

Increasing climate-driven taxonomic homogenization but functional differentiation among river macroinvertebrate assemblages

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Abstract

Global change is increasing biotic homogenization globally, which modifies the functioning of ecosystems. While tendencies towards taxonomic homogenization in biological communities have been extensively studied, functional homogenization remains an understudied facet of biodiversity. Here, we tested four hypotheses related to long-term changes (1991–2016) in the taxonomic and functional arrangement of freshwater macroinvertebrate assemblages across space and possible drivers of these changes. Using data collected annually at 64 river sites in mainland New Zealand, we related temporal changes in taxonomic and functional spatial β -diversity, and the contribution of individual sites to β -diversity, to a set of global, regional, catchment and reach-scale environmental descriptors. We observed long-term, mostly climate-induced, temporal trends towards taxonomic homogenization but functional differentiation among macroinvertebrate assemblages. These changes were mainly driven by replacements of species and functional traits among assemblages, rather than nested species loss. In addition, there was no difference between the mean rate of change in the taxonomic and functional facets of β -diversity. Climatic processes governed overall population and community changes in these freshwater ecosystems, but were amplified by multiple anthropogenic, topographic and biotic drivers of environmental change, acting widely across the landscape. The functional diversification of communities could potentially provide communities with greater stability, resistance and resilience capacity to environmental change, despite ongoing taxonomic homogenization. Therefore, our study highlights a need to further understand temporal trajectories in both taxonomic and functional components of species communities, which could enable a clearer picture of how biodiversity and ecosystems will respond to future global changes.

KEYWORDS

β -diversity, biotic homogenization, climate change, freshwater macroinvertebrates, functional diversity, human disturbance

1 | INTRODUCTION

Global environmental changes are reducing biodiversity globally and altering the functioning of ecosystems through time, primarily through habitat change, pollution and degradation (Cardinale et al., 2012; Hooper et al., 2012; Lefcheck et al., 2015). These processes are altering the distribution of species and the arrangement of communities across the landscape. At the global scale, native species extirpations exceed species colonizations (Jarzyna & Jetz, 2018; Sobral et al., 2016; Urban, 2015). Consequently, observations often indicate that human-induced environmental changes homogenize biodiversity (i.e. reduces spatial β -diversity) through time (Clavel et al., 2011; Gámez-Virués et al., 2015; Iacarella et al., 2018; Magurran et al., 2015). The ecological and evolutionary consequences of this biotic homogenization include reducing overall community and ecosystem functioning (Tilman et al., 1997), stability (Sankaran & McNaughton, 1999), resilience (de Juan et al., 2013) and resistance to environmental change by narrowing the available range of species-specific responses to disturbances (*sensu* McKinney & Lockwood, 1999; Moullot et al., 2013; Olden, 2006; Olden et al., 2004). Empirical biodiversity trends are however highly complex, and reports of a global biodiversity crisis are often seemingly contradictory to documented trends, including increases in β -diversity in response to anthropogenic disturbances (Gutiérrez-Cánovas et al., 2013; Hawkins et al., 2015). These latter observations imply that environmental changes may not always result in habitat simplification, and that a more general and comprehensive understanding of the factors that influence temporal changes in β -diversity is needed.

A trend towards taxonomic homogenization (i.e. an increase in the similarity of species composition among species assemblages over time) has been demonstrated for many taxonomic groups across the globe (Haslem et al., 2015; Kuczynski et al., 2018; Magurran et al., 2015). Taxonomic diversity is, however, often recognized as providing only limited insight into the impacts of disturbance on ecosystem functioning, which may be better predicted using functional trait-based estimates of biodiversity (Gagic et al., 2015; Moullot et al., 2013; Tilman et al., 1997). Increases in the similarity of functional trait composition among species assemblages over time, leading to functional homogenization, are likely to decrease the resistance and resilience capacity of communities facing disturbances (Clavel et al., 2011; de Juan et al., 2013; Olden, 2006). However, in some cases, there may be no direct relationship between changes in taxonomic and functional β -diversity among species assemblages (Sonnier et al., 2014; Villéger et al., 2014; White et al., 2018). For instance, assemblages that exhibit taxonomic homogenization can be functionally differentiated if the newly introduced species in each assemblage are functionally dissimilar to each other (Villéger et al., 2014). Analyses of changes in functional β -diversity are therefore complementary to those of changes in taxonomic β -diversity (Sonnier et al., 2014; Villéger et al., 2014).

In ecosystems, biodiversity patterns are structured by factors operating at multiple, nested spatial scales (Townsend et al., 2003). At the global scale, climate is usually considered the predominant

factor shaping biodiversity patterns, while at more local scales, factors including topography, land-use intensity and natural resource availability become increasingly important (Allan et al., 1997; Chase & Knight, 2013; Chase & Ryberg, 2004; Mykrä et al., 2007). For instance, an ecosystem might be buffered from the full magnitude of climate change by persisting in climate refugia (Hampe & Jump, 2011; Keppel et al., 2012; Roberts & Hamann, 2016). By contrast, local anthropogenic factors may interact with climate change processes to amplify their effects (Comte et al., 2016; Guo et al., 2018; Kuczynski et al., 2018). Hence, causal inferences on climate change effects in ecosystems may sometimes be difficult to distinguish from the potentially confounding effects of human-driven local disturbances (Durance & Ormerod, 2009; Floury et al., 2017; Radinger et al., 2017). However, attempts to disentangle the relative influence of global-to local-scale environmental drivers on the spatial arrangement of communities from both taxonomic and functional standpoints are lacking. This paucity of studies is particularly evident when considering how these patterns and relationships will change in response to global environmental change (Van Looy et al., 2017).

Here, we examined changes in the taxonomic and functional spatial β -diversity of freshwater macroinvertebrate assemblages in 64 New Zealand river sites over a 25-year period. Based on the knowledge gaps identified by Olden et al. (2018), we hypothesized an increasing taxonomic and functional homogenization among freshwater macroinvertebrate assemblages (H_{1a} and H_{1b} respectively). However, we hypothesized that the relationship between changes in each site's contribution to taxonomic and functional β -diversity over time, would differ due to contrasting taxonomic and functional responses to the environment (H_2 ; Sonnier et al., 2014; Villéger et al., 2014). Finally, we hypothesized that changes in climatic conditions over time would be the primary driver of observed changes in β -diversity (H_3 ; Chase & Knight, 2013; Chase & Ryberg, 2004).

2 | METHODS

2.1 | Macroinvertebrate community samples

Macroinvertebrate community samples were collected from 64 sites, located in 35 rivers (mean Strahler stream order = 6; max = 8, min = 3) of mainland New Zealand, between latitudes 46 and 35°S (Figure 1). Sampling surveys were conducted annually from 1991 to 2016, during late austral summers (February to April). These surveys were conducted for New Zealand's National Rivers Water Quality Network (NRWQN, Smith & McBride, 1990), which was operated and maintained by the National Institute of Water and Atmospheric Research (NIWA).

Sampling occurred under baseflow conditions ($Q < Q_{\text{median}}$) no less than 4 weeks after a flood exceeding three times the median flow. Seven Surber samples (0.1 m² and 250 μ m mesh nets) were collected on all sampling occasions and macroinvertebrates were removed from the 0.1 m² area in the sampler down to a depth of c. 10 cm from as many substrate types as possible. Macroinvertebrates

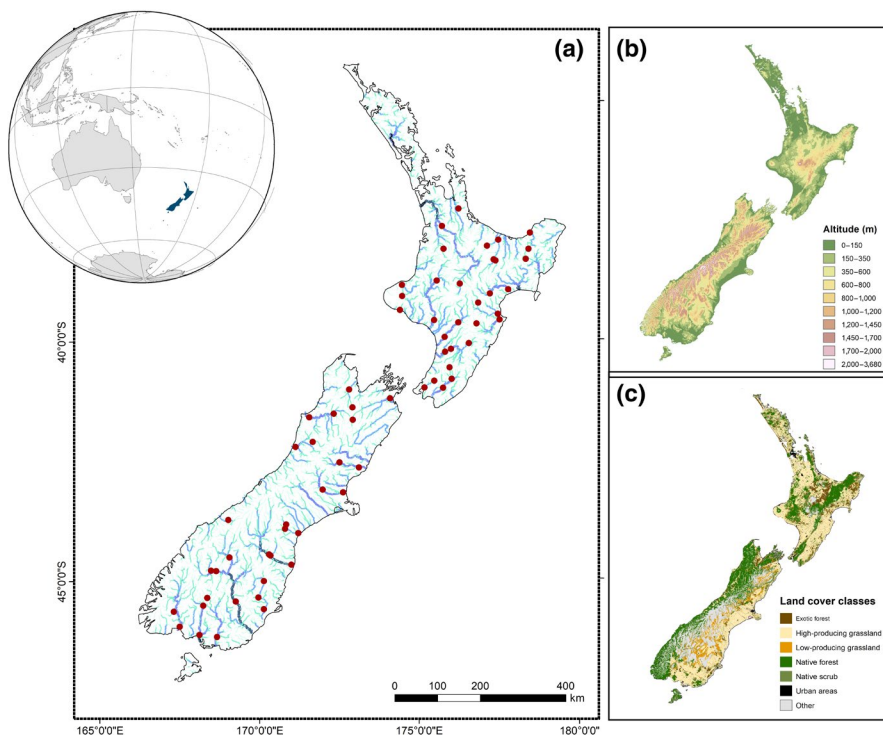


FIGURE 1 Maps of mainland New Zealand showing (a) the location of the 64 sampling sites (red dots). Increases in river size (order > 3) are illustrated using increasing line width and darker blue color. The global inset map shows the location of New Zealand (blue country) in the world. (b) Altitude (m) and (c) Landcover. For a definition of the land-cover classes, see Table S1.2 [Colour figure can be viewed at wileyonlinelibrary.com]

were identified to the lowest practicable taxonomic level (mostly species or genus) following Quinn and Hickey (1990). The same taxonomic resolution was maintained throughout the dataset (Scarsbrook et al., 2000). Further information on site selection criteria, and sampling methodology are available in Smith and McBride (1990) and Davies-Colley et al. (2011).

Macroinvertebrate species were described by functional traits related to morphology, mobility, life-history, dispersal strategies and resource acquisition methods, extracted from the New Zealand freshwater macroinvertebrate trait database (NIWA; https://niwa.co.nz/sites/niwa.co.nz/files/nz_trait_database_v19_2_18.xlsx). Trait combinations govern species interactions through potential competition for habitat and food, or species contribution to ecosystem functioning through nutrient cycling, dispersal and trophic control (Hevia et al., 2017; Sekercioglu, 2010). We used a total of 16 traits, divided into 59 modalities and fuzzy-coded from 0 to 3 following Chevenet et al. (1994; Table S1.1; see also Dolédec et al., 2006, 2011).

2.2 | Environmental descriptors

Environmental characteristics to be used as predictors were grouped according to four different spatial scales: global, regional, catchment and reach scale (Table S1.2). Global-scale predictors used were temporal changes in air temperature and precipitation. At each site, we extracted daily values for the period 1991–2016, from 5 km² gridded layers of New Zealand, using NIWA's Virtual Climate Station Network (VCSN; <https://data.niwa.co.nz/>). We then regressed annual and seasonal (for the winter, spring and summer seasons) mean precipitation, precipitation variability (i.e. the coefficient of

variation $\times 100$), mean air temperature and air temperature variability (i.e. the standard deviation of the mean) against time and used the slopes of each linear regression as estimates of temporal change. Principal component analyses (PCA; Pearson, 1901) were applied individually to air temperature and precipitation variables to reduce the multidimensionality and to eliminate multicollinearity within groups. We scaled all variables prior to PCAs and interpreted the respective first two axes of each PCA as synthetic descriptors of (a) changes in air temperature (TMean), (b) changes in air temperature seasonality (TSeas), (c) changes in precipitation seasonality (Prec CV) and (d) changes in precipitation (Prec; Table S1.3).

Regional-scale predictors were described using four variables, reflecting landscape features that stretch beyond catchment boundaries. Altitude (m) at the sampling site, phosphorus and calcium concentrations and mean hardness (induration) in surface rocks of the upstream catchment (USPhosphorus, USCalcium and USHardness respectively). These variables were extracted for each site from the Freshwater Environments of New Zealand geodatabase, based on a 30 m Digital Elevation Model (Leathwick et al., 2010), using ArcGIS version 10.7 (Esri Inc., 2020).

For catchment-scale predictors, we used the proportion of upstream catchment covered by six land-cover types (intensive agriculture, light pastoral areas, native forest, urban areas, scrub and shrub cover and exotic forest; Table S1.2). We used static, spatial descriptors of land-cover in lieu of estimates of temporal changes in land-cover, as these were found to be major correlates of both spatial and temporal changes in the water-quality of New Zealand's freshwater systems (Julian et al., 2017; Snelder et al., 2018). We created the land cover types by aggregating fine-scale individual classes of the 75 land-cover classes from the New Zealand Land Cover database

version 4.1 (Landcare Research 2015; Table S1.2). The six land-cover metrics were then ordinated using PCA, and the first two axes retained as synthetic land-use predictors (Land-use 1 and Land-use 2 respectively; Table S1.3). Area of the upstream catchment (km^2 ; USCatchArea) and the average slope of the upstream catchment (degrees; USAvgSlope) from each river segment were also used as catchment-scale predictors.

Finally, reach-scale descriptors were defined by the slope (degrees) of the stream segment at each sampling site (SegSlope; Leathwick et al., 2010), the predicted wetted river width (metres) at the 7-day mean annual low flow (WidthMALF; Booker, 2015), the estimated proportion of riparian shading at each river segment (SegRipShade; Leathwick et al., 2010) and temporal changes (1991–2016) in median annual values (mg/m^3) of nitrate ($\text{NO}_3\text{-N}$), ammoniacal-nitrogen ($\text{NH}_4\text{-N}$), dissolved reactive phosphorus and dissolved oxygen concentrations and water clarity (metres; CLAR). Water quality variables were log10-transformed prior to calculating temporal changes, which were then ordinated using PCA. The first axis was retained as a synthetic predictor of temporal changes in water quality (Table S1.3).

The final set of environmental variables consisted of 16 predictors which were not highly correlated (Pearson's $|r| < .65$; Figure S1.1; Zuur et al., 2010).

2.3 | β -diversity measures

To evaluate temporal changes in taxonomic and functional spatial β -diversity, we first $\log(x + 1)$ transformed macroinvertebrate abundances, and replaced the species by site matrix by a community-level (abundance) weighted means of functional trait values (CWM; Lavorel et al., 2008) by site matrix for functional β -diversity analyses. We then measured β -diversity as the dissimilarity among all pairs of sampled sites ($n = 64$) at each annual time step using the percentage difference index (%diff; Odum, 1950; commonly referred to as Bray–Curtis dissimilarity). The percentage difference index between observation S_j and S_k is defined as:

$$\%diff = \frac{(B+C)}{(2A+B+C)},$$

where A is the total abundance of all species found in both S_j and S_k , B is the total abundance of all species unique to S_j and C the abundance of each species unique to S_k . To assess the total variation in composition, we first computed the total sum of squares (SS_{total}) of the dissimilarity matrix by summing the dissimilarities in the lower triangular matrix and dividing it by the number of observations N . We then computed total β -diversity (BD_{Total}) for the North and South Island individually, by dividing SS_{total} by $N - 1$ (Legendre et al., 2005; Legendre & De Cáceres, 2013).

We also measured temporal β -diversity for both islands individually using multiple-year and pairwise dissimilarity of all pairs of sampled years, by aggregating all samples across all sites ($N = 64$) for each individual year ($N = 25$). Pairwise β -diversity

metrics and multi-site β -diversity metrics (i.e. spatial β -diversity aggregated across multiple sites) have been shown to reveal different patterns (Baselga, 2010, 2013a). To test whether temporal variations in β -diversity were mainly due to compensatory changes in abundances or fluctuations in total community abundance, we partitioned total β -diversity into two components, namely abundance replacement (β_{rep}) and abundance difference components (β_{diff}) following Baselga (2013b), Legendre (2014) and Baselga (2017) as:

$$\beta_{\text{rep}} = \frac{2 \min(B, C)}{(2A+B+C)},$$

and

$$\beta_{\text{diff}} = \frac{|B-C|}{(2A+B+C)}.$$

Their contributions to total β -diversity were measured by computing the total sums of squares of each matrix and dividing them by $N - 1$.

Finally, to test the extent to which each sampled site contributed to long-term homogenization or differentiation, we calculated temporal changes in the Local Contribution to Beta Diversity (LCBD; Legendre & De Cáceres, 2013) of each community. LCBD indicates how unique an observation of macroinvertebrate composition is, by assessing its contribution to the total variation in community composition (Legendre & De Cáceres, 2013). LCBD has been found to vary considerably through time in stream ecosystems (Li et al., 2020). We measured LCBD directly from the dissimilarity matrix of all observations as the diagonal elements of the matrix containing the centred dissimilarities, divided by SS_{total} . We then assessed temporal changes in LCBD at each site using the slope of a linear regression against years. Differences in the magnitude of temporal changes between taxonomic and functional LCBDS were tested for significance using paired samples t tests.

2.4 | Drivers of observed changes

Hierarchical Generalized Additive Mixed effects Models (GAMMs) were built to relate temporal changes in taxonomic and functional LCBD to global, regional, catchment and reach-scale processes respectively. Every variable (responses and predictors) was Box–Cox transformed and later standardized to their mean, 1 unit variance. GAMMs were fitted with catchments nested within islands as random effects, using regression splines to account for potential non-linear relationships and restricted maximum likelihood to optimize the parameter estimates. For each change in LCBD, changes were primarily modelled against global climate change descriptors. We kept only the variables that maximized the coefficient of determination (adjusted- R^2) as the best model (Floury et al., 2018; Van Looy et al., 2017). The relative importance of each variable in the model was assessed following methods described in Kuhn (2012). The same step was followed in a descendant way, using successively regional,

catchment and reach-scale descriptors as predictor variables and the residuals from the previous model as a response variable. A smooth product between latitude and longitude was explored as a predictor variable using the residuals from the reach-scale models to account for spatial autocorrelation (Wood, 2017). However, residual spatial autocorrelation was not observed ($p > .05$ for every model). Statistical analyses were all performed under the R environment (version 3.6.2; R Core Team, 2020). CWMs were calculated using the *FD* package (Laliberté et al., 2014), BD_{Total} and LCBD with the *adespatial* package (Dray et al., 2017), β -diversity partitioning with the *betapart* package (Baselga et al., 2012), GAMMs using the *mgcv* package (Wood & Wood, 2015) and the relative influences of the environmental variables in the GAMMs with the *caret* package (Kuhn et al., 2020).

3 | RESULTS

3.1 | Changes in taxonomic and functional β -diversity

We observed overall tendencies towards taxonomic homogenization but functional differentiation of macroinvertebrate communities on both islands of New Zealand (Figure 2a,b). Spatial taxonomic β -diversity declined over the 25 year period in the South Island ($R^2 = .19$, $F = 11.84$, $p < .01$), but not on the North Island ($p = .407$). In contrast, functional β -diversity increased on the North Island ($R^2 = .33$, $F = 24.62$, $p < .001$) but less so on the South Island ($R^2 = .069$, $F = 3.694$, $p = .06$).

Multiple-year and pairwise temporal β -diversity measures were highly similar on both islands and mainly driven by replacements of species abundances and functional traits among communities, rather than unidirectional abundance differences (Table 1). However, abundance replacements were much higher for taxonomic β -diversity (Multiple-year values: $\beta_{rep} = 61.1\%$ on both islands; $\beta_{diff} = 11.1\%$ and 11.2% for the North and the South Island respectively; Average

pairwise dissimilarity: $\beta_{rep} = 37.2\%$ and 39.2% ; $\beta_{diff} = 20.8\%$ and 21.1% for the North and the South Island respectively; Table 1) than for functional β -diversity (Multiple-year dissimilarity: $\beta_{rep} = 20.4\%$ and 21.1% , $\beta_{diff} = 17\%$ and 16% ; Average pairwise dissimilarity: $\beta_{rep} = 12\%$ and 16.4% , $\beta_{diff} = 17.7\%$ and 20.3% , for the North and the South Island respectively; Table 1).

Finally, only 44% of the sites exhibited decreasing taxonomic LCBD, 56% showing flat trends or increasing taxonomic LCBD (Figure 3a), and 56% exhibiting decreasing functional LCBD – 44% showing flat trends or increasing functional LCBD (Figure 3b).

TABLE 1 Taxonomic and functional temporal β -diversity measured as the percentage difference index of dissimilarity ($\beta_{\%diff}$) and its decomposition into replacements of species abundances or functional traits (β_{rep}) and unidirectional abundance gradients (β_{diff}) of macroinvertebrate assemblages collected annually at 64 river sites in New Zealand from 1991 to 2016. To exclude potential spatial variations in species composition, samples were aggregated across all sampled sites ($N = 64$) for each sampled year ($N = 25$; 1991–2016) prior to analyses. Multiple-year dissimilarity corresponds to the dissimilarity after aggregating data across all years. Average pairwise dissimilarity is the average value of each pairwise comparison of sampled years. Values in the table are percentages

Island	Biodiversity facet	$\beta_{\%diff}$	β_{rep}	β_{diff}
Multiple-year dissimilarity				
North	Taxonomic	72.2	61.1	11.1
	Functional	37.9	20.4	17.5
South	Taxonomic	72.3	61.1	11.2
	Functional	37.3	21.1	16.1
Average pairwise dissimilarity				
North	Taxonomic	58.0	37.2	20.8
	Functional	29.7	12.0	17.7
South	Taxonomic	60.4	39.2	21.2
	Functional	36.7	16.4	20.3

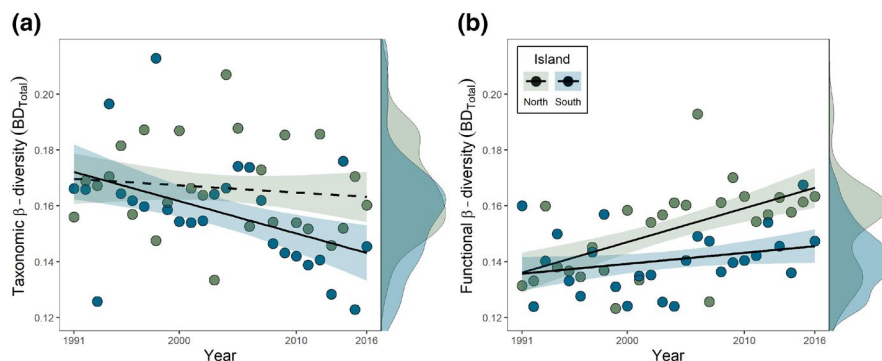


FIGURE 2 Scatter plots illustrating temporal changes in (a) taxonomic and (b) functional β -diversity (BD_{Total}) for the North and the South Island of mainland New Zealand (as indicated by the legend). Solid black lines represent significant ($p < .05$) linear regression models, whereas the black dashed line represents a nonsignificant model ($p > .05$). Density curves on the right of the figures illustrate the density distribution of the corresponding variable [Colour figure can be viewed at wileyonlinelibrary.com]

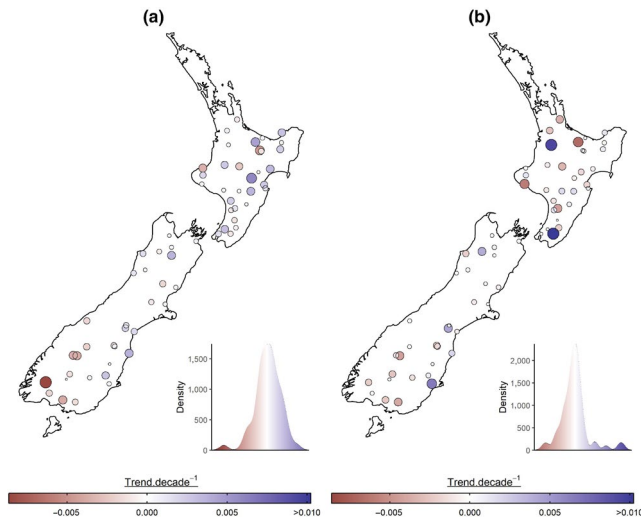


FIGURE 3 Maps of temporal changes (trend.decade⁻¹) in (a) taxonomic and (b) functional Local Contribution to Beta Diversity (LCBD) measured using log($x + 1$) macroinvertebrate abundances and the percentage difference index of dissimilarity. Point size is proportional to the degree of change. Density curves at the bottom right corner of each map illustrate the density distribution of each variable [Colour figure can be viewed at wileyonlinelibrary.com]

3.2 | Relationship between changes in taxonomic and functional local contribution to β -diversity

Changes in taxonomic and functional LCBD were weakly positively correlated on the South Island ($R^2 = .11$, $p = .07$; Figure 4a), but not on the North Island ($p = .69$; Figure 4a). Over both islands, 36% of the sites experienced increasing taxonomic LCBD but decreasing functional LCBD, whereas only 11% of the sites experienced increasing functional LCBD but decreasing taxonomic LCBD. Equal amounts (26%) of the remaining sites exhibited increasing or decreasing taxonomic and functional LCBD. In addition, there were no differences between changes in taxonomic and functional LCBD for all pairs of samples and on both islands individually ($.20 < p < .76$; Figure 4b).

3.3 | Drivers of observed changes

Hierarchical GAMMs explained 38% of the temporal changes for both taxonomic and functional LCBD (Table 2). Changes in taxonomic LCBD were mostly driven by global-scale variables ($R^2 = .25$) and further influenced by catchment- ($R^2 = .07$) and reach-scale descriptors ($R^2 = .07$; Table 2). Changes in functional LCBD mostly responded to global- ($R^2 = .23$) and catchment-scale descriptors ($R^2 = .21$; Table 2).

Eleven drivers of change in taxonomic LCBD were selected in the GAMMs (Figure 5). These were: changes in precipitation seasonality (% of relative influence = 20.7), changes in air temperature (15.6%), altitude (12.1%), stream segment wetted river width at

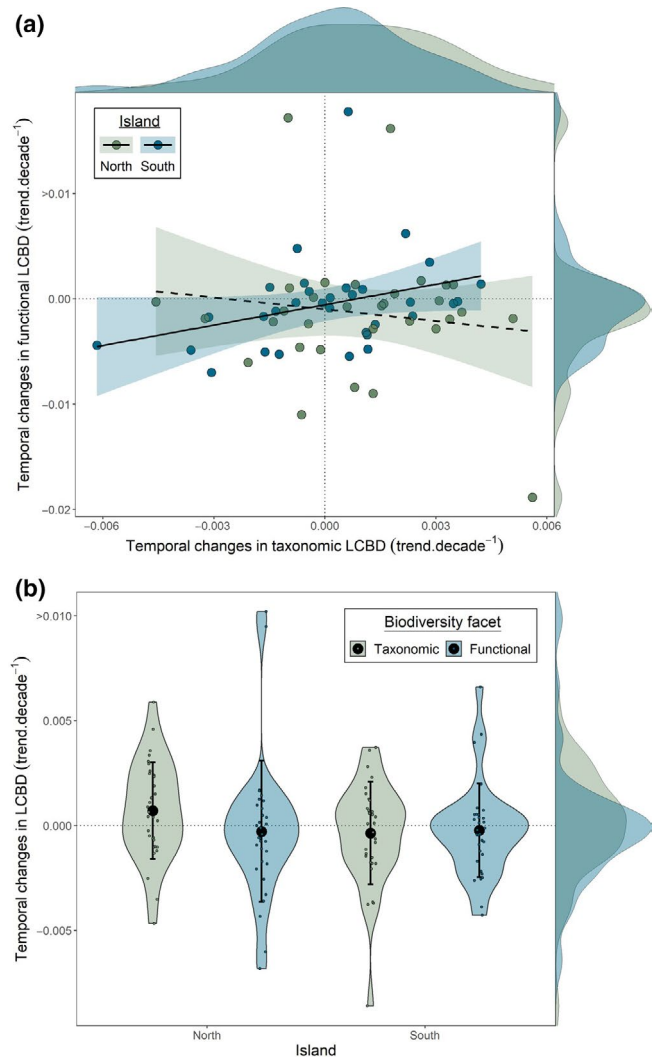


FIGURE 4 (a) Relationships between temporal changes in taxonomic and functional Local Contribution to Beta Diversity (LCBD) for both islands of mainland New Zealand. The solid black line represents a significant ($p < .05$) linear regression model. The black dashed line represents a nonsignificant model ($p > .05$). Shaded areas around the regression lines are 95% pointwise confidence intervals. (b) Violin plots illustrating differences between rates of changes in taxonomic and functional LCBD for the North and the South Island individually. The average rate of change is shown as black points and standard deviation as vertical black lines, in each violin plot. Raw values are shown as colored points. The horizontal dashed line on the plot shows the zero mark. The density curves on the margins of the figures illustrate density distribution of the corresponding variables [Colour figure can be viewed at wileyonlinelibrary.com]

the 7 day mean annual low flow (11.2%), changes in precipitation (11.1%), stream segment slope (10.7%), upstream calcium concentration in surface rocks (7.8%), land-use intensity (Land-use 1:5.8%; Land-use 2:5.7%), upstream catch area (5.4%) and upstream average slope (4.9%).

By contrast, changes in functional LCBD were driven by seven variables (Figure 5). Specifically, upstream catchment average slope (23.91%), changes in precipitation (22.4%), changes in air temperature (16.8%), land-use intensity (Land-use 1 and Land-use 2;

Biodiversity facet	Spatial scale				Total
	Global	Regional	Catchment	Reach	
Taxonomic	0.25	0.05	0.07	0.07	0.38
Functional	0.23	0.01	0.21	<0.001	0.38

TABLE 2 Coefficients of determination (adjusted- R^2) of each generalized additive mixed effect model for each spatial scale and the full model (Total)

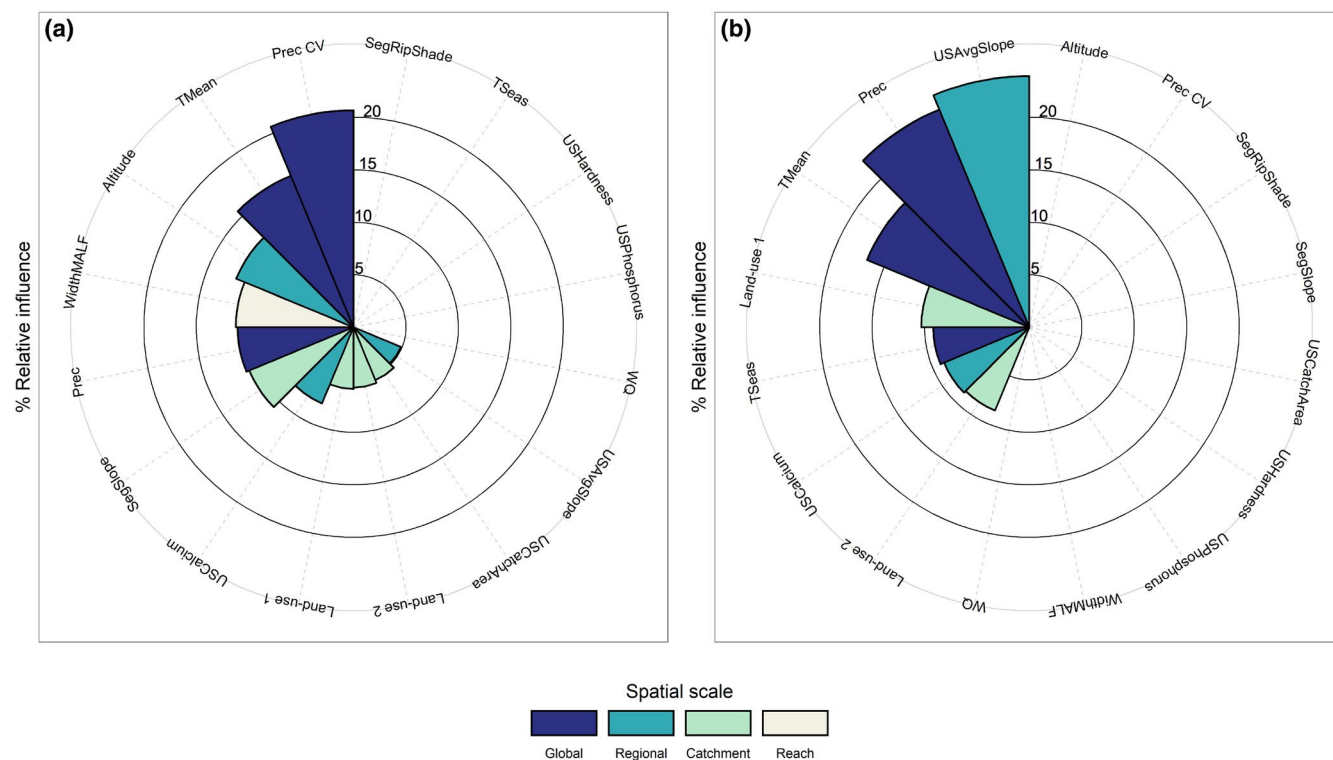


FIGURE 5 Polar diagrams illustrating the percentage of relative influence explained by each environmental predictor in the hierarchical Generalized Additive Mixed effects Models, for (a) taxonomic and (b) functional changes in Local Contribution to Beta Diversity [Colour figure can be viewed at wileyonlinelibrary.com]

10.3% and 8.6% respectively), changes in temperature seasonality (9.2%) and upstream concentration of calcium in surface rocks (8.8%). Marginal effects plots of these relationships are presented in Figure S3.1.

4 | DISCUSSION

Our analyses revealed large-scale declines in taxonomic β -diversity but concurrent rises in functional β -diversity over the 25 year study period, which only partially supports our first hypothesis (fulfilling H_{1a} but rejecting H_{1b}). As expected, we found a weak relationship between changes in each site's contribution to taxonomic and functional β -diversity (accepting H_2). In addition, the mean rate of temporal change in these two metrics did not differ. Finally, our results support H_3 with global-scale climatic factors being the primary determinants of the observed changes in taxonomic and functional β -diversity.

The functional differentiation among freshwater macroinvertebrate assemblages over the 25-year period was contrary to our expectation. However, similar climate-induced large-scale increases

in functional diversity of freshwater macroinvertebrates were also recently observed in rivers of France (Bruno et al., 2019; Flourey et al., 2018), and similar responses to climate change have been observed for other taxa and trophic levels globally (Araújo et al., 2006; Walther et al., 2002). In running waters, this climate-induced process could be due to the increasing prevalence of warm water species in temperate systems, which are promoted by newly suitable (i.e. warmer) conditions (Buisson et al., 2008; Haase et al., 2019). Such a rise in functional β -diversity may also provide greater resilience and resistance capacity to macroinvertebrate communities facing disturbances (de Juan et al., 2013; Isbell et al., 2015; Mori et al., 2013; Van Looy et al., 2019).

Although a relationship between temporal changes in taxonomic and functional LCBD was observed on the South Island, the pattern did not hold on the North Island. This discrepancy highlights the need to consider explicitly both the taxonomic and functional facets of biodiversity, as changes in functional β -diversity cannot necessarily be predicted by changes in taxonomic β -diversity (Baiser & Lockwood, 2011; Villéger et al., 2014; White et al., 2018). More importantly, 36% of the communities (measured as changes in their local contribution to β -diversity) in the present analyses,

differentiated in taxonomic composition, but homogenized in functional composition with accrued time, as opposed to the rest of the communities. This may represent a key mechanism underlying the observed rise of generalist species and replacement of cold-tolerant species with warm-tolerant species that is being observed in temperate macroinvertebrate communities (Floury et al., 2018; Haase et al., 2019; Van Looy et al., 2016). That is, communities comprising functionally similar but taxonomically diverse species are being replaced by functionally diverse but taxonomically similar species, as observed here.

Changes in precipitation seasonality was the most important correlate of taxonomic homogenization. In contrast to temperature, which exhibited a consistent increase across all locations, changes in precipitation and precipitation seasonality were location-specific, with both increases and decreases present across the country (Figure S2.2). These changes, whether an increase or a decrease, tended to reduce a site's contribution to β -diversity. Mainland New Zealand is composed of two mid-latitude islands, with a typically unpredictable climate (Tonkin, Death, et al., 2018) and flashy river flow regimes (Winterbourn et al., 1981) due to its oceanic position. The temporal turnover of stream communities in New Zealand streams tends to reflect this unpredictability, with limited intra-annual differentiation between seasons compared to trends in more predictable climates (Tonkin, Death, et al., 2018). However, our results indicate that patterns of precipitation seasonality in New Zealand has changed over this 25 year period, altering the spatial distribution of river macroinvertebrate communities through time. Similar climate-driven environmental harshness has been observed not only to be important for dynamic systems like these, but also for other ecosystems worldwide. For instance, natural flow intermittence is an important structuring agent for stream macroinvertebrate communities in Mediterranean streams (Belmar et al., 2019). Given the importance of natural cycles of flooding and drought in streams (Aspin et al., 2018, 2019; Poff et al., 1997; Tonkin, Merritt, et al., 2018), it stands to reason that patterns in precipitation seasonality play a key role in structuring stream macroinvertebrate species communities.

Our results clearly highlighted a particularly dominant role of climate change, and less so land-use, in mediating changes in taxonomic and functional β -diversity of these river macroinvertebrate communities. These processes, together, contributed most of the relative influence explained by the variables in our models. Climate change, however, explained 3.6 times more of the variability in changes in taxonomic β -diversity, and 1.3 times more in functional β -diversity, than land-use related variables. This is despite New Zealand having experienced one of the highest rates of agricultural land intensification over recent decades (OECD/FAO, 2015). However, we recognize that this result may be specific to our study area. For instance, the effects of climate change and land-use variables may have differed had we focused on streams of different realms (Heino, 2011) or size (Floury et al., 2018; Radinger & García-Berthou, 2020). Moreover, although we examined the effects of different environmental scales in our models, our

findings could relate to the spatial extent of our analyses (Hewitt et al., 2010; Jarzyna & Jetz, 2018; Wiens, 1989). This can obscure the relative importance of anthropogenic factors that may only operate at local scales (Jouffray et al., 2019), such as human-induced flow alteration, eutrophication and sedimentation within single catchments. Whether a stronger anthropogenic signature would emerge at a finer extent of analyses, therefore, represents an important next step for future work that could better inform local community management.

The responses of communities to changes in climatic drivers were variable. Air temperature warming correlated with decreases in taxonomic and functional LCB. However, decreasing precipitation correlated with decreasing taxonomic LCB but increasing functional LCB. Warming and decreasing precipitation theoretically reduces discharge, hence potentially reduces the connectivity among communities, but at the same time may homogenize mesohabitats in these systems (Aspin et al., 2018, 2019; Rahel, 2002, 2007). Such a mechanism would support the expansion of functionally diverse but homogeneous species assemblages. By contrast, Villéger et al. (2014) observed greater functional homogenization than taxonomic homogenization in European freshwater fish assemblages under climate change due to range expansions in non-native species distributions within European water basins, which supported similar functions to native species. Elucidating which species and functional traits contributed to the changes in β -diversity observed here, may allow further research to understand the evolutionary and ecological consequences of these changes in biodiversity.

Climate models suggest river flow regimes will increase in variability as the climate continues to change (Arnell & Gosling, 2013; Kakouei et al., 2018; Schneider et al., 2013), opening the door to questions of how freshwater macroinvertebrate communities will respond to more intensified and variable flow disturbances. Although these New Zealand streams have seen an increase in functional diversity over the 25 year period, more intensified disturbances are likely to suppress or overturn this trend (Domisch et al., 2013; Kakouei et al., 2018). For example, an increasing number of colonizing warm water species could promote further species losses, by competitive exclusion (Buisson et al., 2008; Radinger et al., 2019). Moreover, the resilience of stream biodiversity in the face of continued global change could also be reduced if spatial insurance effects become less effective, as large-scale disturbances promote greater synchrony among ecosystems (Shanafelt et al., 2015). Our results therefore indicate that the responses of stream biodiversity to ongoing environmental change are overly complex with contrasting taxonomic and functional responses to change. The positive news of increasing functional β -diversity over time, which may provide a greater resilience capacity to communities despite taxonomic homogenization, could only be a transient process that will be overturned in time. To better understand the biodiversity consequences of future global change, we need a greater uptake of studies exploring the combined and interacting responses of both taxonomic and

functional components of biodiversity to ongoing environmental change. As river ecosystem reorganization continues in the Anthropocene in response to climate change (Olden et al., 2018; Tonkin et al., 2019), the value of different ecosystem states and environmental management will likely hinge upon the capacity of those ecosystems to maintain key functional processes despite ongoing taxonomic homogenization.

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AUTHOR CONTRIBUTION

T.L.M., F.S. and P.V. compiled the data. T.L.M. and M.F. designed the study, computed analyses and interpreted the results. T.L.M. and J.D.T. wrote the manuscript with inputs from all co-authors.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from NIWA upon request. Restrictions apply to the availability of these data, which were used under license for this study. Data are available from the authors with the permission of NIWA.

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SUPPORTING INFORMATION

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

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