

Scale dependent effects of productivity and disturbance on diversity in streams

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With 3 figures, 1 table and 1 appendix

Abstract: The effects of productivity and disturbance on diversity vary widely with the spatial scale at which they are examined. Not only do productivity and disturbance have strong influences on diversity patterns at local and regional scales but they can affect the way in which communities assemble and in turn alter beta diversity or community dissimilarity. We assessed whether the form of both the productivity- and disturbance-diversity relationships differed between the spatial scale at which they were examined using experimental stream channels in three Hawke's Bay, New Zealand streams. In place of true local and regional richness, we used the proxies within- and between-stream richness, as well as assessing between-stream community dissimilarity (similar to beta diversity). Our results indicate that productivity and disturbance both affect diversity but at individual scales and in different forms. At the within-stream scale, richness was a u shaped function of productivity whereas at the between-stream scale richness increased monotonically with increasing productivity. Community dissimilarity on the other hand, increased monotonically with increasing rate of disturbance. Rather than a greater role of deterministic assembly with increasing disturbance, our results indicate the opposite, but it appears that communities are simply converging on those found in the surrounding streambed with time since disturbance. Specifically, communities were more similar within individual streams than within disturbance treatments and animals colonizing post-disturbance were simply a subset of taxa present at each site regardless of perceived colonizing ability, rather than a suite of specialist colonizing taxa. These results demonstrate that without a distinction between early and late colonizers, a greater rate of deterministic assembly at high disturbance will not occur.

Key words: assembly rules, alpha, beta, gamma, diversity, macroinvertebrate.

Introduction

The relationship between productivity and diversity can be highly variable with more common trends including unimodal curves (e.g. Grime 1973a, Huston 1979, Rosenzweig 1995, Mittelbach et al. 2001) and linear increases (e.g. Currie 1991, Abrams 1995, Gaston 2000, Mittelbach et al. 2001) in diversity with increasing productivity. However, linear declines, u-shaped relationships and no relationship also occur (Mittelbach et al. 2001); although recent criticisms

have highlighted pitfalls in meta-analyses of the productivity-diversity relationship (Hillebrand & Cardinale 2010, Whittaker 2010). In fact, a recent large scale study on this relationship in plant communities revealed a weak link between the two (Adler et al. 2011).

One explanation for the different outcomes is the difference in the spatial scale of sampling (Currie 1991, Chase & Leibold 2002). Smaller scale studies (e.g. stream reaches) commonly find unimodal relationships between productivity and diversity but

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at increasing spatial scales the pattern is often one of monotonic increases in diversity with productivity (Mittelbach et al. 2001). There are many mechanisms postulated to lead to this unimodal relationship (Rosenzweig & Abramsky 1993, Abrams 1995). For example, Kassen et al. (2000) have shown niche specialization in heterogeneous, but not homogeneous environments can cause this pattern. Chase & Leibold (2002) also found differences in the nature of the relationship when considered from different scales; a hump shaped trend occurred at local scales, a linear pattern at the regional scale and community dissimilarity increased with productivity (see Chase & Leibold 2002 for explanatory mechanisms).

Two factors thought to strongly influence the productivity-diversity relationship are disturbance (Huston 1979, Kondoh 2001) and the history of community assembly (Fukami & Morin 2003). The disturbance-diversity relationship also varies with spatial and temporal scale (Petraitis et al. 1989, Mackey & Currie 2001, Chase 2007), which may be dependent on the competitive-colonizing trade-off distribution of the assemblage at hand (Cadotte 2007). However the prevailing theme in disturbance ecology revolves around the Intermediate Disturbance Hypothesis (IDH) (Grime 1973b, Connell 1978, Sousa 1979), and recently Roxburgh et al. (2004) have shown the promotion of richness at intermediate levels of disturbance can come from many mechanisms. But the requirement for a competition-colonization trade-off (Chesson & Huntly 1997, Roxburgh et al. 2004, Cadotte 2007), and the fact that this has been found to be lacking in many ecosystems, has led many to suggest disturbance simply removes taxa (e.g. Death & Winterbourn 1995). In fact, diversity may be a function of the interaction between disturbance and productivity (Huston 1979, Kondoh 2001, Cardinale et al. 2006), although Tonkin et al. (2013) and Tonkin & Death (2012) found their effects were additive.

Both productivity and disturbance can also alter β diversity and community dissimilarity through changes in assembly sequences (Chase 2007, Lepori & Malmqvist 2009, Chase 2010). Deterministic assembly involves the recruitment of colonists from the regional pool based on niche preferences, whereas stochastic assembly involves random selection of available colonists (i.e. ecological drift). The debate on whether deterministic (Poff 1997) or stochastic determinants (Reice 1994, Hubbell 2001) are more important is long standing, though it is likely that a combination of both occurs (Hart 1992, Thompson & Townsend 2006). Recently, Chase (2010) suggested

that more productive environments lead to higher β diversity through a stronger dependence on stochastic, as opposed to deterministic, community assembly. Deterministic assembly processes will likely be more prevalent in harsh environments where conditions filter out unsuitable taxa; benign environments on the other hand will be governed by more stochastic processes allowing for a greater representation of the regional pool (Chase 2007). This suggests β diversity or community dissimilarity will decline with disturbance rate as a limited range of more specialist traits are required in more disturbed habitats. Nonetheless, Lepori & Malmqvist (2009) found deterministic control (and associated lowest β diversity) was greatest at intermediate levels of disturbance suggesting a more complex interplay between stochastic and deterministic control.

We set out to test the effect of spatial scale on both the productivity-diversity (of stream macroinvertebrates) and disturbance-diversity relationships in experimental stream channels using two levels of productivity and four levels of disturbance. Rather than true α , β and γ diversity, we used within- (local) and between-stream (regional) richness and between stream community dissimilarity (β diversity) for each disturbance and productivity treatment. Based on previous work suggesting productivity sets the upper limit to diversity in streams (Death 2002, Tonkin & Death 2012, Tonkin et al. 2013), we predict that within-stream taxonomic richness will increase log-linearly with productivity and between-stream richness will increase monotonically (Chase & Leibold 2002). Based on the notion that disturbance will simply remove animals and thus taxa (Death & Winterbourn 1995, Death 2002), we hypothesize that within-stream richness will decline with disturbance. Although there is support for increased diversity with disturbance at the regional scale, as it allows for the representation of early colonizing species within patchy environments (Hastings 1980, Pickett & White 1985, Chesson & Huntly 1997), we predict between-stream richness should match within-stream richness and decline. This is because between-stream richness was assessed at the same disturbance rate in all streams, thus disturbance should theoretically be homogeneous between the three locations. We expect greater dissimilarity in community composition (β diversity) at lower rates of disturbance as a result of more stochastic assembly processes (Chase 2003, Chase 2007). As high connectivity between replicates can confound diversity assessments (Warren 1996, Chase 2003, Matthiessen et al. 2010), the scale of this study is such that connectivity between replicates is low.

Methods

Study sites and physicochemical measures

Pastoral farming and wine production dominates land-use of Hawke's Bay, in the East of the North Island of New Zealand; an area characterized by a warm and dry climate with a mean annual rainfall of 783 mm. Three spring-fed streams (EX1-EX3) of relatively similar characteristics (mean width: 1.5–4.7 m; mean depth: 0.15–0.44 m; mean velocity: 0.42–1.52 m s⁻¹) were selected for use in this study in the Ruataniwha Plains. Spring-fed streams were selected for their limited flow variability enabling the experimental manipulation of disturbance, rather than natural fluctuations in flow.

All three streams drain dairy farming catchments and have little to no shading from riparian vegetation, with mostly pastoral grassland surrounding the streams. The riparian zone of EX1 is unfenced and entirely lined with pasture, whereas EX2 has a mixture of pasture and scrub lining the banks. EX3 has been recently fenced with grasses and native flaxes forming the riparian zone. EX1 is the widest (4.7 m) and deepest (0.44 m) of the three streams and EX3 is the narrowest (1.5 m) and shallowest (0.15 m). EX2 has undercut banks through the study reach whereas the remaining two sites have low gradient banks.

Temperature and conductivity in these streams ranged from 15.2 (EX1) to 17.9 °C (EX3) and 160 (EX3) to 220 µS cm⁻¹ (EX2) respectively during the experimental period and streams range in altitude from 134 (EX2) to 146 m a.s.l. (EX1).

A description of benthic communities of the three streams under natural conditions is provided in Appendix 1. This shows the ten most dominant macroinvertebrate taxa in these streams from benthic Surber samples taken in July 2009, five months prior to the present experiment (Tonkin 2010).

Experimental methods

Eight linear 'once-through' plastic channels (1500 mm long × 150 mm wide × 100 mm deep) were placed in the bed of each stream and filled with cobbles. The channels were open ended to allow for colonization and emigration. Cobbles were sourced from within the stream bed and allowed to acclimatize for 21 days before the treatment period. Four disturbance and two productivity treatments were applied within each stream. The disturbance treatments were: no disturbance (after initial disturbance at day 0; dist. 1), every 16 (dist. 2), 8 (dist. 3), and 4 days (dist. 4); and productivity treatments were either high or low. The experiment was run over a 32 day period. This yielded eight treatments: the four levels of disturbance each at low and high productivity levels.

Due to the streams being open-canopied, light level manipulations were applied to create the two productivity treatments as this was predicted to alter primary productivity rates. Thus, productivity was characterized as high or low based on the presence or absence of shading. Shade was applied by covering four of the channels in each stream with 1800 mm × 350 mm metal sheeting approximately 200 mm above the substrate and held in place with metal stakes and rubber grommets.

Channels were placed in pairs of disturbance treatment with one open- and one closed-canopy channel of the same disturbance level placed together. Disturbance treatments were randomized within the stream bed, and channels placed sufficient distance apart so as to not influence other treatments. Disturbance was performed to represent the physical effects of flood

events by movement and turnover of the substrate and subsequent removal of macroinvertebrates. This was implemented by vigorously stirring the full contents (substrate) of the channel to detach macroinvertebrates whilst minimizing removal of periphyton (to isolate the effects of productivity and disturbance) on the substrate for two minutes. However, larger forms of macroalgae were inevitably removed, if present, due to their ease of detachment.

Sampling protocols

Benthic macroinvertebrates were sampled from three random 250 mm sections within each channel. Sampling was performed by inserting a 250 mm modified section of guttering, similar to the artificial channels and with a 250 µm mesh net attached, into the channel and removing all of the contents. Thus abundances per sample are given as individuals 0.038 m⁻². One stone (α axis < 60 mm) was removed from each replicate for later analysis of periphyton biomass. The remaining sample was placed in 70% ETOH and later identified in the laboratory using available keys (e.g. Towns & Peters 1996, Winterbourn et al. 2000). Morphospecies were used where taxa such as Chironomidae were not able to be taken to species level, with the exception of Oligochaeta which was not identified further.

Rather than simply use high and low productivity treatments as factors for analysis, we assessed standing stock of periphyton biomass (chlorophyll-*a*) from single stones within each sample. While not a direct measure of primary productivity, these values were assigned as estimates of primary productivity. Morin et al. (1999) reviewed the relationship between chlorophyll-*a* and primary productivity in streams, finding a strong link ($r^2 = 0.63$); although this was dependent on temperature. Moreover, Tonkin & Death (2012) uncovered a strong link between periphyton biomass on natural *in situ* substrate and accumulation on artificial tiles ($r^2 = 0.74$).

Stones were kept cool and dark on ice in the field before being stored at -20 °C. Photosynthetic pigments were extracted from stones by submerging in known volumes of 90% acetone for 24 hours at 5 °C. Absorbances at 750, 665 and 664 nm were read on a Varian Cary 50 conc UV-Visible Spectrophotometer (Varian Australia Pty Ltd, Mulgrave, Australia) and converted to chlorophyll-*a* pigment concentration using Steinman & Lamberti (1996). These were then corrected for stone surface area (Graham et al. 1988) and halved to account for periphyton being present only on upper stone surfaces.

Statistical analysis

Within-stream ('local') taxonomic richness was calculated as the pooled number of taxa for the three samples within each treatment. Between-stream ('regional') richness was calculated as the total number of taxa for the three samples within each treatment combined for all three streams (nine samples). This represents regional richness (γ) as the total number of taxa in all three streams for each treatment, thus we use the terms within- and between-stream richness. We calculated the dissimilarity in community composition in treatments between streams. These dissimilarity metrics left us with three pairwise comparisons which were averaged to achieve a 'regional' dissimilarity metric. Dissimilarity (100 - similarity) was estimated using the Bray-Curtis similarity metric in Primer v6 (Clarke & Gorley 2006). This method takes into account variation in taxonomic abundance and was performed on raw data. Although this met-

ric is similar conceptually to β diversity, it is a measure of community dissimilarity accounting for abundances rather than the number of unique taxa to each community. Thus, if dissimilarity is zero, all taxa are shared and at the same abundances between all communities and if dissimilarity is 100 then no taxa are shared. In order to assess whether changes in taxonomic richness with productivity and disturbance were due to changes in the density of animals, we also calculated the number of individuals and rarefied taxonomic richness.

To assess one factor of resource heterogeneity we calculated variation in productivity between replicates and streams by summing the differences between chlorophyll-*a* values with each treatment. Similarity Percentages (SIMPER) was used to assess which taxa contributed the greatest to differences between and within treatments using Primer v6 (Clarke & Gorley 2006). Linear and quadratic regression was performed in order to test for relationships between productivity (using measured chlorophyll-*a* rather than productivity categories), disturbance (using disturbance rate) and diversity at the three spatial scales using R 2.13.1 (R Development Core Team 2011). Akaike's Information Criterion (AIC) (Akaike 1974) was used to determine the best fitting model when both linear and quadratic curves were fit. To assess whether treatments altered periphyton biomass and removed animals, two-way Analysis of Variance (ANOVA) was used in R 2.13.1 (R Development Core Team 2011) testing differences in chlorophyll-*a* and the number of animals between productivity and disturbance treatments. We used Analysis of Covariance (ANCOVA) in R 2.13.1 (R Development Core Team 2011) to evaluate the relationship between disturbance rate and productivity on community dissimilarity. Bonferroni correction was applied for concurrent regressions against productivity and disturbance, thus halving the α value. We used non-metric multidimensional scaling (NMDS) ordination on $\log(x+1)$ transformed data using Bray-Curtis similarity to visualize differences in community structure between treatments and locations and tested for significance using analysis of similarities (ANOSIM) (Clarke 1993) in Primer v6 (Clarke & Gorley 2006).

Results

Chlorophyll-*a* was higher in all high productivity treatments but only at $\alpha=0.1$ ($F_{1,16} = 4.09$, $p=0.06$). Chlorophyll-*a* did not differ with disturbance rate ($F_{3,16} = 0.83$, $p=0.50$), and there was no productivity-disturbance interaction ($F_{3,16} = 0.71$, $p=0.56$). The number of animals did not differ between productivity treatments ($F_{1,16} = 0.28$, $p=0.60$) or disturbance treatments ($F_{3,16} = 0.78$, $p=0.52$), and there was no productivity-disturbance interaction ($F_{3,16} = 0.36$, $p=0.78$).

Within-stream taxonomic richness exhibited a u-shaped quadratic response to increasing productivity (AIC: 24.76; Fig. 1, Table 1), with a non-significant linear relationship (AIC: 31.64; $r^2 = 0.02$, $F_{1,22} = 0.41$, $p=0.53$). This u-shaped relationship between productivity and richness at the local scale can be explained by two separate relationships related to the productivity treatment. In the low productivity treatments, richness declined at a decreasing rate with increasing productivity ($r^2 = 0.68$, $F_{2,9} = 9.53$, $p=0.01$, $y = 15.2 - 20.82x + 18.62x^2$). In the high productivity treatments, richness increased monotonically although only at the 10% level ($r^2 = 0.32$, $F_{1,10} = 4.74$, $p=0.06$, $y = 8.84 + 3.58x$). Richness declined monotonically with productivity at medium disturbance sites (8 day disturbance rate) ($r^2 = 0.94$, $F_{1,4} = 59.81$, $p=0.002$, $y = 13.38 - 6.2x$) but was not related at any other disturbance rate.

Between-stream richness increased monotonically with increasing productivity (Fig. 1, Table 1). However, community dissimilarity was not related to productivity (Fig. 1, Table 1) and accounting for disturbance rate did not alter this (ANCOVA: $F_{4,3} = 2.61$, $p=0.23$). The average variation in productivity (a surrogate for resource heterogeneity) increased with increasing productivity but was not significant ($F_{1,6} = 3.33$, $p=0.12$). Rarefied richness was not related to productivity at this scale ($F_{1,6} = 0.05$, $p=0.83$), nor was the number of animals at the 10% level when using Bonferroni correction ($r^2 = 0.44$, $F_{1,6} = 4.71$, $p=0.07$, $y = 28.8 + 108.38x$).

Table 1. Results of linear and quadratic regression analysis for (a) productivity- and (b) disturbance-diversity relationships at within- and between-stream scales and community dissimilarity (100 – Bray-Curtis dissimilarity) in artificial channels in Hawke's Bay, New Zealand streams, December 2009. Bonferroni corrected $\alpha=0.025$ for multiple comparisons.

	<i>F</i>	<i>p</i>	<i>r</i> ²	Equation
(a) Productivity				
Within-stream richness	4.98	0.02	0.32	$y = 13.25 - 23.27x + 11.49x^2$
Between-stream richness	16.68	0.007	0.74	$y = 14.42 + 8.76x$
Community dissimilarity	0.025	0.88	0.004	$y = 66.13 + 4.46x$
(b) Disturbance				
Within-stream richness	0.01	0.92	0.0004	$y = 10.75 + 0.03x$
Between-stream richness	0.028	0.87	0.005	$y = 18.5 + 0.1x$
Community dissimilarity	10.16	0.02	0.63	$y = 48.71 + 7.85x$

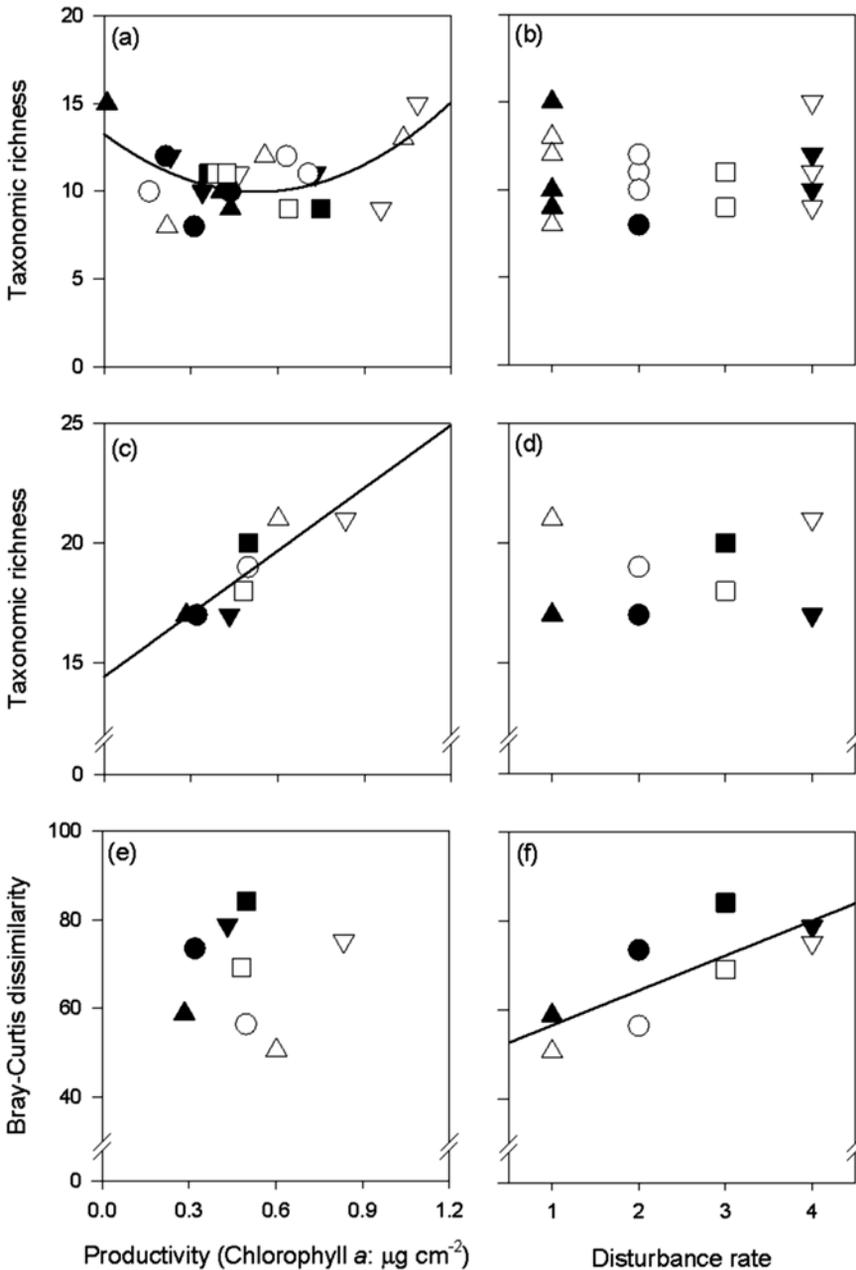


Fig. 1. Linear and quadratic regression between diversity and (a, c, e) productivity and (b, d, f) disturbance at (a, b) within- and (c, d) between-stream scales and (e, f) community dissimilarity ($100 - \text{Bray-Curtis dissimilarity}$) in artificial channels in Hawke's Bay, New Zealand streams, December 2009. Community dissimilarity points represent the average of two-way comparisons for each treatment between streams. Open symbols represent high productivity and closed low productivity treatments. Upright triangles represent disturbance rate of 1 (not disturbed), circles 2 (every 16 days), squares 3 (every 8 days), and inverted triangles 4 (every 4 days).

Within- and between-stream richness were not related to disturbance rate but community dissimilarity increased monotonically with increasing rate of disturbance (Fig. 1, Table 1). The number of individuals increased with increasing disturbance rate at the between-stream level, but only at $\alpha=0.1$ after Bonferroni correction ($r^2 = 0.52$, $F_{1,6} = 6.52$, $p=0.04$,

$y=40.03 + 16.94x$). However, although community dissimilarity showed a slight increase with increasing number of animals per treatment, this was not significant ($F_{1,6} = 3.56$, $p=0.11$). Likewise, rarefied richness was not related to disturbance ($F_{1,6} = 0.06$, $p=0.82$). Resource heterogeneity (productivity variation) within treatments did not increase with distur-

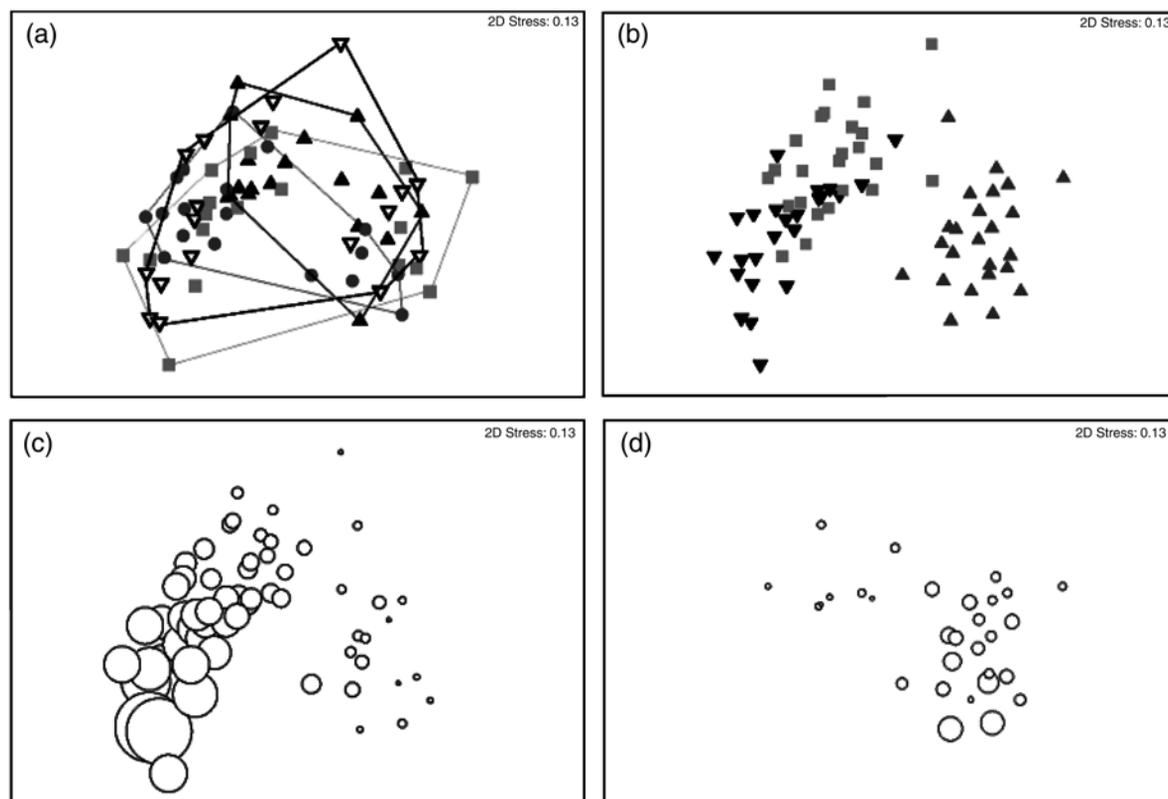


Fig. 2. Non-metric multidimensional scaling (NMDS) ordination of axis one against axis two on raw invertebrate community data from artificial stream channels in Hawke's Bay, New Zealand streams, December 2009 (stress = 0.13). **(a)** Coded based on disturbance treatment: upright triangles = disturbance rate 1 (not disturbed), circles = disturbance rate 2 (every 16 days), squares = disturbance rate 3 (every 8 days), and inverted triangles = disturbance rate 4 (every 4 days). **(b)** Coded on individual streams: upright triangles = EX1 (site 1), inverted triangles = EX2 (site 2), and squares = EX3 (site 3). **(c)** Bubble plot for abundance of *Potamopyrgus antipodarum* and **(d)** *Aoteapsyche colonica*. Bubble scale for both = 0–300 individuals per sample.

bance ($F_{1,6} = 0.15$, $p = 0.71$). Taxonomic richness increased with increasing variation in productivity but was only significant at the 10% level ($r^2 = 0.47$, $F_{1,6} = 5.35$, $p = 0.06$, $y = 15.84 + 3.08x$). Taxonomic dissimilarity was not related to variation in productivity ($F_{1,6} = 2.04$, $p = 0.2$).

Overall community structure differed between the four disturbance treatments ($R = 0.06$, $p = 0.03$; Fig. 2a). However differences between disturbance treatments were largely due to shifts in density of the most abundant taxa rather than change in composition (SIMPER; Fig. 2; Fig. 3). Five taxa contributed on average 77% to differences between disturbance treatments. These were: the snail *Potamopyrgus antipodarum*, Oligochaeta, Platyhelminthes, the mayfly *Deleatidium* spp. and the net spinning caddisfly *Aoteapsyche colonica*. The caddisfly *Pycnocentroides aeris* was one of the most abundant taxa at all sites and treatments (7.3–27.6% contribution) but contributed little to differences between sites and disturbance treatments. Of the top five taxa differentiating treatments,

P. antipodarum (Fig. 2c) and *A. colonica* (Fig. 2d) were the only taxa to respond linearly to disturbance at the between-stream scale and were negatively correlated with each other at both the within-stream scale ($r = -0.45$, $p = 0.03$) and between-stream scale although only at the 10% level ($r = -0.67$, $P = 0.07$; Fig. 3). However, when assessing abundances at each individual site, the responses to disturbance treatment were site specific and varied greatly.

Community structure of undisturbed treatments (dist. 1) were significantly different to all other treatments (dist. 2: $R = 0.11$, $p = 0.03$; dist. 3: $R = 0.08$, $p = 0.047$; dist. 4: $R = 0.12$, $p = 0.01$; Fig. 2). However, there was no difference in community structure between the remaining treatments (dist. 2/dist. 3: $R = 0.02$, $p = 0.22$; dist. 2/dist. 4: $R = 0.05$, $p = 0.09$; dist. 3/dist. 4: $R = -0.01$, $p = 0.52$). Variation within disturbance treatments indicated the number of taxa contributing to differences between replicates declined with increasing disturbance rate. Four taxa (*P. antipodarum*, *A. colonica*, *Pycnocentroides aeris*

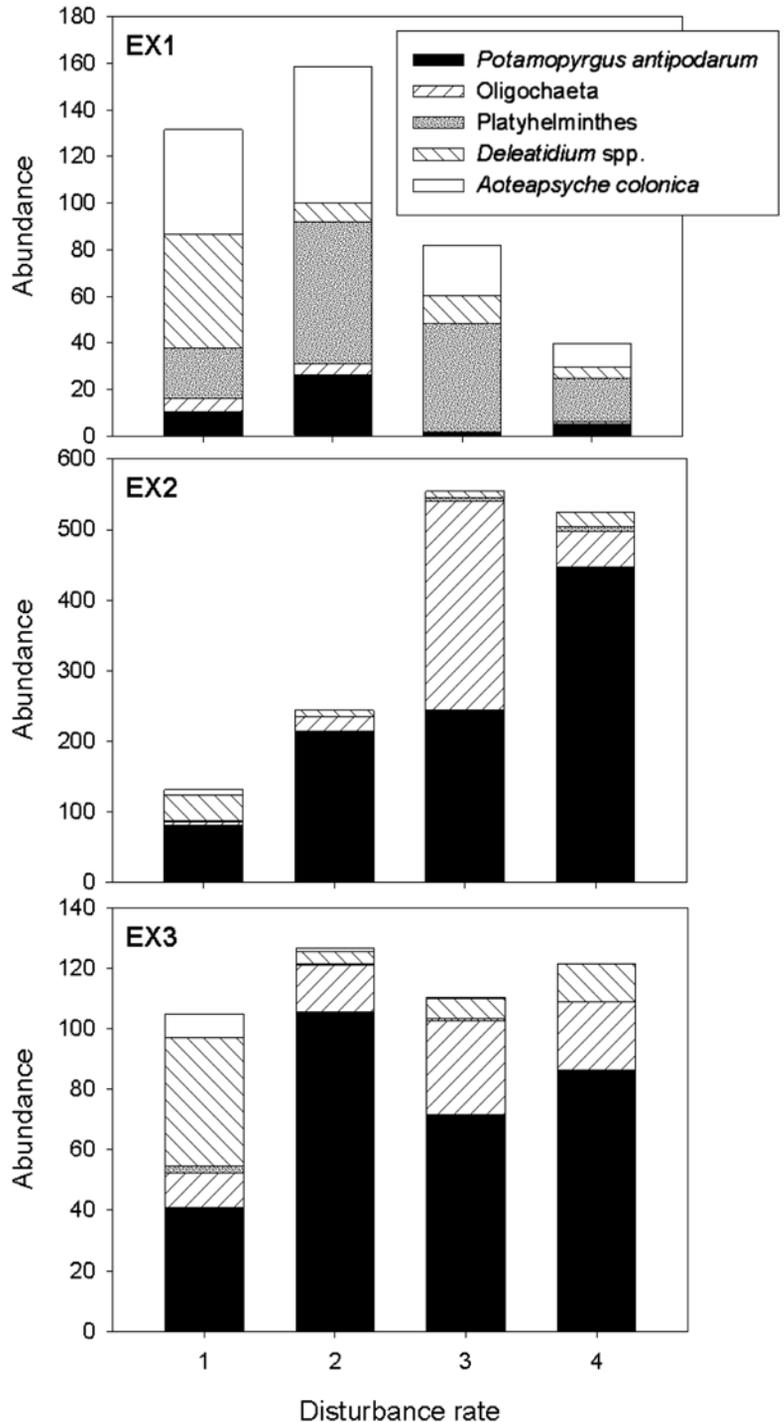


Fig. 3. Mean abundance (ind. 0.038 m⁻²) of five taxa contributing the greatest to difference between disturbance treatments at each disturbance treatment collected within artificial channels in three streams (EX1 – EX3/ site 1 – site 3) in Hawke’s Bay, New Zealand, December 2009.

and *Deleatidium spp.*) each contributed greater than 10% to differences at the lowest disturbance rates whereas *P. antipodarum* was the only taxon to contribute greater than 10% at high disturbance sites. The contribution of *P. antipodarum* to differences between replicates increased with increasing disturbance rate.

P. antipodarum was the most abundant taxon throughout all treatments but abundance of this snail

was lowest at the least disturbed treatments (N=44) and highest at the most disturbed (N=180) and average per treatment increased with increasing disturbance rate ($r^2 = 0.55$, $F_{1,6} = 7.34$, $p = 0.04$, $y = 11.75 + 39.77x$; Fig. 2c; Fig. 3). However, differences in *P. antipodarum* were not significant between disturbance treatments ($F_{3,20} = 0.98$, $p = 0.42$). *A. colonica* declined monotonically with increasing disturbance ($r^2 = 0.79$,

$F_{1,6} = 22.37$, $p = 0.003$, $y = 28.42 - 6.3x$). *P. antipodarum* was negatively correlated with both axis 1 ($r = -0.67$) and axis 2 ($r = -0.45$) of the NMDS ordination (Fig. 2c). *A. colonica* was positively correlated with axis 1 ($r = 0.58$) and negatively correlated with axis 2 ($r = -0.36$; Fig. 2d). *P. antipodarum* was highest at site EX2 (mean = 247 ind./sample) and lowest at site EX1 (mean = 11 ind./sample) ($F_{2,21} = 12.6$, $P = 0.0003$). *A. colonica* was highest at EX1 (mean = 34 ind./sample) and lowest at both EX2 and EX3 (mean = 2 ind./sample) ($F_{2,21} = 15.57$, $p = 0.0001$).

The difference in community structure was more strongly related to individual site differences in composition ($R = 0.65$, $p = 0.001$; Fig. 2b). Communities were more similar at each site regardless of disturbance rate (Bray-Curtis similarity = 46.6–50.1) than between disturbance treatments at all sites (Bray-Curtis similarity = 28.6–40.7). Moreover, when assessing differences in community composition using presence/absence data, communities were more similar at each site regardless of disturbance rate (Bray-Curtis similarity = 61.5–68.3) than between disturbance treatments at all sites (Bray-Curtis similarity = 54.7–57).

Discussion

The response of diversity to both productivity and disturbance varied with the spatial scale at which it was examined in this experiment. This is a common phenomenon when assessing these relationships (Petraitis et al. 1989, Mackey & Currie 2001, Chase & Leibold 2002). In fact, diversity only responded to one of productivity or disturbance at each scale. Tonkin et al. (2013) and Tonkin & Death (2012) found the effects of productivity and disturbance to be additive rather than multiplicative in predicting stream macroinvertebrate diversity. Productivity affected taxonomic richness at within- (local) and between-stream (regional) scales and disturbance affected community dissimilarity (β diversity). Although productivity and disturbance can both affect diversity (e.g. Death & Zimmermann 2005, Tonkin & Death 2012, Tonkin et al. 2013), these often operate in different ways (Connell 1978, Kondoh 2001, Mackey & Currie 2001, Death 2002), varying with spatial and temporal scale (Petraitis et al. 1989). We predicted diversity in these streams at all scales would decline with increasing rate of disturbance but there was no effect of disturbance at within- and between-stream scales. Although experimental studies have struggled to isolate the effects of disturbance and productivity (Robinson & Minshall 1986, Death

1996), we were able to manipulate productivity independent of disturbance as chlorophyll-*a* remained higher in high productivity treatments.

Productivity-diversity relationship

The likelihood of occurrence of u-shaped relationships between productivity and diversity, as found here at the within-stream scale, increases with spatial scale (Mittelbach et al. 2001). Identifying causes for this pattern is difficult as it is not supported by theory and the mechanisms have not been discussed (Mittelbach et al. 2001). While there were two curves forming this trend, this did not fit with the pattern accumulation hypothesis that suggests between-community patterns are an accumulation of local patterns (Scheiner et al. 2000). However, we would need greater replication and spatial extent of sampling to properly test this hypothesis. Richness actually declined with increasing productivity in the low productivity treatments and increased in the high productivity treatments. Most emphasis is placed on identifying humped trends as much of ecological theory predicts this (Mittelbach et al. 2001), but there are reasons to expect other forms of this relationship (Abrams 1995). The more common unimodal relationship at local scales (e.g. Grime 1973a, Huston 1979, Rosenzweig 1995, Mittelbach et al. 2001) is likely to involve competition between animals within heterogeneous habitats (Kassen et al. 2000), but not relatively homogeneous habitats such as in our study.

As predicted, between-stream richness increased monotonically with increasing productivity. This is possibly linked with the increase in resource heterogeneity (although non-significant) with increasing productivity, that would allow greater representation of macroinvertebrate traits to co-exist. The discrepancy in the productivity-diversity relationship found when assessing within- and between-stream scales in this study matches that commonly found between true local and regional scales (Currie 1991, Chase & Leibold 2002). Chase & Leibold (2002) found diversity peaked at intermediate levels of productivity at small scales and increased monotonically at the regional scale in pond communities. Several mechanisms have been put forward to explain the linear increase in richness at regional scales (Currie 1991, Mittelbach et al. 2001) and one likely factor is the inclusion of different niches as spatial scale increases (Kassen et al. 2000). Along with the regional linear increase in richness, Chase & Leibold (2002) found a monotonic increase in community dissimilarity with increasing productivity and more recently Chase (2010) suggested a

greater deterministic control in low productivity environments. Many factors could explain this including increased resource heterogeneity and a greater number of stable states (Chase & Leibold 2002), but due to the nature of this experiment, are not likely to apply. Accordingly, we found no relationship between community dissimilarity and productivity.

Dissimilarity increased with disturbance

Increasing disturbance led to greater dissimilarity between communities; this counters our prediction of greater deterministic control at higher disturbance (Chase 2003, Chase 2007). Often differences in community dissimilarity can be explained by differences in the recolonization process; i.e. deterministic and stochastic assembly patterns. Theory predicts β diversity should decline with increasing environmental harshness due to a greater role of deterministic assembly (Chase 2007), such as that found when comparing spring and runoff-fed stream communities (Barquin & Death 2006). Nevertheless, recent work in lotic systems has demonstrated a greater deterministic control at intermediate levels of disturbance (Lepori & Malmqvist 2009) suggesting the transition from stochastic to deterministic control is not necessarily linear. Disturbance, especially in streams, typically operates at a patchy scale and creates heterogeneous habitat and resources (Doeg et al. 1989, Lancaster & Hildrew 1993). Thus, disturbance can promote diversity within a landscape (β and γ) by allowing both early colonizing and late successional species to co-exist, but this is dependent on low dispersal (Warren 1996, Chase 2003, Matthiessen et al. 2010). Consequently, in natural systems we could have expected the increased dissimilarity with disturbance to be a result of increased resource/habitat heterogeneity. Due to the spatial and temporal scale of this experiment (dissimilarity assessed between equal disturbance treatments), the rate of disturbance was homogeneous between streams. Accordingly, resource heterogeneity (productivity variation) did not increase with disturbance rate nor did community dissimilarity with resource heterogeneity. In fact, resource heterogeneity is likely to be higher in more stable habitats at this scale (Beisel et al. 1998, Barquin & Death 2006).

Whether the increase in dissimilarity with disturbance is a result of greater stochastic assembly in more disturbed treatments is unclear (Chase 2003, Chase 2007). A large proportion of New Zealand benthic invertebrates are capable of living in highly disturbed environments as a result of the high degree of environmental stochasticity and have generalist feeding

habits as a result (Winterbourn et al. 1981, Thompson & Townsend 2000). In fact, there are many that could be considered 'Hutchinsonian demons' – both superior colonizers and competitors (Kneitel & Chase 2004, Cadotte et al. 2006). Essentially the role of deterministic assembly is less pronounced than in other ecosystems where harsh conditions select for few specialized taxa. In these streams, the proportion of taxa within the regional pool able to withstand these conditions is likely to be high.

Given the hypothesized lack of deterministic control in disturbed treatments, we suggest the increase in community dissimilarity with disturbance rate is simply a function of the time since last disturbance (Reice 1994). Considered this way, community dissimilarity declined with time, thus it appears these communities are converging on a single stable equilibrium. If β diversity is not promoted through different assembly processes (multiple stable equilibria), then heterogeneity in resources/conditions between streams (with single stable equilibria) would be required (Loreau & Mouquet 1999, Mouquet & Loreau 2002). Low connectivity between replicates as in this study (dispersal between streams), typically promotes multiple states (Warren 1996, Chase 2003, Matthiessen et al. 2010). Therefore, the apparent convergence on a single stable equilibrium with time since disturbance between the streams indicates little heterogeneity between habitats and resources which was indeed evident in the present study. Nonetheless, community composition remained relatively different between the three locations.

Local suite of colonists

Rather than differences in assembly rules, it appears colonization patterns are simply a function of the local suite of colonizing taxa. Specifically, colonization of channels appears to have come from the small-scale dispersal of animals present within the surrounding benthos of the spring-fed streams in which the study was undertaken; rather than a specialist suite of colonist taxa. Previous experiments of this nature have found this pattern of local arrival rather than the more broad-scale arrival of specialist colonizers (Death 2006). Thus the findings need to be considered with some caution as the colonization patterns do not necessarily match those of large-scale natural disturbances. Communities found within the experimental channels, with a strong contribution of *Potamopyrgus antipodarum*, *Aoteapsyche colonica*, Platyhelminthes, Oligochaeta, *Deleatidium* spp. and *Pycnocentroides aeris* are similar to those found in the benthos in a previous study on these streams around this time (Ap-

pendix 1), and indicate the streams are relatively non-pristine. If ecological theory holds, we would expect high disturbance treatments to be the most similar due to deterministic control selecting for few capable taxa but communities were more similar within streams than within disturbance treatments.

With disturbance not reducing overall animal density, our results suggest the increasing dissimilarity with disturbance rate was due to shifts in abundance of the most dominant taxa, although the mechanisms underlying this are unclear. The most abundant animal, the hydrobiid snail *P. antipodarum*, increased with disturbance rate which opposes research suggesting that this snail is inversely related to disturbance in streams (Holomuzki & Biggs 1999). However, this was only evident at one of the three sites (EX2) with variable results at the other two. Molluscs are generally considered slower colonizers and likely to be competitive dominants (Hemphill & Cooper 1983, Mackay 1992), but the atypical response to disturbance in this instance almost certainly reflects their abundance in the surrounding benthos. The response of *P. antipodarum* to disturbance has been found to be dependent on the type of substrate in the streambed (Holomuzki & Biggs 1999), but this is not likely a factor in the present study as substrates were relatively uniform between treatments.

While disturbance can regulate the rate of competitive interactions between opportunistic early colonizers and competitive dominants (Hemphill & Cooper 1983), the decline of *P. antipodarum* and increase in the hydropsychid caddisfly *A. colonica* with time since last disturbance is not likely due to a competitive interaction. Although the negative trend between these two species occurred within each stream, densities were clearly more site specific than disturbance specific. In fact, there were significant differences between communities of EX1 and the remaining two sites. Despite having similar physicochemical characteristics, EX2 and EX3 had greater interstitial fine sediment and were generally more degraded, which is reflected by the greater number of Oligochaeta in these streams. Moreover, given it is an open canopy spring-fed stream, the presence of high densities of the filter-feeding caddis *A. colonica* in EX1 suggests a reasonable supply of organic matter upstream of the sampling location. Their increase with time since last disturbance most likely reflects the unfavourable conditions for a net building caddisfly created by the regular turnover of substrate. Despite being a successful colonizing species, the mayfly *Deleatidium* spp. exhibited a similar response to *A. colonica*, which in

part reflects their non-specialist nature and competitive ability.

As per previous stream-based studies (Collier & Quinn 2003, Death 2006), no suite of taxa were replaced with time since disturbance. A critical requirement of many relationships in disturbance ecology is that there is a trade-off between competitive and colonizing ability (Chesson & Huntly 1997, Roxburgh et al. 2004, Cadotte 2007). Neutral models have renewed debate on this central tenet in ecology (e.g. Hubbell 2001), but there is still widespread support for these trade-offs (e.g. Kneitel & Chase 2004, Cadotte et al. 2006). The expectation of no competitive displacement led us to predict a decline in richness with disturbance but we found no such pattern. Chase (2010) also found that taxa in low productivity habitats (harsh) were simply a nested subset of those found at higher productivities (benign), and argue that this is likely a more general pattern than previously thought. Indeed, the taxa found in high disturbance treatments in the present study are merely a subset of those found in stable treatments and although *P. antipodarum* declined with increasing stability, it was still dominant throughout all treatments in two of the three sites. More importantly, an underlying competitive interaction between *P. antipodarum* and *A. colonica* does not explain the increase in dissimilarity with disturbance.

Conclusions

Our results demonstrate that spatial scale can affect the way species diversity responds to environmental conditions. We have shown that diversity can respond to both productivity and disturbance but at different spatial scales. Taxonomic richness was lowest at intermediate levels of productivity at the within-stream (local) scale and increased monotonically at the between-stream (regional) scale. Rather than the increase in community dissimilarity previously found with increasing productivity (Chase & Leibold 2002) and the stronger role of deterministic assembly suggested for harsh environments (Chase 2007), we found an increase in dissimilarity with increasing rate of disturbance. Due to the abilities of the pool of colonists to withstand disturbed environments in these streams, communities are converging as a function of the time since last disturbance. Namely, they are simply returning to those found in the surrounding benthos (Appendix 1) as a result of the scale of disturbance and that it is not limiting the species pool. These patterns are highly dependent on the pool of colonists and are un-

derpinned by interactions within each stream. Without a distinction between early colonizing and late successional communities, increased deterministic assembly (and lowering of β diversity) with increasing disturbance will not apply. In fact, depending on the heterogeneity of regional habitats and connectivity between habitats, the opposite pattern may occur as we show here.

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