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Latitudinal metacommunity gradients in New Zealand stream invertebrates

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Abstract

That biodiversity declines with latitude is well known, but whether a metacommunity process is behind this gradient has received limited attention. We tested the hypothesis of a shift from dispersal limitation to mass effects with increasing latitude, along with a series of related hypotheses. We explored these hypotheses by examining metacommunity structuring in stream invertebrate metacommunities spanning the length of New Zealand (~1300 km), further disentangling the role of dispersal by deconstructing assemblages into strong and weak dispersers. Given the highly dynamic nature of New Zealand streams, our alternative hypothesis was that these systems are so unpredictable (at different stages of post-flood succession) that metacommunity structuring is highly context dependent from region to region. We rejected all of our primary hypotheses, pinning this lack of fit on the strong unpredictability of New Zealand's dynamic stream ecosystems and unique fauna that has evolved to cope with these conditions. While local community structure turned over predictably along this latitudinal gradient, metacommunity structure was highly context dependent and dispersal traits did not elucidate patterns. Moreover, the emergent metacommunity types exhibited no trends, nor did the important environmental variables. These results provide a cautionary tale for examining singular metacommunities. The considerable level of unexplained context dependency suggests that any inferences drawn from one-off snapshot sampling may be misleading and further points to the need for more studies on temporal dynamics of metacommunity processes.

Keywords: Metacommunity structure; metacommunity types; latitudinal gradient; environmental stochasticity; stream community

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Introduction

Latitude is a key factor regulating biodiversity globally (Hillebrand 2004, Jocque et al. 2010), but other factors such as seasonality and predictability of local environments can strongly influence this relationship. As a key mechanism behind the latitudinal diversity gradient, climate increases in harshness with increasing latitude (Stevens 1989). However, many other factors influence local climate including island size and the level of isolation. Isolated oceanic islands, for instance, have lower seasonality and predictability than similarly placed continental locations (Tonkin et al. Under review; Fig. 1). Jocque et al. (2010) argue that shifts in climatic stability with latitude drives a dispersal–ecological specialisation trade-off at the metacommunity level, producing gradients in dispersal ability, ecological specialisation, range size, speciation and species richness.

Community differences attributable to latitude are therefore likely to be driven by underlying metacommunity processes. Four metacommunity paradigms have been synthesised to summarise the relative roles of local (niche) and regional (dispersal) processes in community assembly (Leibold et al. 2004, Holyoak et al. 2005): neutral, patch dynamics, species sorting, mass effects (in order of increasing importance of dispersal). The importance of dispersal, in particular, will depend on many factors including the spatial extent of a metacommunity and amount of environmental heterogeneity present between sites (Mykrä et al. 2007, Heino et al. 2015a). Spatial extent can regulate the role of species sorting (i.e. environmental filtering), ranging from mass effects (i.e. dispersal overriding local niche sorting) in highly connected systems to dispersal limitation at large spatial extents (Heino et al. 2015b). What remains to be tested, however, is the influence that latitude has on the roles of different metacommunity processes (Jocque et al. 2010). In a testable hypothesis, Jocque et al. (2010) predicted a stronger role of dispersal limitation in the tropics with a shift to more species sorting and mass effects with increasing latitude.

Situated at mid-latitudes, New Zealand comprises a series of oceanic islands spanning a large latitudinal gradient. With a climate reflecting its oceanic position, rainfall (Fig. 1) and river flow regimes are typically unpredictable (Winterbourn et al. 1981). Coupled with their

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flashy flow regimes comes a lack of seasonality in some food resources because the vegetation is dominated by an evergreen flora (Winterbourn et al. 1981, Thompson and Townsend 2000). These factors ultimately lead to a unique, largely generalist and seasonally asynchronous stream fauna adapted to coping with these harsh conditions and climatic unpredictability (Winterbourn et al. 1981, Thompson and Townsend 2000). Consequently, New Zealand stream communities provide an interesting test case for investigating latitudinal controls on community structure.

To test a series of hypotheses related to metacommunity structuring across a broad latitudinal gradient, we explored gradients of stream invertebrate metacommunity structure (spatial structuring and environmental filtering) spanning the length of New Zealand (~1300 km). As a secondary exploration, we examined the best-fit idealised 'metacommunity types' assigned through the Elements of Metacommunity Structure framework (EMS; Leibold and Mikkelson 2002). To further disentangle the role of dispersal, we deconstructed assemblages into strong and weak dispersers. Doing so can be fruitful for exploring processes behind latitudinal diversity gradients (Kneitel 2016). Taking this multi-faceted approach across this latitudinal gradient allows for identifying complementary patterns in factors shaping metacommunities, compared to local community structure, advancing our understanding of how communities assemble in such dynamic landscapes.

We tested the following primary hypothesis based on the predictions of Jocque et al. (2010): Species sorting and mass effects are the main metacommunity dynamics structuring these assemblages (H_{1a}) and the role of mass effects will increase progressively from north to south (H_{1b}). However, the gradient length of environmental conditions and the spatial extent of metacommunities will interact with latitude to govern metacommunity structuring. The alternative to this hypothesis (H_1A) is that, given the highly dynamic nature of New Zealand streams (Winterbourn et al. 1981), these systems are so unpredictable (at different stages of post-flood succession) that metacommunity structuring is highly context dependent from region to region.

We also tested the following secondary hypotheses: (H_2) In metacommunities with the largest spatial extents, dispersal limitation will be evident, weakening the contribution of

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environmental variables and increasing spatial structuring on local assemblages, particularly for weak dispersers (Heino et al. 2015b). Alternatively, (H_2A) in metacommunities with the smallest spatial extents, mass effects will also increase the amount of variation explained by space through spatial autocorrelation, particularly for strong dispersers (Heino et al. 2015b). If spatial extent and dispersal limitation are interacting, deconstructing the full assemblage into dispersal groups, should elucidate the patterns. H_3: Based on the predictions of Jocque et al. (2010), strong dispersers will increase from north to south. As it was a secondary exploratory analysis, we did not form any specific hypotheses about the gradients of EMS.

Methods

Study sites

We used data previously collected (Astorga et al. 2014) from 120 streams in eight regions (15 sites in each region), spanning a latitudinal gradient of 12 degrees (Fig. 2). Site selection followed a series of criteria to minimize differences between regions. Streams were sampled primarily in protected areas (National or State Forest Parks) and were restricted to those with maximum of 14% exotic forestry and 30% pasture in the upstream catchment. All sites had a minimum intact riparian buffer of 50 m (Freshwater Ecosystems of New Zealand; FENZ) (Leathwick et al. 2010) and were selected in proportion to FENZ classes in regions. Sites were restricted to < 7 m wide headwater streams (order 1-3), with similar aspect and with a rocky substrate, and sampling was confined to the riffle zone. All sites had permanent flow and the large majority of streams were runoff fed.

Benthic macroinvertebrate sampling

Sampling was performed between February and April 2006 (Austral summer/autumn) and benthic macroinvertebrates were sampled using two-minute kick-net (0.3-mm mesh) samples. These were performed with the goal of covering most of the microhabitats present in a ca. 100 m^2 riffle section. This approach captures ca. 75% of the benthic invertebrate species at a site, covering 1.3 m^2 of the benthos (Mykra et al. 2006). Samples were stored in 70%

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ethanol and later sorted and identified to the lowest possible taxonomic level (usually genus or species, but certain difficult-to-identify species, such as chironomid midges were left at higher taxonomic levels), following Winterbourn et al. (2000).

To help understand the role of dispersal (inherent in all of our hypotheses), we focused our analysis on three data matrices: All species combined, species with high dispersal ability, and species with low dispersal ability. These dispersal ability groups were assigned based on pre-defined trait categories established for New Zealand aquatic invertebrates (Doledec et al. 2006, 2011).

Environmental variables

While a plethora of variables can influence the structure of stream communities, we included several previously-identified important local habitat variables, as well as stream order and elevation in our analyses (Table 1). Local habitat variables were as follows: water temperature, electrical conductivity, pH, wetted width, reach slope, water depth, overhead canopy cover, periphyton biomass (chlorophyll *a*), bryophyte percent cover, Pfankuch index (bottom component), and substrate size index (SI).

Depth was measured at 40 random locations in transects across the channel. Canopy cover was measured at 20 evenly-spaced cross-channel transects with a densiometer. Channel slope was measured with an Abney level over 10–20 m. Percentage of bryophytes was visually estimated for each reach. Substrate composition was measured by taking 100 randomly-selected particles at 1-m intervals along a path 45° to the stream bank in a zig-zag manner. Particles were assigned to each of 13 size classes: bedrock, >300, 300–128, 128–90.5, 90.5–64, 64–45.3, 45.3–32, 32–22.6, 22.6–16, 16–11.3, 11.3–8 8–5, and <5 mm. These were then converted to a single substrate size index (SI) by summing the mid-point values of each size class weighted by the number of stones in each class (bedrock was assigned a nominal size of 400 mm).

Stream bed stability was assessed with the bottom component of the Pfankuch Stability Index (Pfankuch 1975). The Pfankuch Index is a visual assessment method designed to give

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an index of channel stability. The index can be broken down into three individual components: upper banks, lower banks and stream bed (bottom). We used the bottom component as it is the most relevant to stream invertebrates (Schwendel et al. 2012). The bottom component consists of six wetted channel attributes (substrate brightness, angularity, consolidation, percentage of stable materials, scouring, and amount of clinging aquatic vegetation), which can be assigned to predetermined categories with weighted scores. The sum of these scores represents the stability of the substrate, where high values represent low stability.

As an assessment of periphyton biomass (measured as chlorophyll *a*: µg cm^2) at each site, five stones were randomly selected from the sample riffle and frozen for later analysis. Pigments were extracted in the laboratory by soaking the stones in 90% acetone for 24 h at 5°C in the dark. Absorbances were read using a Cary 50TM Conc UV-Visible spectrophotometer, and chlorophyll *a* was calculated using the method of Steinman and Lamberti (1996). Stone surface area was corrected using the method of Graham et al. (1988), assuming only the top half of the stone was available for periphyton growth.

Statistical analyses

All analyses were performed in *R* version 3.1.1 (R Core Team 2014).

Summarising patterns across regions

To visualise patterns in the environmental conditions of sites, we used Principal Components Analysis (PCA), performed with the *princomp* function, on the full suite of normalised environmental variables. Similarly, to examine patterns in macroinvertebrate communities across all 120 sites, we performed ordination with non-metric multidimensional scaling (nMDS), on log(x) + 1 abundance data. We ran this using the *metaMDS* function, based on Bray-Curtis distances, in the *vegan* package (Oksanen et al. 2013). To test whether communities differed across the eight regions, we used PERMANOVA, based on the *adonis* function and 999 permutations in *vegan*. To compare the properties of diversity in each of our eight regions, and gain insight into the completeness of sampling for each region, we calculated species accumulation curves (SAC). We did this using the *specaccum* function in

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vegan, based on the *exact* method developed by Ugland et al. (2003).

Given the importance of spatial extent and environmental heterogeneity on metacommunity structuring, we calculated these for each metacommunity. For the spatial extent, we calculated the convex hull of points making up each metacommunity using the *chull* function, followed by calculating the area of the polygon using the *Polygon* function. For environmental heterogeneity, we calculated the homogeneity of group dispersions using the *betadisper* function in *vegan*, following the methods of Anderson (2006).

Metacommunity structuring and role of dispersal ($\mathbf{H_{1\text{-}3}}$)

H_1 and H_2 were tested using a variance partitioning approach (Borcard et al. 1992, Peres-Neto et al. 2006), where we disentangled the relative influence of spatial and environmental variables on metacommunity structure of the eight metacommunities (n = 15) using Hellinger-transformed macroinvertebrate community data. This method uses partial redundancy analysis (pRDA), a constrained ordination technique, to partition the variation into the pure components of space, environment and their shared contribution to the explanation of community structure. This allows isolation of the pure effects of environmental gradients from spatial structure (i.e. environmental filtering) and the pure effects of spatial structure from environmental gradients (i.e. dispersal effects). Shared remaining variation may result from interactive effects such as spatially structured environmental gradients or dispersal that is dependent on topography, for instance. The environmental component in our analysis represents the set of pre-selected local habitat variables, and we represented the spatial structuring through Principal Coordinates of Neighbour Matrices (PCNM).

We created a set of spatial eigenvectors to represent the distribution of sites in space using PCNM (Borcard and Legendre 2002, Dray et al. 2006) with the *pcnm* function in the *vegan* package. This method transforms spatial distances between all sites in a metacommunity based on a distance matrix into rectangular data for use in constrained ordination methods. To do this, we used geographic coordinates to create a distance matrix using Euclidean distances. PCNM vectors represent a gradient of organisation of sites at different spatial scales, ranging from large-scale to small. That is, PCNM1 represents the broadest-scale

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arrangement of sites, through to the last vector representing much finer arrangement. Only eigenvectors with positive eigenvalues were used in the analysis.

Prior to variance partitioning, we first ran global RDA models individually for environment (normalised local habitat, stream order and elevation) and space (PCNM vectors), and tested for significance. We checked for collinearity in the models and excluded variables with a variance inflation factor (VIF) of greater than 10. We removed the variable with the highest VIF first and followed each model sequentially until no variables had a VIF > 10. After this, if the global model was significant, we then performed forward selection to select the most important variables.

For forward selection, we used the *ordiR2step* function in the *vegan* package (Oksanen et al. 2013), which employs the approach outlined by (Blanchet et al. 2008). This method selects variables that maximise the adjusted R^2 (adj. R^2) at each step, and stops when the adj. R^2 begins to decline, exceeds the scope (i.e. full model adj. R^2), or the P value, which we set to be 0.05, is exceeded. If the global model was non-significant, we regarded that dataset to have an R^2 of 0.

Only if both spatial and environmental models were significant, was variance partitioning performed between the two groups. We partitioned the variation between forward-selected environmental variables and forward-selected spatial vectors using pRDA with the *varpart* function in *vegan*, and tested significance of the pure effects of environment and space using the *RDA* function.

Identifying mass effects (high dispersal overrides species sorting) and dispersal limitation is central to testing our hypotheses (H_1 and H_2). These can both be identified by strong spatial control (i.e. spatial variables explain community structure) on metacommunities (Heino et al. 2015b) in the variance partitioning results. However mass effects will be more likely in spatially confined regions and dispersal limitation at large spatial extents. In contrast, species sorting is present where environmental control is strongest.

To test H_3, whether strong dispersers increase from north to south, we calculated the ratio of strong to weak dispersers in each metacommunity in full.

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Elements of Metacommunity Structure (EMS)

In addition to our core hypothesis testing, we employed the EMS framework (Leibold and Mikkelson 2002) as an exploratory examination of metacommunity types along the latitudinal gradient. EMS is an approach used to explore and characterise emergent properties in a site-by-species matrix, using three metrics: (1) coherence, or the degree to which different species respond to the same environmental gradient; (2) turnover (range turnover), or the degree to which species replace each other along the environmental gradient; and (3) boundary clumping, or the amount of (dis)similarity (i.e. clumping) in species range boundaries. EMS differs from the variance partitioning approach in that it concurrently examines multiple idealised types of metacommunities, by comparing observed patterns against null expectation.

Prior to extracting these elements, the site-by-species matrix is organised in the most coherent manner using reciprocal averaging (Gauch et al. 1977). This method arranges sites so that the species with the most similar distributions and sites with similar composition are closest in the matrix (Gauch et al. 1977). This, in essence, arranges sites along a latent environmental gradient which is likely important in structuring species distributions. This ordered site-by-species matrix is then compared with random distributions through permutation of a null matrix.

EMS takes a three-step approach in that only if a matrix has significantly positive coherence, can turnover and clumping be examined. Coherence, the first step, can be differentiated into non-significant (i.e. random: species assemble independent of each other), significantly negative (i.e. checkerboard), or significantly positive (i.e. coherent). Checkerboard patterns represent distributions where species are found in avoidance of each other more often than chance. This was originally thought to reflect competitive exclusion (Diamond 1975), but can also represent a host of other causes such as environmental heterogeneity (Gotelli and McCabe 2002, Boschilia et al. 2008).

At each of the steps, the observed ordinated site-by-species matrix is compared with a null distribution. The matrix is reshuffled based on a predefined algorithm and constraints and permuted a set number of times. The observed value is then compared with the null.

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Coherence is calculated through the number of embedded absences in the ordinated matrix. Embedded absences are gaps in the species range (Leibold and Mikkelson 2002). If there are more embedded absences than expected by chance (i.e. through the null matrix), a metacommunity is considered checkerboarded, and vice versa (i.e. fewer embedded absences than chance). If there is no difference in the observed matrix from chance (null), random assembly is expected. For comparability, both coherence and turnover are tested using the standardised z-test. Coherent distributions suggest communities are structured along an environmental gradient, either individualistically or in groups. Turnover and boundary clumping are then examined on the positively coherent distributions.

The turnover step enables differentiation into the set of gradient models that best fit the data structure. This is measured as the number of times a species replaces another between two sites in the ordinated matrix. Significantly negative turnover points to nestedness in distributions (further described below), whereas significantly positive can be differentiated into Clementsian, Gleasonian or evenly-spaced gradients. These latter three can be distinguished based on the level of boundary clumping in species distributions, using Morista's Index (Morista 1971) and an associated Chi^2 test comparing observed and null distributions. Values significantly greater than 1 point to clumped range boundaries (i.e. Clementsian gradients), less than one point to hyperdispersed range boundaries (i.e. evenly-spaced gradients), and no difference from one points to random range boundaries (i.e. Gleasonian gradients). Nested subsets are also broken down based on their boundary clumping into clumped, hyperdispersed and random range boundaries.

Rather than adopt the approach of Presley et al. (2010), where non-significant turnover is further examined into quasi-turnover and quasi-nestedness, we treated non-significant turnover as a non-structure given that it indicates no difference from the null expectation. This results in eight possible metacommunity types. Detailed explanation and diagrammatic representations of these structures are available in several sources (e.g. Leibold and Mikkelson 2002, Presley et al. 2010, Tonkin et al. 2016a).

We constrained our null models using the fixed-proportional "R1" method (Gotelli 2000). This null model maintains site richness, but fills species ranges based on their marginal

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probabilities. This is a realistic null model from an ecological perspective, given that richness of a site varies along ecological gradients (Presley et al. 2009). Consequently, this model is recommended in the EMS analysis as it is relatively insensitive to type I and II errors (Presley et al. 2009). Other methods can incorporate too much or too little biology into the null model and can be thus prone to type I and II errors (Gotelli 2000, Presley et al. 2009). Using the R1 null model, generated in the *vegan* package (Oksanen et al. 2013), we produced 1000 simulated null matrices for each test. We evaluated EMS on presence-absence data, using the *R* package *Metacom* (Dallas 2014), across the eight metacommunities individually and restricted our examination to the primary axis of the RA ordination as this represent the best arrangement of matrices. Prior to running the analysis, we removed all species that were present in less than two sites, as rare species can bias the EMS results, particularly coherence and boundary clumping (Presley et al. 2009).

Results

The Fiordland and Northland metacommunities had the greatest spatial extents (Fig. 2E), but there was little difference in environmental heterogeneity between the regions (Fig. 2F). The gradient in environmental conditions was weak across the eight regions, with a low percentage of variance explained (37%) by the first two principal components (Fig. 2B). Invertebrate communities differed significantly between the eight regions, with a clear latitudinal trend in assemblage structure (PERMANOVA: $F_{7,112} = 7.30$, $R^2 = 0.313$, $P = 0.001$; Fig. 2C). Regional richness tended to be highest at the North of each island and decline towards the southern zones (Fig. 2D). The regional pool of most regions were well sampled. However, Kahurangi did not reach a clear asymptote and had the steepest species accumulation curve. Moreover, the North Island regions' curves tended to reach a much clearer asymptote compared to those in the South Island.

Metacommunity structuring and the role of dispersal ($\mathbf{H_{1\text{-}3}}$)

There was no gradient with latitude in the relative importance of environmental or spatial control for all species combined and for individual dispersal groups (Fig. 3) suggesting H_1

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can be rejected. Similarly, there was no relationship between spatial extent, dispersal ability and relative role of spatial or environmental components in the variance partitioning models, thus H_2 can also be rejected. Finally, contrary to H_3, the ratio of strong to weak dispersers decreased from north to south (Fig. 4).

When considering all species together, only three of the eight regions had significant environmental and spatial components together, and thus could be considered for variance partitioning (Fig. 3). In the dispersal group datasets, only one of the eight regions had combined significant environmental and spatial components. Environmental control was more commonly important than spatial in structuring these metacommunities. Northland exhibited no spatial or environmental structure for any of the datasets.

Considering all models (including those assigned 0% explained), environmental variables explained more of the variation when the whole community was considered (mean Adj. R^2 = 0.134; 13.4% variance explained) compared to breaking into high (7.1%) and low (4.8%) dispersal ability groups. This was particularly evident for certain regions, such as Westland, which could be explained well when considering the full community (strongest model), but not for the dispersal groups. However, strong dispersers had on average higher adjusted R^2 values (Adj. R^2 = 0.191; 19.1% explained) when only considering the significant models, than all combined (18.0%) or weak dispersers (9.6%). Spatial variables explained less of the variation in community structure than environmental, when non-significant models were included (Adj. R^2 - All: 0.047; High: 0.049; Low: 0.054) but not when only considering significant models (Adj. R^2 - All: 0.126; High: 0.200; Low: 0.143).

Forward-selected environmental variables were highly variable in the RDA models, with no particular variable consistently important across the eight metacommunities (Table 2; Table S1).

Metacommunity types (EMS)

There was no latitudinal trend in metacommunity type for all organisms combined and for each of the dispersal ability groups (Table 3). For the full community dataset, Gleasonian gradients were the most common pattern (five regions), indicating positive coherence and

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turnover, but no boundary clumping. The remaining regions' metacommunity types consisted of two regions with random structures and one with no structure (non-signficant turnover). Clementsian gradients were more common for strong dispersers, with the remaining regions having either random (two regions), Gleasonian or no structure (non-signficant turnover; Table 3). Weak dispersers were much more variable between the regions, often with weaker coherence. In fact, four regions exhibited random distributions represented by non-signficant coherence. The remaining regions had either Gleasonian (two regions), Clementsian and no structure. Egmont (Clementsian) and Westland (random) had the same pattern between high and low dispersal ability groups. Tararua consistently exhibited weak patterns with either random or no structure, and Westland metacommunities were always randomly distributed.

Discussion

As a result of the relatively high latitude of New Zealand and based on the hypotheses of Jocque et al. (2010), we hypothesised (H_1) a dominant role of species sorting and mass effects in structuring these assemblages (H_{1a}) and an increasing role of mass effects from north to south (H_{1b}). However, despite a clear latitudinal gradient in assemblages at the community level, what emerged at the metacommunity level was more idiosyncratic. In particular, there was no latitudinal trend in either environmental vs. spatial control (rejecting H_{1b}) or the idealised metacommunity types tested through the EMS analysis at both the full community level and for dispersal groups. This lack of fit to the hypothesis of Jocque et al. (2010) likely reflects the unique characteristics of New Zealand streams (partially supporting H_1A).

New Zealand comprises a series of mid-latitude oceanic islands, with a typically unpredictable climate (Fig. 1) and flashy river flow regimes (Winterbourn et al. 1981) reflecting its oceanic position. At a single time-point, communities are therefore most likely at different stages of post-flood recolonisation (H_1A). This represents a fundamentally important factor controlling metacommunity dynamics, as the relative role of local and regional processes will depend on the amount of time that has passed for dispersal and colonisation to play out (Brendonck et al. 2014), with preceding flow conditions shaping the metacommunity structure in streams (Campbell et al. 2015).

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The lack of seasonality and predictability in New Zealand's climate likely plays a strong role in the low predictability in metacommunity structuring. The hypothesis of Jocque et al. (2010) does not take into account differences in island size and isolation, fundamental aspects controlling biodiversity (MacArthur and Wilson 1967). Yet, island and mainland locations at similar latitudes do not comprise the same climatic patterns (Tonkin et al. Under review). Continental locations have much greater predictability in their seasonality compared to islands. To demonstrate this point, we compared a 30-y sequence of monthly rainfall totals from central North Island New Zealand with Western Australia, a Mediterranean climate, using wavelet analysis (Fig. 1) (Torrence and Compo 1998). This figure demonstrates clearly the strongly seasonal and predictable pattern apparent in Western Australia, with a significant and repeatable cycle at the 1-y time period over the full sequence. In contrast, New Zealand's climate exhibits no repeatability in the rainfall, with very few time points in the sequence indicating any power at the 1-y period.

New Zealand streams are also unique for a variety of other reasons, including: rivers tend to be short, swift and steep due to the narrow landmass and tectonically active nature; evergreen vegetation dominates the flora; and riparian vegetation is scarce for much of their length leading to a predominance of autochthonous rather than allochthonous control of river food webs (Winterbourn et al. 1981, Thompson and Townsend 2000). As such, New Zealand streams are considered as being physically, rather than biologically, dominated systems (Winterbourn et al. 1981). These factors, in turn, have led to the evolution of a unique stream invertebrate fauna with flexible and poorly synchronised life histories, and generalist feeding behaviour (browsers predominate) (Winterbourn et al. 1981, Scarsbrook 2000, Thompson and Townsend 2000). Under these circumstances, it is not surprising that metacommunity dynamics can be difficult to predict, as we clearly demonstrate, without a strong temporal resolution in the data.

Results were highly idiosyncratic between different regions, with considerable variability in the relative roles of environmental and spatial structuring, the forward-selected environmental variables, and the idealised metacommunity types, with no real match between the two approaches. Contrary to our hypothesis (H_2), this context dependence did not reflect an

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interaction between spatial extent and dispersal ability. While much of this unpredictability may be related to the unique characteristics of New Zealand streams, it is pertinent to recognise that this is a challenge facing many stream metacommunity studies globally, where patterns differ considerably between different catchments (Heino et al. 2012, 2015a, Tonkin et al. 2016b). Lawton (1999) pinpointed this problem of contingency in ecology over a decade ago suggesting that community ecology is rife with contingency, so much so that generality is unlikely. Lawton goes on to highlight that the problem is indeed most severe at the intermediate organisational level of communities, compared to more predictable lower (e.g. populations) or higher levels (e.g. macroecology). Metacommunities are indeed difficult systems to predict, with processes affecting different subsets of organisms and operating at specific times (Driscoll and Lindenmayer 2009). One source of context dependence in metacommunity structuring is differences between different trait modalities, such as dispersal modes (Thompson and Townsend 2006, Canedo-Arguelles et al. 2015, Tonkin et al. 2016c). Thus, if spatial extent and dispersal limitation were interacting, deconstructing the full assemblage into dispersal groups should have elucidated the pattern. Yet, contrary to expectation, examining strong and weak dispersers separately, did not help in explaining discrepancies in our predictions.

Finally, contrary to the expectation of Jocque et al. (2010) that dispersal ability increases moving away from the equator (H_3), we found a decrease in the ratio of strong to weak dispersers moving from north to south. Theoretically, temporal variability in environmental conditions promotes increased dispersal ability of organisms (Jocque et al. 2010); an hypothesis strongly tied with Rapoport's rule of increasing range size with increasing latitude (Stevens 1989). The result we observed may reflect several causes: 1. Lack of time for dispersal and colonisation to play out post-disturbance (Brendonck et al. 2014, Campbell et al. 2015). 2. The requirement of a longer latitudinal gradient for these mechanisms to play out. Over the length of New Zealand, the continuity of habitat availability in space and time, a key mechanism behind Jocque et al. (2010), likely differs very little. 3. Climatic idiosyncrasies not reflecting a north-south gradient and thus not selecting for a gradually increased dispersal ability at higher latitudes.

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Conclusions

Jocque et al. (2010) highlighted the fundamental role of dispersal in driving the latitudinal diversity gradient, suggesting a climate-mediated dispersal–ecological specialisation trade-off as a key factor regulating this pattern. We tested several hypotheses based on those of Jocque et al. (2010) relating to how New Zealand stream invertebrate metacommunity structure changed along a broad latitudinal gradient, and examining the mediating role of dispersal. We rejected all of our primary hypotheses, pinning this lack of fit on the strong unpredictability of New Zealand's dynamic stream ecosystems and unique fauna that has evolved to cope with these conditions. While local community structure turned over predictably along this latitudinal gradient, metacommunity structure was highly context dependent and dispersal traits did not elucidate patterns.

These results, along with other recent findings (Heino et al. 2012, 2015a, Tonkin et al. 2016b), provide a cautionary tale for examining singular metacommunities. The considerable level of unexplained context dependency suggests that any inferences drawn from one-off snapshot sampling may be misleading. Given the importance of understanding metacommunity processes for the successful management of river ecosystems (Heino 2013, Tonkin et al. 2014, Stoll et al. 2016), this level of unpredictability is a major cause for concern. While spatial replication of multiple metacommunities may elucidate some of this uncertainty, studies on temporal dynamics of metacommunity processes are clearly needed. We therefore urge researchers to consider the temporal dynamic, particularly in relation to seasonal cycles and their predictability.

Acknowledgements

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The authors have no conflicts of interest to declare.

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Tables

Table 1: Environmental variables used in the analysis.

Variable	Units	Explanation
Temp	°C	Water temperature
Cond	µS cm^{-1}	Conductivity
pH	-	pH
Width	cm	Wetted width
Elev	m a.s.l.	Elevation
Slope	cm m^{-1}	Slope of the stream reach
Depth	cm	Depth
OHCov	%	Percent overhead canopy cover
Chla	µg cm^{-2}	Chlorophyll *a* (periphyton biomass)
Bryophytes	%	Percent moss cover
Pfankuch_bottom	-	Stream bed stability
SI	-	Substrate size index
Order	-	Stream order

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Table 2: Forward-selected environmental variables used in the variance partitioning analysis when a global RDA model was significant. Only if a global model was significant, was forward selection performed. Forward-selected variables are given in the "Variables" column. Subset = subset of species (All species, and strong and weak dispersers). Full results of both global and forward-selected models, including spatial variables can be found in Table S1.

Subset	Region	F	P	Variables
All	U	2.57	0.00	Temp, pH
All	E	2.96	0.00	OHCov, Elev, SI, Depth
All	K	2.25	0.00	Cond, OHCov
All	A	2.64	0.03	Temp
All	W	4.55	0.00	Cond, pH, Slope
All	F	2.13	0.01	Order
Strong	E	3.83	0.00	OHCov, Elev, SI
Strong	K	2.64	0.01	Cond, Chla
Strong	A	3.20	0.04	Temp
Weak	U	3.32	0.00	Temp, pH
Weak	T	2.57	0.00	OHCov, Pfankuch_bottom, Chla, Depth
Weak	K	2.20	0.02	Cond
Weak	F	2.13	0.02	Order

Table 3: Results of Elements of Metacommunity Structure analysis examining the best-fit idealised metacommunity structure for each metacommunity, including for all species combined, and strong and weak disperser groups. Results are given for the first axis of reciprocal averaging ordination on the species by site matrices testing for coherence, species range turnover and boundary clumping in each metacommunity of 15 sites across eight regions of New Zealand.

			Coherence					Turnover					Boundary Clumping		
Subset	Region	df	Abs	Mean	SD	z	P	Re	Mean	SD	z	P	MI	P	Structure
All	N	58	305	321.1	15.0	1.07	0.2835	2148	1649.8	580.7	-0.86	0.3909	1.17	0.3468	Random
All	U	68	277	386.6	17.7	6.18	< 0.0001	9768	2659.4	823.4	-8.63	< 0.0001	0.85	0.3928	Gleasonian
All	E	62	248	367.8	19.1	6.26	< 0.0001	10931	2978.5	980.3	-8.11	< 0.0001	0.68	0.2683	Gleasonian
All	T	42	168	197.6	12.8	2.32	0.0204	1334	1095.8	388.2	-0.61	0.5394	2.12	0.0044	-
All	K	66	325	384.8	19.5	3.06	0.0022	6293	3145.3	950.0	-3.31	0.0009	1.44	0.1655	Gleasonian
All	A	53	233	340.4	19.3	5.56	< 0.0001	6387	3127.8	1032.9	-3.16	0.0016	1.66	0.0633	Gleasonian
All	W	63	400	425.7	22.7	1.13	0.2591	6969	4705.3	1372.5	-1.65	0.0991	1.18	0.3249	Random
All	F	56	293	354.6	18.3	3.37	0.0008	5885	2942.4	977.6	-3.01	0.0026	1.05	0.4264	Gleasonian
Strong	N	31	117	149.2	9.9	3.24	0.0012	1428	595.7	228.9	-3.64	0.0003	1.74	0.0263	Clementsian
Strong	U	32	127	160.4	11.2	2.99	0.0028	1892	787.7	271.7	-4.06	< 0.0001	2.51	0.0003	Clementsian
Strong	E	31	109	168.7	12.6	4.74	< 0.0001	3552	1283.7	420.1	-5.40	< 0.0001	2.20	0.0019	Clementsian
Strong	T	21	66	83.4	8.1	2.14	0.0322	192	411.9	159.7	1.38	0.1685	1.62	0.0756	-
Strong	K	32	132	167.1	12.6	2.79	0.0053	1712	1303.0	392.7	-1.04	0.2976	1.83	0.0121	-
Strong	A	24	93	134.6	10.7	3.89	< 0.0001	1974	1060.4	352.9	-2.59	0.0096	0.49	0.0894	Gleasonian
Strong	W	30	159	184.3	14.4	1.76	0.0784	2341	2052.6	592.4	-0.49	0.6263	0.52	0.0483	Random
Strong	F	22	112	117.5	9.9	0.56	0.5755	1036	810.8	280.1	-0.80	0.4213	2.29	0.0008	Random
Weak	N	24	119	137.8	10.8	1.75	0.0804	1319	910.3	301.9	-1.35	0.1759	0.92	0.4207	Random
Weak	U	33	128	187.3	13.3	4.45	< 0.0001	3483	1462.2	410.0	-4.93	< 0.0001	0.63	0.1168	Gleasonian
Weak	E	28	111	156.8	11.9	3.83	0.0001	3469	1239.6	385.7	-5.78	< 0.0001	1.96	0.0038	Clementsian
Weak	T	18	87	89.5	8.1	0.31	0.7599	609	513.1	167.7	-0.57	0.5673	1.72	0.0107	Random
Weak	K	31	156	175.7	12.3	1.60	0.109	2108	1282.5	382.4	-2.16	0.0309	1.14	0.3232	Random
Weak	A	26	113	158.0	13.3	3.39	0.0007	2408	1627.6	490.9	-1.59	0.1119	1.50	0.0558	-
Weak	W	30	164	190.1	13.9	1.87	0.0611	2775	1840.7	560.3	-1.67	0.0954	0.74	0.2359	Random
Weak	F	31	147	192.4	13.3	3.42	0.0006	3861	1806.9	557.5	-3.68	0.0002	1.18	0.2630	Gleasonian

Notes: Subset = subset of species (All, and strong and weak dispersers), df = degrees of freedom, Abs = number of embedded absences, Re = number of replacements, MI = Morista's Index, SD = standard deviation. Mean and SD values are those calculated from the 1000 generated null matrices, based on the "R1" null model. Refer to Figure 1 for region names. '-' represents structures with non-significant turnover.

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Figure captions

Figure 1: Wavelet diagram comparing 30-year monthly rainfall values between central North Island New Zealand and Mediterranean-climate Western Australia. Wavelet power increases from blue (low power) to red (high power). Higher power represents greater strength of the periodicity. The figure illustrates clear annual rainfall cycles in Western Australia (i.e. strong and consistent power at the 12-month period over the full 30-year cycle) representative of its Mediterranean climate. This contrasts to the highly unpredictable rainfall cycles in New Zealand. Wavelet analysis was performed using the R package 'WaveletComp' (Roesch and Schmidbauer 2014).

Figure 2: Overview of sites and regional invertebrate assemblages across New Zealand. All plots are colour-coded in the same manner, from North to South. A. Distribution of 120 sites across eight regions of New Zealand. B. First two components of principal component analysis on environmental variables used in the study. Proportion of variation explained: PCA1 = 0.21; PCA2 = 0.17. C. Non-metric multidimensional scaling ordination of invertebrate communities from all 120 sites. 2D stress = 0.21. D. Species accumulation curves for all species for the eight regions. Regions are ordered from North (left) to South (right). E. Spatial extent of each metacommunity (normalised area). F. Environmental heterogeneity of each metacommunity, measured through homogeneity of dispersions.

Figure 3: Results of variance partitioning of spatial and environmental variables on macroinvertebrate communities in eight regions spanning the length of New Zealand. Regions are ordered from North (left) to South (right). Variance partitioning was performed only where global RDA models were significant. Certain regions had non-significant global models for either spatial, environmental or both. Where either spatial or environmental was significant, we plot the results of the global model (and its significance). Significance of the pure effects of space or environment are shown with asterisks. All = all species, Strong = strong dispersers, Weak = weak dispersers.

Figure 4: Ratio of strong to weak dispersers in each metacommunity. 0 = 1:1 ratio of strong to weak dispersers. Above the line represents a higher strong to weak disperser ratio.

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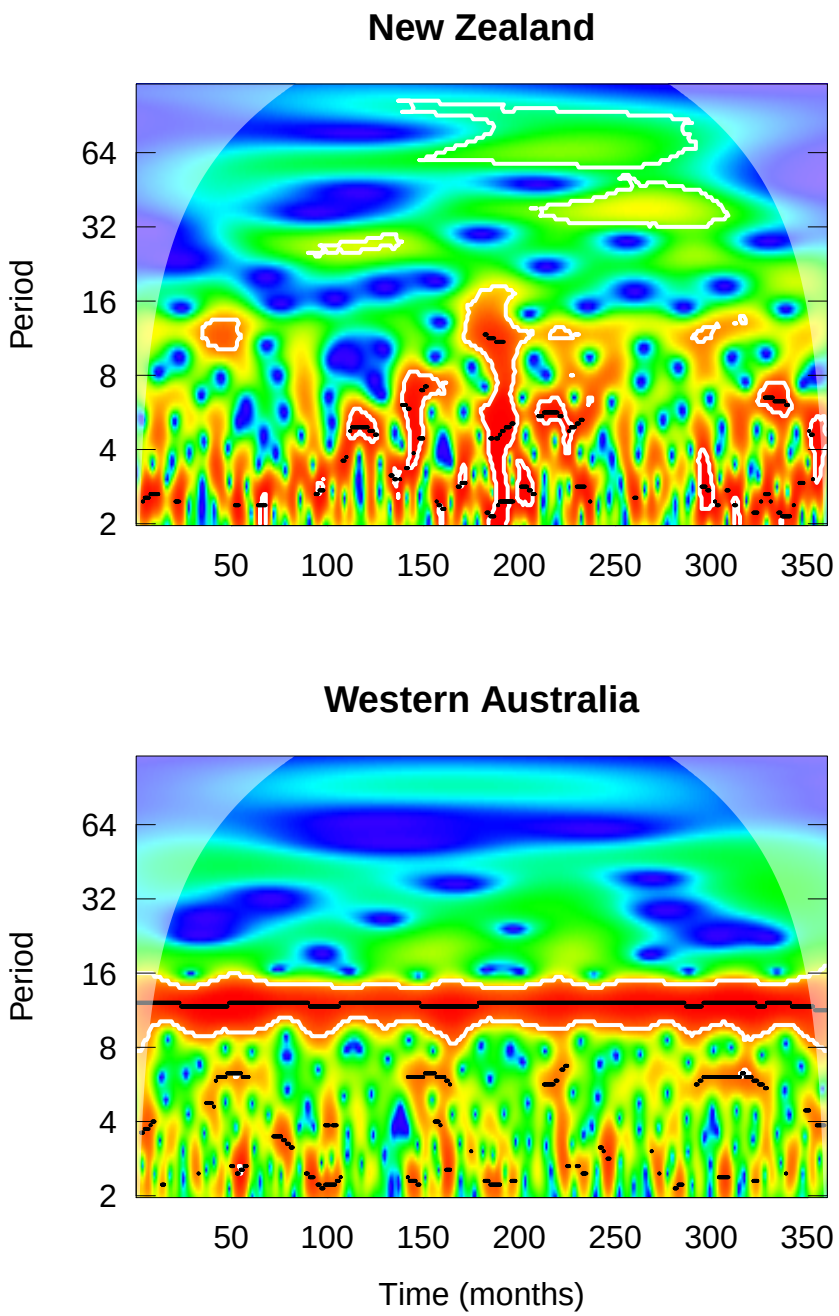

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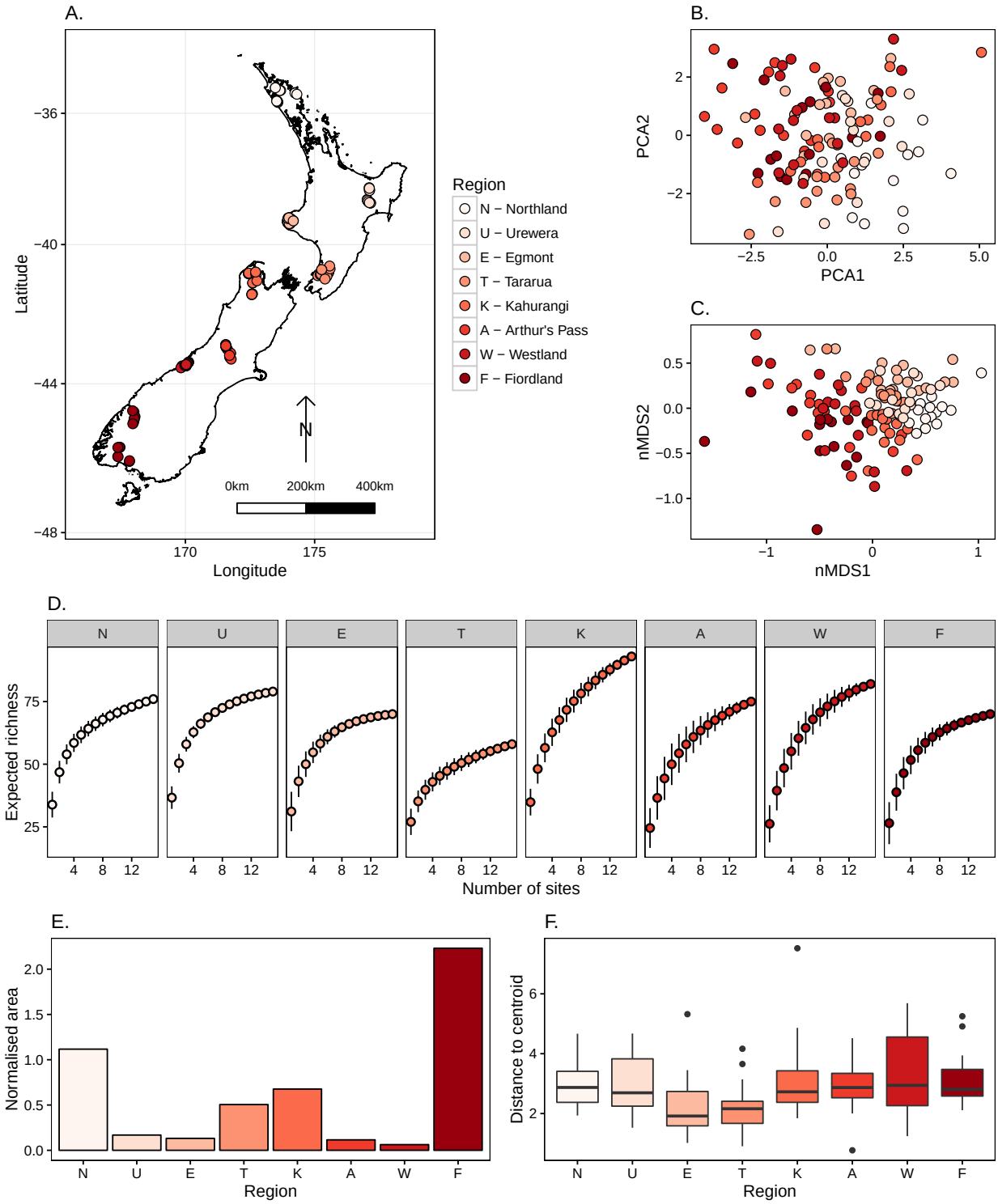

Figure 2: Overview of sites and regional invertebrate assemblages across New Zealand. All plots are colour-coded in the same manner, from North to South. A. Distribution of 120 sites across eight regions of New Zealand. B. First two components of principal component analysis on environmental variables used in the study. Proportion of variation explained: PCA1 = 0.21; PCA2 = 0.17. C. Non-metric multidimensional scaling ordination of invertebrate communities from all 120 sites. 2D stress = 0.21. D. Species accumulation curves for all species for the eight regions. Regions are ordered from North (left) to South (right). E. Spatial extent of each metacommunity (normalised area). F. Environmental heterogeneity of each metacommunity, measured through homogeneity of dispersions.

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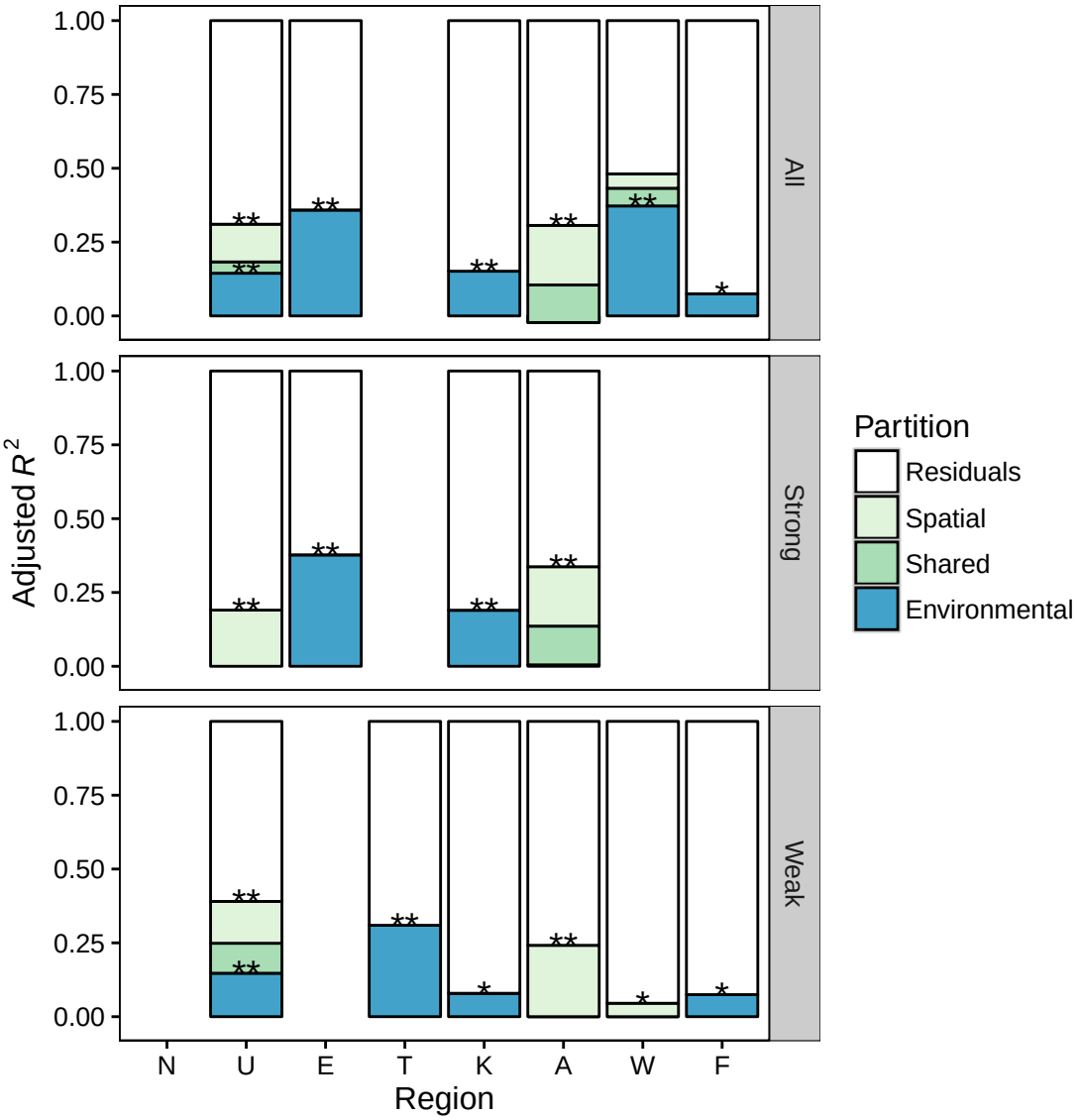

Figure 3: Results of variance partitioning of spatial and environmental variables on macroinvertebrate communities in eight regions spanning the length of New Zealand. Regions are ordered from North (left) to South (right). Variance partitioning was performed only where global RDA models were significant. Certain regions had non-significant global models for either spatial, environmental or both. Where either spatial or environmental was significant, we plot the results of the global model (and its significance). Significance of the pure effects of space or environment are shown with asterisks. All = all species, Strong = strong dispersers, Weak = weak dispersers.

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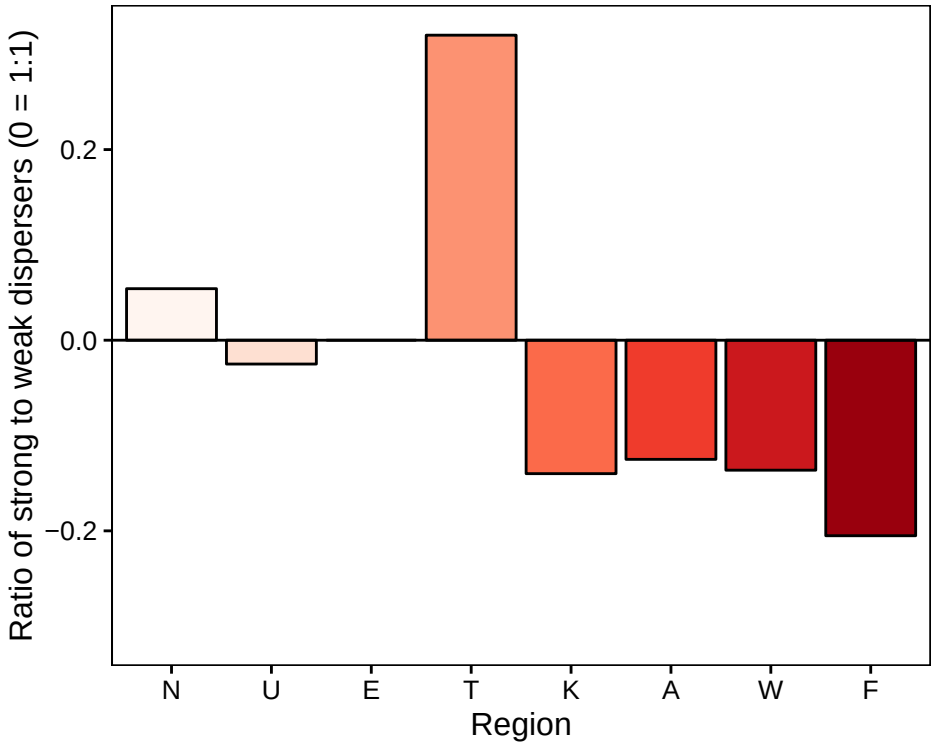

Figure 4: Ratio of strong to weak dispersers in each metacommunity. 0 = 1:1 ratio of strong to weak dispersers. Above the line represents a higher strong to weak disperser ratio.

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Supplementary material

Table S1: Results of forward selection on both spatial and environmental variables for the eight metacommunities. If a global model was significant, forward selection was performed. Forward-selected variables are given in the "Variables" column. Subset = subset of species (All, and strong and weak dispersers). Global model sig. = Global model significant or not (N: no; Y: yes).

Subset	Region	Data	F	P	Model	Sig.	Variables
All	N	Environmental	1.02	0.50	Global	N	
All	N	Spatial	0.90	0.69	Global	N	
All	U	Environmental	1.46	0.03	Global	Y	
All	U	Environmental	2.57	0.00	Fwd. sel.		Temp, pH
All	U	Spatial	1.60	0.02	Global	Y	
All	U	Spatial	2.39	0.00	Fwd. sel.		PCNM1, PCNM3
All	E	Environmental	1.72	0.03	Global	Y	
All	E	Environmental	2.96	0.00	Fwd. sel.		OHCov, Elev, SI, Depth
All	E	Spatial	0.84	0.73	Global	N	
All	T	Environmental	1.19	0.28	Global	N	
All	T	Spatial	0.76	0.86	Global	N	
All	K	Environmental	1.66	0.02	Global	Y	
All	K	Environmental	2.25	0.00	Fwd. sel.		Cond, OHCov
All	K	Spatial	0.81	0.85	Global	N	
All	A	Environmental	1.80	0.02	Global	Y	
All	A	Environmental	2.64	0.03	Fwd. sel.		Temp
All	A	Spatial	1.97	0.00	Global	Y	
All	A	Spatial	3.29	0.00	Fwd. sel.		PCNM1, PCNM2, PCNM3
All	W	Environmental	2.08	0.03	Global	Y	
All	W	Environmental	4.55	0.00	Fwd. sel.		Cond, pH, Slope
All	W	Spatial	1.80	0.05	Global	Y	
All	W	Spatial	2.70	0.03	Fwd. sel.		PCNM9
All	F	Environmental	1.78	0.01	Global	Y	
All	F	Environmental	2.13	0.01	Fwd. sel.		Order
All	F	Spatial	1.33	0.12	Global	N	
Strong	N	Environmental	1.07	0.42	Global	N	
Strong	N	Spatial	0.96	0.58	Global	N	
Strong	U	Environmental	1.47	0.07	Global	N	
Strong	U	Spatial	1.71	0.02	Global	Y	
Strong	U	Spatial	2.64	0.00	Fwd. sel.		PCNM1, PCNM3
Strong	E	Environmental	2.07	0.03	Global	Y	
Strong	E	Environmental	3.83	0.00	Fwd. sel.		OHCov, Elev, SI
Strong	E	Spatial	0.81	0.74	Global	N	
Strong	T	Environmental	1.02	0.45	Global	N	
Strong	T	Spatial	0.66	0.92	Global	N	
Strong	K	Environmental	1.84	0.02	Global	Y	
Strong	K	Environmental	2.64	0.01	Fwd. sel.		Cond, Chla
Strong	K	Spatial	0.59	0.96	Global	N	
Strong	A	Environmental	2.18	0.02	Global	Y	
Strong	A	Environmental	3.20	0.04	Fwd. sel.		Temp
Strong	A	Spatial	2.27	0.01	Global	Y	
Strong	A	Spatial	4.48	0.00	Fwd. sel.		PCNM1, PCNM2
Strong	W	Environmental	1.82	0.09	Global	N	
Strong	W	Spatial	1.62	0.12	Global	N	
Strong	F	Environmental	1.78	0.08	Global	N	
Strong	F	Spatial	1.20	0.35	Global	N	
Weak	N	Environmental	1.16	0.28	Global	N	
Weak	N	Spatial	0.82	0.82	Global	N	
Weak	U	Environmental	1.64	0.02	Global	Y	
Weak	U	Environmental	3.32	0.00	Fwd. sel.		Temp, pH
Weak	U	Spatial	1.63	0.02	Global	Y	
Weak	U	Spatial	2.50	0.00	Fwd. sel.		PCNM1, PCNM5, PCNM2
Weak	E	Environmental	1.37	0.18	Global	N	
Weak	E	Spatial	0.78	0.81	Global	N	

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Subset	Region	Data	F	P	Model	Sig.	Variables
Weak	T	Environmental	1.71	0.04	Global	Y	
Weak	T	Environmental	2.57	0.00	Fwd. sel.		OHCov, Pfankuch_bottom, Chla, Depth
Weak	T	Spatial	0.82	0.77	Global	N	
Weak	K	Environmental	1.54	0.05	Global	Y	
Weak	K	Environmental	2.20	0.02	Fwd. sel.		Cond
Weak	K	Spatial	1.31	0.10	Global	N	
Weak	A	Environmental	1.05	0.42	Global	N	
Weak	A	Spatial	1.60	0.02	Global	Y	
Weak	A	Spatial	2.49	0.00	Fwd. sel.		PCNM1, PCNM5, PCNM2
Weak	W	Environmental	1.17	0.24	Global	N	
Weak	W	Spatial	1.44	0.03	Global	Y	
Weak	W	Spatial	1.67	0.02	Fwd. sel.		PCNM6
Weak	F	Environmental	1.71	0.02	Global	Y	
Weak	F	Environmental	2.13	0.02	Fwd. sel.		Order
Weak	F	Spatial	1.44	0.07	Global	N	