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Research Article

Asynchronous river floodplain environment dampens ecological variability across scales

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Stability patterns can vary across scales within ecological systems. Understanding cross-scale stability patterns can be important for informing conservation and management in landscapes. To identify underlying drivers of stability at local (habitat) and regional (floodplain) scales, both compositional and aggregate variability in terrestrial and aquatic invertebrates, and variability and synchrony between aquatic invertebrates and fish, were investigated in a dynamic floodplain landscape. Synchrony between local aquatic invertebrate communities was low, likely driven by local differences in flood disturbance. However, terrestrial invertebrates had high composition and biomass synchrony, consistent with more homogeneous terrestrial conditions (e.g. temperature). Fish biomass had lower variability than aquatic invertebrates, indicating mobile predators may benefit from spatially heterogeneous conditions. Preserving spatial environmental heterogeneity will therefore likely be important for maintaining landscape-scale stability across multiple trophic levels in dynamic river environments.

Keywords: floodplain, landscapes, metacommunity, meta-ecosystem, mobile consumers, temporal variability

Introduction

Scale of observation can mask patterns and processes in ecology (Wiens 1989), and investigating scale influences on ecological stability is important for a fuller understanding of stability mechanisms (Pimm 1984, McCluney et al. 2014). Variability is one component of stability frequently measured in empirical studies, and insights from across-scale variability patterns are important for informing conservation in complex and dynamic landscapes where landscape properties often emerge from underlying local processes (McCluney et al. 2014, Gounand et al. 2018, Scholl et al. 2023). However, understanding variability patterns at larger spatial scales requires quantifying impacts of both local and regional spatial heterogeneity on community variability (Wang and Loreau 2014, Lamy et al. 2021). Given the complexity of gathering sufficient spatial

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and temporal data, particularly in dynamic landscapes, an empirical understanding of the spatial aspects of community variability is still developing, including relationships between communities, trophic levels, and ecosystems. Bridging the gap between theory and empirical research for complex landscapes will not only aid conceptual understanding of stability but also increase application to conservation of threatened landscapes.

Identifying changing patterns of temporal variability from local patches to whole landscapes is a key challenge in this quest for understanding mechanisms that dampen variability in empirical systems. Organisms across trophic levels, sizes and behavioural patterns interact with landscapes at different scales, such that observed patterns depend on scale (Wiens 1989). Yet, the drivers of variability across spatial scales, and the relationship between communities of resources and communities of consumers across spatial scales, are not well understood in empirical settings. It is possible consumers moving at larger spatial scales than their prey should have dampened regional variability by taking advantage of dampened regional resource variability (McCann et al. 2005, Siqueira et al. 2024). However, consumers also typically have smaller populations thus could be more stochastic or impose strong top–down controls increasing consumer–resource boom bust dynamics, both mechanisms which would show patterns of increased consumer variability (Siqueira et al. 2024). Incorporating both metacommunity and foodweb theories can inform how dampened variability could propagate through food chains and across species operating at different scales, thereby enhancing our understanding of landscape scale variability (Siqueira et al. 2024). Such insights suggest that classifying the mechanisms important for dampening ecological variability at larger spatial scales will be particularly useful for directing the management needed to maintain complex ecosystems threatened by incremental reductions in physical heterogeneity (Caruso 2006, Molina et al. 2018).

Interpreting the underlying processes driving patterns of variability requires investigating both species composition and aggregate biomass dynamics (Micheli et al. 1999, Lamy et al. 2021). The contributions of spatial biodiversity mechanisms, and the stabilising role of biodiversity, could both be of high importance to landscape-scale stability. For example, connected systems involving species with varying environmental responses may result in different species phenologies driving temporal asynchrony in population biomasses (compensatory dynamics). Additionally, species richness can create shared functional diversity for maintaining ecosystem processes (portfolio effects; de Mazancourt et al. 2013, Loreau and de Mazancourt 2013, Hallett et al. 2014). Conversely, spatially aggregate biomass dynamics could indicate whether environmental drivers are spatially coupled or decoupled, thereby clarifying when environmental processes are contributing to (a)synchrony and consequently stability (Rooney et al. 2006, Wang and Loreau 2014, Lamy et al. 2021). Therefore, both compositional diversity and environmental variability could confer stability in landscapes, necessitating the investigation of both (de Mazancourt et al. 2013, Hallett et al. 2014, Lamy et al. 2021).

River floodplains are complex landscapes where interactions between habitat heterogeneity, diversity and connectivity form an ideal case study for investigating such cross-scale variability (Hauer et al. 2016, Harris et al. 2024). These ecosystems likely have different patterns of landscape and channel scale variability and are threatened by anthropogenic simplification (Ward and Stanford 1995, Opperman et al. 2010, Doering et al. 2011). In particular, braided rivers have mobile and differentially-disturbed channel types formed across lateral floodplains with strong differences in physical characteristics, such as flow, size, temperature and turbidity (Gray and Greenwood 2016, Harris et al. 2024). Moreover, these channels are linked by fish and bird species moving throughout the landscape and likely have tightly interlinked cross-ecosystem subsidies (Greenwood and McIntosh 2008, Hauer et al. 2016). These rivers are model landscapes for investigating the primary mechanisms dampening variability across scales, because species movement and channel dynamism create conditions where multiple stability mechanisms are possible. Braided river floodplains in Aotearoa New Zealand represent a globally threatened environment type, facing pressures such as land encroachment, weed invasion, and water abstraction that can lead to a loss of connectivity with lateral springs and eventually more channelised river systems (Gray and Greenwood 2016). Thus, braided rivers provide an opportunity to apply this theory to a threatened ecosystem.

Here, we investigated how variability changed across scales in a braided river landscape, focussing on how local-scale spatial heterogeneity influenced temporal cross-scale community variability of fish and both land-based and aquatic macroinvertebrates. Using variability scaling frameworks allows insight into the relative contributions of local processes, such as biodiversity and spatial asynchrony, to the dampening of regional variability. We hypothesized that (H1) dampened regional variability would be primarily driven by spatial asynchrony in community biomass rather than compositional asynchrony and other population level processes. If high spatial asynchrony was detected, we hypothesized that (H2) high environmental spatial heterogeneity would be enhancing the asynchrony of local aquatic communities, because patterns in invertebrate community abundance and composition would be filtered by asynchronous environmental conditions such as flow and temperature. On the other hand, if aquatic communities were synchronous, connectivity and dispersal were likely having larger impacts than expected (Rooney et al. 2006, Danet et al. 2021, Siqueira et al. 2024). Furthermore, we expected that (H3) fish would have lower local- and regional-scale variability than aquatic invertebrates, because mobile consumers should have better access and choice of sites and thus show dampened dynamics if taking advantage of multiple areas of the landscape (Rooney et al. 2006, Danet et al. 2021, Siqueira et al. 2024). By investigating patterns of variability across spatial scales, ecosystems, and trophic levels in one river with high levels of replication we provide a rare case of empirical work on a single, highly dynamic system, where inference of cross-scale and cross-trophic level relationships can begin to be drawn. Additionally, these patterns are complemented by a large amount of abiotic data for the aquatic system,providing glimpses of the underlying biotic-abiotic relationships in the same study.

Material and methods

Study system

Between May 2022 and February 2024, we studied Te Awa-a-Takatamira, Cass River, Takapō, New Zealand (43°52’60”S, 170°29’05”E, ~ 700 m a.s.l.), a relatively intact braided river (38 km long and up to 1.5 km wide), with channels that vary in space and through time (Harris et al. 2024, Fig. 1A, Supporting information). Different channel types in intact braided rivers such as this house different invertebrate taxa and have diverse hydrological patterns (Gray and Harding 2010, Karaus et al. 2013, Fig. 1A).

Sampling regime

We quantitatively sampled fish and aquatic invertebrates within a 3.5 km long by 1.5 km wide area on the lower Te Awa-a-Takatamira (Fig. 1A). We took samples from channels intersecting four transects within this area every 6–10 weeks. Five channel habitat types were delineated based on Gray and Harding (2007): 1) lateral springs, 2) lateral tributaries, 3) minor channels, 4) major channels, and 5) mid-channel springs. We sampled invertebrates from five rocks (15–30 cm in length) in each channel with a kicknet, with up to three channels of each ‘type’ sampled on each transect. This gave a measure of area (rock area) to standardise invertebrate counts and provided robust but feasible invertebrate density measures across channel spatial heterogeneity, whilst maintaining reasonable sample processing time (Calow 1972, Bergey and Getty 2006). Fish were sampled every second visit (12–20 weeks), with three 2-m^2 reaches in each channel using an electrofishing machine (Smith-root LR-24), and push net. Captured fish were identified, counted, total length was measured, and then they were returned to the river.

To investigate variability across spatial scales of invertebrates in a contrasting environment to those of the aquatic systems, we used pitfall trap samples collected in the same area as the aquatic samples, with some overlap in timing between field campaigns. Terrestrial invertebrates were sampled with land-based pitfall traps during the summer months (November–February) for four years starting in November 2019 and ending in December 2022. The traps were placed every 6 m in a line, with five traps along three lines 100–300 m apart. Each trap contained 33% solution of ethylene glycol (Brown and Matthews 2016) and was placed with four guiding barriers (metal strips, 500 mm long by 100 mm high) positioned in a cross from the edge of each trap. The traps were left open for five nights and six days to give consistent catch per unit effort (CPUE).

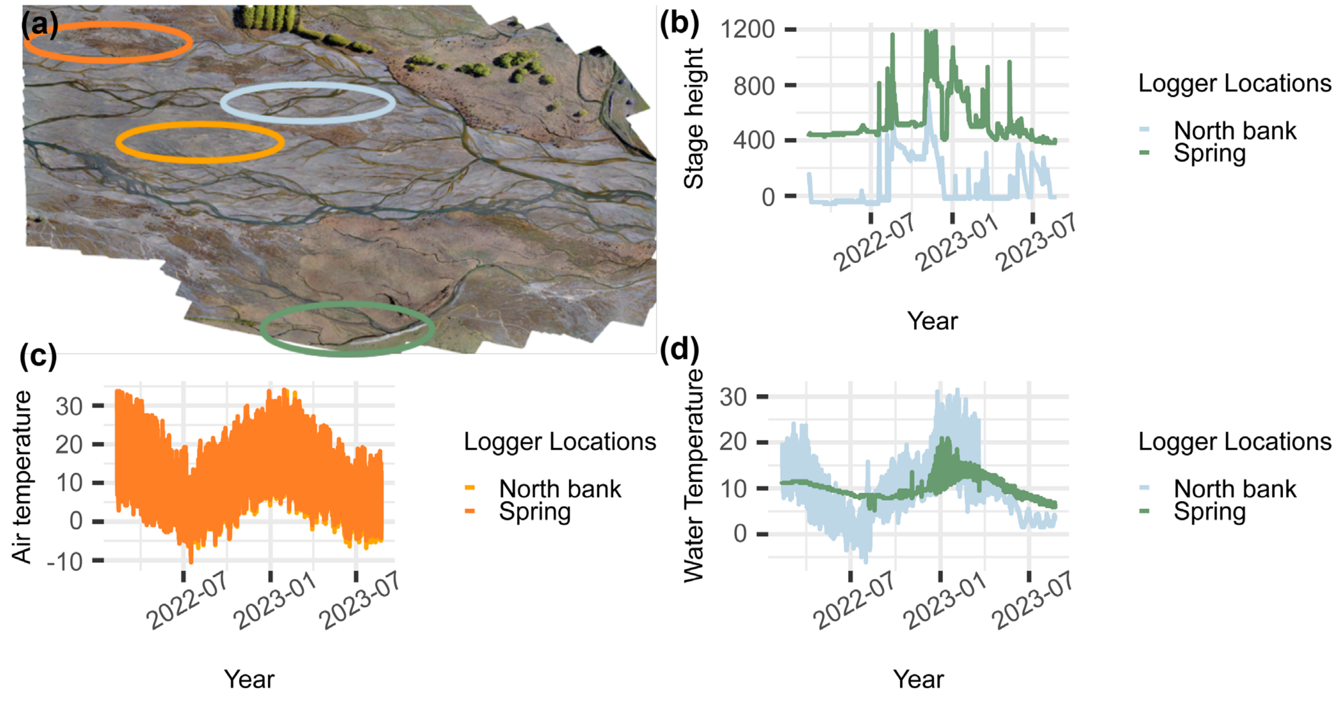

Figure 1. Patterns in measured braidplain meta-ecosystem physical systems over time where different habitats (highlighted with different colours) were either spatially heterogeneous like aquatic minor channels and springs (examples in blue and green in (a), respectively) indicated by water temperatures (°C) and flow gauge stage heights (mm; (b) and (d)), or homogeneous, like terrestrial gravel and cushion vegetation habitats (light and dark shades of orange in (a), respectively) indicated by air temperatures (°C; (c)). Abiotic data (b–d) here is continuous data used for illustration and was not the abiotic spot measures used in analysis.

Abiotic data

At each channel temperature (°C) and dissolved oxygen (DO, mg l^{-1}, YSI EcoSense ODO200), turbidity (NTU, Eutech TN100), three cross-sectional widths (m), and six depths across the channel (m) were measured.

Flow-related disturbances were calculated using two metrics. First, aerial imagery was taken for the whole study area during each sampling period with a Phantom 4 drone. From this imagery, we calculated a metric of channel presence over time, giving a proxy disturbance metric for each individual channel sampled (Supporting information). This metric was calculated as proportion of images that a sampled channel was present in, divided by total number of images that had been taken at the time of sampling. Thus, a value closer to 1 would be considered a channel present more consistently and closer to 0 would be a channel that disappeared very quickly. Second, a regional flow-disturbance metric was calculated from four stage height loggers placed across the braidplain: 1) at the bridge upstream from the study area, 2) the north bank of the study area gravel plain, 3) the south bank of the study area gravel plain, and 4) the groundwater spring at the southern end of the study area. These loggers continuously measured variability in water height and temperature, and air temperature across the braidplain. The stage heights were averaged then subset into the stage heights measured in the month prior to each sampling. The maximum stage height within each of those periods was used as the maximum river height for that period thus giving an indication whether a potentially synchronising flood event had occurred prior to sampling.

Biotic data

Samples from each rock were pooled to channel site level, and aquatic invertebrates were identified to the lowest taxonomic unit (predominantly genus; Winterbourn 2006). The first 11 individuals of each taxon at each site were measured using a calibrated eyepiece micrometre on a compound microscope and all subsequent individuals were only identified and counted. For each taxon at each site, a normal distribution (bounded by 0) was created from the first 11 measurements and values from these distributions were assigned to the non-measured taxon to produce length estimates for all non-measured individuals (similar to Danet et al. 2021). Length-dry weight regressions were applied to all fish and aquatic invertebrate lengths to calculate individual biomass (Towers et al. 1994, Stoffels et al. 2003, Jellyman et al. 2013). Biomass was then divided by area sampled (6 m^2 for fish, total rock area for invertebrates) to get a measure of biomass per square meter.

Pitfall invertebrates were placed in 75% ethanol and invertebrates > 2 mm were identified to the lowest recognizable taxonomic unit (RTU; Oliver and Beattie 1993) and counted by an expert at the Department of Conservation using reference specimens and photographic reference collections.

Variability calculations

To understand the different components of variability, such as changes in composition and changes in biomass, we followed the methods of Wang et al. (2019) and Lamy et al. (2021), calculating biomass variability (squared temporal coefficients of variation, all reported as CV^2, from g m^{-2} or counts). These values were calculated at a local (α), and regional (Υ, whole-river aggregate) scale, and at both community and population levels for aquatic invertebrates. Only community level values at local and regional scales were calculated for pitfall invertebrates respectively and fish, separately, as the focus of this study is primarily on community level dynamics, and fish communities had only small numbers of species ($n=2$–4). Additionally, turnover (Hellinger beta diversity) was calculated for aquatic invertebrates and terrestrial invertebrates at local and regional scales. Hellinger beta diversity accounts for the relative abundances of different species between sites, thus allowing comparisons between sites and between scales (Lamy et al. 2021). Finally, synchrony (φ) between local and regional community biomass variability and between local and regional beta diversity was calculated following Lamy et al. (2021), to understand the contributions of local community composition and variability to regional dynamics.

Communities (local scale, α) and meta-community (regional scale, Υ) sites for aquatic invertebrates and fish were delineated following methods in Gray and Harding (2007) where each channel type (major, minor, mid-channel springs, springs, and tributary) was used as alocal scale community and all channels summed together were used as the landscape scale (hereafter referred to as regional scale, Υ).

Both pitfall and aquatic invertebrates had the same number of total temporal samples ($n=12$) and were sampled over their respective active seasons within years, thus the values calculated are considered relevant to the biological organisms involved. Means per-channel 'type' (for aquatic invertebrates and fish), or 'line' (for land-based invertebrates) were used, which allowed assessment of the within-habitat spatial uncertainty and calculation of more reliable estimates of temporal means at larger scales. Pitfall invertebrate communities were delineated to the pitfall 'line' scale with the regional scale including all pitfall lines. Invertebrates in pitfalls could not be combined into the same analysis as aquatic invertebrates due to methodological sampling differences; however, synchrony between spatial scales is important to within-system variability dampening, and can be contrasted between systems, thus have been included for completeness. For more details on variability metrics and calculations see the Supporting information.

Asynchrony in abiotic measurements

Asynchrony between physical characteristics of different abiotic channels (spot measurements from channels) and air temperature from three continuous stage height loggers across the floodplain (north bank, south bank and bridge site) was measured following Dunkle et al. (2025). Scaled data were z-transformed and correlation between habitats was calculated using mean pairwise Pearson correlation coefficients.

Relationships between environmental variables and biomass

To test the relationship between biomass at each site and the environmental characteristics of sites, we used a generalised linear mixed model (GLMM, Gaussian distribution). The GLMM had an autoregressive component to account for temporal autocorrelation between months, and spatial autocorrelation within transects. Biomass was $\log_{10}$-transformed to meet the assumptions of normality and homoscedasticity. The model was analysed with the 'glmmTMB' package ver. 1.1.10 (Brooks et al. 2017). The 'performance' package ver. 0.12.4 (Lüdecke et al. 2021) was used to test for overdispersion (not detected), and likelihood-ratio test was performed to test the model fit against a null model.

Measuring the impact of habitat accrual on regional variability

To test the influence of channel habitat type and increasing spatial heterogeneity on regional community variability of our aquatic invertebrates across a range of all possible sampled values the raw data was bootstrapped. Data was bootstrapped as it was outside the scope of this study to additionally sample across a range of similar river systems with varying degrees of spatial homogenisation incorporating enough replication to compare changes statistically. While the bootstrap is not always an appropriate analytical technique, here we have a large empirical sampling regime to draw from, giving more confidence in the distribution of possible biomass values that could be found in a given channel type, thus giving more confidence in the true potential distribution of values (Rubin 1981). This approach allowed us to leverage the existing data to firstly, identify both potential asymptotes in variability associated with the number of channel habitats accrued and the range of possible outcomes in regional variability when specific habitats were lost across a broad range of possible values. Secondly, the bootstrap allowed the identification of the relative contributions of specific habitats to variability dampening at certain stages of habitat loss (decreasing number of habitats) or restoration (increasing number of habitats). The aim of this bootstrapping was thus to provide an evaluation of the practical implications from variability scaling theory using empirical data and so provides a starting point for future work and management.

To bootstrap these data, random samples were drawn 999 times from the possible biomass sums measured in each channel at a given time and for a given channel type (Supporting information). This gave 999 draws of possible biomass for each channel type at each time, thus amplifying the variety of possible sampled biomass values in a channel type. From these draws, 100 samples were taken for each habitat at each timepoint, thus generating 100 'river' data frames. Five different regional community $CV^2\Upsilon$ values were calculated from these data frames, each $CV^2\Upsilon$ with an additional channel type. This resulted in 500 values of $CV^2\Upsilon$ with 100 values for each level of channel type accrual, representing scenarios with one channel type to scenarios with up to five channel types. The addition of channel types was first done in non-random order (major, minor, mid-channel spring, spring, tributary) mimicking the sequence that habitats are typically lost and disconnected from these types of river floodplains. For example, due to environmental pressures such as land encroachment and weed invasion, lateral springs are typically disconnected from the central gravel braidplain or lost completely, and with increasing pressure and encroachment flows become more channelised until a once highly dynamic braided river can end up with one major channel or with the occasional minor channels and some additional minor channel formation with increasing flows (Barquín and Scarsbrook 2008, Gray and Greenwood 2016, Stecca et al. 2019).

To test whether the non-random loss of specific channels led to higher variability at each level of channel habitat aggregation than expected from random, this process was then repeated but randomly selecting channel types for each of the 1–5 habitat aggregations, allowing many combinations of channel types for each level of aggregation (Supporting information). The random combinations thus provided a null model for each level of aggregation (except the combination of all five channel types, where all combinations are the same between random and non-random). We used a paired t-test to compare the regional $CV^2\Upsilon$ calculated with the non-random method to the random method of habitat accrual. This allowed some inference around what may happen to regional $CV^2\Upsilon$ with the non-random loss of habitat, and whether some habitats were contributing more than others to differences in regional variability.

Measuring the change in variability between trophic levels

Finally, for each of the 100 randomly sampled communities with all five channel types, we compared the local variability and synchrony of invertebrates to the local variability and synchrony of fish to see whether there was a significant reduction in local scale variability and an increase in synchrony with an increase in trophic height (from invertebrates to fish). The invertebrate biomasses were subset to the same sample dates as the fish to make temporal variability of the different trophic levels comparable. We used a Welch two sample t-test to test for differences in local variability, regional variability, and synchrony between aquatic invertebrates and fish which allowed us to test H3. Local and regional standard deviations were also compared and reported in the Supporting information.

All analysis was conducted in R ver. 4.3.1 'Beagle scouts' (www.r-project.org).

Results

Cross-scale invertebrate variability

We describe variability patterns between local (α) and regional (ϒ) scales for aquatic and terrestrial invertebrates below, starting with aquatics. Aquatic invertebrate community biomass was more variable at local ($CV^2\alpha_{community} = 0.54$; Supporting information) compared to regional scales (CV^2

$\Upsilon_{community} = 0.12$), with invertebrate community biomass peaking at different times in different channel types throughout the study period (Fig. 2A). For example, biomass in spring channels peaked in February and April 2023, whereas minor channel biomass increased from April through June

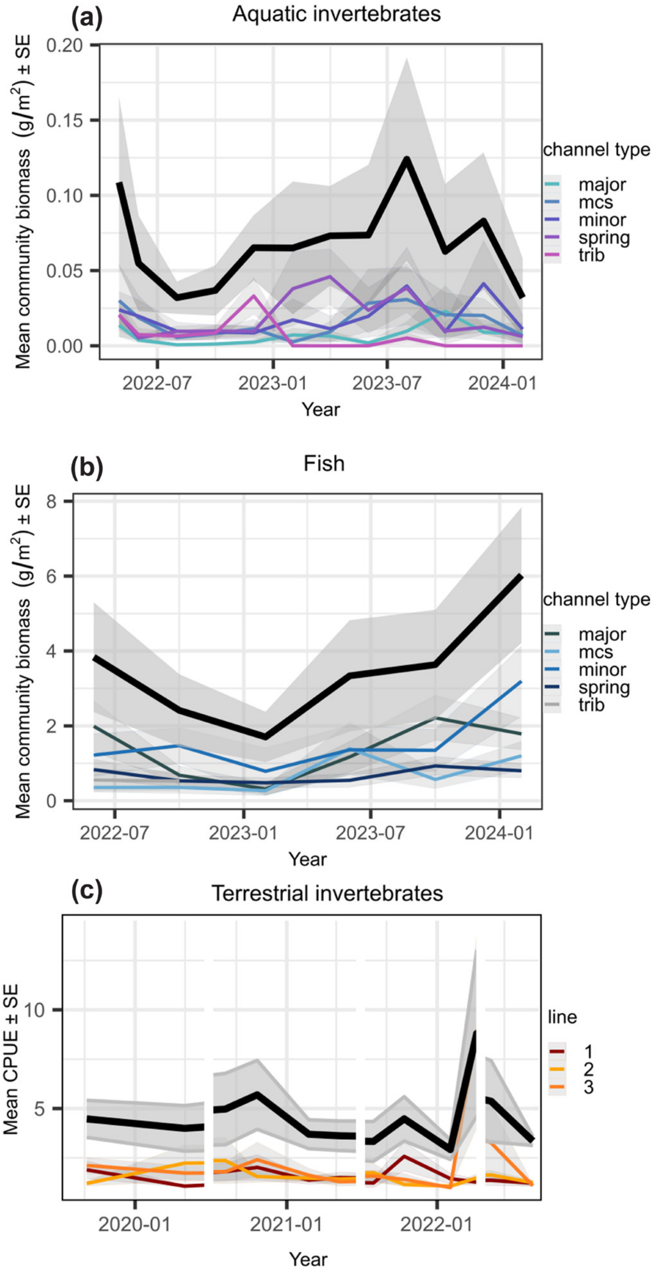

Figure 2. Contrasting temporal patterns in community biomass at regional scales (black lines) for aquatic invertebrate (a) and fish biomass (b), and pitfall trap terrestrial invertebrate catch per unit effort (CPUE, number per trap; (c)) measured across Te Awa-a-Takatamira | Cass River. Coloured lines indicate the underlying community biomass for each channel type (greens (a) and blues (b) respectively), or each pitfall line (oranges (c)) and grey ribbons show the standard error for each community. Note differences in y-axis for greater clarity in patterns, and differences in date for (c) relating to different datasets.

2023 (Fig. 2A, Supporting information). This variable timing of biomass peaks in different channel types led to low synchrony in biomass between channel types, with a synchrony (φ) value of 0.23 (Supporting information), where 1 is completely synchronous and 0 is completely asynchronous.

The compositional turnover in aquatic invertebrate species that underlie these local-scale aquatic biomass dynamics appear largely synchronous between sites (Supporting information). However, there were some subtle differences in population-level biomasses between sites. For example, Chironomidae had the largest biomass across all channel types and while their biomass peaked over summer in all local sites and dipped again the following winter, there were smaller peaks in abundance through winter in the mid-channel and minor springs (Supporting information). Additionally, there was some biomass asynchrony between populations of Ephemeroptera, Plectoptera and Simulidae within channels, and some asynchrony within populations between channels (Supporting information). These between channel type differences in population dynamics (compensatory dynamics) were particularly pronounced in the minor channels, where timing of biomass peaks varied between species (Supporting information). By comparison, population biomasses in major channels were more synchronous (Supporting information).

These patterns in population biomass contributed to both dampened local community stability ($CV^2\ \alpha_{population} = 2.11$ to $CV^2\ \alpha_{community} = 0.54$; Supporting information) and dampened regional community stability ($CV^2\ \Upsilon_{population} = 0.85$ to $CV^2\ \Upsilon_{community} = 0.12$, Supporting information). Additionally, there was some dampened temporal turnover (compositional variability) of aquatic invertebrate species at a regional scale because the invertebrate beta diversity metric declined from 0.34 at the local scale ($Beta^2\alpha$) to 0.23 at the regional scale ($Beta^2\Upsilon$; Supporting information). While most biodiversity was shared between channel types, the spring channel community composition had little overlap with other channel types increasing regional species richness (portfolio effects, Supporting information). Despite these subtle changes in species composition and dampened regional turnover, beta diversity synchrony between channel types was high, at 0.67 (Supporting information). Overall, there was a complex interplay between asynchronous habitats and asynchronous species biomasses across local braidplain habitats.

In contrast to the aquatic invertebrates, invertebrate counts from terrestrial pitfall traps were largely consistent between pitfall lines (Fig. 2C). These terrestrial invertebrates had high local scale (i.e. between line) count synchrony ($\varphi = 0.71$, Supporting information). Temporal beta diversity turnover of terrestrial invertebrates was also high locally ($Beta^2\alpha = 0.66$) and regionally ($Beta^2\Upsilon = 0.51$), but beta diversity synchrony between pitfall lines was also high, measured as 0.77 (Supporting information). Thus, terrestrial turnover in invertebrate composition was similar between lines. Peaks in Hymenoptera were observed during the last summer period of sampling in 2022/2023, driving a peak in total CPUE (Fig. 2C). Overall, terrestrial invertebrates were much more spatially synchronous that aquatic invertebrates.

Physical landscape heterogeneity

The spatial variability in invertebrate communities observed mimicked the dynamism in the physical environment. Aquatic invertebrate biomass was correlated with channel disturbance, which varied among channel types, maximum flow from the month prior to sampling, and channel temperature (Supporting information). Thus, spatial asynchrony in aquatic invertebrate biomass could be associated with a combination of seasonal differences in temperature, the different flood disturbance regimes affecting channel types, and whether there had been a synchronising disturbance event (Supporting information, Fig. 1B–C).

Large-scale environmental drivers such as temperature and disturbance history set the scene for the degree of synchrony in local scale biomass dynamics occurring across different local communities (Fig. 1B–D, Supporting information). There were differences in stage height peaks at different locations across the river and temperature was less variable in springs than connected channels such as main braids (Fig. 1B–C, Supporting information). The most pronounced differences in the environment were either seasonal, for example temperatures in all areas of the river were lower in the winter than the summer, or aseasonal where large flow events synchronously disturbed almost the whole river (Supporting information). However, there were still marked differences in disturbance history and turbidity measured between channel types. By comparison, air temperature was synchronous across the river (Fig. 1D, Supporting information). Correlation coefficients between aquatic sites varied between 0.57 (57% synchronous) and 0.87 (87% synchronous) when considering all abiotic variables measured. Major and minor channels were the most synchronous and springs and minor channels were the least synchronous (Supporting information). Thus, there were measurable spatial differences in the physical properties of the various aquatic environments, and they were stronger than the spatial differences measured in the terrestrial environment. Flow variability, measured by channel presence over time and maximum stage height before sampling, had a strong effect on aquatic invertebrate biomass (Supporting information). Other environmental variables such as turbidity and channel width had weak negative effects on aquatic invertebrate biomass while temperature had a weaker positive effect (Supporting information).

Differences in community variability and synchrony across trophic levels

Next, we compared aquatic invertebrate variability to that of fish to measure how variability transferred across trophic levels. Fish biomass had significantly lower variability than invertebrates at both local ($t=-145.06$; df, 197.65; $p < 0.001$) and regional scales ($t=-151.48$, $df=195.45$, $p < 0.001$). This can be seen in Fig. 2, where aggregate fish biomass at local sites was variable, but with smaller differences between the peaks and dips than that of the equivalent invertebrates. Additionally, fish had lower biomass synchrony among channel types than invertebrates ($t=-32.38$, df $=99.01$, $p < 0.001$). Overall, fish showed dampened dynamics compared to that of the aquatic invertebrates despite being subjected to the same local scale environmental pressures.

The impact of spatial heterogeneity on regional variability

Finally, we examined the relationship between channel type and regional regional-level aquatic invertebrate variability, to gain a greater understanding of how the relationship between increasing physical habitat heterogeneity and decreasing regional biomass variability might be influenced by particular habitats, and variability within habitats. The channel type accrual effect had diminishing returns on the bootstrapped reduction in regional variability, with the change from one to two channel types resulting in the highest reduction in regional variability, and regional CV beginning to approach an asymptote at 4–5 habitats (Fig. 3). The sequential non-random addition of channel types to the regional pool resulted in significantly lower regional variability at one and two channel types than the random addition of channel types, but higher variability than random at three and four habitat types (Supporting information). This demonstrates that the non-random loss of certain aquatic habitat types could have a large impact on variability when there are fewer habitats. Habitats such as minor channels contributed disproportionately to creating asynchronies within the river than others when there were fewer habitats in the scenario, and thus higher regional-scale variability would be expected without them (Supporting information). The bootstrapping approach provides evidence that even across the large range of possible biomass values that are found in these different channels there is high likelihood that braided rivers preserving 4–5 habitats will have lower regional variability than those with fewer habitats despite the wide range of potential values found in these channel types (Fig. 3).

Discussion

Understanding the processes driving stability of large complex ecosystems is integral to maintaining the biodiversity and processes they support (Peipoch et al. 2015, Donohue et al. 2016, Hauer et al. 2016). Our unveiling of differences in patterns of community variability across scales and between trophic levels in an empirical setting reveals the components required to dampen variability of a complex landscape. Our results showed, firstly, that aquatic invertebrate biomass was driven by channel disturbance history and flow, which varied between channel types resulting in asynchronous biomass fluctuations (H1 and H2). Secondly, some habitats, such as minor channels, contributed disproportionately to the spatial dampening of biomass variability, and others such as the springs contributed to the spatial portfolio of invertebrate species within the braidplain (H1 and H2). Finally, variability of the higher trophic level mobile species, the fish, was lower than that of the invertebrates sampled within the same location (H3). This indicates mobile predators may be able to take advantage of the spatial heterogeneity and more

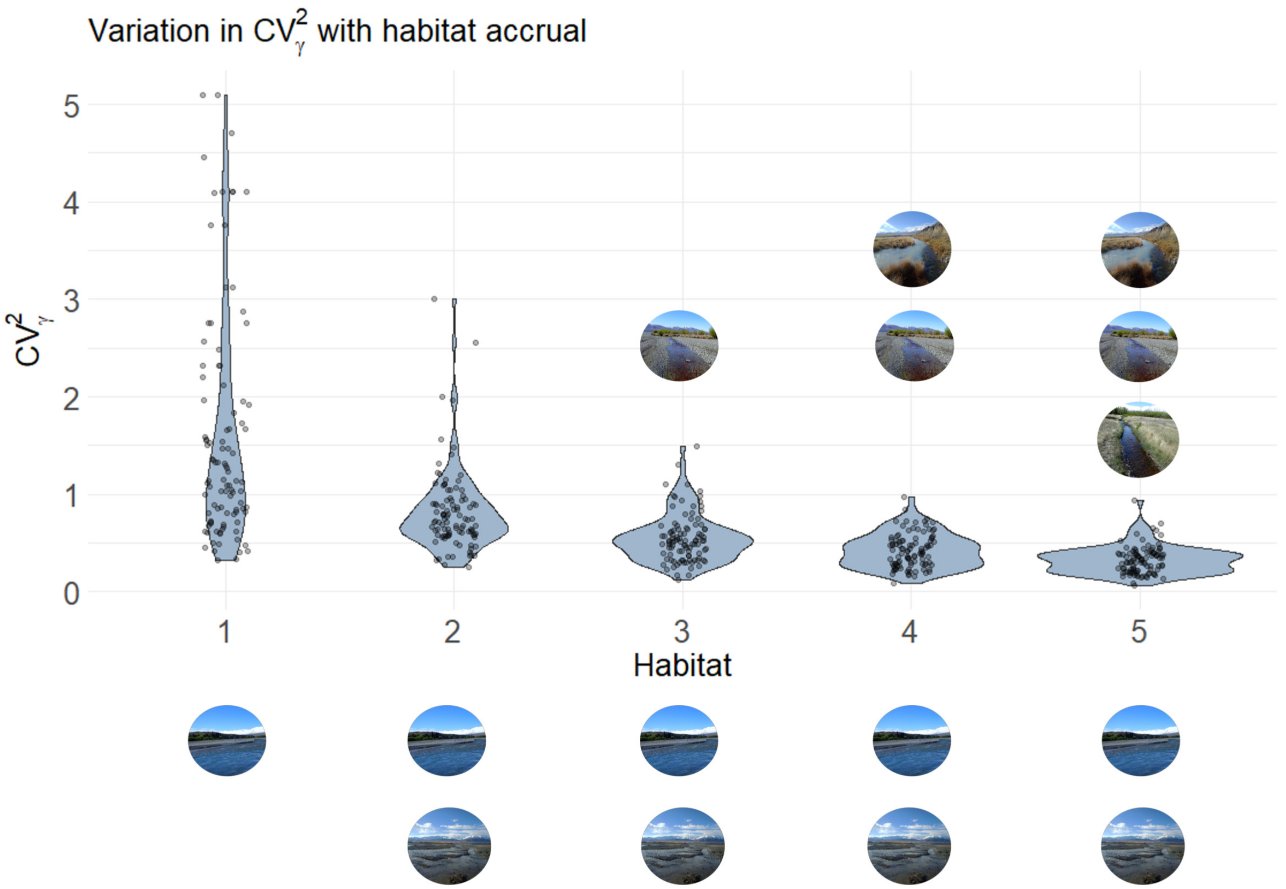

Figure 3. Bootstrapped regional coefficient of variation (CV2ϒ) with changing number of aggregated habitats within a landscape, and violin shapes indicating the changing distribution of data along the y-axis for each increase in habitat number. In this analysis habitats were added sequentially, with 1) habitat corresponding to a river with a major channel; 2) habitats corresponding to major and minor channels; 3) corresponding to major, minor, and mid-channel springs; 4) corresponding to major, minor, mid-channel springs and lateral springs; and five corresponding to major, minor, mid-channel springs, springs and tributaries.

consistent landscape-scale resource availability. Thus, we have shown empirically that landscape heterogeneity not only produces less variable metacommunities but could set a template for more stable food webs. This finding provides important support from a real ecosystem to theory in a burgeoning field of spatial food web dynamics. Below, we discuss the patterns that underpin this general conclusion and consider the implications of our findings for both heterogenous landscapes generally and the river floodplain ecosystems we examined.

Asynchrony promotes dampened variability in meta-populations and communities (Liebhold et al. 2004, Abbott 2011, Wang and Loreau 2014). In our system, the underlying drivers of asynchrony between aquatic invertebrate communities were likely to be environmental processes such as flow-driven habitat heterogeneity that was correlated with invertebrate biomass (Hallett et al. 2014, Wilcox et al. 2017, Lamy et al. 2019, Wang et al. 2019, Walter et al. 2023). Our aquatic invertebrates were much less variable at broader spatial scales (H1) due to asynchronies in local communities, driven by spatial differences in flow-disturbance (H2). Specifically, the high disturbance rates of major channels and minor channels, compared to mid-channel and lateral springs, resulted in community biomass suppression in parts of the river during high flow events, but not the whole river. These results are consistent with prior findings from Te Awa-a-Takatamira, suggesting disturbance plays a large role in invertebrate biomass dynamics (Pierce 1986). This spatial heterogeneity in flow-related disturbance likely contributes to meta-community stability by both counteracting any synchronising effects of movement and mass dispersal in connected systems and contributing to the environmental filtering of species within a local area (Liebhold et al. 2004, Abbott 2011, Wang and Loreau 2014). However, differential responses of species were still important, highlighted by low population biomass synchrony but high compositional synchrony between habitats, suggesting that while species were present in habitats there were still between-habitat differences in biomass. Taken together, it is likely contextual spatial processes and the heterogeneous environment drove the dampened variability of communities within the complex regional landscape of our river floodplain system.

Spatial heterogeneity in disturbance appears to play a prominent role in driving community asynchrony but species trait differences can generate similar effects. For example, phenological responses of different species to the environment could generate asynchrony thereby dampening community and metacommunity dynamics (de Mazancourt et al. 2013, Wang et al. 2019). There were likely some compensatory dynamics in our river system, indicated by the dampened regional scale compositional turnover, however, species turnover synchrony was high. High compositional synchrony shows species composition among local communities underwent similar temporal shifts, reducing capacity for species portfolio effects and compensatory dynamics. Additionally, flow and disturbance history of a channel type was a significant predictor of total channel biomass. Together, these results are consistent with findings that high flow stochasticity leads to fewer phenological responses than systems with highly predictable environmental processes (Tonkin et al. 2017, Walter et al. 2023). However, differences in population biomass within communities and between sites still contributed to dampened variability in communities and metacommunities. Therefore, it is likely that there is an interaction between population portfolio effects, compensatory dynamics, and spatial variability in abiotic habitat conditions contributing to dampened regional variability.

The high variability observed in the aquatic environment contrasts with our observations of the terrestrial environment where there was higher spatial synchrony in invertebrate assemblages between different sampling locations. In our study, land-based taxa were likely subjected to much more homogenous large-scale contextual drivers such as air, temperature, and light, which were much more spatially homogenous across our river braidplain than the aquatic system. Thus, in our study system the spatial dynamics of invertebrate species appear largely dependent on the spatial scale of environmental heterogeneity. For example, the strong local variation in flow-related disturbance in the aquatic realm contrasted with the terrestrial variability in temperatures, which likely occurred at much broader scales. These findings indicate the context of the environmental forcing likely determines the relative importance of spatial synchrony or diversity mechanisms, such as grasslands varying in rainfall or river plant communities (Holdaway and Sparrow 2006, Hallett et al. 2014). However, importantly with variability metrics there is a temporal-scaling component, where interannual differences could be the greatest source of variability for some communities and seasonal differences could be more important for others (Tonkin et al. 2017). Thus, understanding variability across different types of communities requires acknowledging species traits, and the potential for interactions with other species and different abiotic drivers across many timescales leading to a myriad of complex outcomes (González-Varo and Traveset 2016, Bieg et al. 2023). Here, it is likely that the spatial and temporal scale of environmental processes plays an important role in the tightly interlinked roles of heterogeneity, biodiversity and asynchrony, particularly in identifying the relative importance of heterogeneity on cross-scale stability.

Regardless of the mechanisms, the dampened regional variability of aquatic invertebrates we observed likely creates more stable food resources for predators that can move between local areas in the landscape (Quévreux and Loreau 2022, Siqueira et al. 2024). In our study system, fish variability at local and regional scales was lower than that of invertebrate communities subject to the same environmental conditions. This finding is consistent with food-web theory, showing spatially coupled resources, through movement or subsidies, create weaker interaction strengths and thus perturbations and disturbances in a food web are dampened (McCann et al. 2005, Bellmore et al. 2015, Quévreux and Loreau 2022). If we had observed higher fish variability, strong top–down local interactions may have played a role in food-web dynamics or stochastic processes may have been more important than local prey dynamics (Siqueira et al. 2024). However, that was not the case, suggesting that food webs in systems with local-scale environmental heterogeneity could be bottom–up driven with spatial asynchrony between locations creating more consistent prey availability (Rooney et al. 2008, Rip and McCann 2011, Siqueira et al. 2024).

Spatial heterogeneity is not the only potential mechanism explaining dampened predator variability; omnivory and reduced intra-specific competition could also play a role (Nakazawa 2014, Gutgesell et al. 2022). However, spatial mechanisms connected to movement and subsidies likely play a larger role in this system. Omnivory requires changes in abundance of prey species over time, but we found species compositional dynamics that were largely synchronous, with certain groups such as Chironomidae and Ephemeroptera consistently more abundant. Additionally, despite kōaro *Galaxias brevipennis* and other fish species being generalists (McIntosh 2000), these fish also prey on the most abundant food resources (McIntosh 2000), which were consistently *Chironomidae* and *Deleatidium* across all channel types. Furthermore, fish consume food from multiple habitat types, presumably in this river system by moving (Harris et al. 2026a), highlighting the importance of bottom–up asynchrony effects on mobile predator variability of species such as fish. Thus, spatial environmental processes likely have propagating impacts, not only on the stability of metacommunities, but also meta-food webs.

Implications for river floodplain systems

Understanding spatial processes, such drivers of asynchrony and how they contribute to the persistence of ecological properties, will underpin informed management decisions affecting landscape heterogeneity (Nyström and Folke 2001, Blüthgen et al. 2016, Larkin et al. 2016). Without distinct local habitats resulting in community asynchronies within a river like ours, there is a much higher chance both of local extinctions and insufficient resources through time for higher level consumers due to increased regional variability in invertebrates. Additionally, we have shown that the non-random loss of habitats could lead to more landscape variability, and the loss of more than two habitats in a system such as this will lead to much more variability in the river system. This is a key finding and additionally we have highlighted that some habitats, such as the minor channels, likely have high contributions to dampening landscape-scale variability whilst others, such as the springs, also contribute to landscape scale diversity. While decreasing regional CV with increasing habitat is, in general, a statistical inevitability, our results demonstrate this reduction occurring across the range of many possible values that could be found in braided river channels and highlight how dramatic increases in regional CV will be much more likely after a specific number of habitats are lost (two or more). To our knowledge the theoretical understanding of CV dampening is rarely applied to habitat management in this way, despite the frequent homogenisation or loss of habitats from ecosystems (e.g. a melting cryosphere; Dunkle et al. 2025). However, for some ecosystem components, such as the terrestrial invertebrates in our system, it is likely that the area required to dampen variability during environmental perturbations is much higher (even multiple river scale) due to high synchrony between local sites on a river. Thus, management decisions need to first identify ecological properties of priority concern before they can begin to identify the appropriate scales of landscape context for management (Guerrero et al. 2013, Herse et al. 2022). Determining scales of management from conservation priorities is particularly important given our results suggest some habitats may not contribute to dampening total variability yet house specific species that are disproportionately valued.

The loss of disproportionately important habitats from these complex rivers landscapes is a significant threat (Gray and Greenwood 2016). For example, synchronising pulse disturbances (such as large-scale flood disturbances) and press disturbances (such as weed invasions) are likely to be of substantial concern because of the ecosystem's reliance on asynchrony and heterogeneity to support rare and threatened wildlife (Peipoch et al. 2015, Gray and Greenwood 2016, Tonkin 2022). These results together suggest that pulse disturbances increase the landscape-scale variability of river systems when they become large enough to spatially synchronise habitats. This will be particularly important when habitats such as springs become lost, with compounding effects of land-encroachment and weed invasion also reducing the heterogeneity of the whole landscape. Our results, consistent with prior findings (Cross et al. 2013, Chanut et al. 2019), suggest that the impacts of changing disturbance pressures and loss of habitat heterogeneity on invertebrate metacommunities will likely have effects that could propagate through food webs to consumer species.

Conclusions

Our observations highlight the importance of incorporating multi-scale and multi-species information into our understanding of ecosystem variability (Lamy et al. 2021, Siqueira et al. 2024). We have shown that maintaining spatial heterogeneity through the conservation of multiple channel types across a braidplain will likely dampen variability within the floodplain landscape, not only of invertebrate metacommunities, but also of species that consume them such as fish. Additionally, while some habitats contribute more to dampening variability than others, these are not necessarily the same habitats that contribute to increasing landscape scale biodiversity, so diversity and variability should be considered concurrently. These results are useful not only in supporting ecological theory but importantly show the value of theoretical ecology for informing landscape-scale management decisions in complex environments. Thus, we highlight the importance of considering spatial scales and trophic levels together in stability research to improve understanding of the effects of environmental and biodiversity processes on enhancing ecosystem stability.

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Author contributions

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Data availability statement

Data are available from the Figshare: https://figshare.com/s/4845ee6e5aa141b52300 (Harris et al. 2026b).

Supporting information

The Supporting information associated with this article is available with the online version.

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