Landuse intensity in stream catchments affects the benthic food web: consequences for nutrient supply, periphyton C:nutrient ratios, and invertebrate richness and abundance

Antonia Liess[1], Ariane Le Gros[2], Annika Wagenhoff[3], Colin R. Townsend[4], AND Christoph D. Matthaei[5]

University of Otago, Department of Zoology, PO Box 56, Dunedin, 9054, New Zealand

Abstract. Anthropogenic nutrient enrichment increases the supply ratio of N and P to aquatic ecosystems and can affect the identity of the limiting nutrient. Here we focus on how stream communities change along gradients of N and P supply and stream catchment landuse intensity. We used a survey approach in 41 southern New Zealand tributaries to investigate how much changes in water N and P concentrations are reflected in periphyton C:nutrient ratios (C:N or C:P) and how much food quality (high food quality corresponds to low periphyton C:nutrient) is reflected in the abundance and taxonomic richness of benthic invertebrate primary and secondary consumers. We measured streamwater nutrient state, periphyton nutrient ratios, biomass (as chlorophyll *a* in µg/cm^2), algal taxon richness, and macroinvertebrate abundance, taxonomic composition, and richness. We also estimated stream habitat and catchment characteristics, such as current velocity, shading, substrate, geology, and landuse intensity. We calculated the Akaike information criterion (AIC) for each possible multiple linear regression model to select the best predictive models for each response variable. C:nutrient ratios were more strongly negatively related to water-column N than P availability. Neither N nor P availability covaried with periphyton biomass. Lower periphyton C:N partly explained higher grazer, but not predator, abundance. Increased % runoff from pasture and periphyton N:P co-occurred with a decrease in invertebrate taxon richness. For example, a 4× increase in periphyton N:P was related to the loss of ~½ of invertebrate species, but with high uncertainty ($R^2 = 0.13$). We conclude landuse intensity affects these southern New Zealand streams, and these effects are mediated by agricultural N runoff into streams (among other factors). Further shifts toward high-intensity farming within stream catchments may lead to losses of benthic species at all trophic levels.

Key words: nutrient ratios, species richness, ecological stoichiometry, benthic algae, benthic invertebrates, grazers, land use, eutrophication, N-cycle, stream ecosystem.

Human activities affect almost all natural ecosystems, and agricultural intensification is one of the most widespread causes of loss of biodiversity in terrestrial and aquatic ecosystems (Matson et al. 1997). Agriculture releases nutrients (Smith 2003), fine sediments, and other contaminants (Sala et al. 2000) into adjacent water bodies, and these effects can have profound consequences for stream ecosystems. Fertilization of terrestrial and aquatic environments can

increase primary producer biomass, especially in freshwater habitats (Gruner et al. 2008), and can reduce plant species richness (Hillebrand et al. 2007).

Anthropogenic eutrophication can alter the supply ratios of nutrients, potentially shifting nutrient limitation from one nutrient to another. For example, atmospheric N deposition, caused mainly by fossil fuel combustion and agricultural fertilizer use, has increased the amount of circulating bioavailable N by >100% since the industrial revolution (Galloway et al. 2008). This change has dramatically increased the N:P ratio of inputs to aquatic ecosystems. In lakes, increased N deposition can shift phytoplankton from N to P limitation (Bergström et al. 2005, Elser et al. 2009) and may intensify P limitation of benthic primary producers (Liess et al. 2009a). The discussion about N vs P limitation of aquatic ecosystems and the best ways

[1] Present address: Department of Ecology and Environmental Science, Umeå University, 90187 Umeå, Sweden. E-mail address: antonia.liess@emg.umu.se

[2] E-mail addresses: ariane.le_gros@agroparistech.fr

[3] annika.wagenhoff@gmail.com

[4] colin.townsend@stonebow.otago.ac.nz

[5] christoph.matthaei@otago.ac.nz

to remedy eutrophication is still ongoing (Conley et al. 2009). Eutrophication-related problems are a particular threat to streams and rivers because of their proximity to population centers and vulnerability to landuse changes (Malmqvist and Rundle 2002). Stream eutrophication can lead to human health issues, changes in species abundance, and loss of biodiversity.

Agriculture in New Zealand has been shifting from low-intensity sheep farming to high-intensity dairy farming, which involves continuous irrigation and fertilization. One result of this shift is increased agricultural runoff into adjacent water bodies. Agricultural runoff has led to a large increase in bioavailable N and an associated shift in N:P supply ratios in agricultural streams (McDowell et al. 2009). Shifts in streamwater nutrient state change benthic algal species composition (Lange et al. 2011) and species richness (Liess et al. 2009b) and may influence the biomass and nutrient state of periphyton (Stelzer and Lamberti 2001). Nutrient-induced changes to food availability and quality may directly affect density and community composition of grazers and detritivores and indirectly affect predators (Stockner and MacIsaac 1996, Moore and de Ruiter 2000, Cross et al. 2006, Davis et al. 2010). Changes in resource quality through P enrichment can contribute to large-scale losses in macroinvertebrate diversity in streams (Singer and Battin 2007, Evans-White et al. 2009). An explanation for this pattern could be that P-rich food allows faster-growing taxa with high P demand to out-compete slower-growing taxa (Evans-White et al. 2009). Increased N availability appears to have similar consequences for stream invertebrate diversity (Yuan 2010), but the mechanisms behind this connection are unclear. Benthic stream communities across a gradient of agricultural intensification provide an excellent system to explore the consequences of nutrient availability within a stoichiometric framework.

We conducted a stream survey across a gradient of streamwater N and P concentrations resulting primarily from differential catchment land use to elucidate the pathways that lead to loss of biodiversity in streams. Benthic algae (periphyton) constituted the 1st trophic level at these sites and, in turn, sustained a rich and diverse invertebrate assemblage. We measured periphyton biomass, C:nutrient ratios, and taxon richness, and invertebrate abundance, community composition, and taxon richness. Our hypotheses were that: 1) periphyton C:nutrient ratios track water-column N and P availability, 2) periphyton C:nutrient ratios affect benthic algal and invertebrate abundance and taxon richness, and 3) taxon richness of algae and invertebrates declines with increasing landuse intensity.

Methods

Study sites and site characteristics

We selected 41 stream sites in the province of Southland on the South Island of New Zealand to encompass a gradient of catchment land use from native forest to high-intensity dairy farming, with consequent differences in dissolved and total nutrient levels (Appendix S1; available online from: http://dx. doi.org/10.1899/11-019.1.s1). We sampled all sites once for water chemistry, and collected algal and invertebrate samples from a riffle habitat (relatively shallow and fast flowing in comparison to pool habitats) after ≥ 3 wk of undisturbed baseflow conditions in late summer/early autumn 2009 (4 February–1 April). After a flood affected 7 sites, we discontinued sampling for 3 wk to allow the stream communities to recover. Stream order ranged from 2nd to 6th, and study sites fell into 1 of 3 landcover categories (Snelder et al. 2004): 1) native forest spatially dominant (6 sites), 2) tussock grass spatially dominant (2 sites), or 3) pasture (33 sites). We classified surficial geology according to New Zealand's River Environmental Classification (REC) (Appendix S1; Snelder and Biggs 2002). Stream sites differed in the proportion of their catchment devoted to pastoral land use (range: 0–~100%). We used % annual runoff from pasture as our index of land use for each site. For more information about the study sites see Wagenhoff et al. (2011).

We estimated river width and main-channel surface current velocity (as the time required for a tennis ball to float over a defined stream length) at each site (average length = 30 m). We classified the dominant substrate type in the stream bed into one of 5 categories (boulder: >26 cm, cobble: 6–26 cm, gravel: 2–59 mm, sand: 0.06–1.9 mm, slit and clay: <0.06 mm) (Gordon et al. 1992) and estimated the degree of shading by riparian plants. Two of 4 streams with a mostly closed canopy were forested. Most riparian trees in New Zealand are evergreen, so large amounts of leaf litter and shredding invertebrates are rare. We are convinced that benthic algae was the primary food sustaining the invertebrate assemblage in all our study streams. Latitude, longitude, elevation, and water chemistry characteristics of the streams are in Appendix S1.

Dissolved nutrient samples

We collected 1 filtered (glass-fiber filter [GF/C]) and 1 unfiltered water sample in accordance with Southland's Regional Council protocols at each site from the main stream channel in plastic bottles and

kept them on ice until arrival at the laboratory where we froze them until analysis. We analyzed filtered samples for dissolved inorganic N (DIN) and soluble reactive P (SRP), and unfiltered samples for total N (Tot-N) and total P (Tot-P). We measured DIN, SRP, Tot-N, and Tot-P with standard methods (APHA 1998). We measured both total (Tot-N, Tot-P) and dissolved (DIN, SRP) nutrients to assess which were the better predictors in our models because of controversy regarding the utility of these variables as indicators of the nutrient status of stream water (Dodds 2003).

Periphyton samples

At each stream site, we sampled periphyton at 3 locations: upstream riffle, mid-riffle, and downstream riffle. At each location, we selected 5 rocks along a transect perpendicular to flow and spanning water depths from 5 to 15 cm. We subsampled the 5 rocks with a periphyton sampler that cleared an area of 3.14 cm^2 (Peters et al. 2005) and combined the slurry into 1 composite periphyton sample. Thus, each periphyton site mean was based on 3 composite periphyton samples (1/transect) that incorporated the high spatial heterogeneity of the periphyton matrix (Kahlert et al. 2002). We used only site means for figures and in data analyses. We kept periphyton samples on ice and processed them within 1 d of collection. We divided each sample into 4 subsamples. We filtered 3 subsamples onto replicate precombusted GF/C filters for analysis of epilithon C and N (1 filter), P (1 filter), and chlorophyll *a* (Chl *a*; 1 filter). We preserved the 4th subsample with Lugol's iodine solution and stored it at 4°C until taxonomic analysis within 3 mo. We dried the filters and immediately analyzed C, N, and P content of epilithon samples. We measured C and N with a CHN-Analyzer (LECO CHNS-932; Leco Corporation, St. Joseph, Michigan), and P as PO_4^{3-} (after hydrolysis by heating and potassium persulfate) with a spectrophotometer (Grasshoff et al. 1983). We assayed Chl *a* spectrofluorometrically (APHA 1998).

We measured algal taxon richness and relative abundances of each taxon in periphyton samples under an inverted light microscope (Olympus BX 51; Olympus America, Center Valley, Pennsylvania) at 125 to 787.5× magnification following the guidelines in Biggs and Kilroy (2000). First, we scanned the whole slide at 125× magnification and noted all taxon names. Then we scanned again at 787.5× magnification and checked the original identifications. We ranked taxa according to their abundance and assigned scores as described in Biggs and Kilroy

(2000) (range: 0–8, where 0 = absent, 1 = rare, 8 = dominant). We identified all taxa to genus or, if possible, to species level with the standard key for stream periphytic algae (Biggs and Kilroy 2000).

Invertebrate samples

We collected benthic invertebrates from the same reach of stream (upstream of the riffle, mid-riffle, downstream of the riffle) as periphyton samples. We used the standard method used by resource management agencies (Regional Councils) throughout New Zealand and described in detail by Stark et al. (2001). We took 1 standardized semiquantitative macroinvertebrate sample with a D-shaped hand net (0.5-mm-mesh size) in each stream. In hard-bottomed streams (37 of 41), we collected macroinvertebrates with the kick-sampling method. We standardized sampling effort and area by disturbing an area of 0.1 m^2 in each of 5 locations across the sampling reach (1 each upstream of the riffle, mid-riffle, downstream of the riffle, and 2 between). In soft-bottomed streams (4 of 41), we sampled different habitat units, such as bank margins, macrophytes, and woody debris, in proportion to their frequency of occurrence. These samples added up to 5 D-net swipes and a similar total area (0.5 m^2) sampled as in hard-bottomed streams. We pooled invertebrate samples collected within each site and preserved them in 80% ethanol.

We placed invertebrate samples in gridded trays to assess invertebrate abundance and composition. We randomly chose quadrats, counted invertebrates within them, and identified the invertebrates to the lowest possible taxonomic level until 200 individuals had been counted (Stark et al. 2001). We scanned the remainder of each sample for rare taxa. We extrapolated the total number of invertebrates/taxon in the sample from the number of quadrats counted. We identified invertebrates with the standard taxonomic key for New Zealand's benthic invertebrates (Winterbourn et al. 2006), and we categorized each taxon by functional feeding group (Dolédec et al. 2006, Wagenhoff et al. 2011). We classified taxa that were predominantly grazer/scrapers and predators for further analyses (Appendix S2; available online from: http://dx.doi.org/10.1899/11-019.1.s1).

Statistical analyses

We used linear regressions and Pearson's correlations to explore univariate relationships and correlations among predictor variables. We used multiple regressions to test the explanatory power of the predictor variables for our data (using site means for algal abundance data). Predictor variables for periphyton

responses were current velocity, degree of shading, REC geology, main substrate type, % runoff from pasture, DIN, SRP, Tot-N, and Tot-P. Predictor variables for invertebrate responses and algal taxon richness were all the above predictor variables, periphyton nutrient ratios, and Chl a (μg/cm^2). Predictor variables for predator responses were all the above predictor variables, *Potamopyrgus antipodarum* abundance, grazer abundance, and grazer taxon richness. We tested all combinations of these predictor variables and their interactions when ecologically relevant (e.g., the interactive effect of degree of shading and SRP/DIN on periphyton C:nutrient ratios). We used Akaike's information criterion (AIC) to select the best-performing model for each response variable. AIC selects the model with the best combination of predictor variables for explaining the variation in the data while requiring the fewest possible predictor variables. We never used highly correlated predictor variables in the same model during the model-selection process. We $\log_{10}(x)$- or $\log_{10}(x + 1)$-transformed variables as needed for normality. We arcsin($\sqrt{x}$)-transformed percentage data. We used Statistica (version 7.0; StatSoft, Tulsa, Oklahoma) for all analyses. We present only significant ($p < 0.05$) results unless stated otherwise.

Results

Stream environmental variables and streamwater nutrient concentrations

Sampling sites spanned a range of environmental variables and varied markedly with respect to their dissolved and total N and P concentrations (Appendix S1). DIN ranged from 29 to 2564 μg/L and SRP from 1 to 258 μg/L. Water N:P molar ratios ranged from 1.2 to 330. The highest SRP value (258 μg/L), which was well above values at other sites, was confirmed by survey data from the previous year (Wagenhoff et al. 2011). Nutrient levels tended to be higher where % runoff from pasture was higher (Fig. 1A), and SRP levels decreased with increasing current velocity (Fig. 1B). The best model for DIN included current velocity, % runoff from pasture, and REC geology (Table 1). The best model for SRP included only current velocity (Table 1). DIN:SRP increased with faster current velocity and higher % runoff from pasture (best model: current velocity + % runoff from pasture; Table 1).

Periphyton

Nutrient ratios.—Periphyton C:nutrient ratios decreased with increasing concentrations of streamwater nutrients. The best model for explaining periphyton

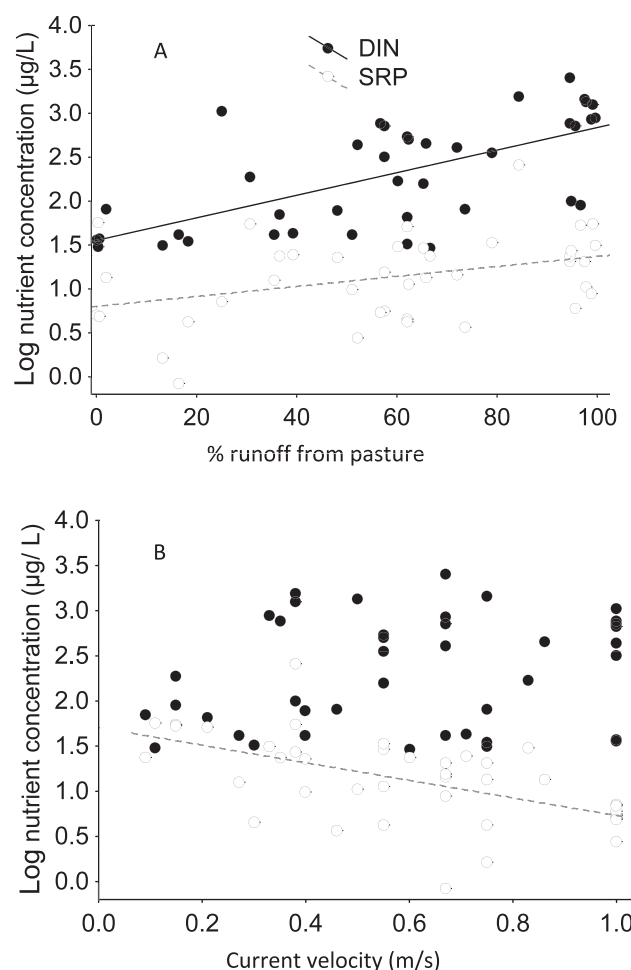
FIG. 1.   Relationships between $\log_{10}(x)$-transformed streamwater nutrient concentrations (dissolved inorganic N [DIN] and soluble reactive P [SRP]) and % annual runoff from pasture (A) and current velocity (B). Points represent individual measurements. Only significant ($p < 0.05$) linear regression lines are shown.

C:N was % runoff from pasture and 2nd-best was streamwater DIN (Table 1, Fig. 2A). The best model for explaining periphyton C:P was streamwater SRP (Table 1, Fig. 2B). However, without the low SRP/high C:P site at Mararoa River, this model was not significant (Fig. 2B). Without the Mararoa River site, the best model explaining periphyton C:P was % runoff from pasture ($R^2 = 0.12$, $p = 0.023$). Periphyton N:P was best explained by SRP concentration, but this model was not significant (Table 1).

Biomass.—Chl a and amount of C (μg/cm^2) (data not shown) were both highly variable among sites, and no significant model with stream environmental variables and streamwater nutrient concentrations as predictor variables could be found (Fig. 2C).

TABLE 1. Results of multiple regression analyses, testing the ability of: 1) environmental variables to explain streamwater nutrient concentrations; 2) environmental variables and streamwater nutrients to explain periphyton nutrient ratios and algal biomass; and 3) environmental variables, streamwater nutrients, and periphyton variables to explain invertebrate abundance and species richness. The best models for each response variable are listed, and >1 model is shown when Akaike Information Criterion (AIC) values were similar (ΔAIC $\leq$ 2), alternative models were needed to test hypotheses, or causal relationship of the best model was ambivalent (explaining predator taxon richness). Models with lowest AIC are ranked first. CR = coefficient of regression, DIN = dissolved inorganic N, SRP = soluble reactive P, REC = New Zealand River Environmental Classification. Bold indicates $p < 0.05$.

Type	Response variable	Best models with lowest AIC	AIC	R^2	CR	p
Streamwater nutrients	DIN[a]	Current velocity (+), % runoff from pasture (+)[c], REC geology	−27.8	0.61	0.67, 1.0	**<0.0001**
		Current velocity (+), % runoff from pasture (+)[c]	−27.0	0.54	0.78, 1.4	**<0.0001**
	SRP[a]	Current velocity (−)	−31.4	0.32	−0.97	**0.0001**
		Current velocity (−), % runoff from pasture (+)[c]	−29.2	0.37	−0.90, 0.34	**0.0002**
	DIN:SRP	Current velocity (+), % runoff from pasture (+)[c]	158	0.41	235, 133	**<0.0001**
		Current velocity (+)	163	0.28	206	**0.0004**
Periphyton nutrient ratios	Periphyton C:N	% runoff from pasture (−)[c]	20.6	0.43	−4.5	**<0.0001**
		DIN (−)[a]	24.4	0.33	−2.2	**<0.0001**
	Periphyton C:P	SRP (−)[a]	158	0.18	−78	**0.006**
	Periphyton N:P	SRP (−)[a]	61.2	0.09	−3.5	0.06
Invertebrate abundance	Invertebrate abundance[b]	Periphyton C:N (−)	−42.1	0.24	−0.072	**0.001**
		% runoff from pasture (+)	−41.6	0.22	0.49	**0.001**
	Grazer abundance[b]	Periphyton C:N (−)[c]	−41.3	0.22	−0.069	**0.002**
		% runoff from pasture (+)[c]	−39.8	0.15	0.41	**0.013**
	Potamopyrgus antipodarum abundance[b]	SRP (+)[a]	−1.49	0.28	1.2	**0.0004**
		% runoff from pasture (+)[c]	0.17	0.20	1.5	**0.004**
	Predator abundance[b]	Grazer abundance (+)[b]	−41.8	0.25	0.63	**0.0009**
Algal and invertebrate taxon richness	Algal taxon richness	Periphyton C:P (+)	51.2	0.11	0.016	**0.033**
		Periphyton C:N (+)	51.9	0.10	0.59	**0.042**
	Invertebrate taxon richness	% runoff from pasture (−)[c], periphyton N:P (−)	59.4	0.32	−8.0, −0.38	**0.001**
		% runoff from pasture (−)[c]	61.8	0.18	−7.7	**0.007**
		Periphyton N:P (−)	62.7	0.13	−0.39	**0.021**
	Grazer taxon richness	% runoff from pasture (−)[c], periphyton N:P (−)	36.2	0.35	−4.1, −0.23	**0.0004**
		% runoff from pasture (−)[c]	38.7	0.18	−4.1	**0.007**
		Periphyton N:P (−)	39.0	0.17	−0.23	**0.006**
	Predator taxon richness	Grazer taxon richness (+)	20.1	0.45	0.48	**<0.0001**
		% runoff from pasture (−)[c], periphyton N:P (−)	24.8	0.33	−3.6, −0.10	**0.0007**
		% runoff from pasture (−)[c]	25.3	0.24	−3.4	**0.001**

[a] Variable was $\log_{10}(x)$-transformed
[b] Variable was $\log_{10}(x + 1)$-transformed
[c] Variable was $\arcsin(\sqrt{x})$-transformed

Invertebrate abundance

Grazers.—Invertebrate and grazer abundance were higher where % runoff from pasture was higher (Fig. 3A) and where periphyton C:N was lower (Fig. 3B). The best model explaining invertebrate and grazer abundance was periphyton C:N, and % runoff from pasture was the 2nd-best model (Table 1).

Potamopyrgus antipodarum.—The abundance of this main grazer species, was partly explained by % runoff from pasture (Table 1, Fig. 3A) but not by periphyton C:N (Fig. 3B). However, the best model
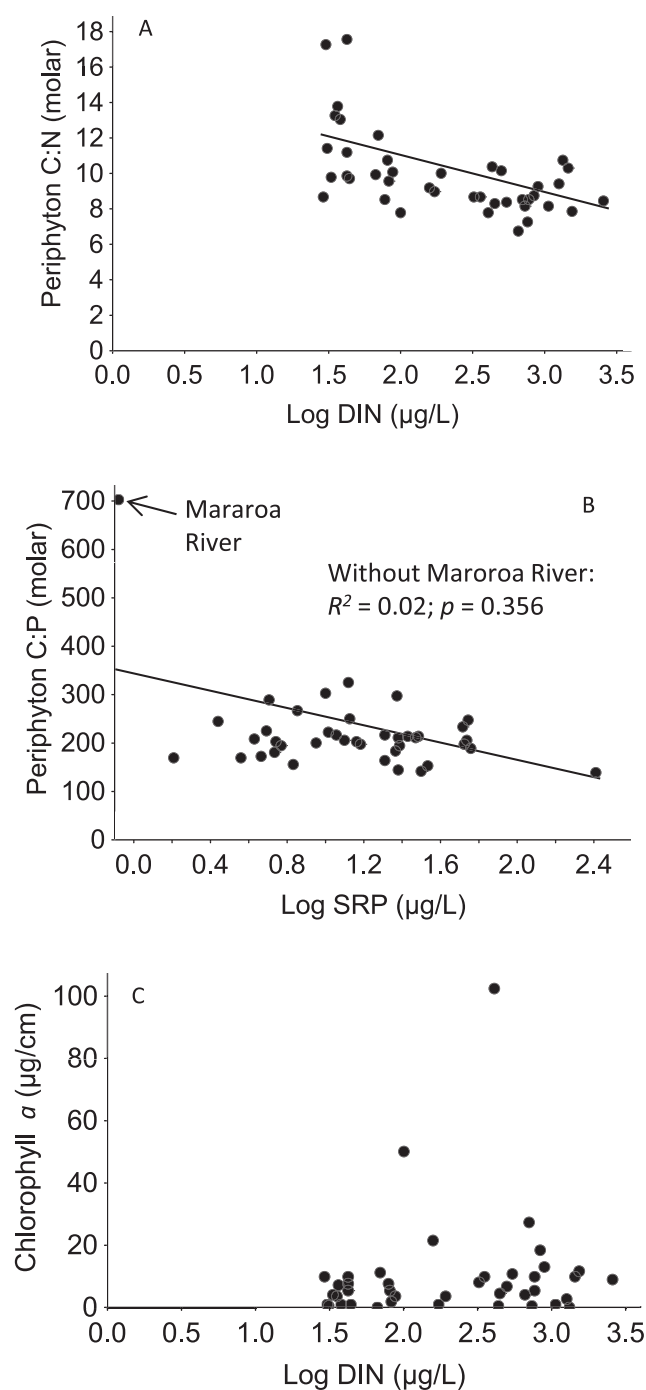
FIG. 2. Relationships between periphyton C:N and $\log_{10}(x)$-transformed dissolved inorganic N (DIN) (A), periphyton C:P and $\log_{10}(x)$-transformed soluble reactive P (SRP) (B), and periphyton chlorophyll a and $\log_{10}(x)$-transformed DIN (C). Points represent individual measurements on the x-axis, but means of 3 replicates on the y-axis. Standard error bars were omitted for clarity of presentation. Only significant ($p < 0.05$) linear regression lines are shown.
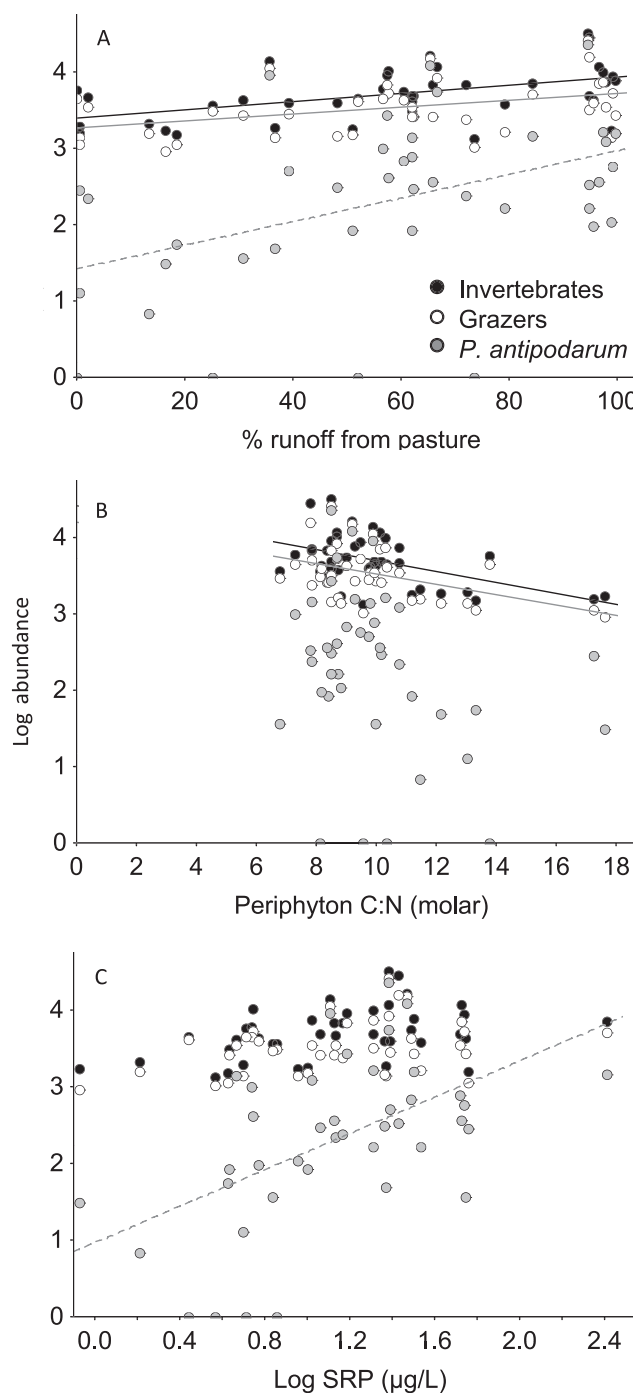
FIG. 3. Relationships between $\log_{10}(x + 1)$-transformed overall invertebrate, grazer, and *Potamopyrgus antipodarum* abundance and % annual runoff from pasture (A), periphyton C:N (B), and $\log_{10}(x)$-transformed soluble reactive P (SRP). Points represent individual measurements except for periphyton C:N, which are means of 3 replicates. Standard error bars were omitted for clarity of presentation. Only significant ($p < 0.05$) linear regression lines are shown.

for *P. antipodarum* abundance was streamwater SRP (Table 1, Fig. 3C). This result was surprising because SRP (alone or in combination with other predictors) was not a good predictor for invertebrate or grazer abundance.

Predators.—The best model for predator abundance was grazer abundance (Table 1, Fig. 4A–C). Predator abundance showed no relationships with % runoff from pasture (Fig. 4B) or periphyton C:N (Fig. 4C).

Algal and invertebrate taxon richness

Increasing periphyton C:P (best model) or C:N best explained increasing algal taxon richness. These were the only significant models, and both relationships were quite weak (Table 1). The 1st model was significant only because 1 site had particularly high values for both algal taxon richness and C:P ratios (Mararoa River, data not shown).

Invertebrate taxon richness decreased with an increase in predictor variables connected to landuse intensity. Percent runoff from pasture + periphyton N:P best explained invertebrate taxon richness and grazer taxon richness (Table 1). Increased % runoff from pasture alone also well explained decreased invertebrate taxon richness (Table 1, Fig. 5A). The same was true for grazer taxon richness (Table 1, Fig. 5A). Increased periphyton N:P also partly explained decreased invertebrate and grazer taxon richness (Table 1, Fig. 5B). Predator taxon richness was related positively to grazer taxon richness (Fig. 6A, Table 1). However, increased % runoff from pasture, alone or in combination with periphyton N:P also predicted the loss of predator taxon richness well (Table 1, Fig. 6B).

Description of algal and invertebrate communities

Diatoms and cyanobacteria dominated the algal community. Of the 14 most widespread taxa (present at $>\frac{1}{3}$ of the sites), *Phormidium* spp., followed by *Navicula* spp., *Nitzschia* spp., and *Melosira* spp., were the most widespread. *Melosira* spp. were present at 35 sites and dominated the algal community (i.e., was the most abundant taxon) at 19 sites (Appendix S3; available online from: http://dx.doi.org/10.1899/11-019.1.s1). *Potamopyrgus antipodarum* GRAY was the most common invertebrate species, present at 37 sites and often in very high abundances, ranging from 0% to 70% (mean: 13%) of the invertebrates in our samples. We also identified common taxa (present at $>\frac{1}{3}$ of the sites) and present their feeding modes and abundances (Appendix S2).
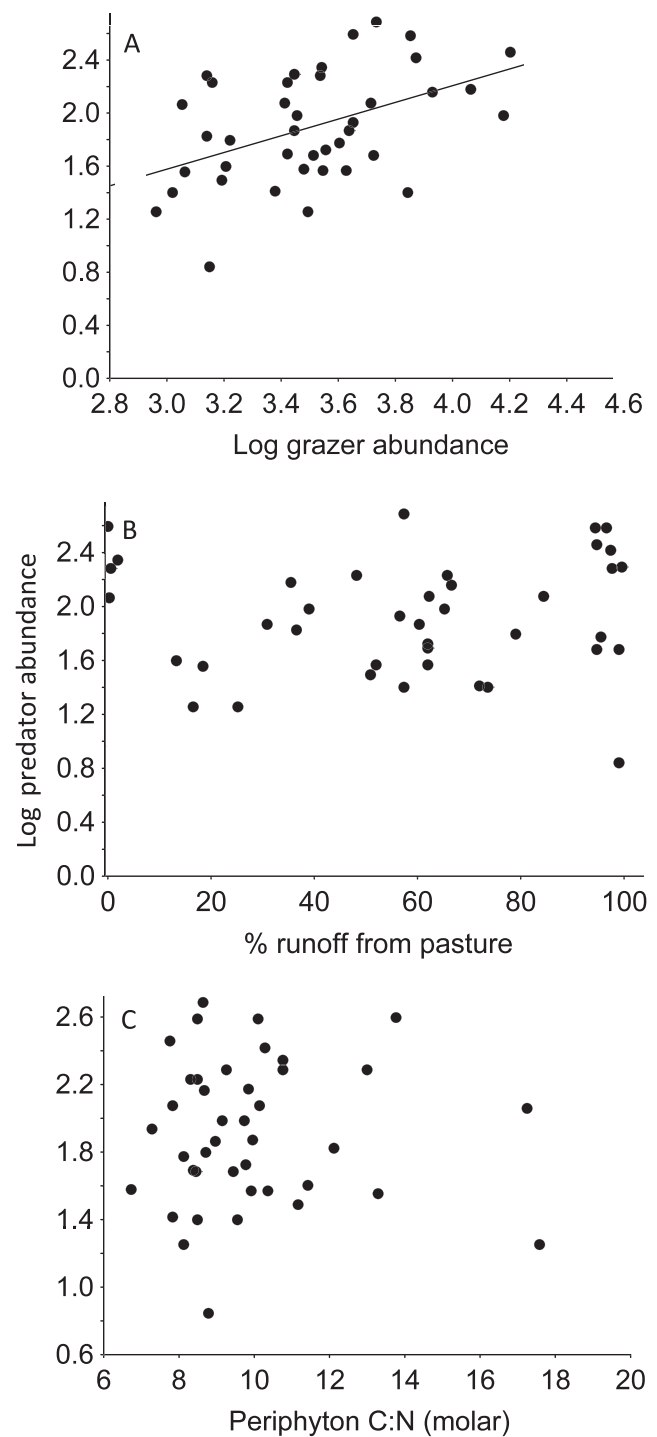

FIG. 4. Relationships between $\log_{10}(x + 1)$-transformed predator abundance and $\log_{10}(x)$-transformed grazer abundance (A), % annual runoff from pasture (B), and periphyton C:N (C). Points represent individual measurements except for periphyton C:N, which are means of 3 replicates. Only significant ($p < 0.05$) linear regression lines are shown.
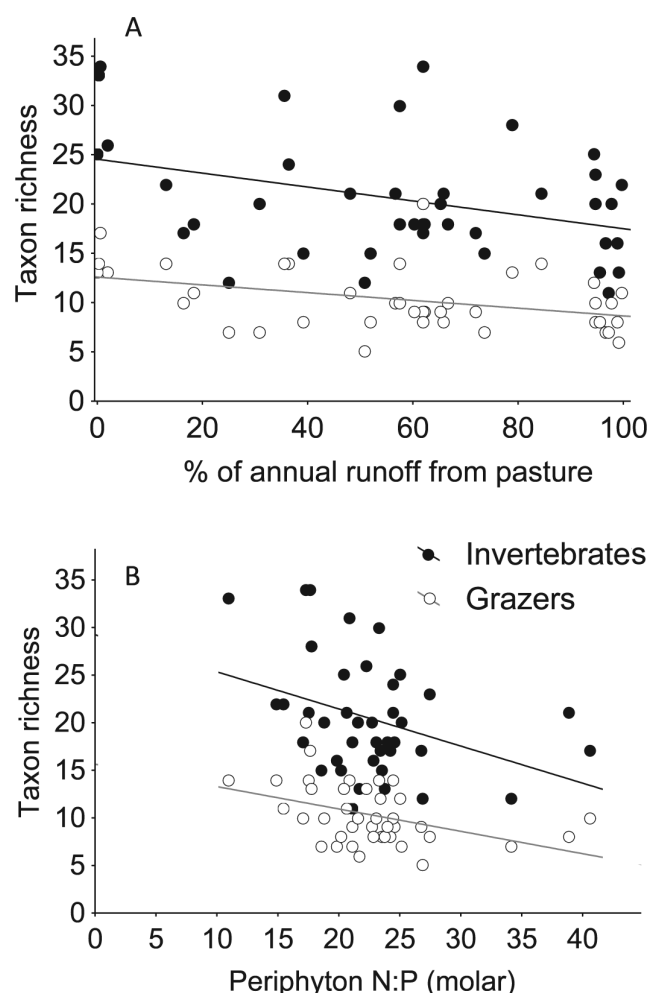
FIG. 5. Relationships of overall invertebrate and grazer taxon richness and % annual runoff from pasture (A) and periphyton N:P (B). Points represent individual measurements except for periphyton N:P, which are means of 3 replicates. Only significant ($p < 0.05$) linear regression lines are shown.
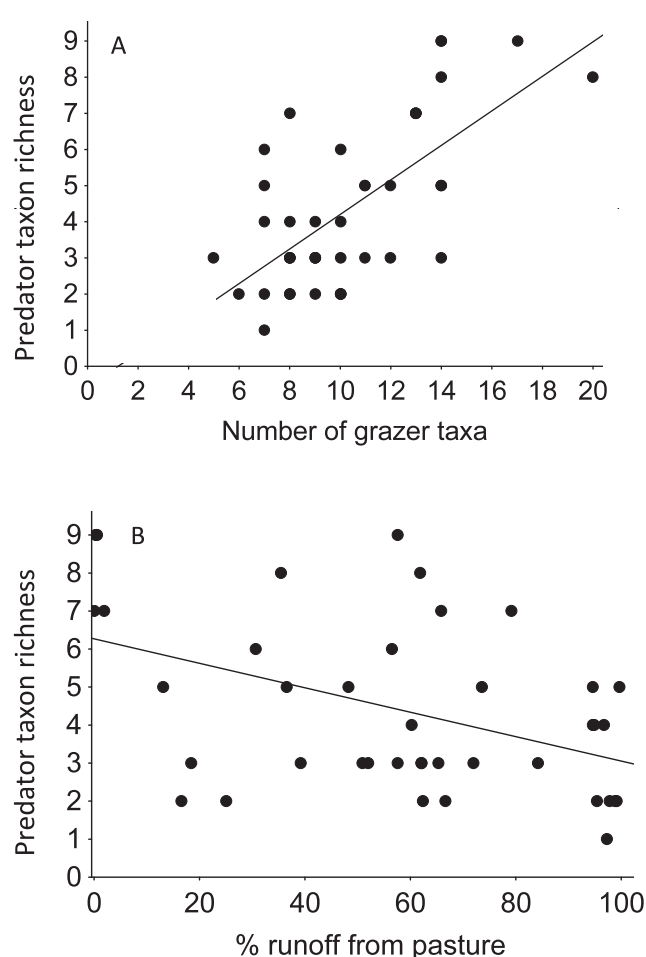

FIG. 6. Relationships between predator taxon richness and grazer taxon richness (A) and % runoff from pasture (B). Points represent individual measurements. Only significant ($p < 0.05$) linear regression lines are shown.

Discussion

Overview

Changes in streamwater N and P availability (DIN and SRP) reflected periphyton nutrient ratios (supporting hypothesis 1). Periphyton C:N usually better predicted algal taxon richness and benthic invertebrate taxon richness and abundance than dissolved nutrients from the sampling day (supporting hypothesis 2). Taxon richness of invertebrates (grazers and predators) was negatively associated with increased landuse intensity, streamwater N concentrations, and periphyton N:P (supporting hypothesis 3). Our results indicate that higher landuse intensity increased invertebrate abundance, especially at the grazer level, but reduced

taxon richness at all trophic levels. Finlay (2011) reported similarly strong effects of human activities on stream characteristics and biodiversity. We found that periphyton nutrient ratios mediated these effects to some degree, probably together with other anthropogenic factors associated with changes in landuse intensity, such as fine sediments (Wagenhoff et al. 2011), eutrophication, toxins, water removal for irrigation, and changes to river beds, fish communities, and riparian zones (Malmqvist and Rundle 2002, Finlay 2011).

Steamwater nutrient concentrations

As desired, nutrient concentrations in our set of 41 study sites varied 2000-fold, with N varying somewhat more than P. Our results showed that landuse intensity in the catchment and current velocity influenced streamwater nutrient state and N:P. A

previous study of the same sites supported this result, showing that nutrient concentrations of stream water reflected the intensity of catchment land use (Wagenhoff et al. 2011).

Periphyton nutrient ratios and biomass

Nutrient ratios.—Higher DIN was correlated with a decrease in periphyton C:N (increased food quality), which could indicate that less-impacted reference streams are still primarily N limited in New Zealand. However, more strongly impacted streams (high-N streams) were P limited, as shown for streams around Christchurch, New Zealand (Biggs and Close 1989). Increased landuse intensity augments streamwater N:P, especially under higher current velocities (>0.5 m/s), thus shifting stream communities into secondary P limitation. In Swedish lakes, increased N inflow via atmospheric N deposition similarly co-occurred with a decrease in periphyton C:N, a result indicating N limitation in low N-deposition areas and secondary P limitation in high N-deposition areas (Liess et al. 2009a). In a study done in artificial stream channels, Stelzer and Lamberti (2001) found that streamwater N:P ratios affected periphyton nutrient stoichiometry. In their study, periphyton N:P and C:P reacted most strongly, indicating that the limiting nutrient before nutrient addition was P instead of N. Nevertheless, many other factors, such as the proportion of detritus in the periphyton (Frost et al. 2005), algal species composition (Liess and Kahlert 2009), nutrient cycling by grazers (Liess and Hillebrand 2004), and light (Liess et al. 2009b) can affect periphyton composition and growth (Larned 2010) and, thus, periphyton nutrient stoichiometry. Some of these factors might be responsible for the large proportion of unexplained variation in our data set.

Biomass.—Chl *a* and C (µg/cm^2 of stream bed) varied strongly among our streams. Confounding effects of other factors that can influence periphyton biomass, such as sloughing, grazing, light, current velocity, and identity of the dominant species (Stevenson et al. 1996), and the extreme patchiness of the periphyton mat within streams could have caused the absence of a significant correlation between streamwater N and periphyton biomass. Another explanation for the lack of nutrient effects on periphyton biomass might be top-down control by grazing. If increased streamwater nutrient concentrations increased periphyton food quality, releasing grazer growth from possible food-quality limitation, then increased periphyton productivity would lead to increased grazer biomass instead of increased algal standing stock (Feminella and Hawkins 1995).

Invertebrate abundance

Grazers.—The abundance of invertebrates in general, and of grazers in particular, was higher in streams with lower C:N (higher food quality). However, landuse intensity explained roughly the same amount of variation in invertebrate and grazer abundance. Food quality could have mediated the positive effect of landuse on invertebrate and grazer abundance because periphyton C:N and land use were associated with each other. In our survey, periphyton C:N, but not periphyton C:P, affected grazer abundance. This result implies that N more than P availability probably constrained grazer abundance.

Predators.—Changes in food quality of periphyton, in terms of C:N or C:P, was not reflected by changes in predator abundance. However, predator abundance was positively correlated with grazer abundance. This result shows some bottom-up effect of streamwater nutrient concentration via periphyton and grazers on predators. However, we could not detect any effects of streamwater nutrient concentrations on predators after passing through so many trophic levels. In long-term stream fertilization experiments, higher trophic levels, such as fish or invertebrate predators, show weak positive responses to nutrient addition (Slavik et al. 2004, Cross et al. 2006). However, predator responses are usually weaker than grazer/shredder responses to nutrient enrichment. The effects of nutrient fertilization tend to be less strong or nonexistent at higher trophic levels because other factors, such as prey edibility, start constraining population densities of predators (Davis et al. 2010).

Potamopyrgus antipodarum.—Surprisingly, the pattern of abundance of the main grazer, the New Zealand mudsnail *P. antipodarum*, was markedly different from that of other invertebrates. Increased streamwater P concentration best predicted increased *P. antipodarum* abundance. This fast-growing snail has relatively high body P content and can be P limited in its growth and reproduction in streams in the USA (Tibbets et al. 2010). However, similar effects of food quality on growth rate have not been found in New Zealand (Liess and Lange 2011). No evidence was found that the positive effect of streamwater P on *P. antipodarum* abundance was mediated through periphyton C:P. Other factors, such as temperature, scouring floods, and fish predation, might have affected *P. antipodarum* densities.

Taxon richness

Invertebrates.—Landuse intensity negatively affected invertebrate taxon richness, as shown before by Finlay (2011). Landuse intensity explained between 13% of

the variation in overall invertebrate taxon richness and 20% of the variation in predator taxon richness. Streamwater N strongly reflected landuse intensity in our study. In a recent analysis of stream survey data from 827 sites, Yuan (2010) found a strong negative relationship between streamwater Tot-N and invertebrate species richness. However, the connection between Tot-N and invertebrate richness was partly a result of covariation between Tot-N and other environmental variables. Yuan (2010) found that Tot-N together with 6 other variables explained 49% of the variation in invertebrate taxon richness, but accounting for these variables greatly reduced the relationship between Tot-N and invertebrate species richness. In our study, landuse intensity also might have covaried with a range of other stream characteristics. In New Zealand, changes in land use from lightly grazed or native grassland to high-intensity grazing usually are associated with an increase in nutrient subsidies to streams and with an increase in fine sediments in streams. Several investigators have shown that these fine sediments reduced invertebrate taxon richness in particular and stream health in general (Riley et al. 2003, Niyogi et al. 2007, Wagenhoff et al. 2011).

Variation in periphyton N:P explained a similar proportion of the variation in taxon richness of invertebrates and grazers. This result suggests that more invertebrate species were adapted to N limitation (high periphyton N:P ratios) than to P limitation (low periphyton N:P). However, periphyton N:P and landuse intensity together explained only 30 to 34% of the variation in invertebrate, grazer, and predator taxon richness. A possible explanation for this result is that the adverse consequences of landuse intensity depend on the interaction with other stressors, such as fine sediments (Wagenhoff et al. 2011), scouring flood frequency, stream hydrology, and toxins.

Predator taxon richness also increased with grazer taxon richness. This result could be caused by covariation with another variable, if the same variables affected both grazer and predator taxon richness. Another possibility is that a causal relationship exists between grazer and predator taxon richness. A trade-off between being a good resource competitor and a hard-to-catch or inedible prey would prevent competitive exclusion under a common predator and promote prey coexistence if the better resource competitor also were more susceptible to predation (Leibold 1996). Thus, a more diverse predator community could favor more diverse prey strategies and higher prey species richness. The causal connection also could be reversed. A more diverse prey community could favor coexistence of more predator species.

Benthic algae.—We found only weak explanatory models for algal taxon richness. Decreased periphyton C:P or C:N explained some loss of algal taxon richness. However, these 2 models explained at most 11% of the variation in algal taxon richness, and periphyton C:P significantly predicted algal taxon richness only because of the high periphyton C:P/ high algal taxon richness site at Mararoa River. Thus, we need to investigate further variables that might influence algal taxon richness in streams.

Conclusions

Increasing agricultural landuse intensity in stream catchments had negative effects on benthic diversity of all trophic levels. Runoff of bioavailable nutrients into streams was partly responsible for shifting invertebrate communities toward species-poor assemblages, dominated by few opportunistic species or taxa, e.g., the snail *P. antipodarum*. Its abundance and relative contribution to the invertebrate community increased in streams with higher P concentrations. Our findings further indicate that changes in N availability may lead to losses of algal and invertebrate diversity. We think that N inflow is especially disturbing to aquatic communities in areas that experience low ambient rates of atmospheric N deposition, such as New Zealand. However, a reduction of agricultural nutrient leakage into streams probably will be only a small step toward improved stream health because other landuse-associated stressors, such as fine sediments (Wagenhoff et al. 2011), toxins, changed hydrographs, water removal for irrigation, and changes to riverbeds, fish communities, and the riparian zone (Malmqvist and Rundle 2002) also have negative effects on stream benthic communities.

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