

Aquatic insect β -diversity is not dependent on elevation in Southern Rocky Mountain streams

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SUMMARY

1. Relatively high β -diversity among aquatic insect communities inhabiting high-elevation streams is most commonly presumed to result from increased dispersal limitation between isolated mountain-top 'islands'. However, these elevational patterns of β -diversity have been predominately drawn from observed changes in community composition along single-thread channels, where the downstream increase in habitat size and hydrologic connectivity provides potential alternative explanations.
2. In this study, we applied an alternative conceptual 'tributary model' to ask whether patterns of aquatic insect β -diversity in similar-sized, hydrologically disconnected streams showed a similar elevational gradient in diversity patterns as previously reported for conceptual 'mainstem model' studies. Aquatic insects were sampled from 24 low-order, montane streams that are tributaries to larger rivers in three adjacent catchments spanning c. 2000–3500 m in elevation. We used relative abundance data to quantify two types of β -diversity: (i) community turnover- β , or the change in local diversity among adjacent streams along the elevational gradient within each catchment, and (ii) community variation- β , or the change in local diversity among all streams within three elevation zones combined across catchments.
3. Our results provided evidence of no relationship between β -diversity and elevation in aquatic insect communities in small montane streams. Community turnover- β was found to be consistently high among sites within catchments and displayed no significant trend across the elevational gradient for any catchment. Community variation- β showed a nonlinear response to elevation, with sites in the high-elevation and low-elevation zones having similarly high community variation- β compared to sites in the mid-elevation zone.
4. Our 'tributary model' results provide the first evidence that β -diversity among small, isolated streams can have similar turnover rates across broad elevational gradients. Our results also show similar patterns of β -diversity among low- and high-elevation tributaries, suggesting that dispersal limitation is not restricted to high-elevation streams.

Keywords: elevational gradient, habitat connectivity, species turnover, stream tributaries, β -diversity

Introduction

A fundamental objective of community ecology is identifying the patterns and processes underlying spatial variation in biodiversity (Rosenzweig, 1995). Historically, the majority of research has focussed on documenting trends in the local richness within a given community

(i.e. α -diversity) and/or the regional richness summed across all communities within a given landscape (i.e. γ -diversity). These efforts resulted in widely recognised large-scale patterns such as the negative correlation between diversity along increasing latitudinal and elevational gradients (Gaston, 2000; Willig, Kaufman & Stevens, 2003) and the positive relationship between

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diversity and habitat heterogeneity at regional scales (Lack, 1969; Ricklefs & Lovette, 1999).

More recently, attention has shifted towards understanding the relationship between regional and local diversity and the variation in local community composition within a region (i.e. β -diversity), and interest in this topic continues to grow exponentially (Anderson *et al.*, 2011). The identification of β -diversity patterns along environmental and spatial (distance) gradients offers insight into our understanding of the local versus regional processes that regulate community assembly (i.e. niche filtering versus dispersal limitation) (Shmida & Wilson, 1985; Mouquet & Loreau, 2003). Therefore, determining patterns of β -diversity and the associated mechanisms maintaining diversity across the landscape can inform the conservation management of vulnerable species and ecological communities (Condit *et al.*, 2002; Ferrier *et al.*, 2007; McKnight *et al.*, 2007). The importance of understanding patterns of β -diversity is becoming increasingly important in stream and river ecosystems, as they are comprised of some of the most imperilled taxonomic groups in the world (Richter *et al.*, 1997; Ricciardi & Rasmussen, 1999; Dudgeon *et al.*, 2006). Although considerable attention has been devoted to examining relationships between aquatic insect β -diversity along environmental gradients and spatial distances (Heino *et al.*, 2012, 2013; Al-Shami *et al.*, 2013; Astorga *et al.*, 2014), general patterns of β -diversity among stream ecosystems are often unpredictable (Heino *et al.*, 2015).

Mountain ranges provide an opportune landscape for identifying and understanding patterns of β -diversity, as environmental conditions change rapidly with elevation over a relatively small spatial scale. Consequently, compared to latitudinal gradients, elevational gradients enable the ability to partition the relative influence of habitat suitability and dispersal ability in shaping β -diversity patterns (Tang *et al.*, 2012). Furthermore, by virtue of their dendritic network structure, stream networks in montane regions are arranged adjacently along an elevational gradient, where environmental conditions are highly variable within a single catchment (Fagan, 2002; Grant, Lowe & Fagan, 2007). However, environmentally similar habitats (e.g. similar stream size and thermal characteristics) may be separated by long dispersal network distances across catchment boundaries. Due to this spatial arrangement of stream channels, β -diversity in montane stream ecosystems can be conceptualised in two different ways (*sensu* Anderson *et al.*, 2011): (i) community turnover- β , or the variation in community composition among adjacent streams within each

catchment, and (ii) community variation- β , or the variation in community composition among all streams within distinct elevation zones. Both measures of β -diversity are useful measures for understanding the degree of biotic heterogeneity among stream ecosystems and for providing insights into processes potentially maintaining diversity across a regional scale.

Despite the negative relationship between local α -diversity and elevation commonly reported, theoretical and empirical evidence often suggests that high-elevation stream communities exhibit higher measures of both community turnover- β and community variation- β than do low-elevation streams (Allan, 1975; Ward, 1986, 1994; Perry & Schaeffer, 1987; Jacobsen, Schultz & Encalada, 1997; Jacobsen, 2003, 2004; Finn & Poff, 2005; Finn, Khamis & Milner, 2013). Higher community turnover- β at high elevations within catchments is typically explained as resulting from abrupt changes in climatic conditions that characterise high montane or alpine environments (Allan, 1975; Ward, 1986; Perry & Schaeffer, 1987; Finn *et al.*, 2013). Additionally, the greater community variation- β observed among high-elevation streams (across catchments) is often explained as the result of increased dispersal limitation between isolated mountain peak 'islands' (Ward, 1994; Finn & Poff, 2005; Finn *et al.*, 2013). Consequently, high-elevation stream communities are often viewed to be comprised of many endemic taxa with narrow distributions.

These inferred patterns and processes of β -diversity have been predominantly drawn from studies that have applied a conceptual 'mainstem model' of stream elevation change, in which changes in community composition are compared along the longitudinal profile of a stream, from higher elevation headwater streams to lower elevation mainstem channels (Allan, 1975; Ward, 1986; Perry & Schaeffer, 1987; Finn & Poff, 2005; Wang *et al.*, 2012; Finn *et al.*, 2013). However, interpreting the effects of elevation on β -diversity using this 'mainstem model' is problematic because elevation is confounded by associated changes in stream size and habitat connectivity (Jacobsen, 2004). First, due to their small catchments that are contained within a relatively narrow elevation range, small (low-order) streams may have variable terrestrial settings from one another and therefore often exhibit higher environmental heterogeneity among habitats compared to larger (mid- to high-order) streams that they flow into (Lowe & Likens, 2005; Meyer *et al.*, 2007). Additionally, because small streams are tributaries to the mainstem, they are relatively disconnected from each other hydrologically; thus, they are expected to have lower rates of inter-site dispersal than

within-mainstem channels, where higher hydrologic connectivity facilitates dispersal (Fagan, 2002; Grant *et al.*, 2007). As a result of their smaller size and reduced connectivity, small tributary streams are characterised by relatively low α -diversity compared to low-elevation mainstem streams; however, small headwater streams are often reported to maintain disproportionately higher β -diversity within a catchment (Clarke *et al.*, 2008; Finn *et al.*, 2011).

An alternative approach to explaining patterns of β -diversity in montane streams would be to apply a conceptual 'tributary model', in which patterns of diversity are compared among similarly small, isolated streams along an elevation gradient. This approach controls for stream size and minimises hydrologic connectivity among sites. Utilising a 'tributary model', we expect both community turnover- β and community variation- β will be consistently high along the elevational gradient. Therefore, contrary to previous 'mainstem models' which have reported highest values of both turnover- β and variation- β at highest elevations, application of this alternate conceptual model may provide new insights into patterns and processes of β -diversity along elevational gradients. Few studies have employed such a 'tributary model' to examine patterns of aquatic insect β -diversity along an elevational gradient, and of these studies, inconsistent patterns have been reported, including positive trends (Jacobsen *et al.*, 1997; Jacobsen, 2003, 2004), negative

trends (Gill *et al.*, 2014) or no apparent trend between β -diversity and elevation (Jacobsen, 2004; Gill *et al.*, 2014). Unpredictable patterns of β -diversity resulting from these 'tributary model' studies may be explained by intermittent sampling along an elevational gradient and/or variation in spatial extent among regions sampled (Jacobsen *et al.*, 1997; Jacobsen, 2003, 2004), or restricting sampling to only the most 'dominant' taxa (Gill *et al.*, 2014). Our study addresses these shortcomings and is the first 'tributary model' study to quantify both community turnover- β and community variation- β across multiple adjacent catchments for complete aquatic insect communities.

In the current study, we employ a 'tributary model' to examine whether β -diversity of aquatic insects changes along an elevational gradient at two spatial scales: within a catchment and across catchments. We sampled aquatic insect communities at 24 streams sites (1st–3rd order) ranging from *c.* 2000 to 3500 m a.s.l. within three distinct catchments in northern Colorado, U.S.A. We used taxonomic composition (63 total taxa across sites) and abundance (*c.* 14 000 individuals enumerated) to examine patterns of community turnover- β and community variation- β to test two predictions that follow from the observation that small streams are more hydrologically isolated than mainstem streams. First, turnover in β among small streams within a catchment does not increase along the elevational gradient. Second, variation in β among small streams occurring at similar elevations

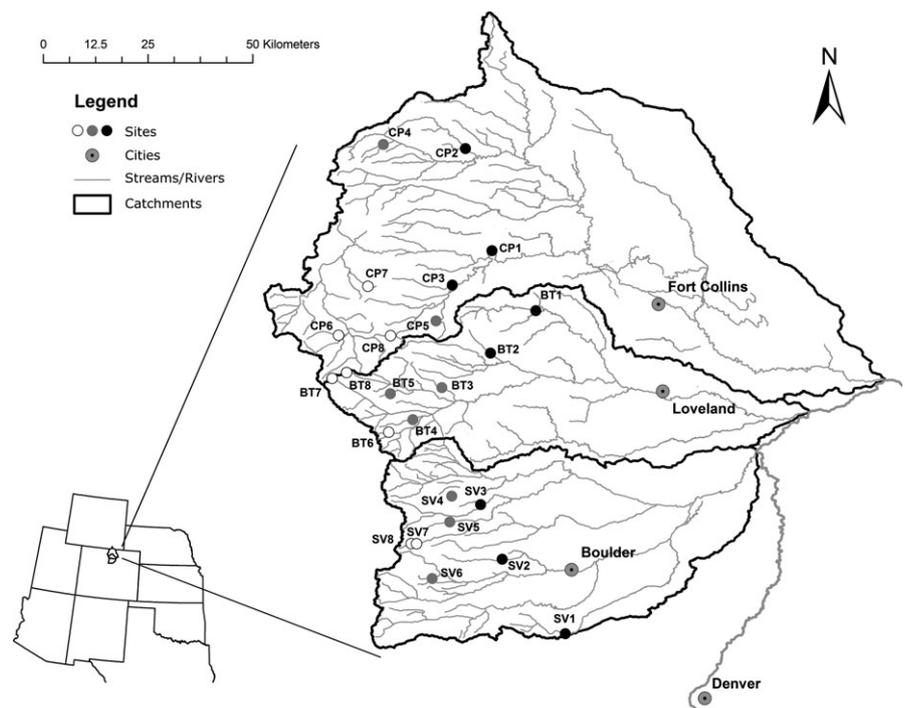


Fig. 1 Map of the study area, depicting all 24 sampling sites. The bottom left inset locates Colorado within the United States and the three catchments in the Front Range of Colorado. Sites CP1-CP8, BT1-BT8 and SV1-SV8 are located within the Cache la Poudre River, the Big Thompson River and the Saint Vrain Creek catchments, respectively. Furthermore, sites located within the low-elevation zone, mid-elevation zone and high-elevation zone are denoted by black circles, grey circles and white circles, respectively. Refer to Table 1 for site elevations.

across adjacent catchments is not different within low-, mid- and high-elevation zones.

Methods

Study area

The study streams were located along the eastern slope of Colorado's Front Range in the Southern Rocky Mountains, within an elevation range that spanned foothills to alpine ecotones (ca. 2000 m to 3500 m a.s.l.). We considered this elevation range to be comparable to the majority of previous 'mainstem model' studies, which have covered roughly 1000–1500 m in elevation (Allan, 1975; Ward, 1986; Perry & Schaeffer, 1987; Finn & Poff, 2005). We selected eight separate low-order tributaries (Strahler order 1st–3rd) at ca. 200-m elevation intervals from each of three adjacent catchments: the Cache la Poudre (CP), the Big Thompson (BT) and the Saint Vrain (SV) (Fig. 1). The resulting 24 study sites are hereafter referred to by their two-letter catchment code followed by a numerical value representing their position along the elevational gradient (#1–8, increase in elevation) (Fig. 1, Table 1).

Table 1 Elevation (m), elevation zone and taxonomic richness from each site location within each catchment in the Front Range of Colorado. Alphanumeric IDs for each site indicate the catchment and position along the elevational gradient. Refer to Fig. 1 for map of site locations

Catchment	Site ID	Elevation (m)	Elevation zone	Taxonomic richness
Cache la Poudre	CP1	1992	Low	32
	CP2	2181	Low	28
	CP3	2411	Low	21
	CP4	2590	Mid	23
	CP5	2775	Mid	15
	CP6	3060	High	17
	CP7	3166	High	16
	CP8	3397	High	17
Big Thompson	BT1	2001	Low	32
	BT2	2252	Low	20
	BT3	2443	Mid	21
	BT4	2573	Mid	20
	BT5	2900	Mid	18
	BT6	3051	High	15
	BT7	3364	High	17
	BT8	3478	High	5
Saint Vrain	SV1	2015	Low	16
	SV2	2189	Low	26
	SV3	2388	Low	25
	SV4	2643	Mid	21
	SV5	2830	Mid	25
	SV6	2964	Mid	18
	SV7	3249	High	14
	SV8	3348	High	15

All streams were tributaries to the mainstem river in the respective catchment. They varied in average width from 1.6 to 7.6 m, with no significant correlation between elevation and average width ($r = -0.25$, $P = 0.23$) or width-to-depth ratio ($r = 0.13$, $P = 0.53$).

We partitioned all sites into one of three elevation zones based on the eight sites that occurred within the lowest elevation range (c. 2000–2400 m), a middle elevation range (c. 2450–2950 m) and the highest elevation range (c. 3050–3500 m) (Table 1). These three zones correspond roughly to previously described vegetation zones (Peet, 1981) and snow cover zones within Colorado's Front Range (Richer *et al.*, 2013), and thus, they represent different terrestrial and hydrologic settings. Application of a PERMANOVA procedure in PC-ORD using the Sørensen's distance measure (McCune & Meford, 2011) showed that the aquatic insect community composition among the three elevation zones was significantly different ($P < 0.0002$, all pairwise comparisons: $P < 0.005$).

We selected sites with minimal human disturbance (e.g. no upstream dams, diversions), and no sites were located downstream of any major natural lake outlet. High-elevation streams originate within protected areas of Rocky Mountain National Park and Indian Peaks Wilderness, and mid- and low-elevation streams are located within either federally or municipally protected lands. We sampled all sites one time in the summer of 2011 between the dates of 26 June and 12 August, starting at low elevation and moving uphill as the season progressed. Similar single-sample 'snapshot' studies are commonly used to capture the response of community composition along environmental gradients (Stoddard *et al.*, 2005; Paulsen *et al.*, 2008).

Aquatic insect sampling

At each study site, we sampled benthic insects along a 200-m stretch using a D-frame kicknet (mesh size 500 μm). This semi-quantitative sampling technique enables the sampling of multiple microhabitats and provides a more comprehensive sampling of total richness than fixed area samplers (Resh & Rosenberg, 1984). Sampling effort per site was standardised using a five-minute timed collection in which time spent per microhabitat was adjusted according to the proportion of each microhabitat type per site (e.g. riffles, runs, pools, boulders and woody debris). Samples were preserved in 95% ethanol and later identified to the lowest practical taxonomic unit (typically genus) and enumerated; over 14 000 individuals were identified from all 24

streams (see Appendix S1). Abundances were summed across the lowest shared taxonomic unit, and chironomid midges, identified to family only, were omitted as they occurred at every site.

Data analysis

Prior to examining patterns of turnover- β along elevational gradients and variation- β within elevation zones, we used partial Mantel tests to determine the pure effects of elevation versus geographic distance on β -diversity (Legendre & Legendre, 2012). Partial Mantel tests were applied using three different distance matrices that consisted of community β -diversity values, elevational distances and straight-line Euclidean distances between all possible pairs of sites. The significance of partial Mantel tests was assessed using 9999 permutations. Using relative abundance data, pairwise β -diversity values were calculated using the quantitative Sørensen Index (i.e. Bray–Curtis dissimilarity index). Multivariate dissimilarity measurements of β -diversity are sensitive to differences in species richness and/or abundance (Morlon *et al.*, 2008); however, desirable features of the quantitative Sørensen index are its relatively low sensitivity to under-sampling and its invariance to the total abundance of species (Legendre & De Cáceres, 2013). This index is commonly used to quantify β -diversity among ecological communities along spatial and environmental gradients (Faith, Minchin & Belbin, 1987; Clarke, 1993; Anderson *et al.*, 2011).

Patterns of community turnover- β along the elevational gradient were determined using pairwise β -diversity values, ranging from zero (i.e. complete similarity) to one (i.e. zero similarity or 100% β -diversity), which were calculated only between the adjacent pairs of sites within each catchment. Values of turnover- β were regressed against the average elevation between each pair of sites, individually both for all pairs of sites within each catchment and for all pairs of sites within the region (i.e. for three catchment). However, because pairwise calculations are inherently not independent, we performed a multiple regression on distance matrices (MRM) to test the significance of these relationships. MRM is a permutational regression approach which utilises a Model I regression and permutation tests of significance for R -squared; 9999 permutations were used (Legendre, Lapointe & Casgrain, 1994; Lichstein, 2007).

Community variation- β within elevation zones was determined using pairwise β -diversity values that were calculated among all possible pairs of sites across the three catchments that were within each predefined ele-

vation zone. We applied global and pairwise PERMANOVA procedures on the resulting β -diversity values to test for differences in the values of community variation- β between low-, mid- and high-elevation zones. Although PERMANOVA is relatively unaffected by heterogeneity for balanced designs, we also used PERMDISP to test the homogeneity of dispersions and to identify whether differences among groups were location versus dispersion effects (Anderson & Walsh, 2013). All analyses were carried out in PC-ORD and in R using the 'vegan' and 'ecodist' packages (Goslee & Urban, 2007; Oksanen *et al.*, 2007; McCune & Meford, 2011).

Results

Aquatic insect collection

Overall, we identified 63 aquatic insect taxa from all 24 study locations (see Appendix S1), with an average of 19 taxa per site. Local richness at individual sites (α -diversity) displayed a negative relationship with increasing elevation ($r = -0.76$, $P < 0.001$), with the number of individual taxa ranging from 32 taxa at sites BT1 and CP1 (in the lowest elevation zone) to 5 taxa at site BT8 (in the highest elevation zone) (Table 1). Of the 64 total taxa identified, 50 of these were present at low-elevation sites (Zone 1), 41 at mid-elevation sites (Zone 2) and 35 at high-elevation sites (Zone 3), indicating the spatial distribution of shared and unique taxa across elevation zones (Fig. 2).

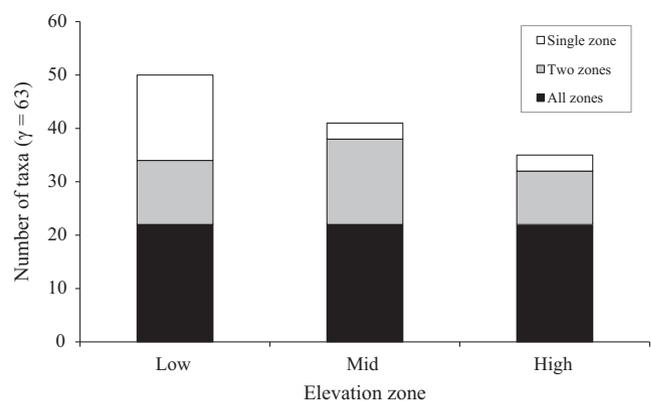


Fig. 2 Histogram depicting the number of taxa collected within each elevation zone (i.e. low, mid or high) out of the total 63 taxa identified. Within each elevation zone, the total number of taxa are partitioned into the number of taxa that were collected only within an individual zone (white fraction), the number of taxa collected within two zones (grey fraction) and the number of taxa collected within all three zones (black fraction).

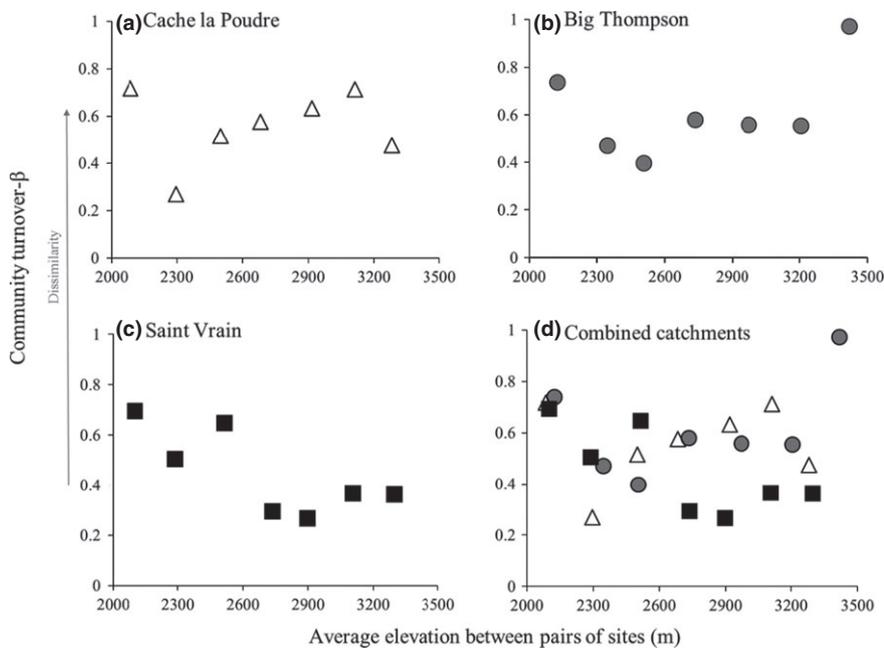


Fig. 3 Regression plots displaying pairwise community turnover- β values (quantitative Sørensen Index) across the average elevation between all pairs of adjacent sites within each catchment. Values are plotted for sites within (a) the Cache la Poudre River, (b) the Big Thompson River and (c) the Saint Vrain Creek, and for all sites combined across catchments.

Spatial analyses

Partial Mantel tests confirmed our assumption that pure effects of elevational distance after partitioning out the effects of straight-line Euclidean distance significantly explained the β -diversity among communities in the study region ($r = 0.49$, $P < 0.001$). Furthermore, partial Mantel tests showed that the pure effects of straight-line Euclidean distance did not significantly explain the β -diversity among communities ($r = -0.05$, $P = 0.662$).

Community turnover- β

Across all elevational gradients, pairwise community turnover- β had a mean rate of 0.54 (SD = 0.18) with highest values peaking among pairs of high-elevation sites in both the BT and CP catchments, and at low-elevation sites in all three catchments (Fig. 3). Results from the MRM permutation analysis indicated that community turnover- β was not significantly correlated with elevation, when data were analysed for either single catchment (CP: $r^2 = 0.002$, $P = 0.865$, BT: $r^2 = 0.091$, $P = 0.200$, SV: $r^2 = 0.205$, $P = 0.056$) or all three catchments combined ($r^2 = 0.015$, $P = 0.147$) (Fig. 3a–d).

Community variation- β

Community variation- β varied between high-elevation ($\bar{X} = 0.62$, SD = 0.24), mid-elevation ($\bar{X} = 0.45$, SD = 0.10) and low-elevation ($\bar{X} = 0.61$, SD = 0.15) zones. Results from the PERMANOVA procedure showed that varia-

tion- β values were significantly different among elevation zones ($P < 0.001$), with pairwise comparisons showing significant differences between the mid-elevation zone and the low- and high-elevation zones (both, $P \leq 0.001$), which were themselves not different ($P = 0.78$) (Fig. 4). Results from the PERMDISP test also showed an overall significant difference in group dispersion among elevation zones ($P = 0.002$), with pairwise comparisons indicating robust differences in dispersion between high- and mid-elevation zones ($P = 0.002$) and moderate differences between high- and low-elevation zones ($P = 0.042$), and between low- and mid-elevation zones ($P = 0.074$) (Fig. 4).

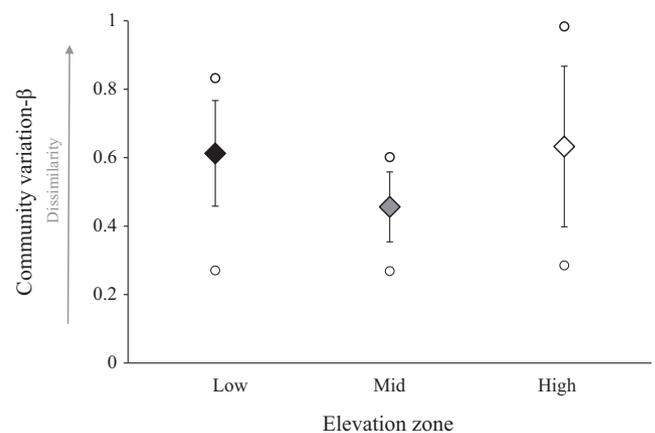


Fig. 4 Mean pairwise community variation- β (quantitative Sørensen Index) within each elevation zone (i.e. low, mid or high). Error bars depict \pm one standard deviation between all pairwise values within each elevation zone. Maximum and minimum pairwise community variation- β values from each zone are displayed (O).

Discussion

Our study quantitatively examined changes in whole community β -diversity of aquatic insect communities in small, tributary streams within and across catchments. Contrary to patterns generally observed in previous studies, our results demonstrate that β -diversity does not increase with elevation in small streams. Thus, our results afford new insights into patterns of aquatic insect diversity in small, wadeable mountain streams.

Community turnover- β

We observed consistently high rates of turnover- β within catchments; however, there was no trend along the elevational gradient (Fig. 3a–d). Variation in the magnitude and location of turnover- β values most likely reflects our ability to capture the gain and/or loss of taxa at the limits of their elevational ranges with a resolution of *c.* 200 m in elevation between streams.

However, most previous studies of β -diversity along elevational gradients have employed the 'mainstem model' and documented patterns of relatively low rates of turnover- β along the gradient, with a peak at higher elevations (Allan, 1975; Ward, 1986, 1994; Perry & Schaffer, 1987; Finn *et al.*, 2013). Although lack of quantitative measurements from many previous studies hinders the contrast of turnover- β rates to those reported in the current study, direct comparison of our data with historical 'mainstem model' data indicates higher rates of turnover- β using the 'tributary model' (see Figure S1).

This discrepancy in results from 'mainstem model' studies may best be explained by the confounding changes in habitat size and habitat connectivity associated with elevation, and the positive relationship between these variables and local α -diversity (Vannote *et al.*, 1980; Jacobsen, 2004). Although both α -diversity and γ -diversity are expected to increase with decreasing elevation (Allan, 1975; Ward, 1986), α -diversity is likely to increase considerably faster than γ -diversity when coupled with increasing habitat size and connectivity. If so, β -diversity in previous 'mainstem model' studies would certainly be lower among low-elevation sites, resulting from the dependence of β -diversity on α -diversity and γ -diversity (Anderson *et al.*, 2011; Chase *et al.*, 2011). We recognise that because of the dependence of β -diversity on both α -diversity and γ -diversity, a null model (e.g. the Raup–Crick measure) would be necessary to determine whether the observed β -diversity values from our 'tributary model' study are in fact higher than would be expected by chance (Anderson *et al.*,

2011; Chase *et al.*, 2011). Unfortunately, the Raup–Crick measure is only suitable for dissimilarity metrics based on presence–absence data and not appropriate for multivariate dissimilarity measures of β -diversity using abundance data such as ours (Chase *et al.*, 2011). However, based on our reported values of α -diversity and γ -diversity along the elevational gradient, it appears as though our measured values of β -diversity do result from the variation in community structure as opposed to variation in α -diversity or γ -diversity as expected from 'mainstem model' studies (see Table 1 and Fig. 2).

Given the confounding effects of habitat size and connectivity with elevation, a couple of additional explanations may account for the differences in patterns of turnover- β between our 'tributary model' results and those of previous studies using the 'mainstem model'. First, small streams are more strongly influenced by the surrounding terrestrial ecosystem than are larger mainstem channels that comprise the lower elevation sites in 'mainstem model' studies. For example, they have smaller catchments that are defined by a smaller elevation range than larger catchments, which may span the entire elevation gradient. The decoupling of larger streams from local terrestrial conditions generally results in lower environmental heterogeneity among habitats than is exhibited among small, tributary streams; therefore, among-stream habitat heterogeneity should be high in small streams compared to larger mainstem streams (Lowe & Likens, 2005; Meyer *et al.*, 2007). Both theoretical and empirical evidences suggest that higher habitat heterogeneity at the regional scale can generate increased β -diversity among small streams (Grönroos *et al.*, 2013; Astorga *et al.*, 2014). Because we sampled only small tributary streams, our finding of consistently high community turnover- β across the elevational gradient is perhaps not surprising.

Second, the dendritic network characteristic of stream systems inherently results in the hierarchical connectivity of habitats and dispersal rates through increasingly larger mainstem segments (Grant *et al.*, 2007; Clarke *et al.*, 2008). Evidence from recent studies suggests that mainstem channels often exhibit significantly lower β -diversity than tributary streams within the same catchment, a pattern that has been attributed to higher potential dispersal rates associated with hydrologic connectivity (Mackay, 1992; Brown & Swan, 2010). Therefore, observations from previous 'mainstem model' studies of lower turnover- β downstream of only the highest elevations may be attributed to higher dispersal rates and saturation of local communities (Mouquet & Loreau, 2003). Furthermore, overland dispersal among

headwater streams is often limited to the closest adjacent streams (Clarke *et al.*, 2008); thus, higher values of turnover- β from our 'tributary model' may be a result of reduced dispersal ability within the network.

Community variation- β

Our 'tributary model' findings of high variation- β across multiple catchments are the first to show that low-elevation stream communities along major mountain fronts can be equally dissimilar as are high-elevation streams (Fig. 4). Previous 'mainstem model' findings have argued that high variation- β for high-elevation streams results from dispersal limitation, exacerbated by the physical isolation of mountain peak 'islands' that are separated by physical barriers of steep topography and harsh climatic environments (Finn & Poff, 2005; Finn *et al.*, 2013). Species dispersal through the network itself is precluded due to thermal barriers encountered in moving along mainstems to lower elevations where confluences would allow upstream movement to another isolated, headwater 'island' (Deshmukh, 1986; Ward, 1994; Finn & Poff, 2005, 2008; Finn *et al.*, 2013). Several recent studies of high-elevation aquatic insect populations have shown significant genetic structure across a small spatial scale; results suggest that dispersal limitation of these taxa may drive high variation- β among high-elevation streams (Hughes *et al.*, 1999; Wishart & Hughes, 2003; Finn & Adler, 2006; Finn *et al.*, 2006; Finn, Blouin & Lytle, 2007; Finn & Poff, 2011).

Results from our 'tributary model' indicate that low-elevation streams can exhibit equally high levels of variation- β as observed in high-elevation streams in the same catchments (Fig. 4). The mechanisms for this low similarity among sites at similar elevation are not clear; however, habitat isolation and dispersal limitation are likely to play a role. Small low-elevation streams in our study region are widely separated and are probably further isolated within a landscape that has been extensively altered by human activities, including urbanisation and stream diversion. At the regional scale, the availability of suitable ('undisturbed') habitat at low elevations is restricted, likely increasing isolation of and thus distances that aquatic insects must disperse to successfully colonise. Patrick & Swan (2011) found that high β -diversity of aquatic insects within a historically disturbed catchment was primarily driven by dispersal limitation between suitable habitats. Another possible explanation for higher levels of β -diversity at lower elevations may be explained by higher habitat heterogeneity among streams, as habitat heterogeneity has been

found to be a stronger predictor of community structure and β -diversity than spatial distance (Grönroos *et al.*, 2013; Astorga *et al.*, 2014). However, analysis of multiple reach-scale variables collected June–August 2011 showed no indication of higher habitat heterogeneity among low-elevation sites when compared to mid- or high-elevation sites (see Appendix S2 and Figure S2). Interestingly, variation- β among mid-elevation streams was significantly lower than both high- and low-elevation streams, and we can offer no suitable explanation in terms of among-site habitat heterogeneity or effective dispersal distance. Although high dispersion of community variation- β values among high-elevation sites could be contributing to differences found between high and mid-elevations, dispersion did not account for differences between low and mid-elevations. Ongoing research on genetic divergence among key species at different elevations may shed some light on movement of organisms between small tributary streams, but that remains to be resolved.

Our results from similar-sized tributaries demonstrated that community turnover- β across elevation was consistently high and displayed no elevational trend and that community variation- β across high-elevation communities was not significantly different than low-elevation community variation- β . Therefore, application of the 'tributary model' reveals that β -diversity among low-elevation communities is equivalent to high-elevation communities, providing the first evidence that small streams across broad elevational gradients can be inhabited by many unique taxa (Fig. 2). In addition to habitat heterogeneity along the elevational gradient, dispersal limitation between isolated communities may potentially contribute to maintaining considerable biotic heterogeneity among small montane streams.

Importantly, our findings support the previous understanding that small tributary streams, despite having low individual α -diversity, collectively exhibit high β -diversity (Clarke *et al.*, 2008; Finn *et al.*, 2011). Narrow distributions of taxa may be driven by a combination of reduced dispersal ability and/or specific niche requirements. In any case, small tributary stream communities, regardless of elevation, are potentially similarly vulnerable to reduction in β -diversity from landscape-scale human disturbances (Hawkins *et al.*, 2014) including rapid climate change. This possibility presents important implications for understanding the impacts that habitat fragmentation and habitat homogenisation have on the diversity throughout entire river catchments. However, as it is likely that the relative influences of these regional and local mechanisms vary spatially in drainage

networks, elucidating the resultant pattern diversity will require considerable effort. Further examination of the relationship between both community composition and key ecological traits in response to environmental, spatial and disturbance variability across elevations is needed to illuminate a greater understanding regarding the conservation of biodiversity in these diverse and ubiquitous systems.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Abundance of taxa collected from each study site.

Appendix S2. Measurements of environmental habitat variables from each study site.

Figure S1. Community turnover- β compared to historical “mainstem model” data.

Figure S2. Pairwise environmental dissimilarity values within each elevation zone.

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