lower dissimilarity through time than an unstable community (Pimm, 1984)	Quantified as the Jaccard dissimilarity (Jaccard, 1912) between each pair of years in the matrix	$\text{diss} = \text{JC}[\text{yr1}, \text{yr2}]$ where JC is the Jaccard dissimilarity of taxa presence/absence for each pair of years in the matrix
Density-*weighted* community *turnover*	Change in community structure through time, incorporating taxon densities as well taxonomic change. A more stable community shows less change in composition and taxon densities through time than a less stable community	Quantified as Bray–Curtis dissimilarity of log (macroinvertebrate density) data between each pair of years in the matrix	$w\,\text{turn} = \text{BC}[\text{yr1}, \text{yr2}]$ where BC is the Bray–Curtis dissimilarity of taxa density data for each pair of years in the matrix

where λ_i is the *i*th eigenvalue derived from the covariance matrix for each time period. Relative semi axis length was calculated by standardising all semi axis lengths by the longest axis length in that time period. This measure allows comparisons to be made about the overall shape of an ellipsoid compared to the null distribution. A cigar-shaped multidimensional stability ellipsoid has lower dimensionality than increasingly spherical ellipsoids.

Ellipsoid volume describes the overall amount of space occupied in multidimensional stability space by components from each time period. Volume was calculated for separate time periods and the permutated ellipsoid dataset using the formula:

$$V = \frac{\pi^{n/2}}{\Gamma\left(\frac{n}{2}+1\right)} \prod_{i=1}^{n} (\lambda_i^{0.5}), \quad (2)$$

where λ_i is the *i*th eigenvalue derived from the covariance matrix for each time period, *n* is the number of different stability components and Γ is the gamma function. Volumes were compared statistically to the null distribution of volumes from the permuted dataset using permutation tests. All analyses were undertaken using R (R version 3.5.1).

3 | RESULTS

Forty-six taxa were identified in the benthic macroinvertebrate community at WPC from 2000 to 2017. NMDS analyses indicated differentiation between the four time periods (Figure 1).

3.1 | Event 1 November 2005 flood

Dissimilarity demonstrated a small but insignificant increase from pre-event 1 [0.4 ± 0.1 (*SD*)] to post-event 1 (0.6 ± 0.1), and no change was observed in the other four stability components (Figure 2). No significant differences were observed in individual stability components between pre- and post-event 1 time periods.

Pre-event 1 stability components generally showed moderate (±0.5) to strong (±0.7) correlations (8 of 10 pairwise comparisons; Figure 3a). *Dissimilarity* was positively and strongly correlated with *extinctions*. *Weighted turnover* was strongly and positively correlated with all other components. During this time period, semi axis 1 has a length of 1.87, semi axis 2 had a length of 0.96 and semi axis 3 has a length of 0.66 (Figure 4).

All eight pairwise stability component relationships observed during pre-event 1 decreased in strength during the post-event 1 time period. Only the moderate positive relationship between *colonisations* and *dissimilarity* and the strong relationship between *dissimilarity* and *weighted turnover* persisted from pre-event 1. The weak positive correlation between *colonisations* and *extinctions* (0.33) observed during the pre-event 1 period shifted orientation, demonstrating a weak negative relationship (−0.44) during the post-event 1 period.

Stability ellipsoid form changed from pre-event 1 to post-event 1 with a shorter of semi axis 1 (1.87 to 1.57) and longer semi axis 2 (0.96 to 1.27) and 3 (0.66 to 0.75) during the post-event 1 period compared to pre-event 1. The relative length of semi axes 2, 3 and 4 during the pre-event 1 time period were significantly shorter than the null model (all $p < 0.05$). The relative lengths of semi axes 5 were not different to those of the null model. During the post-event 1 period, no semi axis relative lengths were significantly different from the null model. Semi axis 2 relative length during the post-event 1 period (0.81) was longer than that observed during the pre-event 1 time period (0.51). Ellipsoid volumes pre-event 1 was significantly different to the null model ($p = 0.015$) with a smaller volume than ellipsoids derived from permuted datasets, while post-event 1 was not significantly different from the null model.

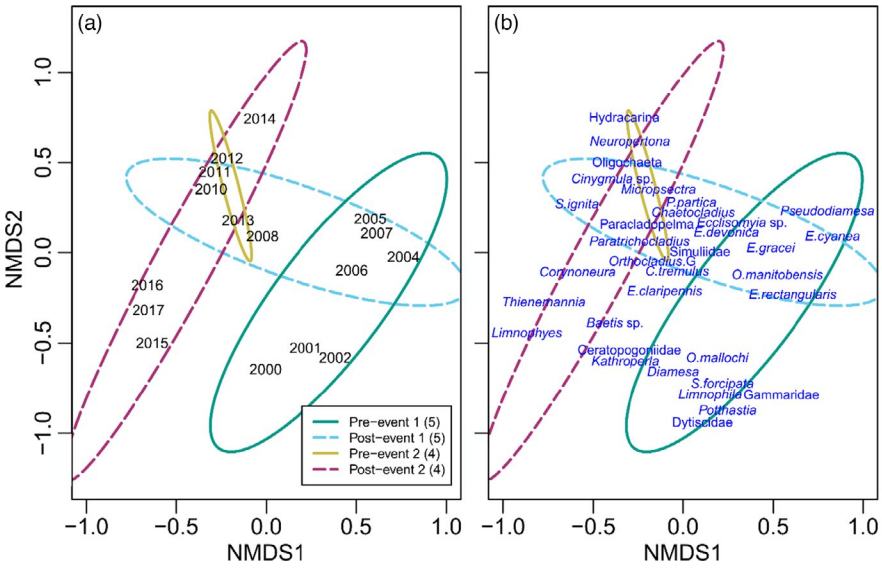

FIGURE 1 Non-metric multidimensional scaling of taxonomic data with (a) 95% (standard deviation) confidence ellipse around the centroid of each time period, (b) taxon biplot with taxa recorded in only one year removed for clearer visualisation. Number in parentheses equals sample size for each time period

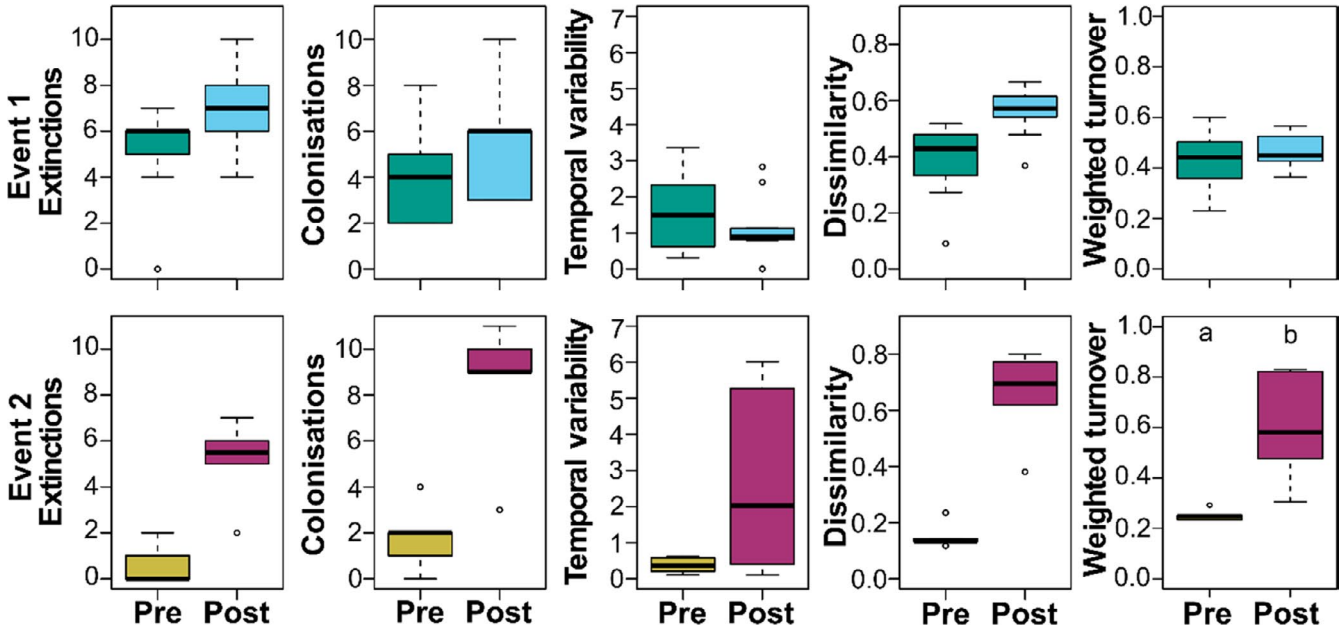

FIGURE 2 Box plots of community stability components pre-event 1 ($n = 9$), post-event 1 ($n = 9$), pre-event 2 ($n = 6$) and post-event 2 ($n = 6$) each disturbance event. Letters above boxes indicate significant differences at the adjusted $p < 0.05$ level. Box plots report median (central line), interquartile range (box), min/max (whiskers) and potential outliers (open circles)

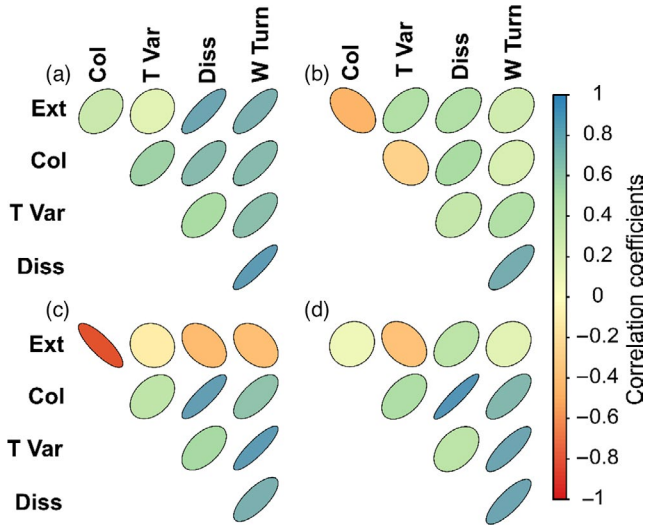

FIGURE 3 Pairwise correlations for (a) pre-event 1 ($n = 9$), (b) post-event 1 ($n = 9$), (c) pre-event 1 ($n = 6$) and (d) post-event 2 ($n = 6$). Ext = Extinctions, Col = Colonisations, T Var = Temporal Variability, Diss = Community Dissimilarity and W Turn = Weighted Turnover. Ellipses represent the correlation between the pair of stability components; a circle indicates no correlation and cigar-shaped ellipse indicates strong correlation. The orientation of the ellipse indicates the sign of the correlation. Colours indicate correlation coefficients. Scatter plots are provided in Figure S4

3.2 | Event 2 summer floods 2014

Density-*weighted turnover* demonstrated a significant difference between pre- and post-event time periods ($W = 0.00$, $p < 0.01$) with an increase in turnover from pre- to post-event. No other individual components demonstrated a significant difference between pre- and post-event time periods. Although *extinctions* and *dissimilarity* fell on the significance level cut-off ($p = 0.05$).

Relationships between components of stability varied in their strength and direction during the pre-event 2 time period. During this time period, a strong negative correlation was observed between *colonisations* and *extinctions* developed from a weak negative relationship directly following the 2005 floods (Figure 3c). Strong positive correlations were observed between *colonisations* and *dissimilarity* as well as *weighted turnover* and both *temporal variability* and *dissimilarity*. Pre-event 2, the ellipsoid of community compositional stability suggested a decreased overall dimensionality with a semi axis 1 length of 1.84, a semi axis 2 length of 1.07 and a semi axis 3 length of 0.64 (Figure 5).

Following the extreme high-frequency summer floods (post-event 2), three strong pairwise correlations persisted from the pre-event 2 time period. These strong correlations were between *colonisations* and *dissimilarity* as well as *weighted turnover* and both *temporal variability* and *dissimilarity*. In addition, the weak positive relationship between *colonisations* and *temporal variability* observed pre-event 2 strengthened, demonstrating a moderate correlation post-event 2 (0.50). In contrast, the strong negative correlation previously observed between *extinctions* and *colonisations* was not observed following the floods.

Limited increased dimensionality was evident following event 2 with a shorter semi axis 1 length (1.84 to 1.76) and longer semi axis 2 (1.07 to 1.18) and 3 lengths (0.64 to 0.69) post-event 2. Semi axes 2 and 3 demonstrated an apparent longer relative length than the pre-event 2 period. However, no semi axis relative lengths were

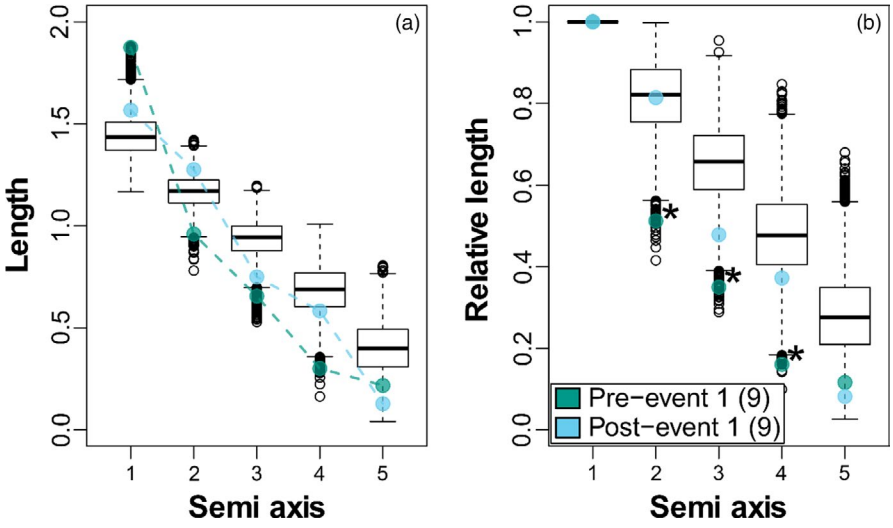

FIGURE 4 Event 1 (a) semi axis lengths and (b) relative semi axis lengths for pre- and post-event 1 time periods (points) plotted over null model box plots. *Denotes significantly different relative semi axis length compared to random permutations of the stability component data (null model) using a permutation test at adjusted $p < 0.05$

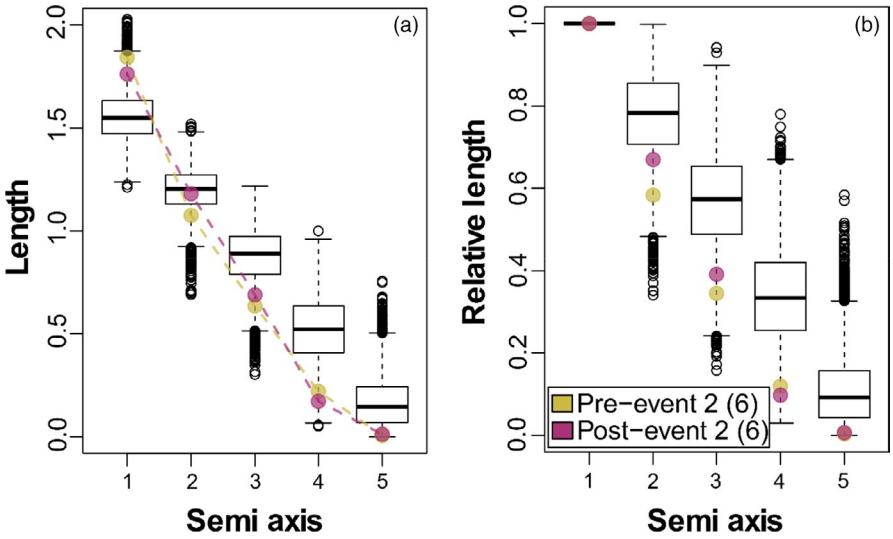

FIGURE 5 Event 2 (a) semi axis lengths and (b) relative semi axis lengths for pre- and post-event 1 time periods (points) plotted over null model box plots

significantly different to the null model. Neither time period's ellipsoid volume was significantly different to those of the null model.

4 | DISCUSSION

Our study illustrates that the multidimensional stability concept can be applied successfully to long-term, observational macroinvertebrate community data with results demonstrating clear, yet temporally variable responses to flood disturbances in Wolf Point Creek. The first hypothesis H_1 that stability will show low dimensionality during the period prior to the first extreme flood was supported as the dimensionality of stability of the invertebrate community was lower at this time compared to subsequent time periods. Our study provides the first evidence of this stability dynamic in a natural system, and is broadly consistent with previous experimental studies of multidimensional ecological stability (Donohue et al., 2013; Hillebrand et al., 2018). Consistency is observed despite differences in ecosystems, study communities, disturbance types, the temporal scale (over 18 years with a single sampling time each year) and spatial scale of research (one sampling reach in a single catchment). This observation may suggest that low dimensionality of stability is a common element of broadly undisturbed ecosystems. Furthermore, our findings indicate low dimensionality persists through less extreme disturbances in natural systems (Ives & Carpenter, 2007), as observed in the particularly wet summer in 2002 (Milner et al., 2018). Less extreme disturbances (i.e. smaller flow events to 1 in 2-year return intervals) may influence relationships between components in time-series datasets to a lesser degree or over a time period shorter than our annual sampling, yet appeared to be insufficient to diminish the utility of the dimensionality of stability approach in our study.

4.1 | Invertebrate community response to flood disturbance

Pre-event 1 ellipsoid form suggests that a single or a group of underlying processes acting in a cohesive manner govern the response of

a suite of stability components in a consistent linear pattern. Species sorting, associated with cold water temperature and unstable channels, is thought to govern assembly during initial invertebrate colonisation of WPC with the importance of competitive exclusion and meta community processes known to increase with glacier retreat before flood event 1 (Brown & Milner, 2012; Milner et al., 2008). At WPC and elsewhere globally, the influence of patch dynamics, including both stochastic and deterministic elements, increases as glacier cover is lost (Brown et al., 2018).

The 2005 flood (event 1) degraded the dominant first dimension of community stability, offering some support for H_2 that post-flood dimensionality would be higher than pre-flood. Shifts in community composition during the post-flood time period were consistent with the dominant response in experimental studies of pulse disturbances (Hillebrand & Kunze, 2020). Indeed, over 12 years following the 2005 floods, compositional recovery to the pre-flood community did not occur in WPC (Milner et al., 2018). These changes to composition were associated with alterations in the river's hydromorphology, including the loss of slow flow habitats (e.g. pools) following each event (Eagle et al., 2021; Milner et al., 2013). In addition, the low dispersal capacity of some displaced taxa (e.g. Gammaridae, Planorbidae) and potential colonisers may govern the community's potential for taxonomic recovery in the physically isolated catchments of Glacier Bay (Hou et al., 2014).

Environmental stochasticity is thought to impact relationships between elements of stability. The flood time series in our dataset may indicate reddening (increasingly positive autocorrelation) of environmental noise, which has been suggested to result in driving higher temporal variability and reducing the capacity of communities to resist disturbance (Yang et al., 2019). Our findings that overall dimensionality of stability increased by this final time period (after two major flood disturbance events) are broadly consistent with these effects.

4.2 | Disturbance sequences

The absence of significant low-dimensionality pre-event 2 may indicate that legacy effects of the 2005 flood persisted when the 2014 floods occurred (Franklin et al., 2000; Pulsford et al., 2016). Legacy effects can be underlain by alterations to the environment (habitat and resource availability) and biotic interactions (resource use and priority effects) post-disturbance (Cawley et al., 2014; Ledger et al., 2006). Through these biotic and abiotic changes, legacy effects could influence the form and extent of the post-flood stability response to subsequent disturbances (Buma & Wessman, 2011). In this study, high-resolution environmental data through which the ability to unpick indirect stability effects or potential alterations to competitive and trophic interactions were not available owing to the extreme remoteness of the study sites which makes sustained repeat visits difficult.

Where deterministic assembly is impacted during initial disturbances, and the importance of second and third dimensions of stability remains high in the post-disturbance ecosystem, this could limit or even mask further alterations to the dimensionality of stability following subsequent disturbances. This perhaps suggests that the dimensionality of stability in natural ecosystems may have an upper boundary which subsequent disturbances cannot surpass. Nevertheless, shifting relationships observed between post-disturbance periods suggested subsequent disturbances may still impact elements of stability in different manners.

Both extreme flood disturbances (2005 and 2014) caused the breakdown of at least some stability component relationships. However, our study offered little support for hypothesis H_3 that a compound disturbance effect of the 2005 and 2014 floods would be observed on dimensionality of stability. The event 2 response was less substantial than event 1, with relative semi axis lengths and volumes not different to those of the null model. Despite similarities in form to the null model, an increasing total semi axis length was observed in the first three dimensions by post-event 2. Such a response may be observed if post-flood stability is governed by a suite of processes that no longer act in a cohesive manner (i.e. become increasingly independent/orthogonal) rather than becoming increasingly stochastic (Radchuk et al., 2019). A number of additional underlying processes could be involved in governing stability during post-disturbance community reassembly. During early post-disturbance years, the high number of new taxa recorded is consistent with (re-)colonisation of capable dispersers which can exploit disturbed systems, with relatively low levels of extinctions perhaps indicating release from interspecific competition (Bengtsson, 1989). The increasing occurrence of extinctions and higher temporal variability in later post-disturbance years is consistent with an increasingly competitive environment in which density-dependent assembly and competitive exclusion become more significant (Liu et al., 2018). The more limited multidimensional response following event 2 is notable as past research has demonstrated significant shifts in community composition following both event 1 and event 2 (Milner et al., 2018).

4.3 | Relating observational results to experimental and modelling studies

Despite consistencies in ellipsoid response between our study and previous experimental work, our findings vary in a number of ways to previous studies. In our study, positive correlations between colonisations and dissimilarity during post-event periods contrast with the experimental plots in Donohue et al. (2013). WPC continues to undergo succession acting under paraglacial processes following glacial retreat (Klaar et al., 2015), with 'colonisations' continually occurring. In addition, experimental work has identified a strong and significant correlation between temporal variability of density and compositional dissimilarity (Donohue et al., 2013), which was weak during both post-flood periods in our work. These contrasts could be associated with differences in the mechanisms which underlie community reassembly in aquatic ecosystems following flood disturbances. Resilient taxa can persist and recolonise rapidly post-flood before the complete recovery of other ecosystem elements

facilitating the recovery of total macroinvertebrate density (Larson et al., 2018; Poff et al., 2018). In contrast, the mesocosms and small-scale trophic exclusion experiments used previously provide simplified representations of natural communities. Such methods may fail to capture the complexities of natural ecosystem response to disturbance under true environmental and ecological stochasticity.

Variation between our findings and those of previous studies may also be the result of differences in the analytical approach used. In our study, the available time-series data included only one study reach on a single river, compared to experimental approaches where these elements of replicability and repeatability can be maximised. Additionally, the differences in data availability for our time-series necessitated adjustments to the calculation method of components which could alter their interpretation compared to previous studies.

A recent meta-analysis of ecosystem stability in experimental studies reported that novel ecosystem trajectories following pulse disturbances are rare although the absence of compositional recovery was regularly recorded (Hillebrand & Kunze, 2020). However, our results indicate that unmodified river systems could respond to disturbances differently to experimental studies, in which the arena is likely to be controlled to enhance replication. Physical disturbances not only have the capacity to directly impact biota but can substantially alter the physical environment within which an ecosystem persists post-disturbance. Extreme floods have been shown to substantially alter river channel and floodplain morphology (Pasternack & Wyrick, 2017) and such extreme alterations to the physical environment may increase the likelihood of novel trajectories and the failure of some taxa to establish post-disturbance.

4.4 | Complexity of the stability response in time-series data

Observational time-series studies of disturbance have reported varied ecological responses depending in part upon the components of stability analysed, for instance the resistance and recovery of community composition (Bêche et al., 2009; Fritz & Dodds, 2004; Woodward et al., 2015) or the variability of abundance, density or biomass (Flecker & Feifarek, 1994; Mathers et al., 2018). In our study, individual stability components demonstrated limited responses to the sequence of floods, in contrast to the shifting dimensionality response observed in ellipsoids. This difference further highlights the opportunity the multidimensional stability approach offers to extending our understanding of the processes which govern ecosystem stability, as individually components may be insufficient to capture the complexities of community response (Donohue et al., 2013, 2016). In the current study, the use of the multidimensional stability approach extends our understanding of community response from a previous study of this river's response to floods (Milner et al., 2018). Our results suggest that the winter flood of 2005 dominated the ecological stability response over the 18-year time period, possibly leading to a persistent decoupling of community assembly processes between floods (2006–2014) and post 2014. The time-series approach used here allows the assessment of natural ecosystem stability dynamics to be made, despite the differences to previous experimental and modelling studies already outlined.

This study represents the first attempt to apply dimensionality of ecological stability concepts developed experimentally to time-series community data from an unmodified river system at larger spatial (10^1 m^2) and temporal (18 years) scale than previous studies. The weakening relationships between stability components observed here following flood disturbance are consistent with past manipulative small-scale spatial and temporal work (Barros et al., 2016; Donohue et al., 2013; Hillebrand et al., 2018) and thus, suggest that there may be common processes occurring across ecosystems to regulate the dimensionality of community stability. Cross-ecosystem studies of long-term datasets, experiments and modelling studies would be a valuable next step to confirm this conclusion. Comparative work would aid in the development of a generalised framework for multidimensional stability, which represents an important advancement to allow reliable identification of processes underlying ecosystem stability.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

A.M.M. initiated the study of WPC and collected many of the pre-flood samples; A.M.M., M.J.K., L.E.B. and L.J.B.E. collected and identified post-flood samples; L.J.B.E. and L.E.B. developed the stability application to time-series data; L.J.B.E. undertook analyses and drafted the manuscript; M.W. contributed to the analytical approach. All authors advanced the concept and contributed to writing the final manuscript.

DATA AVAILABILITY STATEMENT

The data has been deposited in the University of Birmingham eData Repository: https://doi.org/10.25500/edata.bham.00000703 (Milner et al., 2021).

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SUPPORTING INFORMATION

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

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