Riparian shading mitigates stream eutrophication in agricultural catchments

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Abstract: Restoration of riparian vegetation is widely recognized as a tool in stream rehabilitation, but information on whether local riparian characteristics can mitigate the effects of catchment-level stressors on in-stream processes is limited. We measured community metabolism in 21 streams in the Canterbury region of New Zealand along 2 independent gradients of agricultural intensity and riparian cover (from closed canopied to open canopied) to assess relative effects of landscape and local factors on stream trophic state. We measured stream metabolism with the single-station open-channel diel O_2 method. We found a correlation between gross primary production (GPP) and ecosystem respiration (ER), indicating a gradient of trophic states across sites. Streams were strongly heterotrophic with P:R values varying from 0.01 to 0.25. GPP and ER increased with % agriculture and % macrophyte cover, but decreased with % shade from riparian vegetation. Hierarchical partitioning analysis indicated that % agriculture was the only landuse variable to have a significant independent effect on GPP and ER. Among local variables, % shade and % macrophyte cover had significant independent effects on GPP. Percent shade was the only local variable to have a significant independent effect on ER. Percent shade had a stronger effect on both GPP and ER than did % agriculture, and a trade-off exists between the importance of agricultural and forest cover on stream metabolism at different spatial scales. Our results highlight the role of local riparian conditions in controlling trophic state and the importance of riparian buffers as a tool to mitigate eutrophication in streams and rivers.
Key words: land use, trophic state, ecosystem metabolism, gross primary production, ecosystem respiration, P:R ratio, riparian buffer

Increases in the extent and intensity of agriculture have led to widespread and continuing degradation of stream health globally (Foley et al. 2005, Vörösmarty et al. 2010). Agricultural land use influences stream ecosystems by increasing concentrations of sediment, nutrients, microbes, and pesticides in streams; altering flow; and changing riparian and in-stream habitat (Allan 2004). Often, this agriculture-driven degradation of streams is characterized by increases in stream trophic state (Young and Huryn 1999, Fellows et al. 2006b, Von Schiller et al. 2008, Bernot et al. 2010), leading to an increase in the amount of energy available for both autotrophic and heterotrophic metabolism in an ecosystem (Dodds 2007).

Agricultural intensification can alter the trophic state of stream ecosystems via several converging mechanisms. Removal of riparian vegetation for the development of pasture or crop land can boost autotrophic production by increasing light available for photosynthesis (Hill et al. 1995) and decreasing nutrient retention in the soil and root zone along flow paths. Reduced litter-fall can limit the amount of substrate available for heterotrophic respiration (Young and Huryn 1999), but increased autotrophic respiration and heterotroph use of organic runoff in agricultural streams may offset or exceed the loss of litter-based respiration. Increased concentrations of nutrients from nonpoint sources can stimulate algal growth (Rosemond et al. 1993, Mosisch et al. 2001) and increase respiration (Greenwood et al. 2007) by alleviating nutrient limitation. Vegetation removal, tilling, and trampling of the stream bank by livestock increase erosion and turbidity, which in turn, may reduce light available for macrophyte and algal production (Davies-Colley et al. 1992, Young and Huryn 1999). However, more often, the removal of riparian shading and increased sediments facilitate establishment of productive macrophyte beds (Barko 1991).

Riparian buffer zones, strips of vegetation (grass, shrubs, or trees) planted close to the stream channel, are used commonly for mitigating these effects of agriculture on stream health (Lee et al. 2004, Mayer et al. 2005, Craig et al. 2008). In New Zealand, for example, riparian plantings can include native grasses, shrubs, or flax, but more commonly consist of exotic pasture grasses or trees (e.g., willow or mulberry). Vegetation may protect stream health from agricultural influences by reducing excess inputs of sediment (Carver et al. 2006, Canfield et al. 2007) and nutrients (Hopkins and Meals 2002, Craig et al. 2008, Kronvang et al. 2009), moderating stream temperature (Ebersole et al. 2003, Caissie 2006), and reducing available light (Hill et al. 1995). However, where the effects of riparian plantings on stream communities have been evaluated, the success of these rehabilitation projects has been mixed and highly dependent on stream-specific factors, such as up-stream influences, catchment geomorphology, land use, and the age and width of the buffering vegetation (Parkyn et al. 2003, Craig et al. 2008, Wilcock et al. 2009).

Riparian vegetation could influence the trophic state of stream ecosystems directly by enhancing shading and litter inputs and indirectly by reducing landscape inputs of nutrients and other contaminants. Therefore, riparian vegetation is important to the metabolism of organic matter (Bott et al. 1985, Young and Huryn 1999, Hagen et al. 2010), but the relative importance of riparian vegetation for trophic state has been difficult to isolate from catchment influences. For example, Bunn et al. (1999) found a close association between canopy cover and algal production in the Mary River, Australia, but not in other rivers, a result they attributed to effects of intensive land use, such as sediment, nutrients, and salinity. Questions linger regarding whether local factors, such as riparian condition, can mitigate the effects of intensive landuse activities, such as agriculture, occurring at the landscape level.

We investigated the role of riparian cover in regulating stream metabolism by comparing 21 streams in New Zealand. Our key question was, "Can riparian vegetation mitigate some of the impacts of agricultural intensification in stream ecosystems?" To address this question, we tested 3 hypotheses: 1) agricultural land use will increase autotrophic and heterotrophic metabolic rates as a result of increased nutrient concentrations and fine sediment cover, 2) local-level (stream reach) factors, such as riparian cover, will influence stream metabolism by regulating stream temperature, light availability (shade), bed composition, and the standing stocks of autotrophic and heterotrophic resources, and 3) well developed riparian cover will mitigate the effects of agricultural intensification on stream metabolism because local factors will have a greater effect than landscape factors on reach-level stream metabolism.

METHODS
Study area

We selected sites on 21 Canterbury stream reaches that spanned independent gradients of land use and riparian vegetation in 3 regions of the South Island, New Zealand: the Canterbury Plains, Banks Peninsula, and Canterbury Foothills (Fig. 1). All 3 regions have a history of intensive agricultural development, with extensive areas of land used for grazing livestock at varying densities (Taylor and Smith 1997, MacLeod and Moller 2006). Dairy, beef, and sheep farming are common, with lesser amounts of cropping, horticulture, and exotic plantation forestry. Limited fragments of relatively pristine and regenerating native forest also are present in conservation reserves. Riparian vegetation ranges from grass, short shrubs, hedges, and exotic trees to evergreen native forest. In general, riparian vegetation is patchy, and streams with continuous riparian vegetation are extremely rare outside protected nature reserves or commercial forestry plantations.

The 3 regions represent distinct physiographic areas and differ in their intensity of agricultural activity (Fig. 1). The Canterbury Plains is a flat, intensively agricultural area on gravel outwash plains east of the Southern Alps. Streams in this region are often spring fed, with a low gradient (Winterbourn 2008). Throughout most of the last century, agriculture in this region consisted of improved pasture (i.e., pasture that is intensively managed through the planting of introduced forage grasses, fertilization, and irrigation) for livestock grazing. However, in the last decade the region has undergone a rapid transition to higher-intensity dairy farming. The Banks Peninsula is a hilly region of volcanic origin with hillslope-dominated streams. Agricultural activities are often less intensive than on the Plains, but dairy, sheep, and beef farming still occurs at moderate stock densities (Wilson 2008). The Foothills region rises to the west of the Canterbury Plains, at the base of the Southern Alps, and consists of hills and outwash fans of greywacke material. Areas of native southern beech forest are common, and agriculture consists of dairy, beef, sheep, and deer farming (Meurk 2008).

Study design

We selected streams to span a gradient of catchment landuse intensity from native forest to intensive agriculture (dairy farming). Orthogonal to this gradient, we also selected sites to represent a gradient of riparian vegetation cover, from closed- to open-canopied streams. We sampled in the late austral summer 2010, between February and April, and included streams from all 3 regions to capture both agricultural and riparian-cover gradients adequately.

Based on previous research (Greenwood et al. 2012), we selected variables to serve as proxies of agricultural
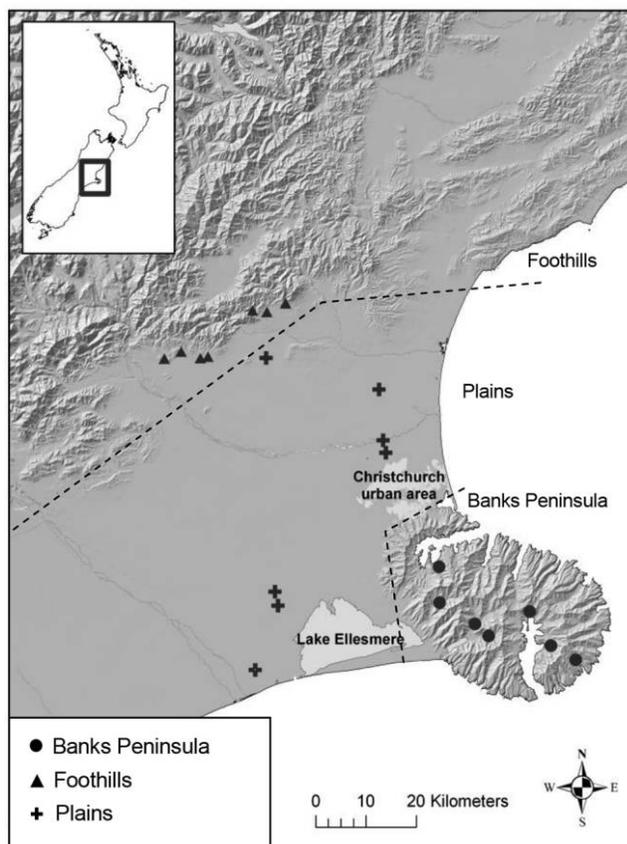
Figure 1. Map showing the Canterbury region, South Island, New Zealand. We selected sites along a gradient of riparian cover in 3 subregions: Canterbury Foothills, Canterbury Plains, and Banks Peninsula.

landuse intensity that may influence stream metabolism, including % agricultural landuse in the catchment (% agriculture), region, NO_3^-, soluble reactive P (SRP) concentration, and fine sediment cover (fines). We also selected variables representing local conditions that might influence stream metabolism, including shading by riparian plants (% shade), temperature, % macrophyte cover, chlorophyll *a* (chl *a*), median substrate size (D_{50}), and fine particulate organic matter (FPOM). In total, we had 11 predictor variables in 2 categories (land use and local).

To incorporate the effects of landscape spatial complexity, we compared the relative independent effects of 3 landuse types (forest, scrub, and agriculture) on stream metabolism at 3 spatial scales (catchment-, network-, and reach-scale). The catchment scale represents activities occurring within the catchment of each stream. The network scale represents land cover ≤100 m of either stream bank for all tributaries in the upstream network and emphasizes the importance of local upstream activities. The reach scale represents activities occurring within the 10-m riparian zone on either side of the stream reach.

Field methods   At each stream, we established a 150- to 200-m sampling reach. We measured channel characteristics at 10 transects along each reach. We recorded stream depth, substrate size (largest axis width) and macrophyte presence/absence at 10 points along each transect, and wetted width. We classified fine particles as sand (0.06–2 mm) or silt (<0.06 mm). We used a densitometer to measure channel shading in the center of each channel transect (Lemmon 1956). We collected duplicate water samples at 8 locations evenly spaced along the stream reach, filtered samples in the field through GF/F glass-fiber filters, and transported them on ice to the laboratory. We selected 5 fist-sized cobbles from throughout the reach for chlorophyll *a* (chl *a*) analysis. We kept cobbles on ice during transport, froze them, and extracted chl *a* later in hot ethanol (Murdock and Dodds 2007). We sampled FPOM with a stove-pipe corer (radius = 10 cm) at 3 locations (downstream, midstream, upstream) along the reach. We stirred sediment down to a depth of 10 cm within the corer, recorded stream depth, and took a 1-L sample of the suspended material.

At each site, we characterized riparian condition on ten 10-m transects extending to either side of the stream (20 transects in total). We measured canopy cover in the buffer, vegetation type, and vegetation height at 1-m intervals along each riparian transect. We calculated total cover of each vegetation type as the number of points in each category divided by the total number of transect points (200/site).

We deployed a calibrated O_2-sensing data logger (D-Opto Logger; Zebra-Tech, Nelson, New Zealand) in the thalweg at the most-downstream station of each stream. Sondes were programmed to record dissolved O_2 concentration at 5-min intervals and left in each stream for 3 to 5 d to ensure that we collected measurements during ≥1 d without cloud cover in each logging period. We used dissolved O_2 measurements to estimate ecosystem respiration (ER) with the single-station open-channel method described below (Bott 2007).

We measured gas exchange in each reach by propane evasion (Bott 2007). We bubbled propane into the top of each stream reach along with a conservative tracer (either rhodamine or NaCl) as a continuous addition and collected water samples at 8 stations along the reach once steady state (3× travel time) was reached. We analyzed these water samples later for propane and NaCl or rhodamine concentration. To sample propane, we took 50-mL water samples with a syringe and injected 5 mL of He with a 3-way stop valve. We shook samples for 5 min to facilitate fractionation of propane from water into He. We injected the headspace from each sample into a He-flushed and evacuated 4-mL glass vial (vial type 2; Exetainer, Labco, Buckinghamshire, UK).

Laboratory methods We used automated colorimetry (EasyChem Plus; Systea Scientific, Anagni, Italy) to analyze water samples for NO_3^- (Cd-reduction) and SRP (molybdate reduction) (APHA 1995). We dried particulate matter at 50°C for ≥48 h, weighed and combusted it (540°C, 4 h), and reweighed it to find the masses of organic and inorganic particulate material (Wallace et al. 2007). The mass of particulate matter was adjusted for water volume to give an estimate per benthic area. We extracted chl *a* from whole rocks to avoid scraping error (Murdock and Dodds 2007). We immersed rocks in a known quantity of ethanol, incubated them in a water bath (78°C) for 5 min, and then refrigerated them for 12 to 18 h. We measured chl *a* concentration of the ethanol with a bench-top fluorometer (Trilogy Laboratory Fluorometer; Turner Designs, Sunnyvale, California) using the chlorophyll acidification method (Sartory and Grobbelaar 1984).

We analyzed propane samples by gas chromatography (Shimadzu GC-2010 with a flame ionization detector; Shimadzu Scientific Instruments, Kyoto, Japan; column: Restek RTX-5Sil-MS, inlet temperature = 220°C with a split of 10∶1, column flow = 1.2 mL/min, He carrier with control by linear flow, initial temperature = 50°C, rising at 10°C/min to 100°C, then rising at 100°C/min to 200°C for 4 min; detector temp = 280°C). We corrected the propane concentration for dilution using the concentrations of the conservative tracer. We calculated the reaeration rate of propane from the rate of propane decrease over the reach and converted it to that of O_2 by multiplying it by an empirically derived conversion factor of 1.39 (Mulholland et al. 2005). In several Plains streams, the reach length was insufficient to detect a statistically significant decrease in propane (Coults Stream, Boggy Creek, Plasket Drain). In these cases, we used the nighttime regression method as the best alternative technique for determining reaeration (Aristegi et al. 2009). In the nighttime regression method (Odum 1956), reaeration rate is estimated by plotting rates of O_2 change against the O_2 saturation deficit (in 25-min bundles to reduce noise) for the time directly after sunset (Odum 1956). The slope of this relationship is equal to the reaeration rate (K). We corrected all estimates of reaeration rate to a standard temperature.

We corrected O_2-saturation values from each stream to pressure at mean sea level using barometric pressure data from the nearest weather station (CliFlo 2010). We calculated gross primary production (GPP) and ER for each stream in 5-min intervals by assuming that changes in O_2 concentration (ΔO_2) between successive readings were caused only by production during GPP, consumption during ER, and exchange between water and air (K) (ΔO_2 = GPP + ER + K). We calculated respiration over 5-min periods from the nighttime rate of O_2 change and K. During the night, ΔO_2 = ER + K. We estimated daytime ER as the average of predawn (midnight–dawn) and postsunset (sunset–midnight) ERs, corrected for temperature. Thus, GPP = ΔO_2 − (ER + K).

The 1-station method we used measures metabolism over a length of stream defined by K. We calculated the effective reach length (L_m) as $1/(3K)$ (Grace and Imberger 2006). In most cases, this length approximated the length of the study reach. In 2 agricultural streams on the Canterbury Plains, we could not access the entire effective reach length (Otukaikino River and Coults Stream). In these streams, we used satellite imagery to estimate % channel shaded in the portions we could not reach and assumed other variables were homogenous along the reach.

We assembled light data from the national climate database CliFlo, which stores data from a network of weather stations across New Zealand (CliFlo 2010). We used daily solar global radiation data (radiation from direct sunlight and scattered by clouds) from the nearest sampling station to each stream (generally <30 km). We also generated a measure of available light, which was equal to the % stream channel not shaded multiplied by daily radiation.

We quantified the areas of landuse types within each catchment using land-cover information from the New Zealand landuse database (LUMv003; Ministry for the Environment, Wellington, New Zealand). This information is based on satellite images taken between 1990 and 2008. We used geographic information systems (GIS) software (ArcMap version 9.3; Environmental Systems Research Institute, Redlands, California) to delineate the catchments of each site, and we recorded the area of each landuse category within each catchment. Land cover in the database is divided into many categories, including forest, woody grassland, high- and low-production grassland, and cropland. For the purposes of this study, we pooled landuse categories as follows: agriculture consisted of high-productivity grassland and short-rotation crops; forest consisted of all native, deciduous, and conifer forest types; and scrub consisted of gorse, manuka, and low-productivity grassland.

Statistical analysis

We checked the distribution of each variable for normality with Shapiro–Wilk tests and transformed variables when necessary to achieve normality and homogeneity of variance before analysis. We used Pearson product–moment correlations to examine the effects of independent variables on GPP and ER and the extent of multicolinearity among independent variables. We discarded riparian, catchment, or in-stream variables that were not significantly correlated with metabolic rates from subsequent analysis.

We tested the 1st and 2nd hypotheses (landuse and local factors) by using hierarchical partitioning to select those landuse and local variables that had the strongest independent effects on GPP and ER (Chevan and Suth-

erland 1991, Mac Nally and Walsh 2004). Hierarchical partitioning is a multiple-regression-based method that applies goodness-of-fit measures to all possible models for a given set of predictor variables. The process then partitions the independent contribution of each individual predictor variable (Mac Nally 2002). Hierarchical partitioning alleviates the effects of multicolinearity among predictor variables (i.e., the total independent effect represents the effect of the predictor variables independently of the collinearity of other predictor variables) (Mac Nally 2002). We then used 500 matrix randomizations to determine the statistical significance of independent effects of each variable (Mac Nally 2002). We tested the 3rd hypothesis by using model selection in multiple regression to identify which of the top landuse and local variables had the greatest effect on GPP and ER (Burnham and Anderson 2002). We compared 4 possible configurations of each model (i.e., containing top landuse variable alone, top local variable alone, top landuse and top local variables, and top landuse and local variables plus their interaction) based on Akaike's Information Criteria for small sample sizes (AIC_c). To examine the effects of spatial landscape complexity, we used hierarchical partitioning of our 3 land-cover classes on stream metabolism at each spatial scale. We did all statistical tests with R statistical software (version 2.15; R Project for Statistical Computing, Vienna, Austria).

RESULTS

Streams were 1st or 2nd order, with a median width of 2.7 m (range: 1.1–7.6 m) and a median depth of 0.12 m (range: 0.07–0.37 m). Discharge ranged from 3 L/s to 590 L/s with a median of 24 L/s. Streams were mostly cobble-bottomed with a median D_{50} of 4.3 cm, but substrate cover ranged widely among streams from fine-

sediment-dominated drains to boulder-strewn hill streams (D_{50} range: 0.01–17 cm). Piston velocities of gas exchange ($K_{20} \times$ depth) were positively correlated with stream slope ($R^2 = 0.47$, $p < 0.01$). Regional patterns of nutrient concentrations were strong. NO_3^- concentrations were highest in the Plains region (1.0–8.5 mg/L) and were linked to its history of intensive agriculture, and SRP was highest in the Banks Peninsula region (10–50 μg/L) because of the prevalence of P-rich volcanic basalts in the region's geology. Foothill streams had low NO_3^- (<0.1 mg/L) and SRP (<15 μg/L) concentrations.

Considerable collinearity existed among predictor variables (Table 1), mostly because of regional differences in agricultural intensity and geology. Agricultural intensification was associated with increases in NO_3^- ($r = 0.801$), fine sediments ($r = 0.603$), % macrophytes ($r = 0.638$), and stream temperature ($r = 0.717$). The boulders in the P-rich hillslope streams of the Banks Peninsula ($r = 0.665$) led to the correlation between large substrates (D_{50}) and SRP ($r = 0.604$), and to the association between D_{50} and % shade ($r = 0.516$).

GPP ranged from 0.04 to 2.78 g $O_2 m^{-2} d^{-1}$ (median: 0.27 g $O_2 m^{-2} d^{-1}$), and ER ranged from 1.4 to 33.3 g $O_2 m^{-2} d^{-1}$ (median: 5.39 g $O_2 m^{-2} d^{-1}$). Log(x)-transformed GPP and ER were strongly positively correlated ($r^2 = 0.68$, $p < 0.01$). All streams were heterotrophic with production to respiration ratios (P:R) <<1 (range: 0.01–0.25; median: 0.05). Higher P:R in some streams generally was caused by higher GPP rates rather than reduced ER. Metabolic rates were correlated with several of the independent variables (Table 2). Percent agriculture was positively correlated with GPP ($r = 0.567$) and ER ($r = 0.462$) (Fig. 2A, B). Percent shade was negatively correlated with GPP ($r = -0.841$) and ER ($r = -0.678$) (Fig. 2C, D). Macrophytes were the dominant autotrophs

Table 1. Correlation matrix of independent variables from study streams. Bold correlation coefficients are statistically significant. Sed. = sediment, SRP = soluble reactive P, chl a = chlorophyll a, D_{50} = median particle size, FPOM = fine particulate organic matter, temp. = temperature. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Variable	Fine sed.	NO_3^-	SRP	Region	% shade	% macrophytes	Chl a	D_{50}	FPOM	Temp.
% agriculture	**0.603****	**0.801*****	−0.158	**−0.682*****	−0.287	**0.638****	−0.085	−0.361	0.373	**0.717*****
% fine sediment		0.225	−0.320	**−0.624*****	−0.349	0.377	**−0.568****	**−0.545****	**0.518***	0.291
NO_3^- (mg N/L)			−0.146	**−0.693*****	−0.078	**0.495***	0.318	−0.300	0.165	**0.693*****
SRP (μg P/L)				**−0.496***	0.210	−0.187	0.022	**0.604****	−0.058	0.196
Region					0.359	**−0.511***	0.048	**0.665*****	−0.331	−0.308
% shade						**−0.571****	0.060	**0.516***	−0.192	−0.205
% macrophytes							0.104	**−0.503***	0.335	0.359
Chl a (mg/m^2)								0.054	0.001	0.160
D_{50} (mm)									−0.267	0.000
FPOM (g/m^2)										0.228

Table 2. Correlations between stream metabolism (GPP = gross primary production, ER = ecosystem metabolism) and independent variables. Bold correlation coefficients are statistically significant. SRP = soluble reactive P, chl a = chlorophyll a, D_{50} = median particle size, FPOM = fine particulate organic matter. * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

Category	Variable	Log(GPP)	Log(ER)
Landuse variables			
	% agriculture	**0.567****	**0.462***
	Fine sediment	0.393	0.362
	Log(NO_3^-)	0.428	0.184
	SRP	−0.316	−0.215
	Region	−0.368	−0.172
Local variables	% shade	**−0.841*****	**−0.678*****
	√(% macrophytes)	**0.687*****	**0.521***
	√(chl a)	0.161	−0.052
	D_{50}	**−0.590****	**−0.538***
	FPOM	0.256	0.049
	Temperature	0.407	0.167

responsible for the pattern of primary production ($r = 0.687$), with epilithic algae (as chl a) playing a secondary role.

Among the landuse variables, only % agriculture had significant independent effects on GPP and ER (Fig. 3A, B). Many correlations were found between region and landuse/reach variables, but none were found between region and metabolism (GPP or ER) (Table 2). Among the local variables, % shade and % macrophytes had significant independent effects on GPP (Fig. 3C). Shade was the only local variable to have a significant independent effect on ER (Fig. 3D). Macrophyte cover was correlated with both % agriculture and shade (Table 2), so it was excluded from the multiple-regression model.

Two variables best represented landuse and local effects on stream metabolism: % agriculture and % shade, respectively. Based on AIC$_c$ selection, the best configuration of the model for GPP included both % agriculture and shade (Table 3). Within the best model, shade had the greater effect (Table 4). The 2nd-best model included a % agriculture × shade interaction, but the interaction term was not statistically significant. The best model for ER also included % agriculture and shade, with shade again having the greater effect (Table 4). The 2nd-best model for ER included shade alone.

The relative importance of agriculture and forest cover shifted between spatial scales. At the catchment scale, agriculture had a stronger effect on stream metabolism than forest cover (% shade). Conversely, at the reach scale, for-

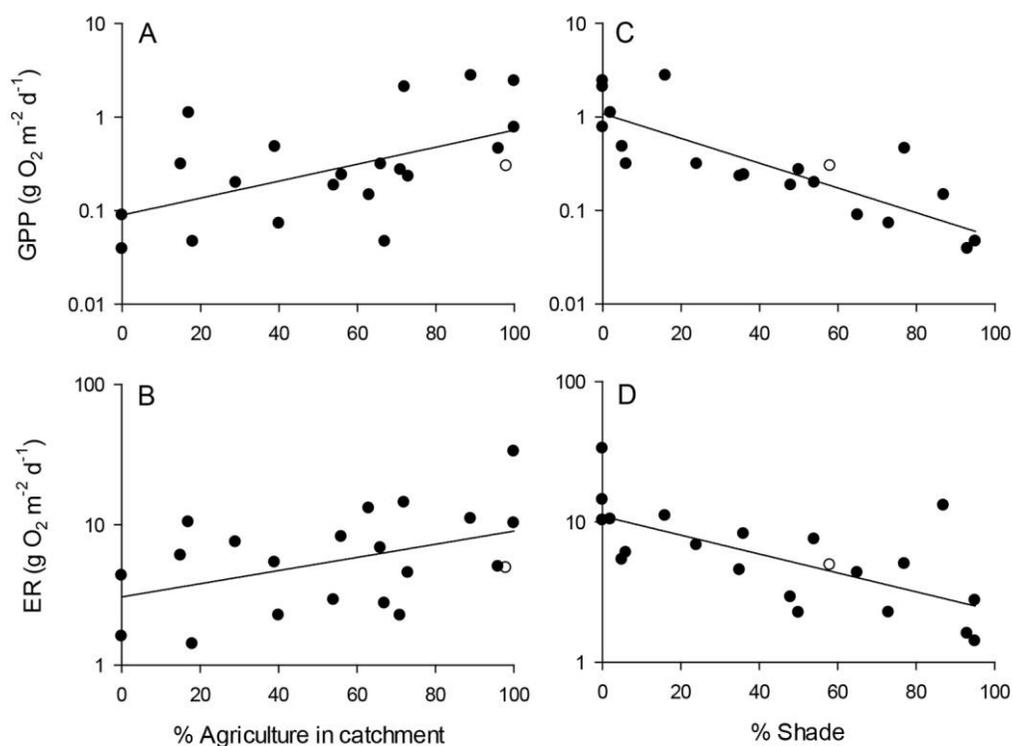Figure 2. Regressions for gross primary production (GPP) (A, C) and ecosystem respiration (ER) (B, D) with respect to % agriculture in the catchment (A, B) and % shade at the stream reach (C, D). At the landscape level, GPP and ER were closely correlated with % agricultural land use in the catchment, whereas at the local level GPP and ER were closely correlated with shading by riparian vegetation.
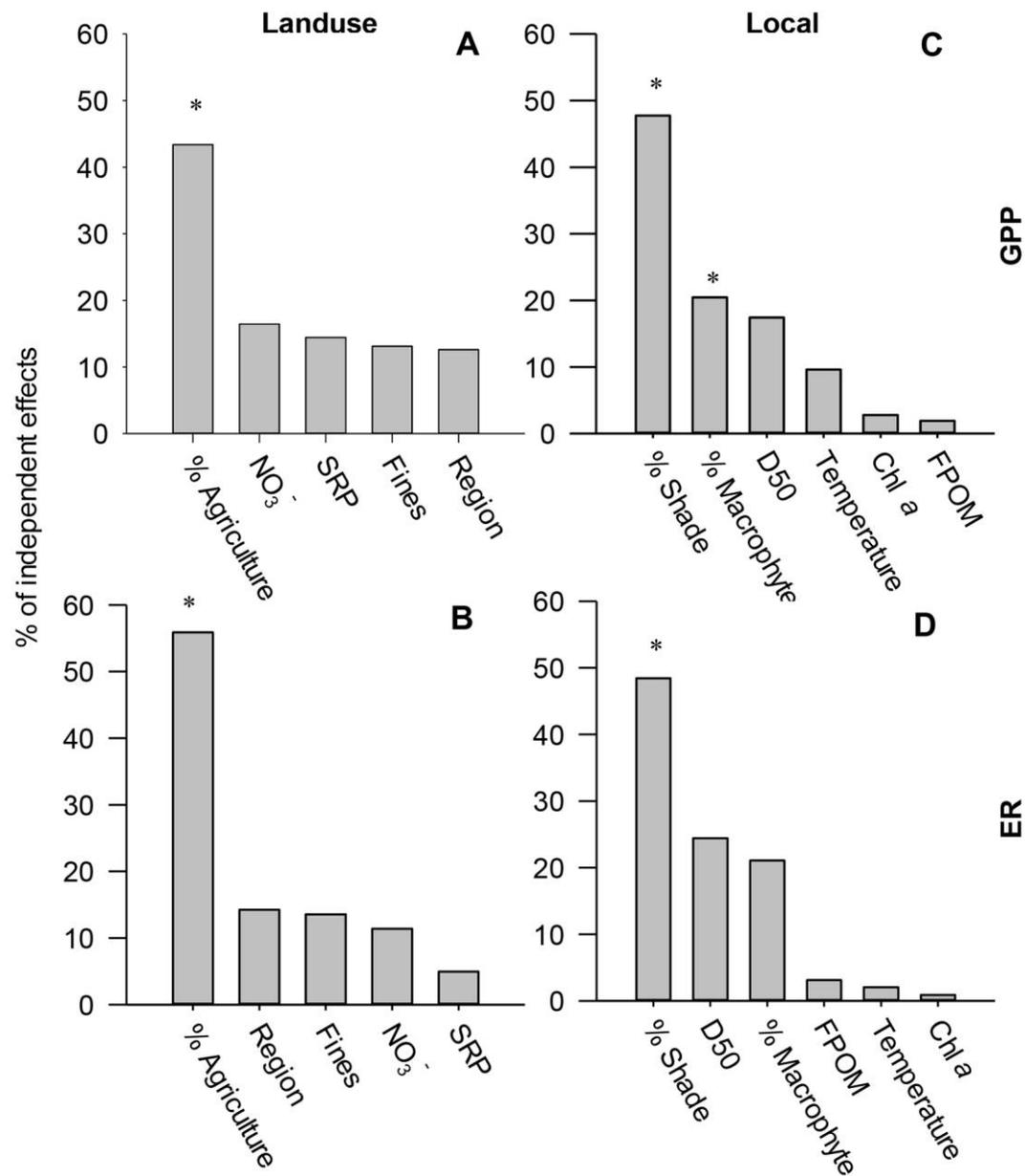
Figure 3. Percent of independent effects from hierarchical partitioning analysis for landuse variables on gross primary production (GPP) (A) and ecosystem respiration (ER) (B) and local variables on GPP (C) and ER (D). * Indicates statistical significance at $\alpha =$ 0.05. SRP = soluble reactive P, fines = fine sediment, D_{50} = median particle size, FPOM = fine particulate organic matter, chl a = chlorophyll a.

est cover had a stronger influence than agriculture because of riparian shading. The shift in influence of forest cover relative to agriculture happened gradually as the scale decreased from landscape to local for both GPP and ER (Fig. 4A, B).

DISCUSSION

The streams in our study formed a strong gradient of trophic states with increases in both autotrophic and heterotrophic activity spanning several orders of magnitude. Activ-

ity ranged from very low autotrophic and heterotrophic productivity in the forested streams of the Banks Peninsula and Foothill regions to high autotrophic and very high heterotrophic productivity in the agriculturally dominated streams of the Canterbury Plains. Despite the large increases in GPP, all streams were net heterotrophic (i.e., P:R always <1) because GPP and ER increased together across the gradient from oligotrophic to eutrophic states. Agricultural land use had a significant effect on streams, but the predicted proximate mechanisms (higher nutrient con-

Table 3. Multiple linear regression model selection for gross primary production (GPP) and ecosystem respiration (ER) using Akaike's Information Criteria for small sample sizes (AIC_c).

Model	AIC_c	$\Delta_i AIC_c$	Model R^2
Log(GPP) = % shade + % agriculture	6.23	0.00	0.823
Log(GPP) = % shade + % agriculture + (% shade × % agriculture)	7.93	1.70	0.834
Log(GPP) = % shade	14.04	7.81	0.707
Log(GPP) = % agriculture	31.33	25.10	0.322
Log(ER) = % shade + % agriculture	6.86	0.00	0.537
Log(ER) = % shade	7.39	0.53	0.460
Log(ER) = % shade + % agriculture + (% shade × % agriculture)	9.94	3.08	0.537
Log(ER) = % agriculture	15.26	8.40	0.214

centrations and fine sediment cover) were not responsible for this increase. Stream shading was the main local factor influencing stream metabolism that led to lower rates of GPP and ER. We also observed an increase in GPP with increased macrophyte cover. Agricultural cover in the landscape heavily influenced the metabolic rates in our streams, but riparian vegetation mitigated the effects of agricultural development on stream metabolism by shading the stream channel.

Increased in-stream production resulting from high-intensity agricultural land use has been attributed to increased nutrient supply and decreased canopy cover (McTammany et al. 2007, Bernot et al. 2010). However, the response of ER to agricultural intensification is not consistent among studies. Von Schiller et al. (2008) and Bunn et al. (1999) found that ER increased with agriculture in European and Australian streams, whereas Young and Huryn (1999), working in a different region in New Zealand's South Island, found that ER decreased with agriculture. Young and Huryn (1999) attributed reduced ER to decreased organic-matter inputs in their agricultural streams relative to in forested streams. Our agricultural streams did not contain less organic matter than forested streams because of an influx of FPOM associated with fine-sediment inputs.

Table 4. Parameter estimates for best multiple linear regression model for gross primary production (GPP) and ecosystem respiration (ER).

Metabolic variable	Variable	β	SE	t	p
GPP	Intercept	−0.22	0.11	−1.945	0.068
	% shade	−1.16	0.16	−7.133	<0.001
	% agriculture	0.51	0.15	3.430	0.003
ER	Intercept	0.91	0.12	7.786	<0.001
	% shade	−0.59	0.17	−3.551	0.002
	% agriculture	0.26	0.15	1.743	0.098

The response of ER to landscape and local tree cover is counterintuitive to what we would normally expect. Streams with riparian trees would be expected to have more organic-matter inputs from falling leaves and woody debris than open, grassy-banked agricultural streams without trees. Similarly, streams with greater forest cover close to the stream network should have higher ER because of downstream movement of coarse and fine organic matter (i.e., Vannote et al. 1980). However, open stream reaches in our study tended to have much higher rates of ER than closed reaches, and upstream forest cover did not have a disproportionate influence on ER. Our streams were all strongly net heterotrophic, suggesting that local autotrophic GPP was not responsible for elevated ER. Macrophyte removal experiments conducted as part of a separate study (JMO, unpublished data) suggest that respiration by macrophytes was not responsible for the elevated rates of ER observed in the open agricultural streams. Our data suggest that open agricultural streams are receiving an alternate form of labile organic matter from the landscape, such as grass detritus, livestock effluent runoff, or dissolved organic matter, that is serving as the main source of metabolic C in these streams.

Riparian plants exerted the strongest control on metabolism by shading the stream channel. The effect of riparian shading on stream metabolism was stronger than either land use or local characteristics (i.e., standing stocks of organic matter or nutrient concentrations). Shading was associated with decreased rates of GPP and ER, but had a stronger effect on GPP by inducing light limitation. The relationship between riparian shading and metabolism has been noted previously (Bunn et al. 1999, Fellows et al. 2006b) and is widely applicable for managing stream trophic state.

In our study, changes in GPP were associated with the abundance of macrophytes rather than of benthic algae. One possible reason for the lack of influence by benthic algae is the inconsistent relationship between chl *a* concentrations and algal productivity (Fellows et al. 2006a, Baulch et al. 2009). In summer, macrophytes are a major
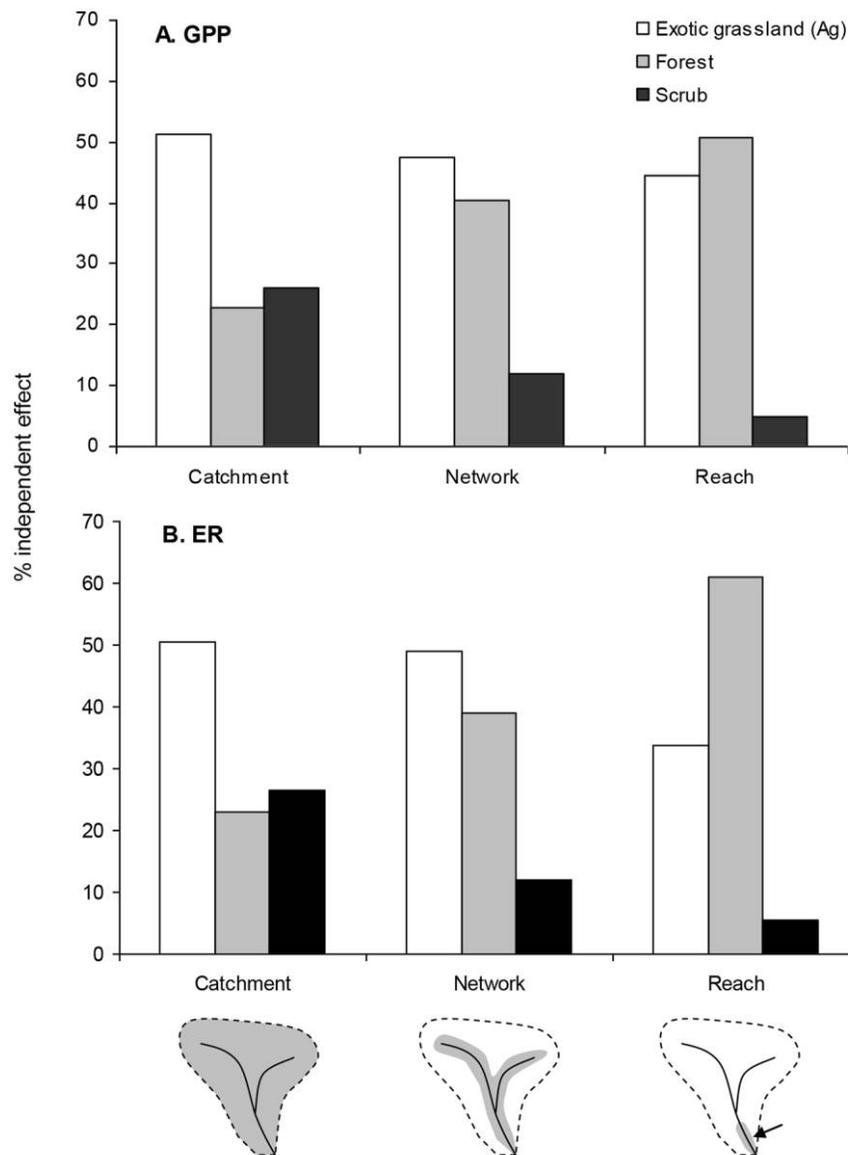
Figure 4. Percent of independent effects from hierarchical partitioning analysis for landuse variables on gross primary production (GPP) (A) and ecosystem respiration (ER) (B) at 3 different scales. Catchment = land cover in drainage catchment, network = land cover within 100 m of the stream network, reach = vegetation cover within a 10-m riparian zone along the 150- to 200-m study reach. For both GPP and ER, the influence of tree cover increases relative to intensive grass cover as the scale decreases. Ag. = agriculture.

component of many lowland waterways and can make up a large proportion of the biomass in a stream channel (Riis et al. 2003). We cannot separate the production of vascular macrophytes from that of the associated epiphytic communities. However, production associated with macrophyte cover is clearly a key driver of trophic state in our streams.

We did not see a strong influence of nutrients on ecosystem metabolism despite wide ranges of NO_3^- (3 orders of magnitude) and SRP (2 orders of magnitude) concentrations in our study streams, possibly because of the dominant influence of macrophytes in our high-productivity

streams. Growth of algae often is influenced by water-column nutrients (Biggs 2000). However, macrophytes can obtain nutrients through both foliar and root uptake and do not respond as readily as algae to increases in water-column nutrients (Madsen and Cedergreen 2002). Fine sediments often are associated with macrophyte beds, but we did not find a strong link between fine sediment cover and macrophytes. Despite the wide range of ecological complexity in our study (including highly impacted landscapes, wide ranges of N and P concentrations, biofilm-smothering fine sediments, and alternation between algae- and macrophyte-dominated systems), light

was the single most important variable determining ecosystem metabolism.

Shading by riparian plants may effectively reduce stream trophic state, but it also may affect other ecosystem processes, such as nutrient cycling. Shaded streams typically have lower rates of nutrient uptake than open algae-dominated streams (Sabater et al. 2000, Fellows et al. 2006b). The role of macrophytes in nutrient cycling and retention has received less attention than the role of algae (Riis et al. 2012) and may greatly influence the relative merits of maintaining open or shaded streams. A potential trade-off between maintaining stream trophic state and enhancing nutrient retention should be explored further, if we plan to manage streams for contrasting ecosystem values and services.

Overall, our study clearly demonstrates that intensive, long-term agriculture at the catchment level increases both GPP and ER in streams, resulting in eutrophication. Forest land use has a limited effect at the catchment scale, but has a disproportionate effect when the trees are closer to the stream, particularly in the immediate riparian zone. The trophic level of streams is important to waterway managers, who often are charged with reducing growth of excessive macrophytes or algae. As a management strategy to prevent eutrophication of agricultural streams, we recommend that land managers plant and protect riparian zones in ways that reduce stream erosion and increase stream shading.

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