Taxonomic richness of stream benthic algae: Effects of flood disturbance and nutrients

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Abstract

We sampled benthic algae monthly for 15 months in 12 New Zealand gravel-bed streams to investigate among-stream differences in algal taxonomic richness and how this might relate to among-stream differences in flood disturbance and nutrient resource regimes. The mean number of benthic algal taxa per month ranged from 9.4 to 21.3 among streams. There were moderate month-to-month fluctuations in richness, partly in response to flood disturbances. Flow perturbations generally reduced richness in streams with unarmored bed sediments but had little or no effect on richness in streams with armored sediments. Richness was moderate within days of floods in most streams but then did not vary significantly for periods of up to 50 d. However, in streams with prolonged periods without bed-moving floods, richness slowly increased after ~100 d, and, in two of these streams, it peaked at 200–300 d before declining. Unexpectedly, there was not a significant pattern in mean monthly richness among the streams as a function of annual flood frequency. Mean richness was strongly negatively related to soluble nutrient concentrations (particularly with soluble inorganic nitrogen [SIN]; $R^2 = 0.511$, $P = 0.018$). However, this was not a direct relationship, because nitrogen-fixing taxa were common in the streams with low SIN, resulting in intermediate to high mat-scale nitrogen concentrations. This possibly shifted these communities to P-limited growth. A combination of disturbance frequency and mat P gave the most parsimonious model of among-stream variations in benthic algal richness ($R^2 = 0.635$, $P = 0.037$). The highest richness occurred in streams with low to intermediate frequencies of flood disturbance (up to 10 bed-moving events yr^{-1}) and intermediate to high concentrations of mat P ($>0.6\%$ P). We could not define an upper nutrient concentration that negatively affected benthic algal richness (perhaps because none of our streams were highly enriched). We discuss our results in relation to three contemporary models of biodiversity.

Streams and rivers are one of the most heavily human-affected environments on Earth (Vitousek et al. 1997). Benthic algae are the dominant primary producers of these environments and provide the main energy base driving production in higher trophic levels in unshaded streams (Lamberti 1996). However, our knowledge of variations in the diversity of benthic algae among streams and factors controlling it is still poor.

The frequency of disturbance by floods is a fundamental determinant of spatial patterns in average benthic algal biomass among streams (Biggs 1996), and it seems reasonable that flood disturbance also might influence patterns in benthic algal taxonomic richness. Indeed, streams in regions of New Zealand with frequent floods appear to have greater mean monthly benthic algal richness than streams in regions with infrequent floods (Clausen and Biggs 1997). Furthermore, within streams, years with more frequent flooding have lower richness than years when flooding is less frequent

(Biggs et al. 1998*a*). These results are likely linked to changes that occur in diversity over successional time. For example, Robinson and Rushforth (1987) demonstrated that richness was lower in early successional communities on frequently overturned substrates compared with late successional communities on more stable substrates. However, the algal succession rate, and thus the duration of the flood disturbance effect, may be quite short. Fisher et al. (1982) found that a relatively high diversity of benthic algae was reestablished within 5 d of a major flood in Sycamore Creek, a Sonoran Desert stream, and diversity did not vary significantly over the 60 d needed to develop a late successional community. Peterson and Grimm (1992), also working in Sycamore Creek, found that diversity was high early in succession on artificial substrates introduced 16 d after a small spate but then declined as succession progressed.

Nutrient enrichment is also a fundamental determinant of benthic algal biomass in streams (Biggs 1996, 2000) and, as with flood disturbance, also might influence patterns in benthic algal taxonomic richness. However, results from previous experimental studies have been equivocal in that they have shown that nutrient additions may either increase (e.g., Pringle 1990; McCormick and Stevenson 1991) or have no overall effect (Stevenson et al. 1991) on richness and/or evenness of stream benthic algae. Furthermore, studies in streams where production is N-limited have suggested that the nitrogen-fixing activity of some taxa can displace succession along a different sere to that occurring in N-replete streams (Peterson and Grimm 1992). Thus, overall, it is still unclear as to how enrichment of streams might influence mean benthic algal taxa richness.

The aim of this study was to assess variability in benthic algal taxonomic richness among streams and how landscape-

Table 1. Summary of physical and water quality characteristics of the study streams (data from Biggs et al. 1999) (D_{84}, median dimension of the 84th percentile sediment particle size; TSS, total suspended solids; SRP, soluble reactive phosphorus). Streams are arranged in decreasing order from most to least frequently disturbed. SE in parentheses.

Stream	Median flow ($m^3\ s^{-1}$)	Width (m)	Flood frequency: D_{84} (No. yr^{-1})	D_{84} (mm)	Tempera-ture (°C)	Conductivity ($\mu S\ cm^{-1}$)	TSS (mg L^{-1})	NH_4-N (mg m^{-3})	NO_3-N (mg m^{-3})	SRP (mg m^{-3})	N:P
Camp	0.63	9.39	28	113	9.8 (0.81)	58 (3.65)	3.3 (0.79)	1.7 (0.25)	37.4 (2.77)	2.0 (0.19)	22.6 (2.87)
Sams	0.23	6.05	24.9	151	9.8 (0.85)	28 (3.35)	0.8 (0.28)	5.1 (0.46)	7.3 (1.00)	1.6 (0.14)	8.5 (0.84)
Rough	0.34	4.79	24.8	158	6.8 (0.71)	45 (3.40)	1.0 (0.40)	1.9 (0.21)	19.2 (1.84)	1.6 (0.14)	15.3 (2.56)
Timber	0.26	4.85	23.2	57	8.2 (0.94)	55 (5.15)	100 (96.67)	2.7 (0.67)	21.0 (5.24)	1.7 (0.28)	12.9 (2.74)
N. Kowai	1.04	4.76	20.5	139	8.2 (1.09)	40 (1.52)	9.5 (8.00)	2.0 (0.29)	18.4 (6.04)	1.8 (0.24)	10.2 (1.63)
Slaty	1.10	12.72	18.4	160	9.4 (0.78)	37 (1.77)	1.2 (0.63)	2.7 (0.29)	17.7 (2.07)	1.7 (0.16)	14.0 (2.00)
Victoria	0.50	4.95	9.6	206	8.7 (1.11)	33 (7.26)	1.08 (0.32)	2.4 (0.19)	5.8 (1.00)	1.3 (0.11)	8.5 (1.68)
Granity	0.20	1.58	6.4	134	11.9 (1.24)	27 (2.06)	4.8 (2.18)	6.8 (0.57)	130 (31.21)	31.6 (29.4)	97.6 (22.64)
W. Kowai	0.46	4.87	3.2	200	9.5 (1.05)	69 (2.65)	3.0 (1.91)	3.4 (0.44)	34.4 (9.85)	1.8 (0.23)	21.7 (3.97)
Woolshed	0.34	7.35	2.4	103	9.2 (1.17)	49 (6.43)	1.1 (0.28)	3.8 (0.71)	218 (43.33)	4.1 (0.51)	55.4 (7.63)
Kyeburn	0.08	3.10	0.1	152	7.6 (1.06)	53 (16.80)	0.77 (0.45)	2.2 (0.23)	4.0 (0.70)	1.8 (0.24)	4.2 (0.72)
Bowyers	0.60	9.38	0	190	7.5 (0.88)	42 (2.25)	2.6 (1.04)	2.7 (0.33)	14.2 (1.87)	2.7 (0.23)	7.3 (1.78)

scale variations in flood disturbance regimes and nutrient resource supply might separately and jointly affect patterns in richness. We also wished to test the applicability of some of the more general contemporary models describing patterns in biodiversity: the intermediate disturbance hypothesis, intermediate productivity hypothesis, and dynamic equilibrium model (Grime 1979; Huston 1994). The knowledge of factors that control the biodiversity of ecosystems is justified as part of a broad effort to stem the loss of Earth's species and will buttress models for predicting stream algal biomass as a function of flow regimes and enrichment (e.g., Biggs 2000). Furthermore, studies in other habitats have suggested that ecosystem functioning can be linked with diversity (e.g., Naeem et al. 1994), and, in streams, some herbivores appear to demonstrate selective grazing on benthic algal taxa (Steinman 1996), whereas some algal taxa appear to be more easily digested by certain grazers (e.g., Peterson et al. 1998). Thus, the diversity of autotrophs might have important implications for some ecosystem processes in streams.

Materials and Methods

Study sites—We sampled benthic algal communities in 12 gravel-bed streams located in the hill country of the South Island of New Zealand. The streams ranged in median discharge from 0.23 to 1.1 $m^3\ s^{-1}$ and were selected in different climatic and geological/land use zones, to give a range of flood disturbance frequencies and levels of nutrient enrichment (Table 1).

All study sites were "runs" (i.e., uniform channel section with moderately swift water and few surface undulations) ~20 m long, with mean depths of <0.3 m and widths of 1.6–12.7 m at median discharge (Table 1). There was little direct shading of sites during the day, although all sites received some shading in the morning and late afternoon from banks and riparian vegetation (more so during winter). Streambed sediments were dominated by gravels and cobbles. Six of the streams (Bowyers, West Kowai, Kyeburn, Granity, Victoria, and Woolshed) had low sediment supply and thus contained relatively armored substrates that were very resistant to movement during most floods (Biggs et al. 1999), whereas the remainder of the streams had relatively high sediment supply and mobile beds during even moderate-intensity floods.

None of the watersheds were intensively farmed, and vegetation cover varied from native beech and podocarp-broadleaf forest (Sams, Rough, Slaty, Camp, Victoria, and Bowyers) to predominantly native snow tussock grassland with sheep or low-intensity cattle grazing (the remaining watersheds). The mean monthly benthic algal biomass varied from <1 to 35 mg chlorophyll *a* m^{-2} among streams (Biggs et al. 1999).

Assessment of disturbance—We quantified the frequency of flow perturbations >3 × median flow (Clausen and Biggs 1997) and movement of the 84th percentile size fraction of bed sediments (Biggs et al. 1999) as the main measures of flood disturbance as follows. First, discharge in each stream was continuously monitored during the 15-month study period by use of pressure transducer water level recorders (NIWA Instrument Systems). Water levels were converted to discharge by use of calibrations based on monthly and supplementary high flow gaugings. Sediment particle-size analysis was carried out at each sampling site by use of the Wolman method (Wolman 1954).

Second, hydraulic surveys of each site were carried out at approximately median flows. These surveys involved 15–20 transects, spaced 5–8 m apart, across each stream. Relative channel elevations, water depths, and velocities (at 0.4 of the depth from the bottom) were measured at up to 15 points across each transect. The average water surface slopes of the sampling reaches were calculated by measuring the relative difference in water surface height with a surveyor's level at each bank and down the center of the main flow path.

Third, sediment stability was assessed by use of the hydraulic data and a method developed for steep streams with bed sediments dominated by cobbles interspersed among boulders and a shallow water depth (i.e., high roughness) (Duncan and Biggs 1998). We used a discharge exceeding that necessary to mobilize up to the D_{84} sediment size (i.e., the 84th percentile of the sediment size distribution) as a threshold for determining the frequency of large-scale bed sediment movement at the sites. Once this size fraction is entrained, mass movement of the bed can be expected. Biggs et al. (1999) found that this method for determining disturbance provided good explanatory power for differences in mean monthly Chl *a* among our study streams.

Assessment of nutrient resource supply—We quantified relative rates of benthic algal nutrient resource supply using mean monthly dissolved nitrogen and phosphorus concentrations and mean seasonal total nutrient concentrations within algal mats. These two measures have given the best correlations with benthic algal biomass in New Zealand streams (Biggs 2000).

Duplicate water samples were collected monthly from each site, chilled to 4°C, then frozen within 6 h until later analysis for dissolved nutrients in the laboratory that used auto-analyzer methods, as summarized in Biggs and Close (1989). Subsamples of algae were removed from the main algal samples each season and analyzed for mat N and P on a Technicon II autoanalyzer after Kjeldahl digestion. Results were normalized to the biomass of the samples by use of ash-free dry mass (AFDM) (see Biggs and Kilroy 2000 for a description of the AFDM method).

Sampling and analysis of benthic algae—Each stream was visited approximately monthly between 1 August 1994 and 30 October 1995, giving a total of 14 or 15 monthly samplings per stream. One or two samplings were missed in eight of the streams because of high water. In each study reach, two transects (1 m apart) were placed across the stream, and five points were located at equal distances across the width. Benthic algae was sampled by collecting a stone located beneath each point across each of the two transects, resulting in 10 replicates per site. Although no conscious bias was used in retrieving stones, this procedure effectively excluded particles more than ~400 mm median diameter because they were too large to lift.

On the stream bank, the a-, b-, and c-axes of each stone were recorded to calculate stone surface areas, according to the method of Biggs and Close (1989). Attached algae was thoroughly scrubbed with a stiff nylon brush from upper stone surfaces into a bucket that contained 1.5 liters of stream water. All 10 stones from a given site were scrubbed in the same water, giving a single composite algal sample for each stream on each monthly visit. The algal slurry was then transferred to a 2-liter plastic bottle, chilled to ~4°C, and sent to the laboratory in a cooler for processing within 36 h.

In the laboratory, each sample was homogenized in a blender. Three aliquots were removed from the suspension (after shaking) and pooled in an inverted microscope chamber and allowed to settle before analysis (as described in Biggs and Kilroy 2000). Because among-sample differences in cell density during enumeration can introduce bias into assessments of microalgal species richness (Stevenson and Pan 1999), samples were diluted or concentrated so that approximately similar amounts of periphyton were analyzed in each subsample. The pooled aliquots were then thoroughly examined by use of a microscope at 400× and 780× magnification, and chlorophyll-bearing algal taxa were identified to the lowest taxonomic level possible and recorded. For some diatom taxa, similar shaped dead/clean frustules were used to help confirm species designations where frustule surface markings were required for identification. The principal taxonomic reference texts were Patrick and Reimer (1966, 1975), Bourelly (1970), Foged (1979), Prescott (1973), and Krammer and Lange-Bertalot (1986, 1991). Many taxa of Cyanobacteria and Chlorophyta could be defined only to genus level (hence, we do not use the term ''species'' richness) because of a lack of essential distinguishing characteristics (e.g., reproductive structures in the Chlorophyta). For several genera, we were able to separate morphologically distinctive forms. One of us (R.A.S) did all the taxonomic analyses, to maintain consistency with definition. However, because of difficulties with identifying some taxa, the results should be viewed more as indicative of ''relative responses'' in richness than absolute responses.

The relative biovolume of taxa per sample also was assessed. The taxon with the highest biovolume in each sample was first defined (i.e., a visual integration of frequency × size), followed by the biovolume of all other taxa rated on an eight-point linear scale in relation to the dominant taxon. If two taxa were codominant, they were both given a score of 8 (see Biggs and Kilroy 2000 for further details of the method). Generally, one–four taxa made up ~70% of the biovolume of each sample. Equitability (Simpson's index) was calculated by use of the relative biovolume ranks, but these data were not included here because the results were so highly correlated with richness (Pearson correlation $R = 0.923$, $N = 12$, $P < 0.001$).

Data analysis—Principal components analysis was used to discriminate sites on the basis of mean relative biovolume ranking of taxa. Only taxa with a rank of ≥ 2 in at least one site were included. General trends in richness in time after disturbance were investigated by use of correlation and regression analysis. The trends among sites were characterized according to the following criteria: no trend (i.e., the correlation of richness with time was not significant; i.e., $P > 0.05$), a monotonic increase in richness with time (i.e., a significant linear correlation), and a curvilinear change in richness with time (i.e., a significant quadratic regression). We used quadratic regression where we were analyzing trends in mean monthly richness as a function of disturbance frequency and nutrient resources to test for fit of the unimodal intermediate disturbance and intermediate productivity hypotheses because quadratic formulations best match the theoretical shapes of the hypothesized response curves (e.g., Townsend et al. 1997). In a companion study, Francoeur et al. (1999) found that the nutrient (N or P)–limiting periphyton biomass accrual in many of our streams varied during the study period. Thus, we present results for richness as a function of both N and P.

Stepwise multiple regression with backward elimination was used for analysis of joint effects of disturbance and nutrient resources on richness. We also used quadratic formulations for this analysis, because Huston (1994, fig. 5.6) depicts the response of richness to be a power curve with a positive exponent of <1, a unimodal curve, or a power curve with an exponent less than −1, depending on the level of resource supply across the gradient of disturbance frequency and for different levels of disturbance across the gradient in resource supply. Quadratic expressions can give adequate fit to all such responses. All statistical analyses were performed with SYSTAT (1998), version 8.0.

Results

Floods and nutrients—No clear seasonality in floods occurred in the streams with a moderate to high frequency of events, but floods were more frequent in winter and spring (July–October in New Zealand) in streams with low flood frequencies (West Kowai, Kyeburn, Woolshed, and Bowyers; Fig. 1). Discharge generally returned rapidly to base flows after each flood. Flood frequencies with intensities capable of moving up to 84% of bed sediments varied from 0 to 28 per year (Table 1).

The mean monthly soluble reactive phosphorus (SRP) concentration was <5 mg m^{-3} in all streams except Granity, where it was 31.6 mg m^{-3} (Table 1). Mean seasonal mat P concentrations varied from 0.35% to 1.1% and did not correlate significantly with SRP. Concentrations of ammonia plus nitrate (soluble inorganic N [SIN]) varied from 6 to 222 mg m^{-3}, with values more evenly spread over the range than for SRP. Mean seasonal mat nitrogen concentrations varied from 3.5% to 7.5% and did not correlate significantly with SIN.

Benthic algae—Diatoms made up the largest taxonomic group (57 taxa), followed by Cyanobacteria and Chlorophyta (19 taxa each), Rhodophyta (2 taxa), and Xanthophyta (1

taxon). Sites differed distinctively in terms of mean relative biovolume of taxa (Web Appendix 1 at http://www.aslo.org/lo/toc/vol_47/issue_4/1175a1.pdf, Fig. 2). There was a group of seven streams (Camp, North Kowai, Rough, Sams, West Kowai, and Woolshed) characterized by a mix of the filamentous Cyanobacteria (e.g., *Homeothrix* sp.) and a range of diatoms. Three streams (Granity, Kyeburn, and Timber) had communities most commonly dominated by the filamentous Rhodophyta *Audouinella hermanii,* whereas Slaty and Victoria were most commonly dominated by *Oedogonium* (filamentous Chlorophyta) and *Tolypothrix* (filamentous Cyanobacteria), respectively. Other Cyanobacteria were also common in these streams. Sams, Slaty, Victoria, and Kyeburn were notable for having relatively high biovolumes of the nitrogen-fixing Cyanobacteria *Calothrix* sp., *Nostoc* sp., and *Tolypothrix* sp.

Total taxonomic richness varied from 41 to 59 among sites, with monthly averages of 9.4 (Rough Creek) to 21.3 (Victoria Stream). Richness varied erratically in all streams during the 15-month study period, with no regular patterns (Fig. 1). On any one sampling occasion, 10–20 taxa were usually recorded. There were no significant differences in richness among seasons (ANOVA $F_{3,44} = 0.869$; $P = 0.464$ for the pooled data). Although it might be expected that seasonal effects should become more pronounced in streams with fewer disturbances, no significant difference in richness was noted among seasons in streams with <5 disturbances yr^{-1} (ANOVA of mean monthly values from four streams grouped by season; $F_{3,12} = 0.389$, $P = 0.763$).

Flood disturbance effects—On many occasions richness declined after floods (e.g., Timber Creek) (Fig. 1). However, this effect was not general among the streams, nor was it associated will all floods in any given stream. Richness declined as a function of flood magnitude in the streams with unarmored bed sediments (Fig. 3). In streams with more stable, armored sediments, there was no such trend, and even very intense floods often did not reduce richness. Thus, the following analysis only uses the frequency of flood events capable of moving the majority of bed sediments (84th percentile) as a measure of disturbance of the benthic algal communities.

Richness was usually moderate very soon after floods (within a week) and did not correlate with time since bed-moving floods in seven streams (Sams, Camp, Slaty, Granity, North Kowai, Timber, and Victoria) that were subject to frequent flood disturbances (Fig. 4). In four streams with infrequent flood disturbances (West Kowai, Kyeburn, Woolshed, and Bowyers), richness gradually increased beyond the initial colonization phase and correlated significantly with time since disturbance. All of these streams covered accrual periods of >100 d. In two of the streams (Kyeburn and Woolshed), richness peaked 200–300 d postdisturbance and declined thereafter, giving a significant unimodal trend ($R^2 = 0.975$, $N = 13$, $P < 0.001$ for Kyeburn and $R^2 = 0.923$, $N = 15$, $P < 0.001$ for Woolshed for quadratic regressions). For the combined data set, taxonomic richness was significantly related to time since disturbance, but the variance explained was small ($R^2 = 0.082$, $N = 152$, $P = 0.002$; Fig. 5A). There was no significant relationship between mean
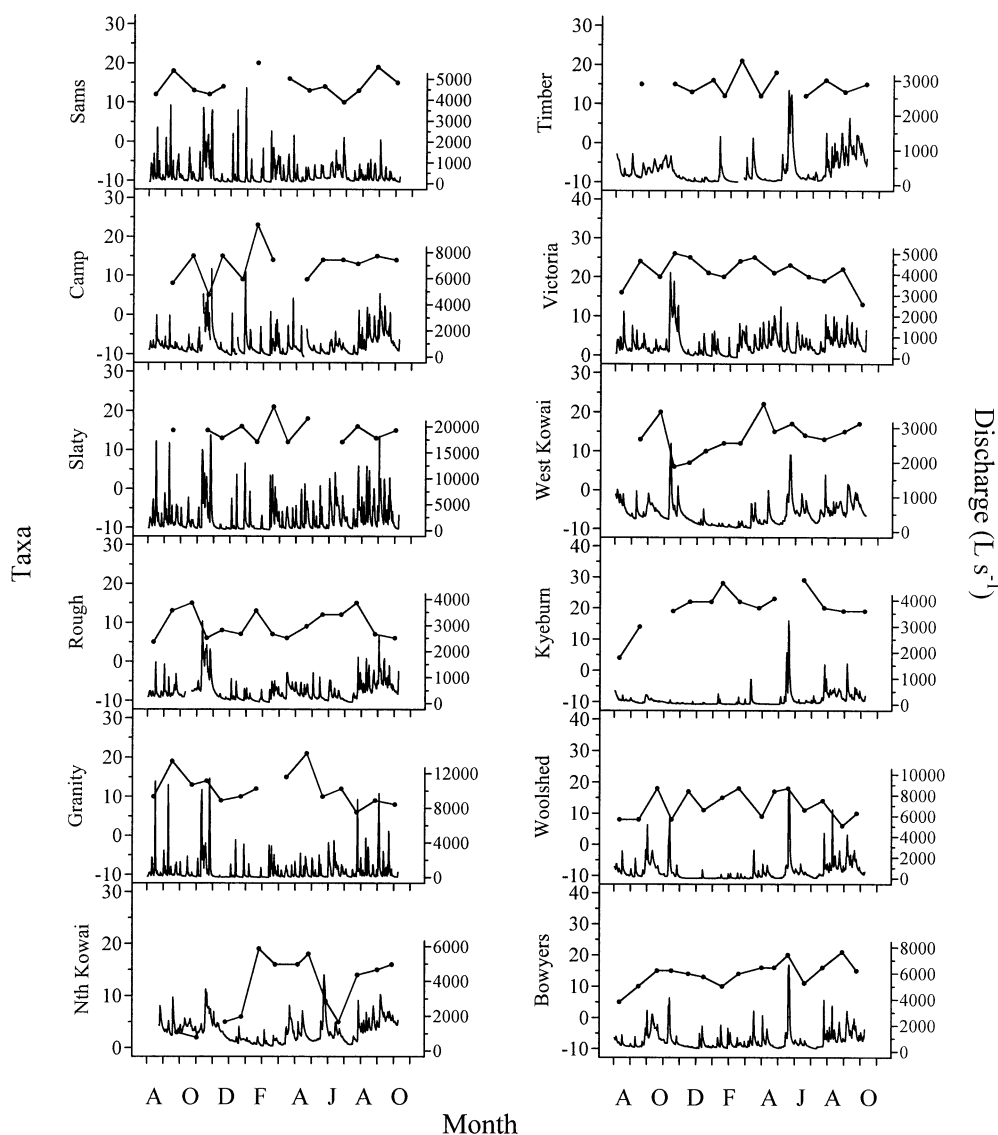
Fig. 1. Time series of taxonomic richness and discharge for each study stream.

monthly richness and annual frequency of disturbance ($R^2 = 0.115$, $P = 0.576$; Fig. 5B).

Nutrient effects—Temporal variations in richness over the 15-month study period were not significantly correlated with SRP concentrations in any of the streams and not in 11 of 12 streams for SIN. In Camp Stream, richness was negatively correlated with SIN ($R^2 = 0.368$, $N = 13$, $P = 0.028$). For the combined data set, richness was not significantly correlated with SRP or SIN, although the latter correlation did display a weak negative relationship ($R^2 = 0.012$, $N = 166$, $P = 0.071$).

Overall, the mean monthly richness was highest at sites with low mean monthly SIN concentrations and then declined as dissolved N concentrations increased ($R^2 = 0.511$, $N = 12$, $P = 0.018$ for a negative quadratic regression; Fig. 6C). However, the phosphorus relationship was heavily influenced by one outlier from Granity Creek and was not

significant. The results for SIN did not agree with those for mat nutrients, whereby mean monthly richness displayed weak unimodal patterns as a function of mat P and N concentrations (mat P, $R^2 = 0.315$, $N = 12$, $P = 0.182$ and mat N, $R^2 = 0.185$, $N = 12$, $P = 0.399$ for quadratic regressions; Fig. 6B,D).

We hypothesized that the above discrepancy in the relationship between soluble and mat nitrogen with richness was due, in part, to N-fixing taxa supplementing N within the mat, because many of the streams with low SIN had intermediate to high concentrations of mat N (e.g., Victoria Stream SIN = 8 mg m^{-3} and mat N = 5.4%). Indeed, the mean monthly relative biovolume of N-fixing taxa increased greatly when the mean monthly ratio of SIN:SRP decreased to <15 and the mean monthly SIN concentration decreased to <25 mg m^{-3} (Fig. 7). In turn, mean monthly richness among our streams was highly correlated with the total relative biovolume of nitrogen fixers ($R^2 = 0.876$, $P < 0.001$;
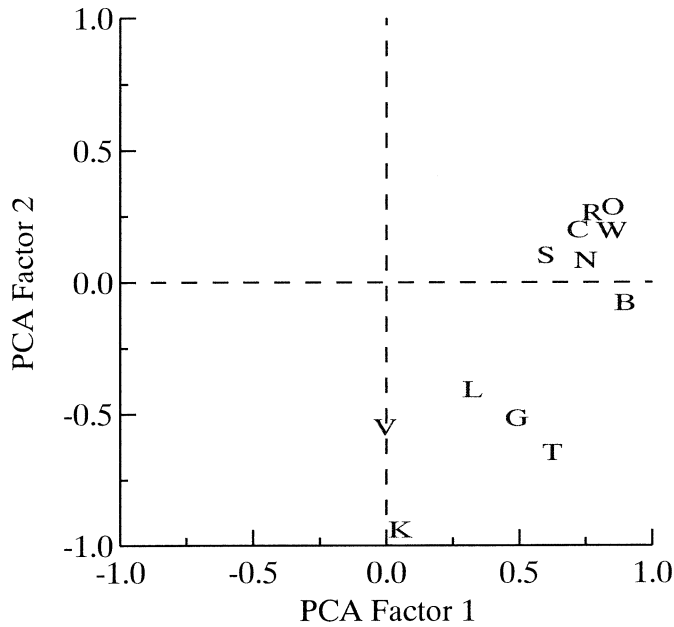
Fig. 2. Factor 1 and 2 scores for a principal components analysis of the mean monthly relative biovolume of benthic algal taxa in the study streams (B, Bowyers Stream; C, Camp Creek; G, Granity Stream; K, Kyeburn; K, North Kowai Stream; R, Rough Creek; S, Sams Creek; L, Slaty Creek; T, Timber Stream; V, Victoria Stream; O, West Kowai; and W, Woolshed Stream).

Fig. 3. Relative change in taxonomic richness (compared with the preceding month) as a function of the magnitude of recent flow events. The latter variable was calculated as the highest flow in the 10-d period prior to sampling divided by the long-term median flow for the stream. The dashed line denotes zero change; the sloping solid line is a linear regression line ($P = 0.033$) for streams with unarmored bed sediments (dots), and the almost horizontal solid line is a linear regression line ($P = 0.332$) for the streams with armored sediments (triangles).
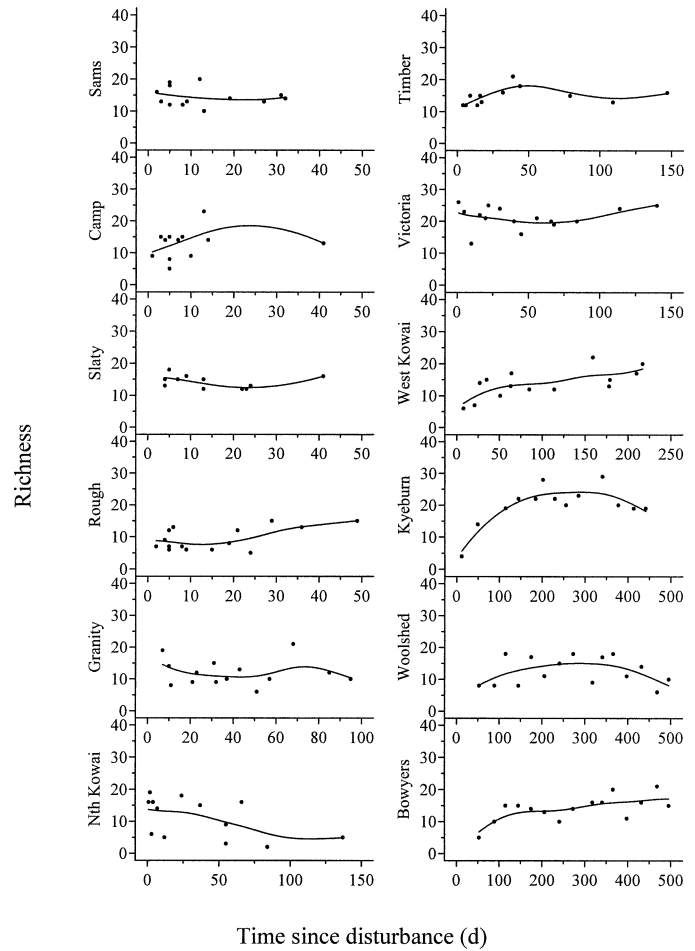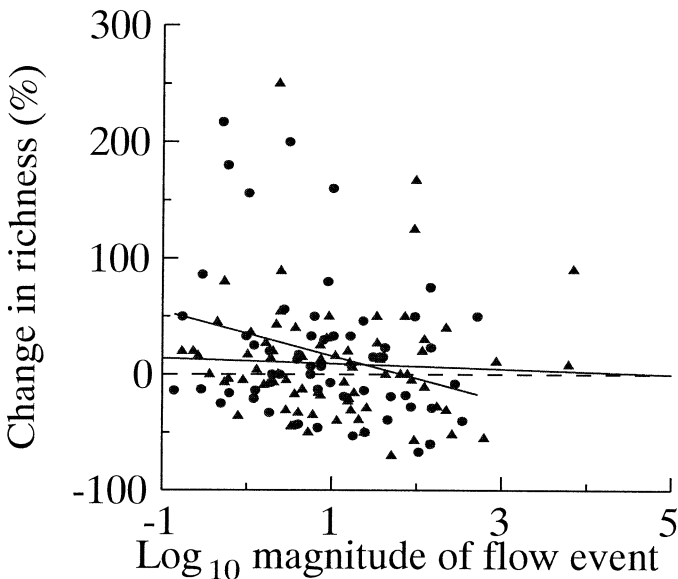

Fig. 4. Richness as a function of time since disturbance. Lines of best fit were generated from distance-weighted least-squares regressions. Note that the scale on the *x*-axis differs among plots.

Fig. 8). This indicated that water-phase soluble inorganic nutrient concentrations did not adequately characterize nitrogen supply to the mat. Consequently, we only use mat nutrient concentrations to assess joint effects of disturbance and nutrients in the following analysis.
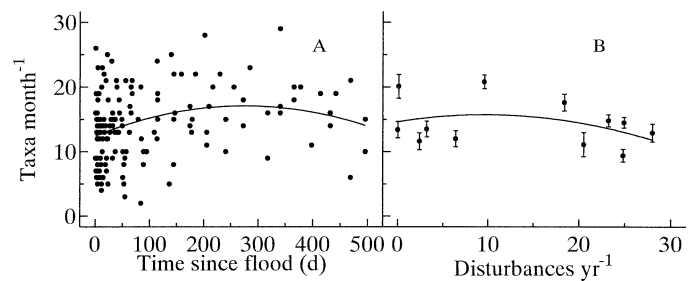

Fig. 5. (A) Richness as a function of time since disturbance for the combined data set. (B) Mean monthly richness as a function of disturbance frequency (± 1 standard error). Lines of best fit were generated from a quadratic regression.
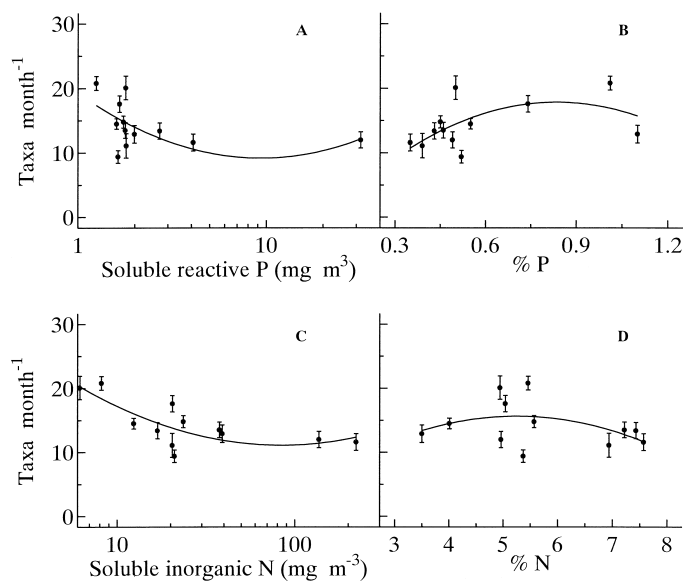
Fig. 6. Mean monthly richness as a function of (A) mean monthly soluble reactive P, (B) mean seasonal mat P (%P), (C) mean monthly soluble inorganic N, and (D) mean seasonal mat N (%N) (± 1 SE). Lines of best fit were generated from distance-weighted least-squares regressions (SYSTAT 1998).

Richness as a combined function of flood disturbance frequency and nutrients—Models that combined disturbance frequency with mat nutrients explained a higher variance in mean monthly richness than either disturbance or nutrients alone, with the P model being statistically significant (Table 2). The highest richness occurred in streams with intermediate to low frequencies of flood disturbance and intermediate to high mat P concentrations (Fig. 9).

Discussion

Flood frequency spanned the range commonly found in New Zealand streams, but nutrient concentrations were not as high as has sometimes been recorded elsewhere (e.g., Biggs and Close 1989; Clausen and Biggs 1997; Biggs 2000), and biomass was generally only moderate to low (see Biggs et al. 1999 for Chl *a* data). However, our streams did represent quite a wide range of physically different systems, and there was a relatively wide range in mean monthly richness. These richness values are similar to the range reported in other studies that have related benthic algal richness to land use and geology in the United States (e.g., Leland 1995; Kutka and Richards 1996).

Unexpectedly, on average, our frequently flooded streams often did not have significantly fewer taxa than infrequently flooded streams (see Robinson and Rushforth 1987; Clausen and Biggs 1997; Pringle and Hamazaki 1997). We sampled the benthic algae in many of our streams very soon after some flood peaks, and although there was always a low biomass (usually 1–10 mg m^{-2} Chl *a*; Biggs et al. 1999, Fig. 5), floods did not always result in a reduction in richness, particularly if the beds were armored. For example, 7–12 taxa were often recorded in the samples collected within the
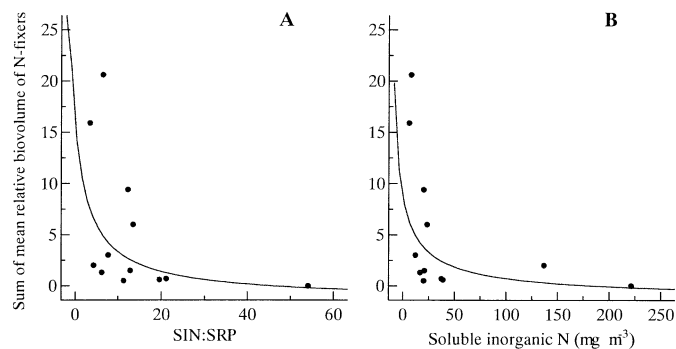

Fig. 7. Sum of the mean relative biovolume of nitrogen-fixing benthic algae (including Cyanobacteria) in the study streams (see Web Appendix 1) as a function of (A) the mean monthly SIN : SRP ratio and (B) the mean monthly SIN concentration.

first 5 d of a flood peak, with the highest number being 26 taxa only 1 d after a flood in Victoria Stream, where bed sediments were very stable.

The lack of a clear flood disturbance effect over short time periods might be due to resistance of the communities to disturbance. For example, many prostrate diatoms (e.g., *Achnanthidium minutissimum*) and some filamentous green algae (e.g., *Stigeoclonium* sp.) that posses tight adhesion structures are well adapted to persist on substrata through high shear stress events (Peterson 1996). Thus, significant relict biomass can remain after even quite severe flood scouring events (Biggs and Close 1989; Grimm and Fisher 1989; Francoeur et al. 1998). Other taxa can survive abrasion through habitation of small refugial crevices on stones (Bergey 1999). Also, patches of stable substrata such as point bars and microform bed clusters occur in steep, hill-country streams and likely provide substantial refugia for benthic
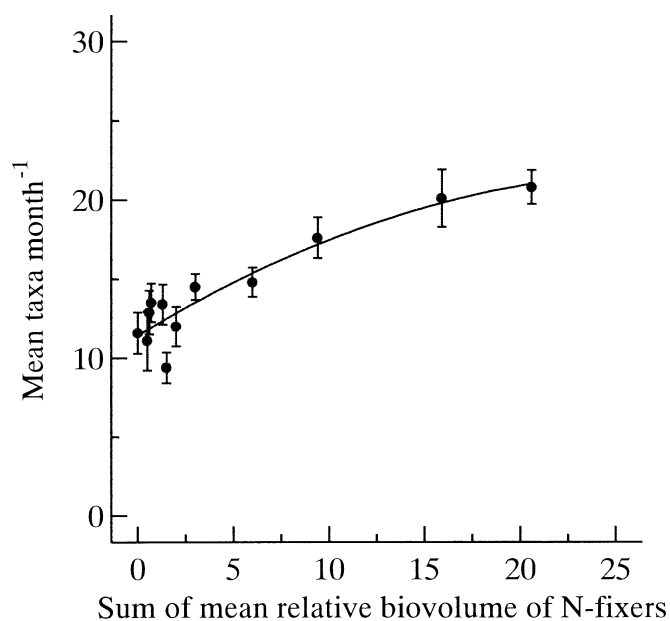

Fig. 8. Taxonomic richness as a function of the sum of the mean relative biovolume of nitrogen fixing benthic algae (including Cyanobacteria) (see Web Appendix 1) in the study streams.

Table 2. Backward elimination stepwise regression analyses of the mean monthly richness as a function of flood disturbance frequency and nutrient concentrations (soluble reactive P, SRP; soluble inorganic N, SIN; mat % P; and mat %N). Only variables with $P < 0.20$ were included in models. $N = 12$ for each analysis.

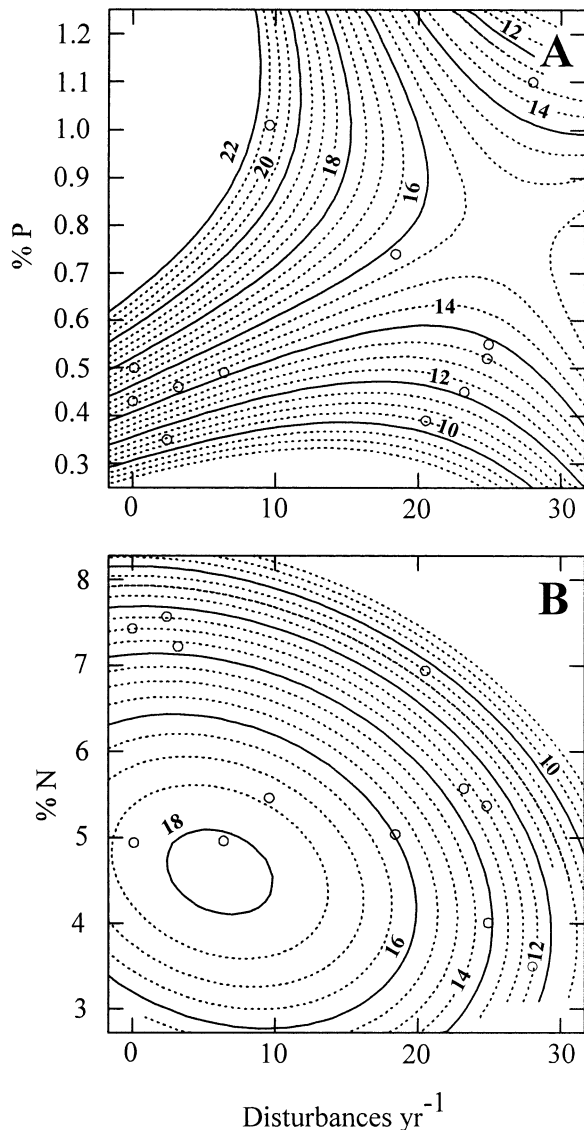| Variable	Coefficient	SE	t	P (two-tail)
Mat % P ($R^2 = 0.635$; ANOVA $P = 0.037$)				
Constant	−3.970	8.428	−0.471	0.650
Flood frequency × Mat % P	−0.339	0.128	−2.646	0.029
Mat % P	54.433	26.321	2.068	0.072
Mat % P^2	−26.663	17.887	−1.491	0.174
Mat % N ($R^2 = 0.382$; ANOVA $P = 0.115$)				
Constant	22.523	3.614	6.231	0.001
Flood frequency	−0.216	0.105	−2.059	0.070
Mat %^{2} N	−0.157	0.074	−2.132	0.062

Fig. 9. Mean monthly richness as a function of annual flood disturbance frequency and (A) mean seasonal mat P and (B) mean seasonal mat N. Contour lines were generated by use of quadratic regression.

algae during floods (e.g., Francoeur et al. 1998). Relict communities on such refugia can have quite high diversity (albeit with low biomass) soon after a flood (e.g., Peterson and Grimm 1992; Francoeur et al. 1998).

The lack of a clear flood disturbance effect may also be related to rapid downstream immigration of some populations (Peterson 1996) from tributaries and the point bar and microform bed cluster refugia. The extent of this immigration effect likely varies among streams according to the density, species composition and physiology of the immigrant pool, and distance to the source of immigrant communities (Peterson 1996). Postdisturbance reestablishment of significant diatom biomass can occur in days to weeks (e.g., Peterson and Grimm 1992; Biggs et al. 1998*a*), which is short when compared with the average return period of weeks to months for floods in many streams (e.g., Fig 1).

However, we also found that richness gradually increased from initially moderate levels over long time periods (6–7 months) where bed-moving floods were infrequent, with peak richness in these streams occurring well after the initial recolonization phase. The reason for this relatively slow successional change in richness, when growth rates can be high (e.g., Stevenson et al. 1991; Biggs and Stokseth 1996), is possibly that only very small pools of late successional taxa survive the reset flood events in these streams. Indeed, these changes in richness were much slower than rates of algal succession in experimental systems that have been documented elsewhere (e.g., Stevenson et al. 1991) or the colonization and growth of communities on new substrates introduced to stable stream beds covered by more mature communities (e.g., Pringle 1990; Peterson and Grimm 1992). However, they are commensurate with results on successional changes after intense, systemwide floods reported from other natural streams (e.g., Biggs and Stokseth 1996; Dent and Grimm 1999).

Thus, we suggest that species accrual in benthic algal mats after extensive flood disturbance is not necessarily a linear process over time but might be biphasic, with different timescales for the two phases. In summary, phase 1, which was common to all streams, occurred very rapidly (days to a week) and was dominated by taxa with high rates of immigration and reproduction (*r* strategists; sensu Grime 1979; also see Biggs et al. 1998*b*) and/or by taxa with high resistance to disturbance, which were probably derived from

local refugia. However, phase 2 leading to higher richness required a considerably longer time, was much more variable in duration among streams (1 month to many months), and was probably dominated by taxa with less disturbance resistance and much slower immigration/growth rates (*C* and *S* strategists; sensu Grime 1979; also see Biggs et al. 1998*b*) that perhaps arrived from more distant (perhaps non–main-channel) refugia. Indeed, phase 2 represents a period of much greater biotic complexity and might be more sensitive to among-stream variations in resource supply than phase 1, as is the case for late successional seres in terrestrial plant communities (Grime 1979). Further studies will be required to test this hypothesis in natural streams after systemwide flood disturbances. If correct, the difference in these time-scales and the high temporal variability of the phase 2 processes could have important implications for recognizing and understanding patterns in benthic algal diversity and biotic interactions in stream ecosystems.

Unexpectedly, we recorded the highest richness in streams with the lowest SIN concentrations. However, it appeared that low SIN in many of our streams was driving a shift toward dominance by nitrogen-fixing taxa that then augmented the N supply to the mat, giving higher local levels of nutrient resources than was indicated by SIN concentrations in the overlying waters. Indeed, we found that richness was strongly related to the relative proportion of community biovolume composed of nitrogen-fixing taxa among some of the streams. Pringle (1990) first suggested that such heterogeneity in nutrient supply over time and space should help maintain high species diversity in stream algae, and Peterson and Grimm (1992) refined this idea by suggesting that, as biomass develops after a flood, the importance of allogenic nutrient sources should yield to autogenic sources for stream benthic algae.

Our data on distribution of N-fixing algal taxa suggest that primary production in the streams with low SIN concentrations was N limited, at least early in the successional sere. However, following from the above discussion, this may have been only a temporary phenomenon, and, later in the sere, production could have become P-limited as the N-fixing taxa became more abundant. We speculate that P supply may ultimately have become more important than N in influencing richness in late successional communities not only in the streams with high SIN concentrations but in all our study streams. This may explain some of the discrepancy between streamwater nutrient concentrations and growth responses to mat-scale nutrient additions recorded at these sites by Francoeur et al. (1999).

Intermediate disturbance hypothesis—The intermediate disturbance hypothesis (IDH) proposes that maximum richness occurs at intermediate stages of succession after a disturbance and at sites that receive intermediate frequencies of disturbance. This hypothesis is based on the premise that the identity of dominant species changes after disturbance, with taxa that immigrate and reproduce rapidly (*R* strategists) being the first to exploit newly exposed habitat but then are progressively displaced by more competitive taxa with slower immigration rates (*C* strategists). Richness is hypothesized

to peak where the community is in transition from the initial colonization to the climax state (Grime 1979; Huston 1994).

The first prediction of the IDH is that taxonomic richness will be highest at an intermediate point within a successional sere (Grime 1979). As noted above, taxa richness generally increased to a high level in four hydrologically stable streams after long periods of accrual (i.e., >100 d). In two of these streams, richness did eventually decline, as predicted by the IDH. However, the time required for this was much longer than expected (as noted above).

The second prediction of the IDH—that, averaged over long timescales, richness will peak at sites with an intermediate frequency of disturbances—was not supported by our data. Although there is much theoretical support for this prediction (e.g., Grime 1979), Townsend et al. (1997) claim that there is still only limited empirical evidence for such a phenomenon. For example, Death and Winterbourn (1995) found that species evenness, but not richness, peaked at intermediate frequencies of disturbance for stream invertebrates, whereas Townsend et al. (1997) observed a weak peak in stream invertebrate richness, but not evenness, at intermediate frequencies of disturbance. However, Sousa (1979) and Davis and Wilce (1987) demonstrated clearer intermediate disturbance patterns in richness of intertidal and subtidal cobble benthic algae, including shifts in growth form from dominance by upright species under infrequent disturbance to tightly adhering, crustose species under frequent disturbance.

There may be several reasons for the lack of IDH patterns in relation to disturbance frequency among our streams. Rapid colonization by pioneer taxa, but the highly variable immigration of climax taxa over time among streams, likely masked a peak in mean monthly richness along the flood frequency gradient. Indeed, Dial and Roughgarden (1998) note for plants and intertidal organisms that recruitment and dispersal represent important mechanisms in structuring natural communities in disturbed habitats. Because of the opposing effects of disturbance and settlement, covariation among these two processes can potentially either obscure or accentuate intermediate disturbance effects (Dial and Roughgarden 1998). A clearer IDH pattern for the given range of flood disturbance frequencies also might have occurred had growth-limiting resources been higher among streams (leading to higher rates of competitive displacement). As noted by Huston (1994, p. 138), virtually all the evidence in support of the IDH comes from systems with high growth rates. Our results suggest that, when looking for patterns in richness as a function of disturbance frequency, close attention needs to be paid to variations in timescales for the different stages of succession in relation to the return period for disturbance and levels of nutrient resource supply.

Intermediate productivity hypothesis—Under the intermediate productivity hypothesis (IPH), more species are predicted to coexist as supplies of growth-limiting resources increase. With increasing biomass, competition for resources also increases, eventually leading to resource shortages for some species, and they become eliminated through competitive displacement (Huston 1994). This process is expected to generate maximum richness at intermediate levels of pro-

ductivity. However, as with the IDH, the universality and causal mechanisms of the IPH are still in debate (e.g., Abrams 1995; Dodson et al. 2000).

We did not find intermediate productivity effects with soluble inorganic nutrients in streamwater, but we did find weak unimodal patterns with mat nutrients (with mat P explaining a greater amount of variance in richness than mat N). Experimental studies have shown that nutrient additions may either increase (e.g., Pringle 1990; McCormick and Stevenson 1991) or have no overall effect (Stevenson et al. 1991) on richness and/or evenness of stream benthic algae. Stream benthic algae, lake phytoplankton, and lake benthic algae share many common taxa (at least at the generic level). Results from lake communities, therefore, might provide a useful point of comparison with our results. Recently, Dodson et al. (2000) reported a significant unimodal relationship for mean phytoplankton species richness as a function of phytoplankton productivity among 33 North American lakes. However, within individual lakes subject to experimental enrichment, the results were varied and unpredictable. Other studies have shown that enrichment of substrate patches can reduce benthic algal species richness and evenness in lake littoral zones (e.g., Carrick et al. 1988). Once nutrient stress is relieved in such patches, the community becomes overwhelmed by local taxa that are best able to monopolize resource acquisition at higher supply concentrations. Often, only a few taxa are present with such traits (Carrick et al. 1988).

Our study adds to the debate about mechanisms leading to monotonic or unimodal productivity–richness patterns. In particular, our results indicate that it is important to distinguish allogenic and autogenic nutrient supply processes and incorporate specific measures of these when quantifying production-limiting resource supply regimes. We agree with Abrams (1995), who concluded that there are many viable mechanisms that can produce monotonic or unimodal curves for richness as a function of productivity. Huston (1994) suggested that IPH effects are most likely to be found in communities subject to intermediate to high rates of disturbance, where varying rates of competitive displacement (through different rates of limiting resource supply) become important and, more generally, that resource effects are closely linked to disturbance effects. Thus, there are likely to be interactions between disturbance and resource supply regimes in our streams that will probably influence the manifestation of simple unimodal patterns in benthic algal diversity such as those proposed under the IPH (and IDH).

Dynamic equilibrium effects—In an attempt to resolve some of the IDH and IPH issues discussed above and to provide a more heuristic theory, Huston (1994) argued that local-scale variations in α-diversity are best explained by the *interaction* between local and landscape driven disturbance and resource supply/productivity processes (termed the ''dynamic equilibrium'' model [DEM]). In the DEM, the intensity of competition after disturbance, and therefore the rate that inferior competitors are lost from the community, is determined by resource supply and resultant growth rates of competing populations (Huston 1994). The DEM predicts maximum richness at low to intermediate levels of both resources and disturbance. Few studies have specifically tested

the DEM under adequate natural conditions and covering orthogonal gradients in disturbance frequency and resource supply (Pollock et al. 1998). Death and Winterbourn (1995) tested the model using stream invertebrates and found that the DEM may have some validity, at least at the patch level. Pollock et al. (1998) tested the model with plants in riparian wetlands and found many of the community-level predictions were supported.

Although richness was most strongly correlated with SIN concentrations among our streams, this does not represent a direct relationship. As was discussed above, the communities in the streams with low SIN concentrations were in fact quite enriched at the mat scale through the N-fixing activity of some taxa. A model that combined mat P with flood disturbance frequency did explain a relatively high percentage of variance in mean monthly benthic algal richness (Table 2). This model was the most parsimonious explanation for the variation in algal richness among our study streams and gives some support for Huston's DEM of biodiversity. We note, however, that the location of peak richness on the disturbance–mat P habitat matrix (Fig. 9A) was somewhat different from that predicted in the DEM by Huston (1994, fig. 5.12). In our streams, maximum richness occurred at moderate to high concentrations of mat P (>0.6% P) with moderate to low disturbance frequency (<10 bed-moving events yr^{-1}), instead of Huston's prediction of maximum richness at moderate to low disturbance and enrichment.

However, we caution that we do not expect richness to continue to increase with further (i.e., very high levels of) enrichment in stable streams (Fig. 9A). This is because we expect stronger competitive displacement to occur at higher biomasses than was recorded at our sites (see Biggs et al. 1999), as has been shown for lake phytoplankton (Dodson et al. 2000) and terrestrial vegetation (see reviews by Grime 1979 and Huston 1994). Unfortunately, our streams did not span a wide enough nutrient gradient to test this hypothesis for benthic algal communities. Had this occurred, then our results may have been a better fit with the DEM.

We conclude that the interaction of flood disturbance and nutrient resource regimes strongly influences local taxonomic richness in stream benthic algal communities and that it is important to measure resource supply at a scale that is relevant to the algae living within the mat. Also, very long periods of hydrological stability can be required for high richness to develop in stream algae. In such stable streams, richness can be further enhanced by moderate to high levels of growth limiting nutrient resources. Overall, we conclude that gravel-bed streams with moderate to high hydrological stability and moderate to high mat-scale enrichment (but not necessarily very high) are likely to contain the highest diversity of benthic algae.

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