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RESEARCH ARTICLE

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Long-term changes in macroinvertebrate communities across high-latitude streams

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Abstract

Long-term records of benthic macroinvertebrates in high-latitude streams are essential for understanding climatic changes, including extreme events (e.g. floods). Data extending over multiple decades are typically scarce. Here, we investigated macroinvertebrate community structural change (including alpha and beta diversity and gain and loss of species) over 22 years (1994–2016) in 10 stream systems across Denali National Park (Alaska, USA) in relation to climatological and meteorological drivers (e.g. air temperature, snowpack depth, precipitation). We hypothesised that increases in air temperature and reduced snowpack depth, due to climatic change, would reduce beta and gamma diversity but increase alpha diversity. Findings showed temporal trends in alpha diversity were variable across streams, with oscillating patterns in many snowmelt- and rainfall runoff-fed streams linked to climatic variation (temperature and precipitation), but increased over time in several streams supported by a mixture of water sources, including more stable groundwater-fed streams. Beta-diversity over the time series was highly variable, yet marked transitions were observed in response to extreme snowpack accumulation (1999–2000), where species loss drove turnover. Gamma diversity did not significantly increase or decrease over time. Investigating trends in individual taxa, several taxa were lost and gained during a relative constrained time period (2000–2006), likely in response to climatic variability and significant shifts in instream environmental conditions. Findings demonstrate the importance of long-term biological studies in stream ecosystems and highlight the vulnerability of high-latitude streams to climate change.

KEYWORDS
climate change, diversity, long-term records, species loss, stream communities

1 | INTRODUCTION

High-latitude stream systems are hotspots of biodiversity, supporting unique biological communities with taxa highly adapted to the often-harsh environmental conditions (Tolonen et al., 2018). A major driver of biodiversity in these systems is environmental heterogeneity, driven by variability in different water sources and flow paths (e.g. rainfall runoff, snowmelt, glacial meltwater and groundwater;

Heino et al., 2013). Environmental conditions in these high-latitude streams are responding to climate change and associated hydrometeorological trends—such as increased rainfall runoff in northern hemisphere high latitudes (Arnell & Gosling, 2013; Zhang et al., 2013). There is, however, limited understanding of how these long-term environmental changes affect biotic communities inhabiting streams (Hotaling et al., 2017).

Climate-driven alterations in water sources and flow paths in high-latitude streams present a serious threat to various elements of biodiversity these environments support (Heino et al., 2020). Reductions in glacier ice and snowpacks, and subsequently, meltwater from these sources, will likely drive homogenisation of environmental conditions across streams (Hotaling et al., 2017). Without meltwater, streams in high-latitude systems would be dominated by groundwater and rainfall runoff, especially considering future predicted increases in precipitation (Arnell & Gosling, 2013). This in turn would potentially have significant effects on biodiversity at local and regional scales (see Cauvy-Frauné & Dangles, 2019; also see Muhlfeld et al., 2020). Within meltwater-fed streams, specialist taxa, have evolved to cope with the harsh environmental conditions present in snowmelt and glacial meltwater-fed streams. This loss of specialist taxa adapted to these cool, high-latitude climates (i.e. glacial-meltwater specialists, such as the chironomid genus *Diamesa*; Milner & Petts, 1994) will lead to a turnover of species with a gain of generalist taxa. As the community composition of these streams is variable prior to environmental change, the loss of these specialist taxa and gain of more generalist taxa will be stream-specific, leading to variable changes in alpha-diversity (Cauvy-Frauné & Dangles, 2019), including potential increases (Milner et al., 2017). The loss of these unique taxa in certain streams would also homogenise communities at the regional scale as environmental conditions become more similar, leading to a reduction in beta-diversity and gamma-diversity (Hotaling et al., 2019; Jacobsen et al., 2012). The increase in generalist riverine taxa as the environmental conditions become more homogenised occurs as they can expand their ranges, out-compete specialists and persist in these altered conditions (Culp et al., 2022; Lento et al., 2022). The increasing incidence and severity of extreme events (e.g. floods) alongside changes in water sources will also limit the type of taxa that can persist under the new environmental conditions. All in all, these changes would mean that high-latitude stream system communities are more sensitive to further environmental change (Birrell et al., 2020), with reduced taxonomic (beta and gamma) and functional diversity leading to potential reductions in an ecosystem's ability to respond to climate change (Mori et al., 2013).

Long-term data offer the unique opportunity to understand inter-annual variation related to different biotic and abiotic factors, inter-decadal ecological responses to environmental drivers (e.g. climate change), as well as determining the trajectory of change in ecological communities (Kuebbing et al., 2018). Indeed, to understand the potential effects of climate change on the different components of high-latitude stream biodiversity, these long-term datasets are essential. However, long-term ecological datasets (>10 years) are uncommon (Milner et al., 2016), especially in high-latitude stream systems across the globe.

Here, we investigated long-term trends in high-latitude stream macroinvertebrate communities using a unique 22-year time series (1994–2016) across 10 streams in Denali National Park, Alaska. Three hypotheses were tested:

> **H1.** Alpha-diversity will increases in some streams reflecting climatological and meteorological changes that would allow colonisation by generalist taxa from the regional species pool.

> **H2.** Beta-diversity will decrease over time due to increased homogeneity in environmental conditions across the study region.

> **H3.** Gamma-diversity will decline over time, as driven by the loss of specialist macroinvertebrate taxa and increased domination of generalists.

2 | METHODS

2.1 | Study region

Denali National Park, in central Alaska (Figure 1) covering nearly 2.5 million ha, is one of the largest National Parks in the United States. The streams in this pristine subarctic region are dominated by glacial plains, braiding channels and permafrost, thereby supporting a wide diversity of habitats and organisms. Streams in the study region flow northwards eventually becoming tributaries of the Yukon River.

Studies were conducted in the same 15 m reach across the 10 streams for 22 years (1994–2016) in Denali National Park (Figure 1). Each of the streams was fed by different water sources (snowmelt, glacial meltwater, groundwater and rainfall runoff). These flow pathways influence their flow regimes and physical and chemical conditions (Table 1). Water sources were identified by use of maps, water temperature records and personal observations. Some streams were dominated by individual water sources (e.g. Igloo Creek [snowmelt] and Little Stoney Creek [groundwater]) and some through a combination of water sources (e.g. Highway Creek [snowmelt and rain runoff]).

2.2 | Climate, meteorology and other physical conditions

Large-scale climatological and regional-scale meteorological data were collated for the study period (1994–2016). Phases of the Pacific Decadal Oscillation (PDO), a recurring ocean–atmosphere climate pattern variation with a periodicity of approximately 3–7 years, were used as a key climatological variable for analyses. Changes in the PDO reflect variation in the sea surface temperature and atmospheric pressure in the Pacific Ocean, which in turn drive shifts from a positive (below average winter temperature and above average winter
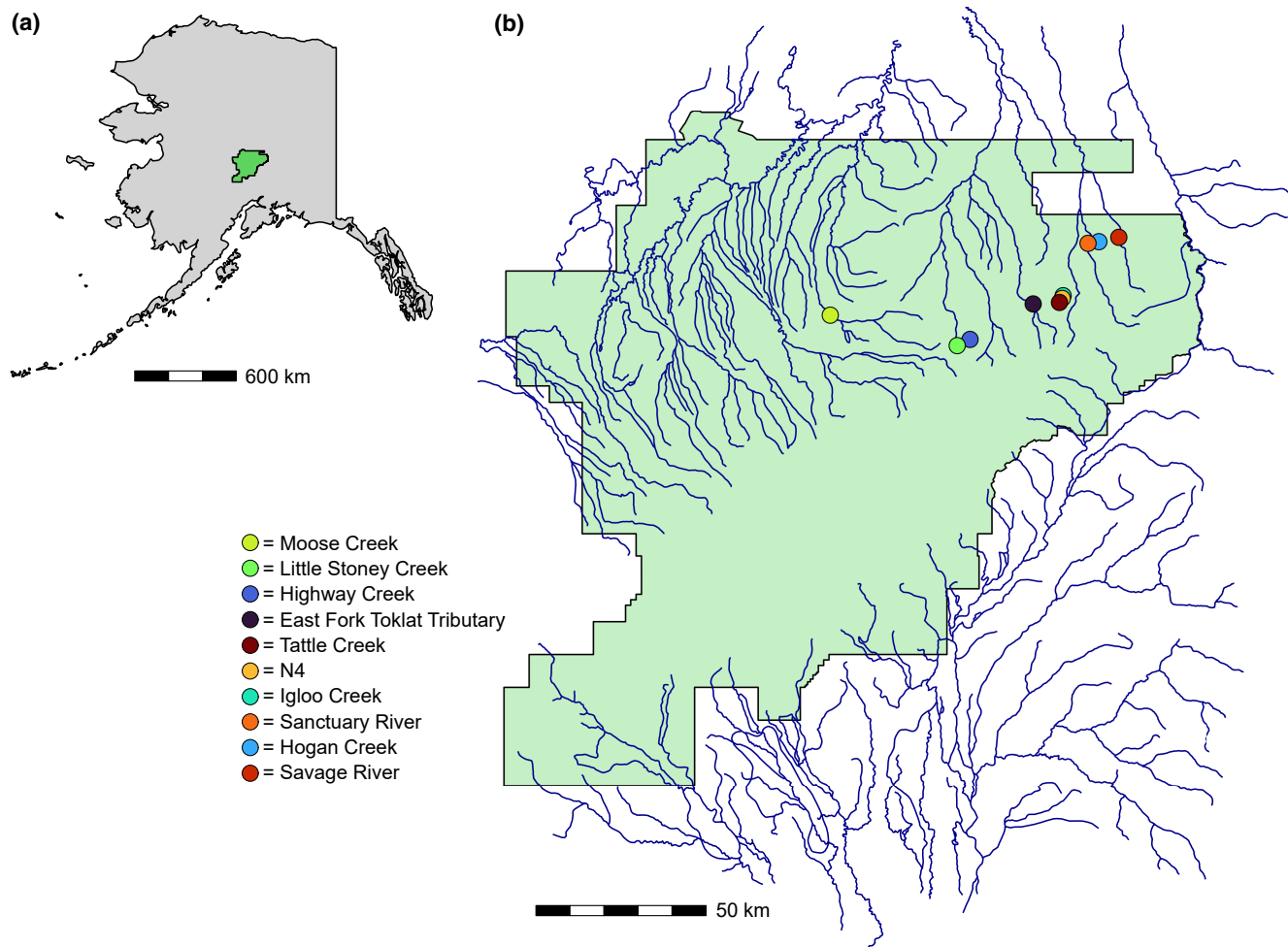
(a)

(b)

- ○ = Moose Creek
- ○ = Little Stoney Creek
- ○ = Highway Creek
- ○ = East Fork Toklat Tributary
- ○ = Tattle Creek
- ○ = N4
- ○ = Igloo Creek
- ○ = Sanctuary River
- ○ = Hogan Creek
- ○ = Savage River

FIGURE 1 The study region and sample site locations across Denali National Park. (a) Denali National Park (green polygon) in Alaska, USA. (b) Locations of sample sites.

precipitation) to a negative (above average winter temperature and below average winter precipitation) phase (Mills & Walsh, 2013). PDO data were collated from the National Oceanic and Atmospheric Administration (NOAA; https://www.ncei.noaa.gov/pub/data/cmb/ersst/v5/index/ersst.v5.pdo.dat). Meteorological data, daily precipitation (mm), snowfall (mm), snowpack depth (mm), minimum, maximum and observed air temperature (°C) were collated from the McKinley Park Station (63°39′05.5′′ N, 148°48′58.4′′ W; 630 m a.s.l; Appendix S1 in the Supplementary Materials).

The bottom component of the Pfankuch Index was used to assess the stability of the sampling section of the stream channel, which incorporates attributes like rock angularity, percent stable materials, degree of substrate packing and erosion and deposition (Pfankuch, 1975). The higher the score, the more unstable the channel is. Gradient was measured using a clinometer over a specified distance.

2.3 | Macroinvertebrate sampling.

Six replicate macroinvertebrate samples were collected every year within August using a 0.093 m^2 Surber sampler with a 335-µm mesh

net. The 15 m sampling section was always upstream of the Park Road by at least 20 m. Samples were preserved with 70% ethanol prior to sorting in the laboratory and taxa were identified to genus level for Ephemeroptera, Plecoptera and Trichoptera and to family for other groups using Merritt and Cummins (2009) and Voshell (2002). The six samples were identified individually in their entirety and then an average density per m^2 was determined for each stream.

2.4 | Statistical analysis

All analyses were completed in R 4.2.1 (R Core Team, 2022). Data and scripts are openly available (DOI 10.5281/zenodo.7648859).

Climatological and meteorological variables were summarised over the year preceding a given sample period, that is, September 1993 to August 1994 for the 1994 sample. The methods of summarising data depend on the variables: (i) cumulative annual (i.e. sum of daily values) and coefficient of variation (CV) for precipitation (PRCP) and snowfall (SNOW); (ii) mean and standard deviation for maximum daily temperature (TMAX), minimum daily temperature (TMIN), temperature at the time of observation (TOBS), annual

TABLE 1 Physical characteristics of the study streams in Denali National Park.

Stream	Order	Predominant water source	Riparian vegetation proximity	Stability (Pfankuch index value)	Gradient (%)	Catchment area (km²)
Moose Creek	3	Mixed (all except glacial meltwater)	Close border	High (27)	2.1	13.1
Little Stoney Creek	2	Groundwater	Close border	High (25)	1.4	1.4
Highway Creek	2	Snowmelt and rain runoff	Absent	Low (42)	7.6	7.6
East Fork Toklat tributary (EFTT)	2	Snowmelt and rain runoff	Close border	Moderate (33)	3.8	67.2
Tattler Creek	1	Snowmelt and rain runoff	Close border	High (30)	4.7	4.7
N4	1	Snowmelt and rain runoff	Absent	Low (40)	17.4	3.4
Igloo Creek	2	Snowmelt	Close border	High (31)	2.8	13.5
Sanctuary River	3	Snowmelt and minor glacial meltwater	>10 m	Moderate (37)	4.4	97.5
Hogan Creek	2	Groundwater	Close border	High (25)	2.0	8.9
Savage River	4	Snowmelt and minor glacial meltwater	>10 m	Moderate (38)	2.6	89.4

Note: Data are from 1995 and adapted from Conn (1998). Stream order refers to Strahler order, where 1 is a headwater stream prior to any confluence. Stability is the bottom component of the Pfankuch Index (Pfankuch, 1975).

snowpack depth (SNWD) and winter snowpack depth (SNWD_winter). Variables were then condensed using principal components analysis (Abdi & Williams, 2010), using the '*prcomp*' function in the '*stats*' package. All variables were initially centred around zero and equally scaled as raw data were on different scales (by an order of magnitude in some cases). We selected principal components (PCs) that significantly explained variation in the meteorological data using a broken stick model (Peres-Neto et al., 2005).

A range of indices were calculated to summarise macroinvertebrate community diversity. For each combination of sample year and site, we calculated alpha-diversity (α_{div}) as the Shannon-Weaver Index (Shannon & Weaver, 1963) using the '*diversity*' function in the '*vegan*' package. We calculated beta-diversity (β_{div}) across streams for each year with an abundance-based index, Bray–Curtis (Baselga, 2017), using the '*beta.multi.abund*' function in the '*betapart*' package (Baselga & Orme, 2012). This method also partitions total β_{div} into balanced variation (β_{divb}; the individuals of some species in one site are substituted by the same number of individuals of different species in another site) and gradient-abundance (β_{divg}; individuals are lost from one site to the other). We also calculated the change in beta-diversity (β_{div}) between streams for pairwise comparisons of years (e.g. 1994–1995, 2002–2003) using the '*ecopart.multi*' function in the package '*ecopart*' (Tatsumi et al., 2022). This method partitions the change in β_{div} ($\Delta\beta_{div}$) into components, reflecting either homogenisation (decrease in β_{div}) or differentiation (increase in β_{div}) through species gains and losses. Finally, gamma-diversity (γ_{div}) was calculated using the Shannon–Weaver Index for macroinvertebrate data pooled across streams for each year (i.e. sum of abundance for all taxa across all streams for each year), again using the '*diversity*' function in the '*vegan*' package.

Macroinvertebrate indices were related to meteorological and climatological variables, in the form of PCs (see above), using

generalised additive models (Wood, 2011) with the '*gam*' function in the '*mgcv*' package (Wood, 2017). Model structures are described in Appendix S2 in the Supplementary Materials. Stepwise backwards selection was used to select the most parsimonious model with the greatest level of deviation explained and generalised cross-validation score (Wood & Augustin, 2002).

To identify species contributing to the patterns in macroinvertebrate indices we investigated variation in macroinvertebrate community structure over time with non-metric multidimensional scaling (NMDS) using the '*metaMDS*' function in the '*vegan*' package (Oksanen et al., 2022). Distance matrices were computed using Bray–Curtis indices across two axes, and a Wisconsin double-rank standardisation was used to account for the effects of rare and common taxa. For the NMDS, we included taxa that occurred at >10 sample units (i.e. greater than 10 occurrences across 220 sample points [10 streams × 22 years]), which resulted in species richness being reduced from 48 to 30 (Appendix S3). This filtering procedure was completed to prevent rare taxa (i.e. 1 Taeniopteryx was recorded in a single sample, across all sites and years) from biasing the results of subsequent analyses (Gauch, 1982). To provide statistical support for the NMDS analyses we used a negative binomial multivariate generalised linear model (M-GLM) using the '*manyglm*' function in the '*mvabund*' package (Wang et al., 2012). We tested for differences in community structure across streams and over time as well as investigated the relationships between community structure and PCs. Finally, to quantify the levels of community variation over time we calculated the perimeter and area of the convex hull for the different sites in NMDS space using the function '*convhulln*' in the '*geometry*' package (Roussel et al., 2022), such that relatively small perimeters and areas would indicate low variation in macroinvertebrate communities and vice versa. Dunn tests (Dunn, 1964) were then used to assess whether the median area and perimeter of the

convex hulls for different streams were significantly different between their stability states – high, moderate or low (Table 1).

3 | RESULTS

3.1 | Climatological and meteorological patterns

Over the period studied (1994–2016), climate and meteorology exhibited significant variation. Meteorological and climatic data were summarised on the first three PCs explaining a total of 72.5% of variation (Table S4). PC1 (36.1%) was dominated by air temperature (maximum, minimum and observed), which was negatively loaded, PC2 (24.3%) was dominated by snowfall and snowpack depth (snowfall, annual and winter snowpack depth) which were negatively loaded, and PC3 (12.1%) was dominated by variation in temperature (maximum, minimum and observed) which were positively loaded (Table S4). PCs varied significantly over the study period (Figure 2) and several years experienced extremes in meteorological and climatological conditions, particularly during 2003 and 2011–2012, where some of the most extreme negative and positive values of PC1 and PC2 were measured.

3.2 | Changes in macroinvertebrate diversity across scales

Over the study period, 48 taxa were collected in the 10 streams, of which Chironomidae and Simuliidae were dominant, but only identified to family. Of the mayflies, *Baetis* was dominant followed by *Epeorus* and *Cinygmula*. *Baetis* was found in all streams over most of the 22-year period. Of the stoneflies, *Capnia* was dominant followed by the nemourids *Podmosta* and *Ostrocerca*. Trichoptera were

less numerous by an order of magnitude than mayflies and stoneflies, with *Glossoma* and *Ecclisomyia* being the most abundant. The streams that supported the most taxa were Hogan Creek, Tattler Creek and Little Stoney Creek whereas the streams with the lowest diversity were N4 and Highway Pass Creek. Oligochaetae were only found at one site for 1 year (Table S3).

Macroinvertebrate α_{div} was highly variable, both between streams and over time (GAM$_{\alpha div}$: Adjusted R^2 = .52, n = 198; Scale estimate = 0.09). Three streams displayed significant and directional temporal variation in α_{div} over time (Hogan, Moose and East Fork Toklat tributary [EFTT]), with others showing high but inconsistent inter-annual variation (Figure 3). Of these three, both stable streams, Hogan Creek and Moose Creek, displayed positive trends over time, whereas EFTT, a less stable stream, showed more variation over the time series. However, temporal variation in Hogan Creek and Moose Creek and all other stable streams was not significantly related to PC1 (Table S2b). However, temporal variation of α_{div} in the less stable streams (Sanctuary, Savage and Highway), was significantly related to PC1 (Table S2b).

The values of β_{div} across these stream systems were high (0.74–0.93), as was temporal variation (total and components) (Figure 4a). This variation in β_{div}, however, was not significantly related to year or PCs in a linear or non-linear manner, with all models failing to explain a significant amount of variation. Although temporal trends were not significant, patterns were observed in $\Delta\beta_{div}$, in particular, subtractive processes (homogenisation and differentiation; Figure 4b) were dominant over the time series, particularly during 1999–2000, indicating species losses caused the observed changes in β_{div}.

Macroinvertebrate γ_{div} was variable over time (GAM$_{\gamma div}$: Adjusted R^2 = .25, n = 22; Scale estimate = 0.06). Although a significant relationship between γ_{div} and the sample year was not found, γ_{div} was significantly related to PC1—with high annual values of PC1 (lower
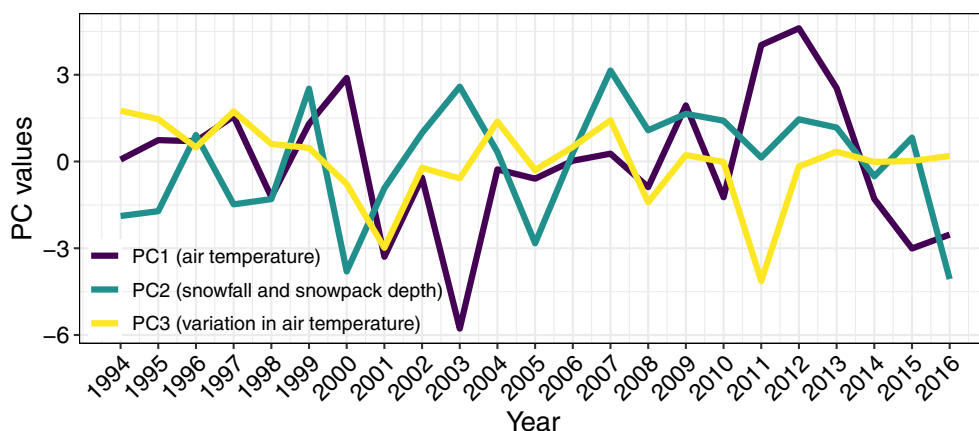

FIGURE 2 Temporal variation in PCs over the study period. For a complete description of variable loadings for each PC refer to Table S4. PC1 positive values indicate low air temperature and negative values high air temperature, PC2 positive values indicate high snowfall and snowpack depth and negative values low snowfall and snowpack depth, and PC3 positive values indicate high variation in air temperature and negative values indicate low variation in air temperature. Note the significant shift in PC1 and PC2 between 1999 and 2000, specifically the high values of PC1 (high air temperature) and the low values of PC2 (high snowfall and snowpack depth) in 2000. PC, principal component.
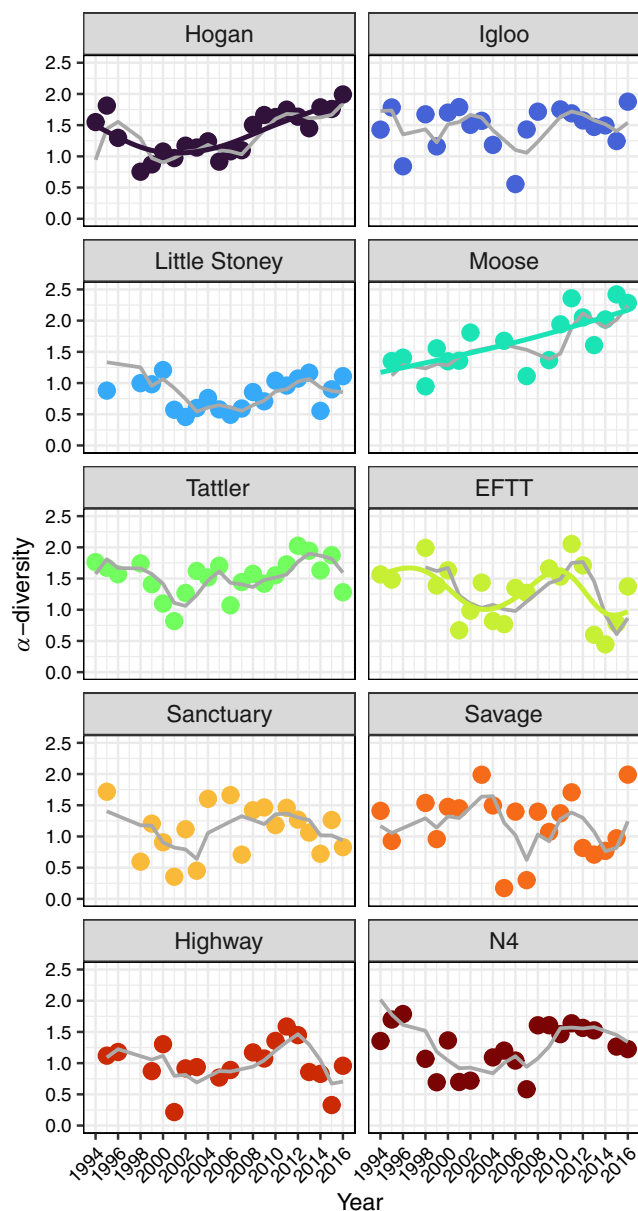
FIGURE 3 Temporal variation in α_{div} across the 10 streams. Grey lines represent the 3-year moving average. Lines with colour for Hogan Creek, Moose Creek and EFTT indicate significant relationships from generalised additive models with the dark grey ribbon representing standard errors. EFTT, East Fork Toklat tributary.

air temperature) related to high values of γ_{div} ($F_{1,22} = 7.93$, $p = .011$; Figure 5b).

3.3 | Variation in macroinvertebrate community structure

Macroinvertebrate community structure was highly variable and the variation was driven by overall shifts in the abundance of different specific invertebrate taxa (Figure 6a). In general, there is a shift in community composition over time in all streams (Figure 6c), which

appears somewhat related to climate and meteorology (Figure 6d) with similar patterns shown in NMDS gradient plots. Nevertheless, an M-GLM ($R^2 = .2$, Likelihood Ratio Test = 51.92, $p = .018$) showed that only the stream and the year, independently, were related to the overall community structure ($w_{9,188} = 1815.1$, $p < .001$; $w_{1,187} = 585.1$, $p < .001$; respectively).

Streams showed generally different temporal patterns in community composition (Figure 6b), yet there were some consistent patterns, with 2007 consistently appearing as an outlier across streams due to the high relative abundance of Diptera (Simuliidae and Chironomidae; Figure 6a). Although the overall differences in convex hull areas between streams with different levels of environmental stability were not significant (Kruskal–Wallis rank-sum test: $\chi^2 = 2.9$, df = 2, $p = .24$), the convex hull area between streams with low and high channel stability was significant (Dunn test: $z = -1.7$, $p = .045$).

Individual taxa, as well as driving changes in the overall community structure (in the case of more abundant organisms), were lost and gained in streams over the study period (Figure 7). *Capnia*, *Doddsia* and *Ostrocerca* were not observed in any streams prior to 2003 and increased in both occurrence and abundance across streams between 2003 and 2016. Conversely, *Despaxia* and *Rhithrogena* were only collected before 2001 and 2006, respectively, and have not been collected in any stream since those years.

4 | DISCUSSION

Macroinvertebrate communities varied significantly in space and time across Denali National Park during the study period 1994–2016. The α_{div} of macroinvertebrate communities exhibited different temporal patterns across different streams. Communities in streams with stable channels and less variable flow regimes (more dominated by groundwater) exhibited more constancy over time, with some increases in macroinvertebrate diversity (Hogan Creek and Moose Creek). In comparison, in streams with less stable flow regimes (i.e. snowmelt and glacial meltwater-fed streams) macroinvertebrate communities exhibited higher variation over time, related to changes in climatological and meteorological conditions (air temperature, precipitation and snowpack depth). Differences in macroinvertebrate communities between streams, and their variable relationships with climate and meteorology, led to high but continually shifting levels of β_{div}. Turnover in β_{div} in both space and time was primarily driven by gains and losses of taxa. In particular, taxa were lost in response to high air temperature and a large accumulated snowpack in 2000 leading to extremely high spring stream flows. At the regional scale, γ_{div} was also variable and was highest during periods with lower air temperature. However, we acknowledge that the sampling points represent a low proportion of streams relative to the large area of catchments in Denali National Park. Nevertheless, our unique long-term study (>20 years) highlights the temporal variability of macroinvertebrate communities across streams supported by different water sources and demonstrates the importance of spatial
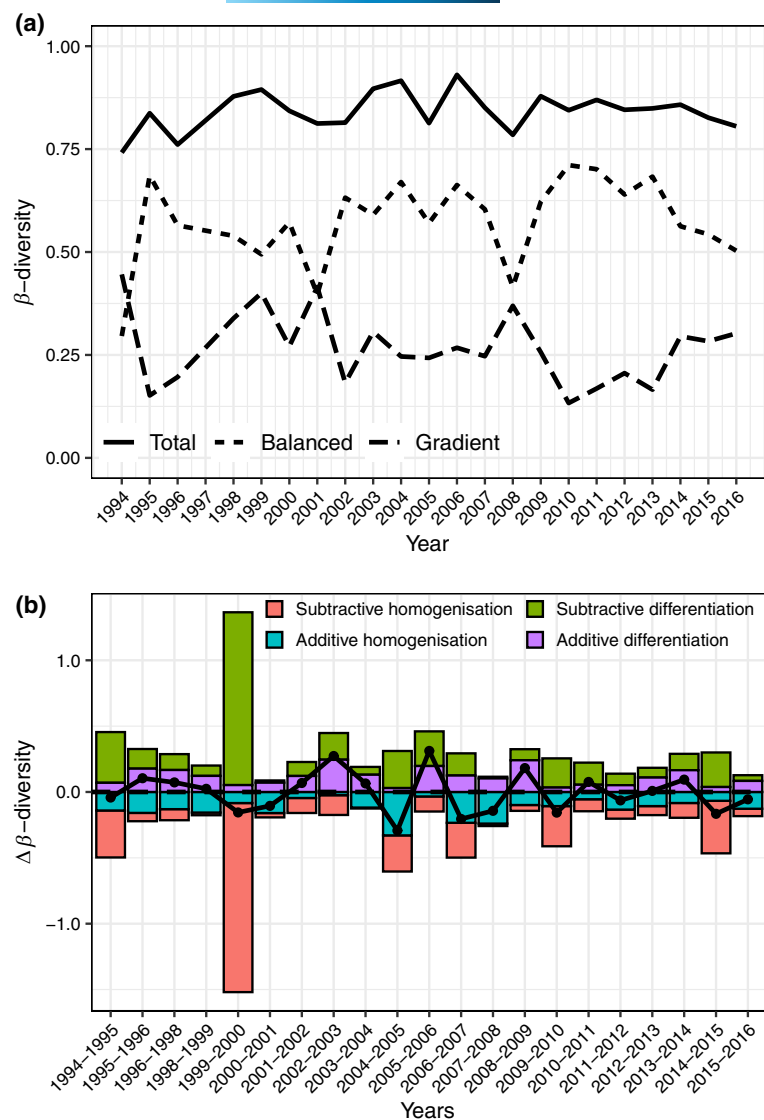
FIGURE 4 Change in β_{div} over time. (a) Temporal variation in β_{div} across all sites. The dotted line indicates balanced variation. The dashed line indicates gradient abundance. (b) Partitioning of $\Delta\beta_{div}$ change between years, either positive or negative, resulting from losses or gains of taxa. Black points indicate $\Delta\beta_{div}$.

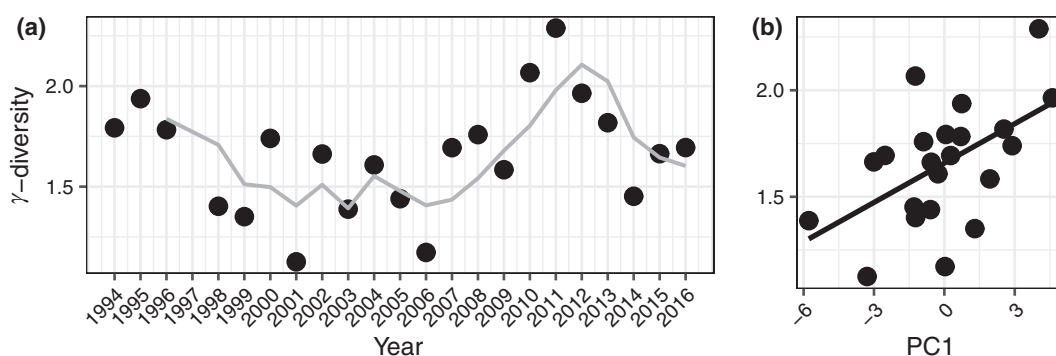**FIGURE 5** Variation in γ_{div}. (a) Temporal variation in γ_{div} (measured using the Shannon–Weaver Index). The grey line is the 3-year rolling average value. (b) Relationship between γ_{div} and PC1 (inverse of air temperature; see Table 1). Grey shading represents a 95% confidence interval. PC, principal component.

variation in macroinvertebrate communities for the persistence of aquatic biodiversity in high-latitude catchments (Lento et al., 2022).

Long-term trends in α_{div} across the streams provided some support for H1, with two streams exhibiting increases in alpha diversity over the time series. Patterns in α_{div} in streams have been investigated in detail across high-latitude streams (Culp et al., 2019; Heino et al., 2013; Lento et al., 2022; Tolonen et al., 2018), including those in Denali National Park (Milner et al., 2006, 2016; Windsor
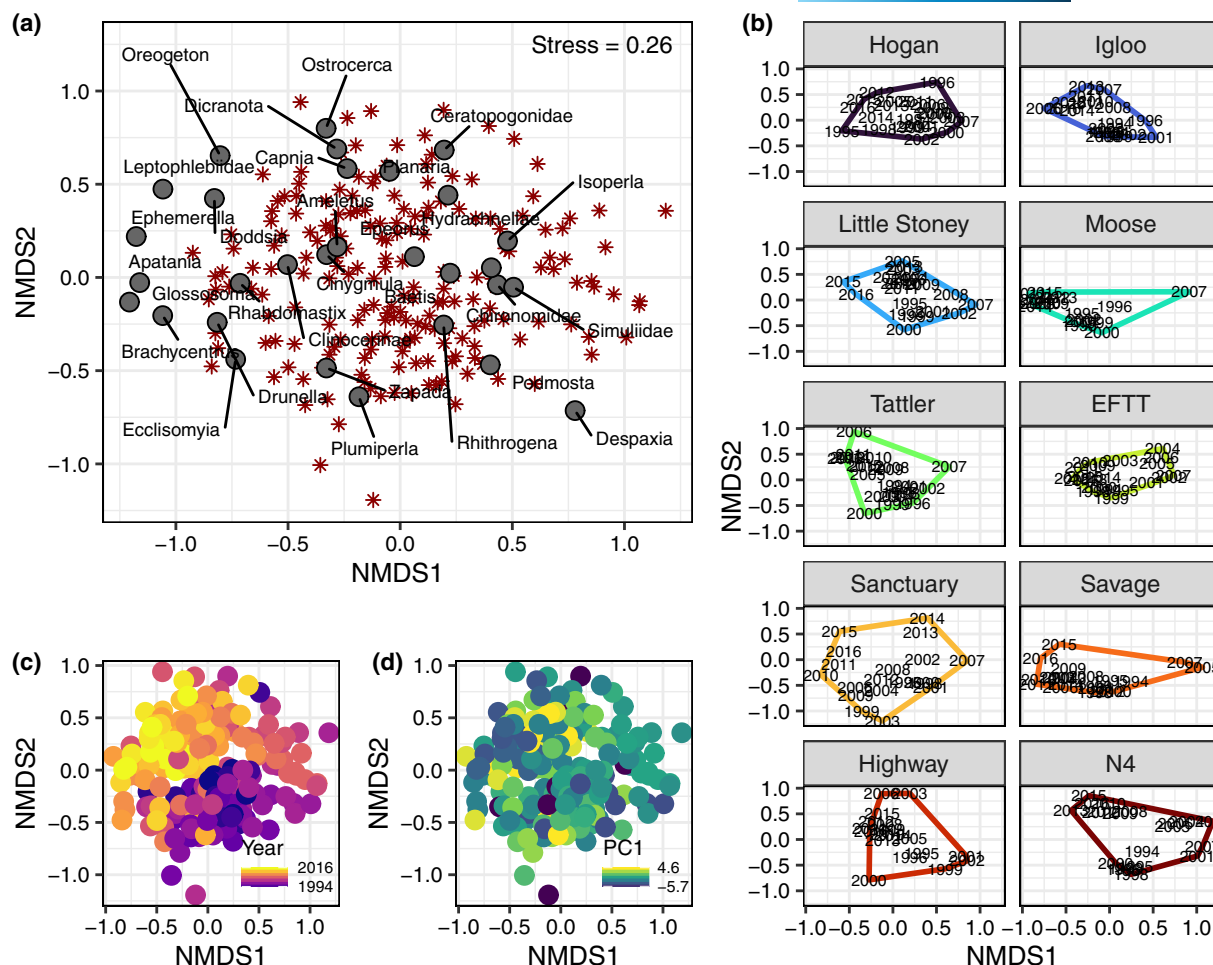
FIGURE 6 Macroinvertebrate community structure. (a) NMDS results for samples (red stars) with species influences (grey circles). (b) NMDS results separated by stream, with points represented as sample years. Convex hulls are drawn for the sites using the 'chull' function. (c) Samples coloured by year. (d) Samples coloured by PC1 value (higher values = lower air temperature). NMDS, non-metric multidimensional scaling; PC, principal component.

et al., 2017). The long-term trends observed here match those observed in shorter studies, with flow and morphological stability responsible for differences in diversity (Brown et al., 2006; Docherty et al., 2018; Milner et al., 2020) and persistence of this diversity over time (Milner et al., 2006). Two stable streams, dominated by groundwater, supported an increase in α_{div} over time, unrelated to climate or meteorology. For these streams, the increase in α_{div} may be a result of an increase in the diversity of flow paths and thus organic matter contributions in these more stable streams, allowing a more diverse macroinvertebrate community to persist (Crossman et al., 2023). Macroinvertebrate diversity in streams with greater contributions from meltwater, both snow and glacial ice, were related to climatic and meteorological variables—especially air temperature and snowpack depth, which act as a useful proxy for meltwater contributions to streamflow in alpine streams (Windsor et al., 2021). As reported in shorter-term studies (Milner et al., 2010), our findings indicate that water source dynamics play an extremely important role in affecting the biodiversity within high-latitude streams.

Differences in the relationships between α_{div}, climate and meteorology across streams were manifested in high levels of β_{div}

and γ_{div}. There was, however, no support for H2, as there was no consistent decrease in β_{div} over time. Over the time series, periods of climatological and meteorological instability (i.e. 1999–2006 exhibited high levels of inter-annual variation), were related to the highest β_{div} values. Thus, stream environmental conditions across streams, supported by different water sources, are likely most different under variable or extreme climate or meteorology (Rolls et al., 2016), and, as a result of environmental heterogeneity across streams, there are large differences in species composition. Under current climate conditions, high inter-annual variability in meteorological conditions promotes high β_{div}, yet with further change (i.e. increases in mean air temperature or net alterations in total precipitation as expected over time with climate change) such variation may lead to reduced macroinvertebrate diversity and a loss of specialist taxa.

Species loss was the main driver of macroinvertebrate diversity patterns in this long-term study. Both homogenisation (loss of β_{div}) and differentiation (gain of β_{div}) driven by subtraction contributed significantly across the study—in particular species loss occurred between 1999 and 2000 as a result of the heaviest snowfall and snowpack
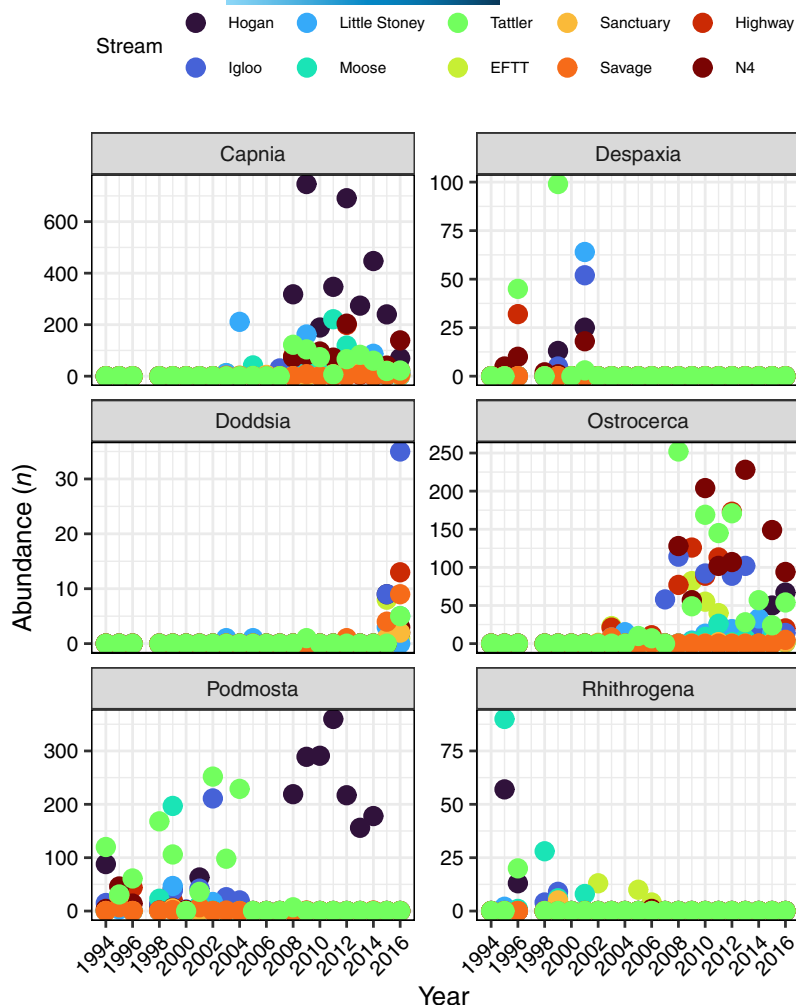
FIGURE 7 Temporal patterns in the abundances of macroinvertebrate taxa gained (Capnia, Doddsia, Ostrocerca) or lost (Despaxia, Podmosta and Rhithrogena) across sites over the time series (1994–2016). Colours indicate different streams. Note the different *y*-axis scales for different taxa.

depth observed, combined with warm air temperatures in spring, resulting in high-flow events in early 2000 (Milner et al., 2006). Two notable taxa lost during the 2000s were *Rhitrogena* and *Despaxia*. *Rhithrogena* are typically reliant on fast-flowing conditions and well-oxygenated waters and are consequently sensitive to climate change (Hauer et al., 1997). The possibility exists that reduced cool-water inputs into streams and increases in water temperature may have led to their loss from streams over the time series. The leuctrid stonefly *Despaxia*, on the other hand, may have been lost due to the semi-voltine life cycle of this genus (2 years; Richardson, 2001) preventing resistance and resilience against extreme events such as the spring floods in 2000. A number of taxa also colonized streams throughout the study. Specifically, winter stoneflies (*Capnia*, *Doddsia* and *Ostrocerca*) increased in both presence and abundance. This is potentially a result of climate change-driven reductions in meltwater contributions or low oxygen concentrations in summer favouring organisms that complete their lifecycles in winter and spring (Stewart & Anderson, 2010) and those which have resilient life cycles (e.g. have a long diapause such as *Ostrocerca*; Harper, 1990). Definitive statements on the drivers of species losses and gains, however, require further studies focusing on understanding the habitat preferences, diet, traits and ultimately the ecological niche of these taxa,

to better understand the mechanisms underlying both the species losses and gains.

At the regional scale, there was a general turnover in macroinvertebrate communities between years, providing limited support for H3, with no clear loss in specialist taxa or domination by generalists over the 22 years, as might have been expected with climate change. Furthermore, regional macroinvertebrate diversity, γ_{div}, did not exhibit a net increase or decrease over the 22-year study period. However, γ_{div} was significantly related to air temperature, with the highest diversity observed under lower temperatures. Firstly, over the duration of the study (1994–2016), there were consistent increases in mean air temperature across interior Alaska (Overland et al., 2019). Although γ_{div} did not clearly decline, the negative relationship between air temperature and γ_{div} indicates that if temperatures are to continue to increase then it is likely that γ_{div} would decrease in the future. Secondly, there are predicted increases in extreme air temperature and precipitation events for Alaska (Bennett & Walsh, 2015), posing a significant future threat to regional diversity in these high-latitude streams. Thus, although as of this moment, there is no marked decline in diversity observed at large scales, it is likely that further climatic change may bring about reductions in stream macroinvertebrate biodiversity across all scales.

5 | CONCLUSION

Long-term studies on macroinvertebrates in streams are rare, yet by exploring trends from 1994 to 2016 we show they are extremely valuable for understanding relationships between community structure and climatic variation. We demonstrate a strong relationship between macroinvertebrate communities (diversity and structure) and climatological and meteorological variables, particularly air temperature and snowpack depth. This informs ecological theory of the dominant role of physical variables in stream ecosystems. Although significant reductions in beta and gamma diversity over time were not observed in the streams of Denali National Park as suggested by ecological theory, the relationships identified in this study provide useful insights into the biodiversity changes that may occur under future climate change.

CONFLICT OF INTEREST STATEMENT
The authors declare no conflict of interest in submitting this manuscript.

DATA AVAILABILITY STATEMENT
Data and scripts are openly available via Zenodo at https://doi.org/10.5281/zenodo.7648859 and Github at https://github.com/fmwindsor/denali-longterm-macros.

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