

Productivity–diversity relationships for stream invertebrates differ geographically

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Abstract More productive environments typically have more species, although the specific form of this relationship is unclear and can vary with spatial scale. This relationship has received little direct attention in lotic systems, and thus the nature of the relationship is unclear, as is any effect of spatial scale. We examined the link between stream primary productivity and macroinvertebrate diversity in Spain and New Zealand and hypothesized that macroinvertebrate diversity would increase log-linearly with increasing productivity in both regions. We sampled 24 streams in Cantabria, Spain, and 24 in the central North Island, New Zealand. Algal primary productivity was approximately three times higher in Spanish streams, but

taxonomic richness of invertebrates did not differ between the regions. Richness and Shannon diversity only responded to productivity in the New Zealand streams, exhibiting the predicted log-linear increase. In the Spanish streams, only the total number of individuals increased with productivity. However, when plotted on the same axes, richness in the Spanish streams simply occurred on the linear portion of the graph to the right of the New Zealand streams. We speculate that productivity in the Spanish streams never became low enough to constrain diversity, but did in the New Zealand streams. Combining results from the two regions, there is no evidence of a decline in diversity with higher productivity.

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Introduction

Predicting diversity remains a fundamental challenge in community ecology (e.g. Huston 1994; Hubbell 2001; Adler et al. 2011). Global patterns suggest diversity is a function of a few broad-scale factors such as latitude, precipitation, temperature, altitude, and land mass (Gaston 2000). Of the multitude of factors that can influence diversity, disturbance (Connell 1978; Wootton 1998; Lake 2000) and productivity (Currie 1991; Mittelbach et al. 2001) remain central,

although universal patterns remain elusive (Mackey and Currie 2001; Mittelbach et al. 2001). What is likely is disturbance and productivity interact to affect diversity but the nature of this interaction remains unclear (Currie 1991; Death and Zimmermann 2005; Scholes et al. 2005; Cardinale et al. 2006). Few systems are more heavily influenced by disturbance than streams (Resh et al. 1988; Lake 2000; Death 2008), but the response of diversity to disturbance is likely to be dependent on productivity (Death and Zimmermann 2005; Cardinale et al. 2006; Tonkin et al. 2013). However, due to the relatively mobile nature of stream invertebrates, successful applications of common models such as the Intermediate Disturbance Hypothesis (IDH) (Grime 1973; Connell 1978) and the Dynamic Equilibrium Model (DEM) (Huston 1979, 1994) are rare (but see Townsend et al. 1997). What makes streams especially unique is the strong association between disturbance and productivity (Lake 2000; Death 2002). Death (2002) proposed a model suggesting disturbance simply resets the colonization process and productivity, rather than competitive interactions, sets the upper limit to richness in streams. However, whether a great enough range of productivity was sampled by Death (2002) to elucidate the full pattern is unclear as this was only assessed in New Zealand forest streams. In order to better understand the interaction between productivity and disturbance, clarification of the productivity–diversity relationship in streams is required.

The two most common forms of the productivity–diversity relationship in all systems are unimodal (e.g. Rosenzweig 1995; Leibold 1999; Mittelbach et al. 2001) and linear (e.g. Currie 1991; Abrams 1995; Gaston 2000; Mittelbach et al. 2001) increases in diversity with increasing productivity (but see Adler et al. 2011). One of the major influences on the form of this relationship is the spatial scale of investigation (Currie 1991; Chase and Leibold 2002) and the type of ecosystem and/or organisms considered; with hump-shaped relationships more common in plant communities and linear relationships in animal communities (Waide et al. 1999; Mittelbach et al. 2001). Moreover, where standardized methodologies are used across systems, patterns have been inconclusive (Adler et al. 2011), and differences in productivity measurements potentially obscure results between systems (Groner and Novoplansky 2003). Studies at smaller spatial scales commonly find unimodal relationships between productivity and diversity,

but at greater spatial scales, this pattern often changes to a monotonic increase in diversity with productivity (Mittelbach et al. 2001; Chase and Leibold 2002). There are many mechanisms postulated to lead to this unimodal relationship (Rosenzweig and Abramsky 1993; Abrams 1995), but these often require some form of competitive trade-off for which there is little evidence in stream communities (Reice 1985; Death and Winterbourn 1995). Little effort has been placed on elucidating the productivity–diversity relationship in isolation from disturbance and other factors in lotic systems. The few to look specifically have found both unimodal (Death and Zimmermann 2005; Cardinale et al. 2006) and log-linear (Death 2002; Tonkin and Death 2012; Tonkin et al. 2013) increases in diversity with increasing productivity.

Not only are the effects of productivity dependent on spatial scale, but regional effects such as the potential pool of colonizers can completely alter the response to environmental factors, although Tonkin and Death (2012) found no differences between two regions of contrasting land-use in New Zealand. When comparing invertebrate communities between Spain and New Zealand, Death and Barquin (2012) found contrasting responses to disturbance rates. Although productivity is often postulated as a potential explanation of weak links in the disturbance–diversity relationship (Huston 1994; Cardinale et al. 2006; Tonkin and Death 2012), Death and Barquin (2012) found no evidence to support this in their study. Thus, we set out to examine whether the response of stream benthic invertebrate diversity to a commonly used proxy of productivity, standing crop of periphyton biomass, differs between these two regions in the Northern and Southern Hemispheres. Based on recent findings (Death 2002; Tonkin and Death 2012; Tonkin et al. 2013), we hypothesize that invertebrate diversity will increase with increasing productivity up to a point before tapering off, despite the different taxonomic composition. As a more stream-specific metric, we also assess whether the percent of Ephemeroptera, Plecoptera, and Trichoptera (% EPT) respond differently than other taxa as they are sensitive to algal proliferations in lotic systems. Finally, because of the strong link between productivity and disturbance in streams, we explore the relationship between stability and diversity in these streams. We hope by expanding the spatial scale of study we can gain more generality in the productivity–diversity relationship of lotic systems.

Methods

Study sites

Twenty-four streams were sampled in each of the Cantabrian Mountains of Northern Spain and Tongariro National Park in the central North Island of New Zealand between February and July 2007 (Appendix 1). Specifically, New Zealand streams were sampled in February–April and Spanish streams in July 2007 representing respective Southern and Northern Hemisphere summers. The Cantabrian Mountains span approx. 483 km east to west along the northern coast of Spain reaching 2,648 m asl at Torre de Cerredo. Average rainfall ranges from approx. 1,200 to 1,600 mm p.a. depending on location within the region. Land-use surrounding sampling sites varied from Atlantic deciduous forest consisting predominantly of oak (*Quercus* spp.) and European beech (*Fagus* spp.) to pasture and small urban settlements. Sites were selected from 6 river catchments: Río Besaya, Río Saja, Río Pas, Río Pisueña, Río Nansa, and Río Ebro. Except for Río Ebro, which drains into the Mediterranean Sea, all rivers flow into the Atlantic Ocean. Altitude ranged from 163 to 1,061 m asl, and average channel width ranged from 1.9 to 30.7 m.

The Tongariro National Park is dominated by the central volcanic massif of Mt Ruapehu (2,797 m asl), Mt Ngauruhoe (2,287 m asl), and Mt Tongariro (1,967 m asl) and the Tihia-kakaramaea volcanic massif to the north. The Kaimanawa Ranges rise to ~1,799 m asl to the east of the Tongariro National Park. Vegetation within and around the park varies from broadleaf-podocarp, mixed beech-podocarp, exotic *Pinus radiata* plantation, native tussock and scrubland to bare ground in the eastern rain shadow of the 3 central volcanoes. The north and west has an average rainfall of 1,800–3,500 mm yr⁻¹ with the south and east only receiving around 1,100 mm yr⁻¹ due to the rain shadow cast by the three mountains from the prevailing westerly winds. Sites ranged from 518 to 1,158 m asl, and average width of stream channels ranged from 1.4 to 30 m.

Sampling protocol

Macroinvertebrates were sampled by taking five 0.1-m² Surber samples (250 µm mesh in New Zealand and 500 µm in Spanish samples but all samples from

both countries were later sieved to 500 µm) from random locations in riffles throughout ~50 m reaches at each site. Samples were stored in 10 % formalin and later sieved to 500 µm and identified in the laboratory to the lowest possible taxonomic level. New Zealand samples were identified using available keys (e.g. Towns and Peters 1996; Winterbourn et al. 2000), and taxa that could not be taken to species level were identified to morphospecies including ‘difficult’ groups such as Chironomidae and Oligochaeta. Spanish samples were mostly identified to morphospecies at the same levels as New Zealand samples, however, where possible these were identified using available keys (e.g. Tachet et al. 2000). Four community metrics were used in this study: number of individuals, number of taxa (richness), Shannon diversity index (H'), and the percent of Ephemeroptera, Plecoptera, and Trichoptera (% EPT animals) (Lenat 1988).

Proxies of primary productivity are often used in ecology (both aquatic and terrestrial) due to the difficulties of measurement in well-spatially or well-temporally replicated studies (Waide et al. 1999; Mittelbach et al. 2001; Gillman and Wright 2006), and primary productivity methods can prove unsatisfactory in streams with low rates of productivity. Therefore, given our approach was to explore spatial patterns of this relationship, rather than measure primary productivity directly, we focused our assessment on standing crop of periphyton biomass using measures of chlorophyll *a* from stream substrata. Chlorophyll *a* and primary productivity in streams, while not directly equivalent, have been found to be well correlated (Morin et al. 1999). Five stones (longest axis < 60 mm) were randomly collected from each riffle for later extraction of chlorophyll *a*. From here, stones were kept cool and dark on ice before being stored at -20 °C. Photosynthetic pigments were extracted from stones by submerging each stone in known volumes of 90 % acetone for 24 h 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) for New Zealand samples and on a Beckman Coulter DU[®] Series 700 UV/Vis Scanning Spectrophotometer (Beckman Coulter Inc., Brea, CA, USA) for Spanish samples and converted to chlorophyll *a* and phaeophytin pigment concentration using Steinman and Lamberti (1996). These were then corrected for stone surface area and halved to account

for just the active growing area of the stone using Graham et al. (1988).

Substrate size composition was assessed using the ‘Wolman Walk’ method where the second longest axis of 100 stones was measured at approximately 1-m intervals across a zigzag transect at 45° to the stream bank (Wolman 1954). Percentage substrate composition of Wentworth scale size classes (Wentworth 1922; Cummins 1962) was converted to a single substrate size index by summing midpoint values of size classes weighted by their proportion. Bedrock was assigned a nominal size of 400 mm for use in the calculations (Quinn and Hickey 1990). Spot measurements of conductivity, temperature, and pH were taken at the time of sampling using Eutech instruments ECScan pocket meter at New Zealand sites and a YSI 556 MPS meter at Spanish sites. Depth and velocity were recorded with a Marsh-McBirney flowmate current meter in the thalweg of each stream at 5 points at equidistant intervals along the study reach. Flow type of each site was assessed visually as percentage of still, backwater, pool, run, or riffle over a 100-m reach.

Bed stability/substrate disturbance was assessed using the Pfankuch stability index (Pfankuch 1975). Only the bottom component of the index (rock angularity, brightness, packing, percent stable materials, scouring, and amount of clinging vegetation) was used, which assesses the substrate component of the stream only, as this is more relevant to stream invertebrate communities (Winterbourn and Collier 1987).

Statistical analysis

For multivariate analysis, physicochemical data were normalized by subtracting means and dividing by their standard deviation using Primer v6 (Clarke and Gorley 2006). Principal component analysis (PCA) was carried out on normalized environmental data to determine whether physicochemical and habitat variables differed between New Zealand and Spanish streams using Primer v6 (Clarke and Gorley 2006). Differences in principal components between regions were tested for with one-way analysis of variance (ANOVA) using the ‘aov’ function in R 2.15 (R Development Core Team 2012). PCA was also performed for each region individually to assess the factors that influenced chlorophyll *a* levels within these streams. Chlorophyll *a* was then regressed against each principal component for each region

individually and for both regions combined using simple linear regression in R 2.15.

Further assessment of whether site characteristics differed between regions was assessed using analysis of similarities (ANOSIM) (Clarke 1993) on normalized physicochemical data using Euclidean distances in Primer v6 (Clarke and Gorley 2006). One-way ANOVA was performed on individual physicochemical and biological data to determine whether there were differences in these metrics between Spanish and New Zealand streams using R 2.15.

Where required, data were $\log(x + 1)$ transformed to meet the assumptions of analysis. To test whether diversity was a log-linear function of chlorophyll *a* as hypothesized, simple linear regression analysis was carried out to explore relationships between diversity and chlorophyll *a* within each region as well as combining both regions and testing for a universal relationship using R 2.15. Finally, to explore whether stability was important at determining diversity patterns in these streams, simple linear regression was performed between the Pfankuch index and invertebrate metrics using R 2.15, and a second term was added if it yielded a better fit. Akaike’s information criterion (Akaike 1974) was used to determine the best fitting curve to the data. This method takes into account goodness of fit statistics and the number of parameters involved in the fitting of the model to select the model most preferred.

Results

Physicochemical variables

Stream habitat and physicochemical conditions were different between New Zealand and Spanish streams (Appendix 2; Table 1). PCA on combined Spain and New Zealand environmental data revealed a strong split in the two regions on principal component (PC) 1 (35.6 % variation explained), but there was no difference between regions on PC2 (16.4 % variation explained; Appendix 2; Table 1). Width, depth, and velocity increased; and conductivity, temperature, and pH decreased with PC1, whereas substrate heterogeneity increased; and substrate size and slope decreased with PC2 (Appendix 2, Appendix 3). ANOSIM confirmed there were strong differences in physicochemical variables between the two regions ($R = 0.53$,

$p = 0.001$). Conductivity ranged from 44 to 298 $\mu\text{S cm}^{-1}$ in New Zealand and 68–402 $\mu\text{S cm}^{-1}$ in Spanish streams and was on average 1/3 higher in the Spanish streams (Table 1). New Zealand streams were more acidic, wider, deeper, and had twice the velocity (Appendix 2; Table 1). There was little or no difference in stream slope, substrate size index, or substrate heterogeneity between the two regions (Table 1). Bed stability, assessed as the bottom component of the Pfankuch index, did not differ between New Zealand and Spain (Table 1).

When assessing New Zealand sites separately, conductivity, temperature, pH, substrate size, slope, and Pfankuch increased with PC1 and velocity and substrate diversity declined (Appendix 3). Width and Pfankuch increased with PC2 and substrate variability declined for the New Zealand sites (Appendix 3). For the Spanish sites, conductivity and substrate variability increased; and width, depth, velocity, temperature, and substrate size declined along the PC1 axis (Appendix 3). Substrate size and slope increased along PC2 and temperature and Pfankuch declined (Appendix 3).

Chlorophyll *a*

Mean chlorophyll *a* ranged from 2.58 to 15.35 $\mu\text{g cm}^{-2}$ in the Spanish streams and averaged 5.84 $\mu\text{g cm}^{-2}$. Chlorophyll *a* was on average three times lower in the New Zealand streams ranging from 0.03 to 5.02 $\mu\text{g cm}^{-2}$ and averaging 1.88 $\mu\text{g cm}^{-2}$ (Table 1). Chlorophyll *a* declined with decreasing bed stability at the New Zealand sites ($r^2 = 0.17$, $F_{1, 22} = 4.46$, $p = 0.046$, $y = 4.04 - 0.06x$); however, there was no relationship between stability and chlorophyll *a* at Spanish sites ($r^2 = 0.06$, $F_{1, 22} = 1.36$, $p = 0.26$).

With all sites combined, chlorophyll *a* declined strongly with PC1 ($y = 3.86 - 1.24x$, $r^2 = 0.50$, $F_{1, 46} = 45.32$, $p < 0.0001$), but there was no relationship with PC2 ($r^2 = 0.008$, $F_{1, 46} = 0.38$, $p = 0.539$). Chlorophyll *a* was not related to PC1 ($r^2 = 0.02$, $F_{1, 22} = 0.43$, $p = 0.519$) but declined linearly with PC2 ($y = 1.88 - 0.48x$, $r^2 = 0.20$, $F_{1, 22} = 5.38$, $p = 0.03$) in New Zealand streams. Chlorophyll *a* increased linearly with PC1 in Spanish streams ($y = 5.84 + 1.13x$, $r^2 = 0.29$, $F_{1, 22} = 9.02$, $p = 0.007$) but was not related to PC2 ($r^2 = 0.01$, $F_{1, 22} = 0.23$, $p = 0.63$).

Table 1 Mean (± 1 SE) physicochemical, periphyton and invertebrate community metrics collected from 24 streams in each of the central North Island of New Zealand and Cantabrian Mountains, northern Spain, between February and July 2007

Variables	New Zealand	Spain	$F_{1, 46}$	P
Width (m)	12.9 (1.95)	7.72 (1.24)	5.04	0.03
Depth (cm)	31.05 (1.85)	18.86 (0.98)	33.86	0.00
Velocity (m s^{-1})	0.89 (0.04)	0.4 (0.03)	98.48	<0.0001
Conductivity ($\mu\text{S cm}^{-1}$)	131.58 (14.15)	205.96 (18.91)	9.92	0.003
Temperature ($^{\circ}\text{C}$)	10.71 (0.45)	15.15 (0.39)	55.98	<0.0001
pH	7.88 (0.12)	8.86 (0.05)	57.09	<0.0001
Substrate size index	152.59 (9.02)	139.11 (6.08)	1.53	0.222
Substrate heterogeneity	1.9 (0.03)	1.98 (0.03)	3.32	0.075
Slope ($\text{m } 100 \text{ m}^{-1}$)	3.77 (0.35)	5.18 (0.61)	4.02	0.051
Pfankuch bottom	36.88 (2.12)	32.75 (1.74)	2.27	0.139
PC1	1.6 (1.19)	-1.6 (0.72)	127.57	<0.0001
PC2	0.19 (1.41)	-0.19 (1.13)	1.1	0.3
Chlorophyll <i>a</i> ($\mu\text{g cm}^{-2}$)	1.88 (0.3)	5.84 (0.72)	26.01	<0.0001
No. of taxa	14.78 (1.02)	15.6 (0.59)	0.48	0.491
No. of animals	327.5 (59.52)	928.23 (406.66)	2.14	0.151
Shannon diversity (H')	1.77 (0.09)	1.63 (0.07)	1.65	0.205
% EPT animals	54.00 (6.00)	57.00 (4.00)	0.24	0.627

F and P values indicate results of one-way ANOVA testing for differences between the 2 regions

PC principal component

Community metrics

We found 76 taxa in Spanish and 82 taxa in New Zealand streams. The mean number of individuals was higher in Spanish than in New Zealand streams, but due to the high degree of variation, this difference was not significant (Table 1). Moreover, the mean number of taxa, Shannon diversity index, and the % EPT animals did not differ between New Zealand and Spanish streams (Table 1).

Density, richness, and the Shannon index increased log-linearly with increasing levels of chlorophyll *a* in the New Zealand streams (Table 2; Fig. 1). The % EPT animals was not related to chlorophyll *a* in either New Zealand or Spanish streams (Table 2; Fig. 1). The number of animals increased linearly with increasing chlorophyll *a* in the Spanish streams, but richness and the Shannon index were not related to chlorophyll *a* in these streams (Table 2; Fig. 1).

Fitting the New Zealand and Spanish invertebrate community metrics together against chlorophyll *a* showed that the New Zealand streams fit along the lower end of the chlorophyll *a* gradient and the Spanish streams were at the higher end (Table 3;

Fig. 2). Both the number of animals and the number of taxa fit similar log-linear curves to those for the New Zealand data (Table 3; Fig. 2). The Spanish data simply placed further to the right along the curve at higher levels of chlorophyll *a* (Table 3; Fig. 2).

None of the four invertebrate community metrics were related to bed stability in the Spanish sites (Table 2). The number of animals declined at an increasing rate with stability in the New Zealand streams, and taxonomic richness and the Shannon diversity index peaked at intermediate levels of stability in the New Zealand streams (Table 2). A second term yielded a better fit to the data for these metrics in these streams. There was no relationship between stability and % EPT animals in the New Zealand streams (Table 2).

Discussion

We set out to test the productivity–diversity relationship in streams in the Northern and Southern Hemispheres and found differing responses of benthic macroinvertebrate diversity to primary productivity,

Table 2 Results of individual regression analysis of invertebrate community metrics as a function of (a) chlorophyll *a* and (b) the Pfankuch bottom component collected from 24 streams

	New Zealand				Spain			
	<i>F</i> (AIC)	<i>P</i>	<i>r</i> ²	Equation	<i>F</i>	<i>P</i>	<i>r</i> ²	Equation
(a) Chlorophyll <i>a</i> (μg cm ⁻²)								
Log ₁₀ no. of animals	36.07	<0.0001	0.62	$y = 2.24 + 0.31\ln(x)$	5.31	0.031	0.19	$y = 2.43 + 0.04x$
Number of taxa	22.93	<0.0001	0.51	$y = 14.41 + 2.79\ln(x)$	0.05	0.83	0.002	Non-significant
Shannon index	9.87	0.005	0.31	$y = 1.75 + 0.18\ln(x)$	0.04	0.83	0.002	Non-significant
% EPT animals	4.15	0.054	0.16	Non-significant	1.14	0.3	0.05	Non-significant
(b) Pfankuch index								
Log ₁₀ no. of animals	12.92 (68.7)	0.002	0.37	$y = 3.38 - 0.03x$	0.68	0.42	0.03	Non-significant
Quadratic	9.43 (58.6)	0.001	0.47	$y = 1.64 + 0.07x - 0.001x^2$				
Number of taxa	4.76 (-31.9)	0.04	0.18	$y = 22.24 - 0.2x$	0.19	0.66	0.01	Non-significant
Quadratic	13.42 (-32.6)	0.0002	0.56	$y = -10.59 + 1.76x - 0.03x^2$				
Shannon index	1.7 (-32.2)	0.21	0.07	Non-significant	0.78	0.39	0.03	Non-significant
Quadratic	7.82 (-39.2)	0.003	0.43	$y = -0.48 + 0.15x - 0.002x^2$				
% EPT animals	1.88	0.18	0.08	Non-significant	0.17	0.69	0.01	Non-significant

Degrees of freedom = 1, 22 for linear and log-linear and 2, 21 for quadratic regressions

AIC Akaike's information criterion where lower numbers represent a better model

Fig. 1 Mean (± 1 SE) (a, b) number of animals, (c, d) number of taxa, (e, f) Shannon diversity, and (g, h) percent of EPT animals as a function of chlorophyll *a* in 24 (a, c, e, g) central North Island, New Zealand, and (b, d, f, h) Cantabrian Mountains, northern Spain streams, collected between February and July 2007. Results of regression analysis are presented in Table 2

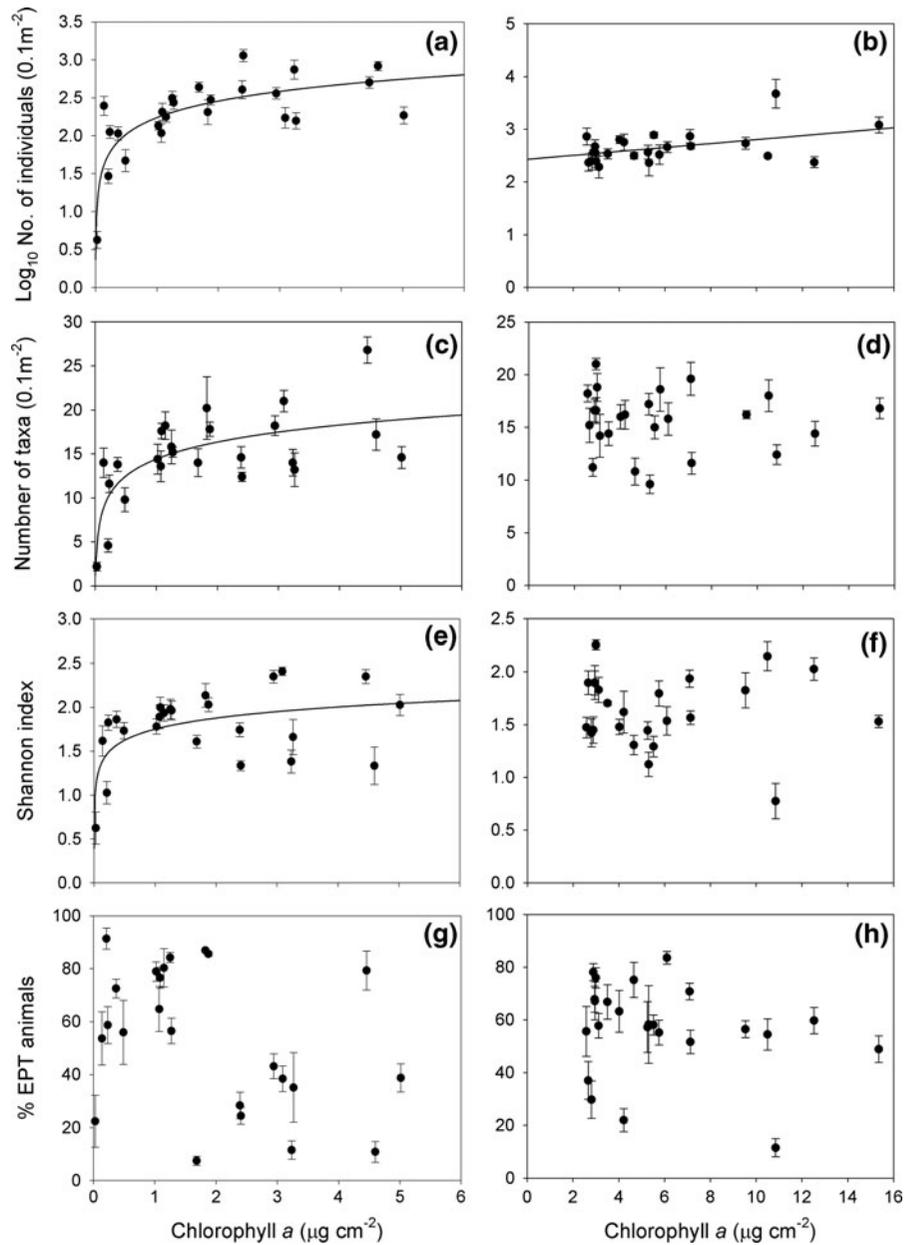
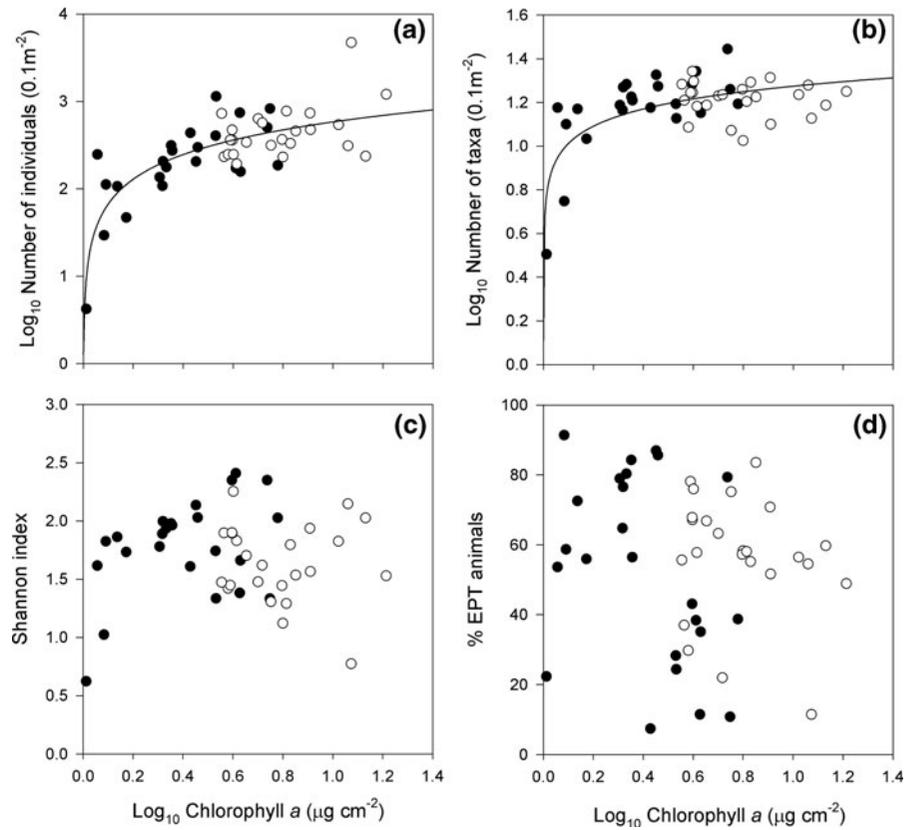


Table 3 Results of combined regression analysis of invertebrate community metrics as a function of chlorophyll *a* collected from 48 streams in the central North Island of New

Zealand and Cantabrian Mountains, northern Spain, between February and July 2007

	$F_{1, 46}$	P	r^2	Equation
Log ₁₀ no. of animals	37.08	<0.0001	0.446	$y = 1.27 + 0.11\ln(x)$
Number of taxa	69.88	<0.0001	0.603	$y = 2.77 + 0.41\ln(x)$
Shannon index	1.36	0.25	0.029	Non-significant
% EPT animals	0.02	0.89	0.0004	Non-significant

Fig. 2 Mean **a** number of animals, **b** number of taxa, **c** Shannon diversity, and **d** percent of EPT animals as a function of chlorophyll *a* in 48 central North Island, New Zealand, and Cantabrian Mountains, northern Spain streams, collected between February and July 2007. Black symbols are New Zealand streams, and white symbols are Spanish streams. Results of regression analysis are presented in Table 3



measured as chlorophyll *a*, between the two regions. While the productivity–diversity relationship is a central theme in many aspects of ecology (Abrams 1995; Mittelbach et al. 2001; Adler et al. 2011), only recently has emphasis been placed on examining this relationship in lotic systems, with strong links being found between the two (Death and Zimmermann 2005; Cardinale et al. 2006; Tonkin and Death 2012; Tonkin et al. 2013). Most studies have found that the productivity–diversity relationship is log-linear at local scales (but see Death and Zimmermann 2005; Cardinale et al. 2006). That is, productivity appears to set the upper limit to richness in streams (Death 2002; Tonkin et al. 2013). Tonkin and Death (2012) found similar patterns in this relationship between two regions of contrasting land-use in New Zealand; thus, we hypothesized that both regions in this study, although separated by considerable distance, would follow the same log-linear increase in diversity with productivity. Invertebrate diversity in New Zealand streams was much more closely linked with chlorophyll *a* and exhibited the hypothesized log-linear relationship. In contrast, given

the large range of chlorophyll *a* found in Spanish sites, we expected a clear invertebrate diversity response, but there was no evidence of a link between productivity and diversity in these streams. In fact, while the range of chlorophyll *a* measured in Spanish sites was more than twice that of New Zealand, the only biological metric linked with productivity was the number of animals, which increased linearly with chlorophyll *a*.

Differences in the relationship between diversity and productivity between the two region's stream communities may simply be a result of sampling at different ranges along a productivity continuum. This may partly be due to different environmental conditions between the two regions such as Spanish streams having warmer temperatures, higher conductivity, and generally being smaller and shallower. In these Spanish streams, and when combined with New Zealand streams, greater chlorophyll *a* occurs when streams are narrower, slower, warmer, and have higher conductivity. Thus, although it appears there are two differing responses of diversity to productivity in the Northern and Southern Hemisphere streams, Spanish

streams had on average three times higher chlorophyll *a* than the New Zealand streams. Essentially, the New Zealand streams examined occurred along the first half of a productivity scale with the Spanish sites along the second half. Combining the two regions indicated density and richness fits the log-linear curve that described the New Zealand data, with no evidence of a decline in diversity at higher productivity. Most prior studies of this nature in New Zealand streams examined the link between productivity and diversity at similar levels of chlorophyll *a* to the New Zealand streams in this study (e.g. Death 2002; Tonkin et al. 2013), indicating these studies may be simply covering the lower half of the more common unimodal pattern often found in plant communities (Waide et al. 1999; Mittelbach et al. 2001). However, Barquin (2004) assessed this relationship in New Zealand streams with up to five times higher chlorophyll *a* than the present study and found no evidence for a decline in richness with increasing productivity.

The lack of decline in invertebrate richness with higher productivity fits with Death's (2002) postulation that productivity, rather than competitive interactions, sets the upper limit to stream invertebrate richness. While commonly searched for, the 'hump-shaped' relationship between productivity and diversity is more commonly found with sedentary organisms such as plant communities (Mittelbach et al. 2001) and has been found with stream primary producer communities (Cardinale et al. 2006); linear increases are more prevalent in animal communities (Waide et al. 1999; Mittelbach et al. 2001). Rosenzweig (1995) provides several explanations for a decline in richness at greater productivity including competitive exclusion, but stream communities are dominated by organisms with a high degree of mobility (Downes 1990; Death 2008). Nevertheless, competitive exclusion does occur in stream communities (e.g. Hemphill and Cooper 1983), but the influence of these interactions appears limited (Reice 1985) and it is more likely in streams with sedentary species (Hemphill and Cooper 1983; McAuliffe 1984).

Although the number of taxa increased with increasing chlorophyll *a*, evenness of communities declined, but this was not a consistent pattern and varied greatly at higher levels of chlorophyll *a* in our study. Within low productivity streams, Death (2002) found stream invertebrate evenness measures are also

positively linked with productivity. The response of community evenness in the New Zealand and Spanish streams was highly variable. In fact, these Spanish communities become increasingly dominated by *Prosimulium* spp. at greater chlorophyll *a* which is linked with a high proportion of filamentous algae in these streams. Although black flies (Simuliidae) do not graze directly upon algae, they can be found in high densities feeding on drifting algal cells (Peterson et al. 1985), and high densities of smaller individuals often attach to filamentous algae (Dudley et al. 1986). Within streams, the invertebrate productivity–diversity relationship is likely to be influenced by the taxonomic composition of the algal communities (Tonkin 2010). Yet although invertebrate communities became dominated by a single taxon at greater productivity, early colonizers which are often associated with low periphyton biomass were not completely replaced by superior competitors (e.g. Death 1996; Collier and Quinn 2003).

The % EPT index is commonly used as a bioassessment tool in streams (e.g. Lenat 1988) as these taxa are considered sensitive to changes in various factors of river condition. In this instance, both within each region and combined, the response was highly variable. In the New Zealand streams, although richness increased in a log-linear fashion, there appeared to be a strong shift in the community from EPT dominated to chironomid dominated at roughly the midpoint ($2 \mu\text{g cm}^{-2}$) on the chlorophyll *a* gradient. When compared to the Spanish streams, this shift in community composition in New Zealand streams occurred at relatively low levels of chlorophyll *a* which likely reflects the mountainous nature of this area; these types of streams can support certain chironomids that tend to flourish with cold water and low environmental stability (Milner and Petts 1994).

We expected that bed stability could provide explanations for variation in the productivity–diversity relationship between streams as productivity is strongly linked with disturbance in streams. Our results indicate that New Zealand stream macroinvertebrate communities respond to bed stability but Spanish streams do not. However, the link between bed stability and periphyton biomass in the New Zealand streams, although present, was weak. This may be a result of the relatively low conductivity, temperature, and bed stability (and associated chlorophyll *a*) of these streams.

Bed stability was not able to predict any of the invertebrate community metrics in Spanish streams. Death and Barquin (2012) found diversity of benthic invertebrate communities was higher in more stable habitats in New Zealand streams but the opposite in Spanish streams. New Zealand stream communities are highly dependent on both productivity and disturbance for the maintenance of diversity (Death 2002; Death and Zimmermann 2005), but these studies suggest the role of disturbance is simply to reset the colonization process (at different rates) allowing habitats to be recolonized. Theoretically, richness is then governed by productivity controlling the maximum diversity at a site; however, there was no evidence of an interaction between productivity and stability in determining diversity in Spanish streams.

This pattern is likely due to a lack of low productivity sites in the Spanish sites; thus, low productivity was not a constraint on diversity of invertebrates. In fact, the sites at the lower end of the chlorophyll *a* spectrum among the New Zealand sites were more alpine sites that tend to be colder and more heavily influenced by snowfall or glacial runoff. This category of site did not exist within the set of Spanish streams. Interestingly, these sites in New Zealand were not inhabited by a specialist suite of taxa but merely fewer numbers of species consisting primarily of relatively common taxa such as the mayfly *Deleatidium* spp., the stonefly *Zelandoperla* spp., and a species of orthoclad midge. At the higher productivity sites, as well as these common taxa, communities were more dominated by several chironomid species and cased caddisflies such as *Beraeoptera roria*. There was no corresponding shift in community composition with increasing chlorophyll *a* in the Spanish streams and the dominance of the three most common species, *Prosimulium* spp., *Baetis* spp., and *Echinogammarus*

spp., exhibited no clear trend with increasing chlorophyll *a*.

The lack of focused assessments of the productivity–diversity relationship in lotic systems has left benthic ecologists with no clear idea of the nature of the relationship. With the strong role productivity plays in streams, especially in conjunction with disturbance (Lake 2000; Death 2002; Cardinale et al. 2006), it is essential to elucidate this relationship. As has been found in recent studies (Death 2002; Tonkin and Death 2012; Tonkin et al. 2013), we suggest the role of productivity is indeed to dictate maximum richness in streams rather than to increase the effect of competitive interactions as suggested by models such as the DEM. The variable response found between the two regions indicates that caution is required when interpreting results along differing scales of environmental variation. What appears to produce the lack of pattern in the Spanish streams found here is that productivity does not fall low enough in the study streams to constrain diversity, whereas it does in the New Zealand streams. However, although this variation occurred, the overall relationship when combining regions lends support to Death's (2002) postulation that productivity sets the upper limit to richness in streams.

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Appendix 1

See Table 4.

Table 4 Latitude, longitude, and altitude of 48 streams sampled in the central North Island of New Zealand and Cantabrian Mountains of northern Spain, between February and July 2007

New Zealand				Spain			
Site	Longitude	Latitude	Alt.	Site	Longitude	Latitude	Alt.
Mangatoetoeenui @ SH1	175.7316156	−39.2363068	971	Río Besaya @ Helguera	−4.03276	43.158628	214
Whakapapa d/s intake	175.4659706	−39.11992199	680	Río Eracia @ Helguera	−4.030378	43.159622	222
Whakapapaitei @ SH4	175.4720796	−39.17692963	859	Río Bisuena @ Barcena de Pie de Concha	−4.06826	43.121292	309
Trib of Ohinepango @ old hut	175.671968	−39.20895258	1106	Ayo. Torina @ Barcena de Pie de Concha	−4.054722	43.126793	299
Waihohonu Springs	175.6654827	−39.18896035	1158	Ayo. Santiurde @ Santiurde	−4.078611	43.063231	634
Wahianoa stream u/s intake	175.6407765	−39.38396292	934	Ayo. Rumadero @ Pesquera	−4.074784	43.083177	574

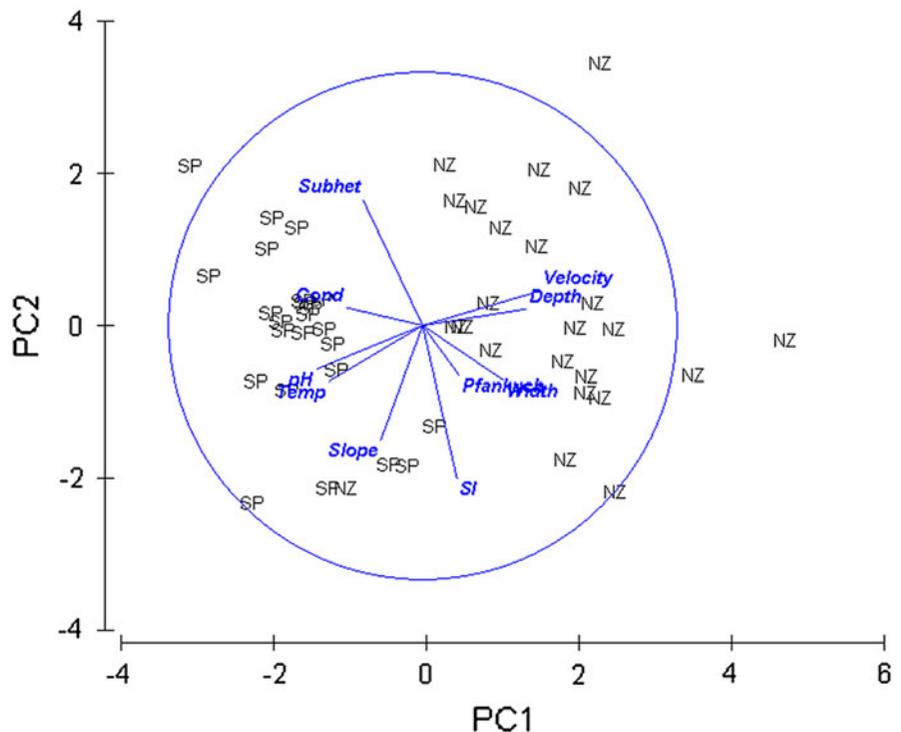
Table 4 continued

New Zealand				Spain			
Site	Longitude	Latitude	Alt.	Site	Longitude	Latitude	Alt.
Te Ununuakapuataeriki stream	175.5593075	-39.4431139	701	Río Leon @ San Martín de Quevedo	-4.038779	43.139996	264
Tongariro d/s Poutu intake	175.8224059	-39.13002278	456	Ayo. Valdeiguña @ Pedredo	-4.067773	43.192911	185
Waipakihi @ end of road	175.7729642	-39.22440144	857	Río Argoza @ Barcena Mayor	-4.232753	43.156963	422
Mangatepopo by camp	175.5633283	-39.06976046	752	Río Saja @ Renedo	-4.30455	43.194076	293
Mangatepopo d/s dam	175.5523842	-39.05335106	624	Río de la Magdalena @ San Andres	-3.897027	43.096378	412
Ohinepango Springs	175.6779304	-39.21838435	1091	Ayo. Salcera @ San Miguel de Luena	-3.899921	43.112736	347
Mangaturuturu river	175.3917215	-39.30696099	820	Río Viaña @ Viaña	-3.804674	43.155633	326
Tongariro d/s Rangipo dam	175.779722	-39.21008569	813	Río Pas @ Pandillo	-3.759107	43.164859	366
Tongariro @ pillars of hercules	175.7881839	-39.18527209	660	Ayo. Llerana @ Coterillo	-3.794589	43.263832	207
Whanganui @ Te Porere	175.5924007	-39.04622437	654	Río Pisuena @ Barcena de Carriedo	-3.823485	43.241998	181
Whanganui d/s intake	175.6010392	-39.01997827	604	Río Nansa @ Puentenansa	-4.406832	43.257111	168
Oturere Stream SH1	175.7576087	-39.18382654	809	Ayo. de Hoyamala @ Puentenansa	-4.406179	43.257101	163
Unnamed @ SH1	175.7578776	-39.1940232	885	Ayo. Lamasón @ Quintanilla	-4.476253	43.25448	238
Whakapapanui @SH4	175.5090823	-39.1491875	835	Ayo. de Traveseras @ Quitanilla	-4.30588	43.256427	239
Unnamed Karioi forest stream	175.6278138	-39.38270332	935	Ayo. Palomba @ Paracuelles	-4.211634	43.019856	895
Poutu Stream	175.7969903	-39.07827181	518	Río Hajar @ Espinilla	-4.226527	43.019571	937
Tauwhitikuri Stream d/s intake	175.5513666	-39.05365336	621	Río Rucebos @ Soto	-4.222249	43.035916	960
Makomiko stream	175.3923096	-39.23638244	746	Río Guares @ Abiada	-4.289066	43.016011	1061

Appendix 2

See Fig. 3.

Fig. 3 Principal component (PC) 1 as a function of PC2 for environmental variables in 24 streams from each of the central North Island of New Zealand and Cantabrian Mountains, northern Spain, sampled between February and July 2007. PC1 explained 35.6 % and PC2 explained 16.4 % of the variation in the data (vectors indicate direction of increase in environmental variables). NZ New Zealand, SP Spain, SI substrate size index, Subhet Shannon substrate heterogeneity, Temp temperature, Cond conductivity



Appendix 3

See Table 5.

Table 5 (a) Eigenvectors and (b) environmental variable loadings for principal component (PC) 1 and PC2 for all 48 streams combined and 24 streams individually from each of the

central North Island of New Zealand and Cantabrian Mountains, northern Spain, sampled between February and July 2007

	All		New Zealand		Spain	
	PC1	PC2	PC1	PC2	PC1	PC2
(a) Eigenvectors						
Eigenvalues	3.56	1.64	2.36	1.84	2.79	2.08
%Variation	35.60	16.40	23.60	18.40	27.90	20.80
Cumulative %Variation	35.60	52.00	23.60	42.10	27.90	48.70
(b) Variables						
Width (m)	0.318	-0.216	-0.038	0.545	-0.443	-0.296
Depth (cm)	0.409	0.065	-0.177	0.276	-0.370	-0.226
Velocity (m s ⁻¹)	0.460	0.136	-0.322	0.277	-0.408	-0.052
Conductivity (μS cm ⁻¹)	-0.299	0.070	0.298	-0.102	0.358	-0.200
Temperature (°C)	-0.368	-0.219	0.332	-0.163	-0.323	-0.324
pH	-0.418	-0.172	0.338	-0.244	-0.017	-0.191
Substrate size index	0.135	-0.602	0.437	0.232	-0.361	0.444
Substrate heterogeneity	-0.234	0.495	-0.278	-0.535	0.365	-0.211
Slope (m 100 m ⁻¹)	-0.165	-0.449	0.434	-0.060	-0.057	0.570
Pfankuch bottom	0.144	-0.197	0.306	0.331	0.007	-0.333

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