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APPLIED ISSUES

Influence of land use on stream ecosystem function in a Mediterranean catchment

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SUMMARY

1. Due to the hierarchical organization of stream networks, land use changes occurring at larger spatial scales (i.e. the catchment) can affect physical, chemical and biological characteristics at lower spatial scales, ultimately altering stream structure and function. Anthropogenic effects on streams have primarily been documented using structural metrics such as water chemistry, channel alteration and algal biomass. Functional parameters, including metrics of nutrient retention and metabolism, are now being widely used as indicators of stream condition.

2. Within this hierarchical context, we used a multivariate approach to examine how structural and functional (i.e. nutrient retention and metabolism) attributes of streams are related to catchment variables, including land use. The study was done in 13 streams located within a single Mediterranean catchment, but draining sub-catchments with contrasting land use.

3. At the catchment scale, results showed two contrasting land use gradients: (i) from forested- to urban-dominated catchments and (ii) from low to moderate agricultural-dominated catchments. Variation in structural and functional parameters was strongly related to these land use gradients. Specifically, NH_4^+ demand (measured as the uptake velocity, V_f) decreased along the gradient from forested- to urban-dominated catchments primarily in response to increases in stream nutrient concentrations [NH_4^+, dissolved organic nitrogen (DON) and carbon (DOC)]. Both primary production and respiration increased along the gradient of agricultural development in response to increases in algal biomass (chlorophyll *a*). Soluble reactive phosphorus demand was not related to any of the land use gradients.

4. Our results illustrate the connections among factors operating at different spatial scales (i.e. from catchments to streams) and their distinct influence on stream ecosystem function. Managers should take into consideration these connections when designing stream management and restoration plans. Because ecologically successful stream management and restoration is expected to restore function as well as structure to streams, the use of appropriate measures of functional processes is required. Nutrient retention and metabolism parameters are good candidates to fill this gap.

Keywords: land use, Mediterranean, metabolism, nutrient retention, streams

Introduction

Stream networks are hierarchically organized systems such that land use changes occurring at larger spatial scales (i.e. the catchment) can affect physical, chemical

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and biological characteristics at lower spatial scales, ultimately altering stream structure and function (Frissell *et al.*, 1986; Allan, 2004; Martí *et al.*, 2006). Because streams provide vital ecosystem services to humans (Palmer *et al.*, 2004), it is important to understand if and how different types of land use in the catchment compromise stream function.

Although human influences on physical, chemical and biological characteristics of streams are well documented, there have been far fewer studies on how humans affect ecosystem processes including biogeochemical cycling, production, respiration and decomposition (but see Bunn & Davies, 2000; Gessner & Chauvet, 2002; Meyer, Paul & Taulbee, 2005; Bott *et al.*, 2006). Ecosystem processes, however, can be ideal measures of stream condition, because they integrate environmental characteristics and may accurately reflect a broad range of catchment disturbances (Bunn, Davies & Mosisch, 1999). Stream management and restoration programs, such as the European Union's Water Framework Directive, are increasingly recognizing the importance of ecosystem processes and are designing programs directed towards maintaining these processes in addition to traditional goals of protecting biodiversity and improving water quality (Vighi, Finizio & Villa, 2006).

Stream nutrient retention, the set of processes by which nutrients are stored, transformed and removed from the water column, can mitigate problems associated with eutrophication, by reducing nutrient delivery to downstream and coastal ecosystems (Alexander, Smith & Schwarz, 2000). Because nutrient retention is now being used as an indicator of stream ecological condition, it is important to understand how human activities influence it (Meyer *et al.*, 2005; Newbold *et al.*, 2006; Roberts, Mulholland & Houser, 2007). Past research shows that some activities reduce retention efficiency (i.e. retention relative to nutrient flux), such as channel modification (Sweeney *et al.*, 2004; Bukaveckas, 2007), nutrient loading (Martí *et al.*, 2004; Bernot *et al.*, 2006; Newbold *et al.*, 2006) and other forms of water pollution that inhibit biological communities responsible for nutrient uptake (Newbold *et al.*, 2006; Lottig *et al.*, 2007). Conversely, retention efficiency may increase with other human activities, such as riparian vegetation removal, through increases in light for primary producers (Sabater *et al.*, 2000).

Stream metabolism can also be used to assess stream condition (e.g. Bunn *et al.*, 1999; Bott *et al.*, 2006; Fellows *et al.*, 2006). Primary production and respiration determine how carbon cycles through streams as well as the oxygen status of streams (Bott *et al.*, 2006). Human land use can influence stream metabolism by altering environmental variables, including light (Bunn *et al.*, 1999; Young & Huryn, 1999), organic matter inputs (Young & Huryn, 1999; Houser, Mulholland & Maloney, 2005) and nutrient availability (Bernot *et al.*, 2006; Gücker & Pusch, 2006).

The majority of studies of how land use changes affect nutrient retention and metabolism have been conducted in streams in temperate regions of North America. Here we study how land use influences stream ecosystems in a catchment situated in the Mediterranean region. Studying the influence of land use on stream function across cultures, landscapes and climates is critical for developing a global view of how land use affects streams. Specifically Mediterranean catchments, such as the ones in this study, differ from those in temperate North America because: (i) they have a longer history of human impact, (ii) they often have mixed land uses so that streams situated in urban and agricultural areas often have catchments dominated by second growth forests, and (iii) they may be more susceptible to human impacts due to the natural deficit of water resources (Alvarez-Cobelas, Rojo & Angeler, 2005).

The aim of this study was to explore how nutrient retention and metabolism are influenced by human land use in the catchment. With this purpose, we used a multivariate approach within a hierarchical context to examine the variability in parameters of nutrient retention and metabolism among streams located within the same catchment, but draining sub-catchments with contrasting land use composition.

Methods

Study sites

This study was conducted in the catchment of the river La Tordera (Catalonia, NE Spain), with an area of 868.5 km^2 and dominated by siliceous geology. Climate in this region is typically Mediterranean, with warm, dry summers and mild, humid winters. The long history of human settlement has created a highly heterogeneous mosaic of human land uses. Most of the valley heads are protected areas dominated by deciduous forests of beech (*Fagus sylvatica* L.) at the higher altitudes and dry sclerophylous forests of evergreen oaks (*Quercus ilex* L. and *Quercus suber* L.) and pine (*Pinus halepensis* Mill. and *Pinus pinea* L.) at the lower altitudes. In the valley plains the forests have been partially substituted by agricultural, urban and industrial areas.

Within this catchment, we selected experimental reaches with relatively unmodified channels from 13 headwater streams draining catchments subjected to a variety of land uses. The length of the reaches ranged from 20 to 200 m, and did not include any tributaries. The catchments above the experimental reaches were characterized for total area, mean altitude, mean slope and percent land use using geographic information system (GIS) data layers. Internet-accessible GIS databases from the Department of the Environment and Housing of Catalonia (http://www.gencat.net/cat/el_departament/cartografia) were used to obtain images, and data layers were subsequently combined using ArcGIS (Environmental Systems Research Institute, Redlands, CA, USA). Land uses were grouped into forested (including all types of forests), agricultural (including irrigated and dry-land crops) and urban (including towns, residential areas, industrial and commercial zones). Other types of land uses (e.g. water impoundments, areas without vegetation, grasslands) found only in discrete (or at single) catchments were not considered in this study.

Field sampling

Field experiments were performed in the early spring (20 March to 10 April) of 2006, a period characterized by moderate temperatures, base flow conditions and relatively high light availability at the stream bottom because leaf emergence had not yet occurred.

Solute additions. We measured nutrient retention metrics and hydraulic characteristics in each stream using short-term constant rate additions of ammonium (NH_4^+, as NH_4Cl) and soluble reactive phosphorus [SRP, as $Na(H_2PO_4){\cdot}2H_2O$] in conjunction with chloride (Cl^-, as NaCl) as a conservative tracer (Webster & Valett, 2006). A Masterflex (Vernon Hills, IL, USA) L/S battery-powered peristaltic pump was used to deliver the addition solution to the stream until conductivity reached plateau (i.e. 1–3 h) at the bottom of the study reach. Conductivity was automatically recorded at the bottom of the reach every 5 s using a WTW (Weilheim, Germany) 340i portable conductivity meter connected to a Campbell Scientific (Logan, UT, USA) data logger. We measured conductivity and collected water samples for NH_4^+, SRP and nitrate + nitrite (NO_3^- + NO_2^-) at eight stations along the reach before the addition for background concentrations (two replicates per station), and once conductivity reached plateau for plateau concentrations (five replicates per station).

Metabolism measurements. Metabolism was estimated in each stream on cloudless days within 5 days of the nutrient addition using an open-system, single-station approach (Bott, 2006). Dissolved oxygen (DO) concentration and temperature were recorded at the bottom of the study reach at 10-min intervals during a 24-h period with a WTW 340i portable oxygen meter. Percent DO saturation was estimated using DO and temperature data together with a standard altitude-air pressure algorithm to correct for site altitude. To estimate mean daily temperature and percent DO saturation we averaged values recorded over the 24-h period. During the same period, photosynthetically active radiation (PAR) was measured every 10 s, and 10-min integrals were logged with a Skye (Powys, UK) SKP215 quantum sensor connected to a Campbell Scientific data logger. Unfortunately, PAR could only be determined in seven of the study streams due to a malfunctioning sensor.

Additional measurements. Water samples (three replicates) for total dissolved N (TDN) and dissolved organic carbon (DOC) were taken at the lowermost station of each reach before the addition. Wetted width (*w*) and percent reach coverage by different substratum types were determined on cross-sectional transects located at each sampling station along the reach. Six cobbles or sand core samples, in streams without cobbles, were randomly sampled from the streambed and transported to the laboratory for analysis of chlorophyll *a*. All water samples for nutrient chemistry were immediately filtered through pre-ashed Albet (Barcelona, Spain) FVF glass fibre filters (0.7 μm retention), stored on ice in the field and then refrigerated at 4 °C or frozen in the laboratory until analysis.

Laboratory analyses

Nutrient chemistry. Concentrations of NO_3^- + NO_2^-, NH_4^+ and SRP in stream water samples were analysed with a Bran + Luebbe (Norderstedt, Germany) TRAACS 2000 Autoanalyser following standard colorimetric methods (APHA, 1995). TDN and DOC concentrations were determined on a Shimadzu (Tokyo, Japan) TOC-VCSH analyser. Dissolved organic N (DON) concentration was calculated by subtracting the sum of the inorganic forms of dissolved N (NO_3^- + NO_2^- and NH_4^+) from TDN.

Algal biomass. Chlorophyll *a* concentration on cobbles or sand cores was estimated following standard protocols (Steinman, Lamberti & Leavitt, 2006). Samples were extracted in 90% v/v acetone over 24 h at 4 °C, sonicated for 2 min and centrifuged for 10 min at 1108 *g*. Absorbance of the resultant supernatant was measured using a Shimadzu UV-spectrophotometer. The chlorophyll *a* content of each sample was corrected for phaeo-pigments by acidification and expressed per unit area of substratum.

Parameter calculations

Hydraulic parameters. Breakthrough curves of conductivity were analysed by visual inspection with a one-dimensional transport with inflow and storage model (OTIS; Runkel, 1998) to calculate stream hydraulic characteristics, including discharge (Q), cross-sectional area (A) and cross-sectional transient storage area (A_s). In this study, we used the ratio A_s/A to characterize water transient storage because it allows for comparison among streams of different size. Mean reach depth was calculated as A/w.

Nutrient retention parameters. Using data from the nutrient additions, we calculated three metrics of retention for each nutrient (i.e. NH_4^+ and SRP) and stream: uptake length (S_w), uptake velocity (V_f) and areal uptake (U). S_w, the average distance travelled by a nutrient molecule before being removed from the water column (Newbold *et al.*, 1981), was calculated as the negative inverse of the slope of the regression of the ln-transformed and background corrected nutrient : conductivity ratio versus distance downstream from the addition point. S_w is an indicator of the nutrient retention efficiency at the reach scale (Webster & Valett, 2006). This metric was converted to V_f, calculated as the stream specific discharge (i.e. Q/w) divided by S_w. Because S_w is strongly dependent on discharge, V_f provides a more appropriate variable for comparison across streams of different size (Webster & Valett, 2006). V_f describes the velocity by which a nutrient molecule is removed from the water column, and it is an indicator of nutrient demand (Hall, Bernhardt & Likens, 2002). U, the mass of a nutrient taken up from the water column per unit streambed area and time, was calculated as V_f multiplied by the ambient nutrient concentration. Because U is an areal measurement it provides a more appropriate variable to examine relationships with areal metabolism measurements. Nitrification could not be estimated with our data for any of the study streams because no downstream increases in NO_3^- along the experimental reaches were observed during the additions.

High nutrient concentrations at plateau resulting from the addition experiments may overestimate S_w at ambient nutrient levels. This can be avoided by using multiple enrichments (Payn *et al.*, 2005) or stable isotope additions (Mulholland *et al.*, 2002). Because of the extensive character of our study, covering two nutrients across 13 streams, we used the traditional short-term addition method and tried to minimize the error associated with this method by maintaining a relatively low and similar nutrient enrichment factor (i.e. plateau/background) among streams. Enrichment factors for SRP (mean ± 1SE = 23.4 ± 8.4) were higher than for NH_4^+ (4.5 ± 0.9), because relatively low ambient SRP concentrations had to be sufficiently increased to ensure reliable analytical detection of concentration changes downstream. Nevertheless, no relationship (Pearson correlation, $P \geq 0.386$) between enrichment factor and S_w was found for either of the two nutrients.

Metabolism parameters. We estimated gross primary production (GPP) and ecosystem respiration (ER), by integrating the DO measurements at a single station during a 24 h period following Bott (2006). Reaeration coefficients (range = 11.3–66.2 day^{-1}) and respiration at night were estimated based on DO change rates and DO deficits using the night-time regression method (Young & Huryn, 1996). Respiration at night was extrapolated to 24 h to estimate ER. GPP was computed by integrating the difference between the measured net DO change (corrected by the reaeration flux) and the extrapolated day-time respiration. GPP and ER were multiplied by the mean reach depth to obtain areal estimates, which allow for comparison among streams of different size. Three other metabolic metrics were calculated: net ecosystem production (NEP = GPP − ER), the production/respiration ratio (GPP/ER) and total metabolism (TM = GPP + ER; *sensu* Meyer *et al.*, 2005).

Statistical analyses

All variables were divided into three groups: catchment variables (Table 1), stream structural variables (Table 2) and stream functional variables (Table 3). To examine which variables contributed to variation among streams at the two different scales (i.e. catchment and stream), we conducted separate principal component analyses (PCA) with the group of variables at each scale. Variables were standardized and a correlation matrix was used for the PCA. Results from the two PCA allowed us to test for correlations among variables within each scale. Results from each PCA are hereafter referred to as catchment-PCA and stream-PCA. The weight of a variable on a PCA component was considered significant when its loading was >0.7. Due to statistical constraints in the number of variables that can be included in the PCA based on the total number of cases, we only used percent fine substratum (i.e. sand + mud) to characterize streambed substratum composition, because this was the substratum type that showed the highest variability among streams. PAR measurements were excluded from the PCA analysis because we only had data for seven streams.

We examined the relationship between catchment and stream environmental variables using simple linear regressions with the scores of the components of the catchment-PCA as independent variables and the scores of the components of the stream-PCA as dependent variables. The relationship between stream environmental variables and functional variables was explored using simple linear regression with the scores of the components of the stream-PCA as independent variables, and nutrient demand (V_f) and metabolism parameters (GPP, ER, NEP, GPP/ER and TM) as dependent variables. The relationship between nutrient retention and metabolism was examined using Pearson correlation analysis with the areal nutrient uptake (U) and metabolism (GPP, ER, NEP, GPP/ER and TM) as variables.

All variables were normalized prior to analysis by $\log_{10}$ or arcsine $\sqrt{(x)}$ (for percent data) transformation. Results were considered significant if $P < 0.05$, and marginally significant if $0.05 < P < 0.10$. Statistical analyses were done with Statistica 6.0 (Statsoft, Tulsa, OK, USA).

Results

Catchment characteristics

Study catchments included a wide altitudinal range (122–1419 m a.s.l.; Table 1). Catchment size of all streams was relatively small, but values varied over

Table 1 Physiographic and land use characteristics of the catchments drained by the study streams. Geographical coordinates correspond to the lowermost station of the experimental reaches

Stream	Code	Longitude 2°E	Latitude 41°N	Mean altitude (m)	Mean slope (%)	Total area (km^2)	Forested area (%)	Urban area (%)	Agricultural area (%)
Aiguaviva Park	AGP	49′04″	44′54″	200	11.2	0.7	23.2	69.0	0.0
Castanyet	CAS	37′25″	53′28″	572	21.7	8.6	99.6	0.0	0.4
Sant Celoni	CEL	27′41″	42′44″	845	21.2	9.3	90.4	0.0	8.9
Santa Coloma Sur	COLs	39′32″	51′48″	554	19.9	45.0	93.7	3.6	2.6
Santa Coloma Norte	COLn	37′52″	52′18″	425	18.7	19.1	92.6	3.7	3.4
Font del Regás	FR	27′00″	49′32″	929	24.5	12.7	99.7	0.0	0.2
Fuirosos	FUI	34′54″	42′14″	361	21.5	14.4	98.1	0.1	1.3
Gualba	GUA	30′17″	44′02″	940	22.6	13.5	96.0	0.6	2.1
Montbarbat	MB	46′54″	44′50″	182	10.8	0.4	8.7	91.0	0.0
Santa Fe	MON	27′42″	46′37″	1419	24.1	2.6	99.4	0.0	0.0
Residential Park	RES	42′08″	46′53″	122	6.9	0.8	27.7	57.2	15.0
Riells	RIE	32′50″	45′27″	716	19.9	15.3	96.1	0.6	3.1
Riudarenes	RIU	42′40″	50′15″	140	6.2	10.3	61.2	3.7	31.6

two orders of magnitude (0.7–45.0 km^2; Table 1). Average catchment slope was relatively similar (*c.* 20%) among most of the streams, except for four streams with slopes ≤11%. In nine of the 13 sub-catchments over 90% of the land was forested (Table 1). In the most disturbed streams, urban land use accounted for >50% of the land area in three catchments, and agricultural land use accounted for 15% and 32% of the land area in two catchments (Table 1). Highly urbanized streams drained the smallest catchments, located at low altitudes with minor slope (Table 1).

The first component of the catchment-PCA explained 68.8% of the variance (Fig. 1a), with a positive loading of percent urban area (0.91), and a negative loading of percent forested area (−0.98), slope (−0.91), altitude (−0.91) and total area (−0.79). The second component accounted for 25.0% of the variance (Fig. 1a), with a negative loading of percent agricultural area (−0.94). Finally, the third component accounted for only 4.0% of the variance, and no variable had a significant loading on it. Thus, the first component of the catchment-PCA indicated a gradient from forested- to urban-dominated catchments associated with concomitant changes in physiographical characteristics. The second component of the catchment-PCA indicated a gradient of agricultural development among catchments.

Stream environmental characteristics

Discharge (0.5–130.4 L s^{-1}), A_s/A (0.04–0.44), percent fine substratum (5.5–100%), conductivity (34–888 μS cm^{-1}) and daily PAR (1.7–19. 2 mol m^{-2} day^{-1}) varied over an order of magnitude among the study streams (Table 2). Water temperature was less variable (7.1–14.9 °C) and >10 °C in all streams except MON, the stream at the highest altitude. Concentrations of inorganic solutes (NO_3^- + NO_2^- [79–989 μg N L^{-1}], NH_4^+ [9–104 μg N L^{-1}] and SRP [0.4–26 μg P L^{-1}]) spanned wider ranges than those of organic solutes [DON (177–571 μg N L^{-1}) and DOC (0.6–3.9 mg L^{-1}); Table 2]. The range in mean daily percent DO saturation was relatively low (88.2–108%), and only four streams were oxygen supersaturated (i.e. DO saturation >100%; Table 2). Chlorophyll *a* per unit area of substratum varied >1 order of magnitude among streams (0.2–7.9 μg cm^{-2}; Table 2).

Table 2 Physical, chemical and biological characteristics of the study streams

Code	Discharge (L s^{-1})	A_s/A	Fine substratum (%)	Conductivity (μS cm^{-1})	PAR (mol m^{-2} day^{-1})	Temperature (°C)	NO_3^-+NO_2^- (μg N L^{-1})	NH_4^+ (μg N L^{-1})	DON (μg N L^{-1})	SRP (μg P L^{-1})	DOC (mg L^{-1})	DOsat (%)	Chlorophyll *a* (μg cm^{-2})
AGP	0.5	0.44	95.0	772	2.2	12.6	296	48	294	19	3.0	88.7	0.6
CAS	27.0	0.06	57.0	170	14.4	10.0	193	16	190	0.4	1.1	95.5	1.5
CEL	21.5	0.08	5.5	98	N/A	12.6	557	11	223	26	1.0	93.9	1.0
COLs	130.4	0.08	34.8	251	N/A	12.4	673	13	180	2	1.1	93.0	5.8
COLn	35.2	0.04	60.8	253	N/A	12.6	633	15	177	1	1.2	101.4	7.9
FR	48.1	0.10	57.0	172	7.2	10.1	79	13	189	1	0.6	108.4	0.5
FUI	12.8	0.05	57.9	170	N/A	11.5	79	9	290	0.4	1.5	100.8	1.0
GUA	65.4	0.07	21.1	85	14.1	12.9	115	10	195	0.5	0.9	98.0	1.2
MB	1.6	0.20	61.5	888	N/A	13.0	356	104	291	1	3.9	92.4	0.2
MON	48.6	0.13	8.2	34	15.4	7.1	115	14	207	2	0.6	97.2	1.1
RES	1.4	0.26	40.0	683	19.2	14.6	444	22	366	20	3.0	88.2	0.8
RIE	50.9	0.09	47.5	114	1.7	11.7	191	11	251	8	1.3	100.7	0.6
RIU	24.3	0.09	100.0	712	N/A	14.9	989	20	571	8	2.0	93.6	5.4

See Table 1 for site code.

A_s/A, relative transient storage; PAR, photosynthetically active radiation; NO_3^- + NO_2^-, nitrate + nitrite; NH_4^+, ammonium; DON, dissolved organic nitrogen; SRP, soluble reactive phosphorus; DOC, dissolved organic carbon; DOsat, dissolved oxygen saturation; N/A, data not available.

Table 3 Parameters of nutrient retention and metabolism in the study streams

	NH_4^+			SRP						
Code	S_w (m)	V_f (mm min^{-1})	U (μg N m^{-2} min^{-1})	S_w (m)	V_f (mm min^{-1})	U (μg P m^{-2} min^{-1})	GPP (g O_2 m^{-2} day^{-1})	ER (g O_2 m^{-2} day^{-1})	NEP (g O_2 m^{-2} day^{-1})	GPP/ER
AGP	335	0.2	8.3	145	0.4	7.3	0.11	0.28	−0.18	0.37
CAS	475	1.2	18.1	978	0.6	0.2	0.02	0.40	−0.39	0.04
CEL	476	1.0	11.7	1083	0.5	11.8	0.10	1.95	−1.85	0.05
COLs	158	6.9	89.5	391	2.8	5.6	0.48	1.00	−0.52	0.48
COLn	370	2.0	28.8	153	4.7	2.9	0.53	2.29	−1.76	0.23
FR	162	5.1	67.9	294	2.8	1.9	0.05	0.96	−0.91	0.05
FUI	173	1.4	12.1	441	0.5	0.2	0.85	0.71	0.15	1.21
GUA	249	3.2	30.6	502	1.6	0.7	0.57	1.22	−0.65	0.47
MB	238	0.5	47.5	64	1.7	1.5	0.01	0.41	−0.40	0.02
MON	162	5.0	68.0	655	1.2	2.0	0.25	1.34	−1.10	0.18
RES	104	1.0	23.4	62	1.8	35.7	1.19	2.42	−1.23	0.49
RIE	532	1.6	18.6	1171	0.7	6.2	0.15	0.34	−0.19	0.43
RIU	433	1.3	25.5	656	0.8	6.6	1.52	2.22	−0.70	0.68

See Table 1 for site code.

S_w, uptake length; V_f, uptake velocity; U, areal rate; GPP, gross primary production; ER, ecosystem respiration; NEP, net ecosystem production.

The first component of the stream-PCA explained 51.2% of the variance, with a positive loading of DOC (0.94), conductivity (0.89), NH_4^+ (0.79), DON (0.73) and A_s/A (0.73), and a negative loading of discharge (−0.84) and percent DO saturation (−0.77; Fig. 1b). The second component accounted for 18.6% of the variance, with a negative loading of chlorophyll *a* (−0.89; Fig. 1b). Finally, the third component accounted for 11.4% of the variance, but no variable had a significant loading on it.

The first components of both the catchment-PCA and the stream-PCA were positively related ($r^2 = 0.94$, $P < 0.001$; Fig. 2a); the variation among streams in hydraulic and chemical characteristics was related to the gradient from forested- to urban-dominated catchments. Similarly, the second components of both the catchment-PCA and the stream-PCA were positively related ($r^2 = 0.71$, $P < 0.001$; Fig. 2b); algal biomass increased along the gradient of agricultural development. No other relationship ($P \geq 0.762$) between catchment-PCA and stream-PCA components was found.

Stream functional characteristics

Streams were generally more retentive for NH_4^+ than for SRP (Table 3). Only in four streams, including the three most urbanized, S_w was shorter and V_f was higher for SRP than for NH_4^+. Similarly, only in the two streams showing the highest SRP concentrations, U was higher for SRP than for NH_4^+. The V_f s for NH_4^+ (0.2–6.9 mm min^{-1}) and SRP (0.4–4.7 mm min^{-1}) spanned similar ranges, and were positively correlated ($r = 0.57$, $P = 0.042$).

GPP and ER were also positively correlated ($r = 0.63$, $P = 0.020$). GPP (0.01–1.52 g O_2 m^{-2} day^{-1}) was lower than ER (0.28–2.42 g O_2 m^{-2} day^{-1}) in all streams except FUI, the only stream showing a positive NEP and a GPP/ER ratio >1 (Table 3). We found a marginally significant relationship ($r^2 = 0.26$, $P = 0.077$) between ER and U-SRP. No other relationship ($P \geq 0.141$) between metabolism parameters (i.e. GPP, ER, NEP, GPP/ER, TM) and retention parameters (U, V_f) was found for either nutrient.

V_f-NH_4^+ and the first component of the stream-PCA were negatively related ($r^2 = 0.63$, $P = 0.002$; Fig. 3a); demand for NH_4^+ decreased with stream hydraulic and chemical changes related to the degree of urbanization at the catchment scale. No relationship ($P \geq 0.457$) between the scores of the two stream-PCA components and V_f-SRP was found. GPP and the second component of the stream-PCA were negatively related ($r^2 = 0.34$, $P = 0.037$, Fig. 3b): GPP increased with increases in algal biomass related to the degree of agricultural development at the catchment scale. This relationship was only marginally significant for ER ($r^2 = 0.29$, $P = 0.060$, Fig. 3b). No relationship ($P \geq 0.148$) between the scores of the stream-PCA components and NEP, GPP/ER or TM was found.

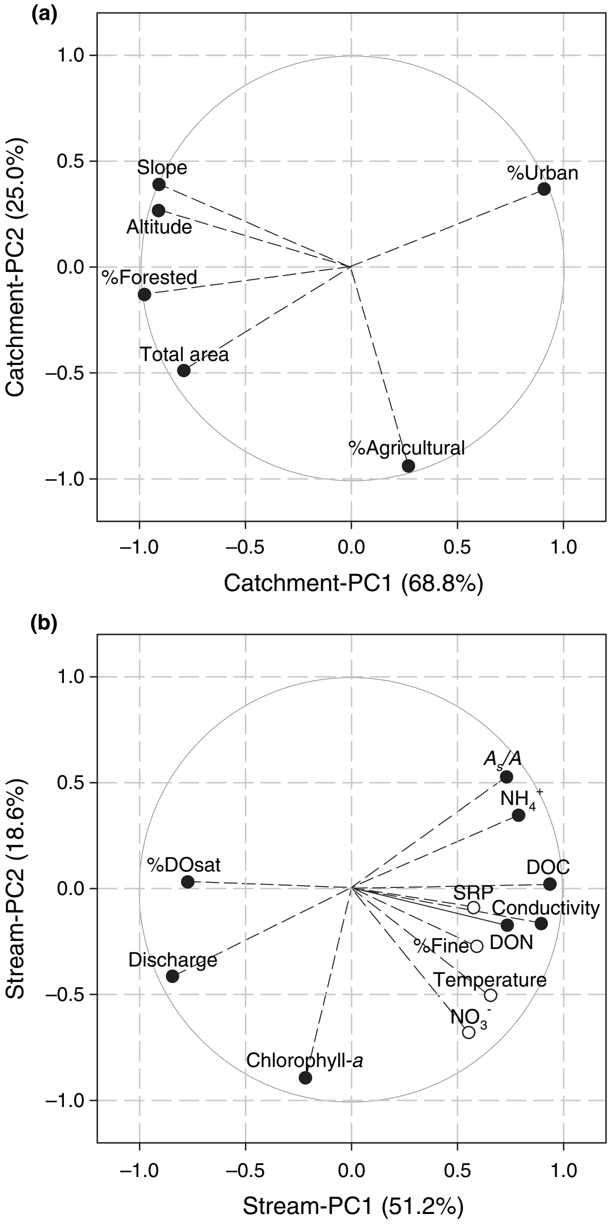

Fig. 1 Principal components analysis (PCA) of selected variables from two different hierarchical scales: (a) the catchment and (b) the stream. The percent values on each axis represent the amount of variance explained by each PCA component. Closed symbols denote significant variables (loading >0.7). See Tables 1 & 2 for a more detailed description of the variables included in each PCA.

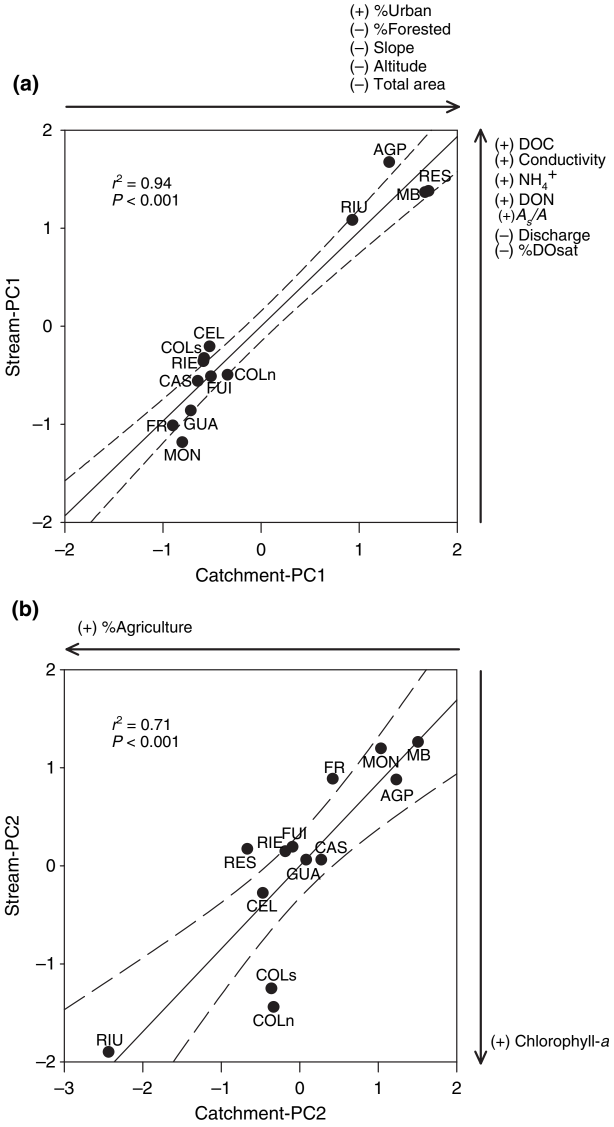

Fig. 2 (a) Linear regression between the scores of the first component of the catchment PCA (indicating a gradient from forested- to urban-dominated catchments) and the scores of first component of the stream PCA (indicating a gradient of stream chemical and hydraulic changes) and (b) Linear regression between the scores of the second component of the catchment PCA (indicating a gradient of catchment agricultural development) and the scores of the second component of the stream PCA (indicating a gradient of algal biomass). Significant variables (loading >0.7) associated with each PCA component are shown on the axes with their respective positive (+) or negative (−) weight. Dashed lines represent 95% confidence regression bands. Point labels correspond to the study streams ($n = 13$). See Table 1 for site code.

Discussion

Stream functional and environmental parameters were strongly related to catchment land use composition. Catchment signatures detected in streams varied depending on the type of land use. Nutrient demand, in particular for NH_4^+, was sensitive to catchment urbanization, whereas primary production and respiration were sensitive to agricultural

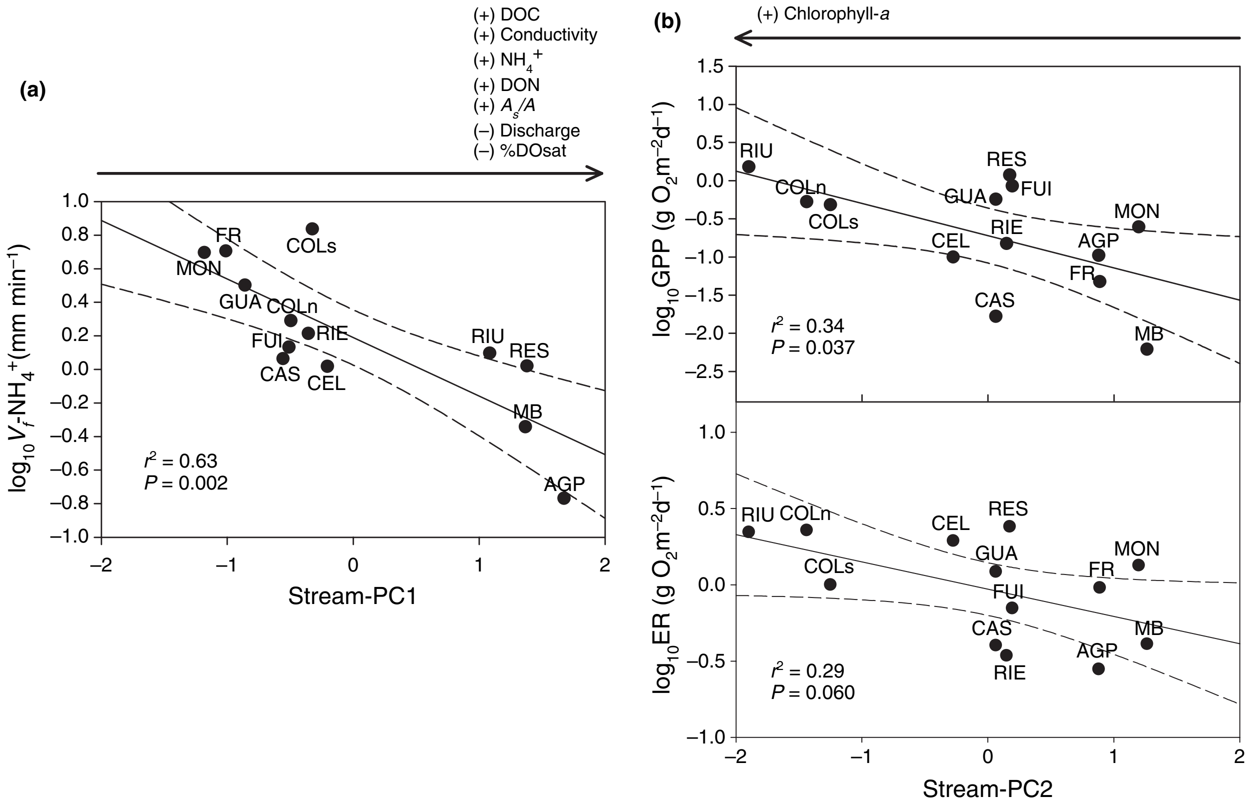

Fig. 3 (a) Linear regression between the scores of the first component of the stream PCA (indicating a gradient of stream chemical and hydraulic changes) and ammonium demand (V_f-NH_4^+) and (b) Linear regression between the scores of the second component of the stream PCA (indicating a gradient of algal biomass) and gross primary production (GPP) and ecosystem respiration (ER). Significant variables (loading >0.7) associated with each PCA component are shown on the axes with their respective positive (+) or negative (−) weight. Dashed lines represent 95% confidence regression bands. Point labels correspond to the study streams (n = 13). See Table 1 for site code.

development. A weak positive relationship between *U*-SRP and ER indicated some coupling between SRP retention and metabolism in these streams, supporting results from previous studies (e.g. Mulholland *et al.*, 1997; Newbold *et al.*, 2006). In contrast to results from other previous studies (e.g. Hall & Tank, 2003; Gücker & Pusch, 2006; Newbold *et al.*, 2006), we did not find a coupling between NH_4^+ retention and metabolism. Stoichiometric imbalances (i.e. differences in the relative availability of nutrients) and variation in abiotic (e.g. sorption, volatilization) and dissimilatory (e.g. nitrification, denitrification) uptake processes among streams may have blurred this relationship in our study, but our data do not allow us to test this hypothesis.

Altered stream hydraulic and chemical characteristics were observed along the gradient of catchment urbanization, the predominant type of land use transformation in our study. Stream water conductivity and concentrations of reduced forms of N (NH_4^+ and DON) and C (DOC) increased, while percent DO saturation decreased. These changes were likely a result of wastewater inputs from point and diffuse sources, which are characteristic of urban streams (Paul & Meyer, 2001; Kaplan *et al.*, 2006; Pellerin, Kaushal & McDowell, 2006). In addition, the more urbanized streams showed higher transient storage (A_s/A) and lower discharge, which enhanced the high solute concentrations in these streams by reducing their dilution capacity. Demand for NH_4^+ decreased with changes in these variables along the forested to urban gradient, but high levels of inter-correlation among them made it difficult to determine which were important in influencing this relationship. Some variables had the expected effect, while others had an effect opposite to that expected. For example, higher concentrations of both NH_4^+ and DON likely contributed to lower V_f-NH_4^+ through the saturation of the N uptake capacity (Newbold *et al.*, 2006). Higher DOC (Strauss & Lamberti, 2000) and lower oxygen (Rysgaard *et al.*, 1994) concentrations may have reduced V_f-NH_4^+ through the inhibition of nitrification. In contrast, higher A_s/A was expected to positively affect V_f-NH_4^+ by increasing the contact time of dissolved nutrients to biogeochemically active surfaces (e.g. backwaters, eddies, sediments; Gücker & Boëchat, 2004). The observed result, however, was the opposite, indicating that other mechanisms, such as nutrient saturation, may have overridden the influence of transient storage on NH_4^+ retention. Results from other empirical studies are also conflicting, with some showing no relationship between nutrient retention and transient storage (e.g. Webster *et al.*, 2003; Niyogi, Simon & Townsend, 2004; Meyer *et al.*, 2005; Roberts *et al.*, 2007), or a relationship opposite to that expected (e.g. Hall *et al.*, 2002; Valett, Crenshaw & Wagner, 2002). Although V_fs for both NH_4^+ and SRP were positively correlated across streams, V_f-SRP was not sensitive to the land use gradients. This result was likely due to the relatively low values and small range of SRP concentrations in comparison with dissolved N concentrations across the study streams. Only three streams showed concentrations >9 μg P L^{-1} and previous studies have demonstrated SRP uptake saturation at concentrations >5–13 μg P L^{-1} (Mulholland, Steinman & Elwood, 1990; Rosemond *et al.*, 2002; Newbold *et al.*, 2006). In addition, co-precipitation of SRP with calcium carbonate, which is an important abiotic removal process in calcareous streams, was probably negligible in the study streams due to the dominant siliceous geology (Reddy *et al.*, 1999).

Decreases in V_f due to increasing urbanization have been also reported from North American catchments. Meyer *et al.* (2005) found that demand for both NH_4^+ and SRP decreased as urbanization increased in streams located in Georgia (USA). The authors attributed this result to the decrease in fine benthic organic matter, an important resource for microbes, along the urbanization gradient. Similarly, in streams from the water-supply source areas of New York City (USA), demand for both NH_4^+ and SRP decreased from forested to more populated catchments mainly due to nutrient uptake saturation and possibly increases in toxic pollutants (Newbold *et al.*, 2006). Finally, in urbanized desert streams from the US Southwest, reduced areal NO_3^- uptake was attributed to reduced channel complexity and reduced primary production due to the presence of algaecides in stream water (Grimm *et al.*, 2005). Results from these streams, located in different biomes of North America, together with our own results from streams in the Mediterranean region indicate that, regardless of the bioclimatic setting, urbanization has a negative effect on stream nutrient retention, a key ecosystem service of streams.

Although there was only a small amount of land allocated to agriculture in this study, our results indicate that the effect of agriculture was primarily through increasing algal biomass and metabolism, including both GPP and ER. Chlorophyll *a* was the only stream environmental variable that significantly responded to the gradient of agricultural development. Both nutrients (Borchard, 1996) and light (Hill, 1996) limit algal growth in many streams. The lack of significant changes in nutrient concentrations along the agricultural gradient indicates that either nutrients were not responsible for the observed increases in algal biomass or excess nutrients were efficiently transferred up the food chain. Although we did not detect a relationship between PAR and chlorophyll *a* among the streams where data were available, results from previous studies have demonstrated the higher importance of light over nutrient limitation on algal growth in some of these streams (von Schiller *et al.*, 2007). GPP and ER were positively correlated and increased with algal biomass along the agricultural development gradient. Despite high nutrient concentrations and light availability, stream metabolism was dominated by respiration (i.e. negative NEP and GPP/ER <1) in all streams except FUI, supporting previous findings for headwater streams (reviewed by Battin *et al.*, 2008). Large patches of filamentous algae contributing to GPP peaks are typical in FUI during early spring (Acuña *et al.*, 2004).

High metabolism measurements associated with agriculture have been reported from previous studies. GPP increased with nutrient concentrations along an agricultural gradient located in the US Midwest (Bernot *et al.*, 2006). In the southern Appalachian Mountains (USA), GPP was higher in agricultural streams with little canopy cover but not in agricultural streams with well developed riparian forests, relative to streams draining forested catchments (McTammany, Benfield & Webster, 2007). Similarly, Young & Huryn (1999) in their study along a gradient of land use conversion to pasture located in New Zealand highlighted the effect of forest canopy on stream metabolism through its control on light availability and organic matter supply. Results from these and other studies (e.g. Bunn & Davies, 2000; Bott *et al.*, 2006) together with our own results indicate that stream metabolism may be more susceptible to human influences on proximate factors operating at a near-stream spatial scale (e.g. riparian vegetation removal) than on distant factors operating at a greater spatial scale (e.g. catchment land use).

This study demonstrates that whole-stream N retention and metabolism are sensitive to human land use pressures. Demand for NH_4^+ was mainly influenced by changes in nutrient availability related to the degree of catchment urbanization, whereas both GPP and ER were influenced by increases in algal biomass related to the degree of agricultural development at the catchment. Both nutrient availability and algal biomass have been used as indicators of trophic state in streams (Dodds, 2007). Our study corroborates the ecological link between these key structural variables and functional attributes of streams in the context of catchment disturbance. Furthermore, by considering the hierarchical organization of stream networks, our results illustrate the connections among factors operating at different spatial scales (i.e. from catchments to streams), and their relative influence on stream ecosystem function. Land management practices can have wide repercussions on the ecological condition of streams (including their functional capacity) at varying scales through diverse pathways and involving complex interactions (Martí *et al.*, 2006). Managers should take into consideration these connections when designing stream management and restoration plans.

Ecologically successful stream management and restoration is expected to restore function as well as structure to streams (Bernhardt & Palmer, 2007), requiring indicators of functional processes. Results from this and other studies have demonstrated that nutrient retention and metabolism parameters are good candidates to fill this gap. This study reports the first measurements of nutrient retention and metabolism in most of these Mediterranean streams. It thus provides a baseline for assessing the impact of further deterioration or the benefits of management practices in these streams and their catchments in the future, which can now be based on measurements of stream ecosystem function in addition to the more traditional biotic and nutrient status indexes.

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References

Acuña V., Giorgi A., Muñoz I., Uehlinger U. & Sabater S. (2004) Flow extremes and benthic organic matter shape the metabolism of a headwater Mediterranean stream. *Freshwater Biology*, **49**, 960–971.

Alexander R.B., Smith R.A. & Schwarz G.E. (2000) Effect of stream channel size on the delivery of nitrogen to the Gulf of Mexico. *Nature*, **403**, 758–761.

Allan J.D. (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. *Annual Review of Ecology and Systematics*, **35**, 257–284.

Alvarez-Cobelas M., Rojo C. & Angeler D.G. (2005) Mediterranean limnology: current status, gaps and the future. *Journal of Limnology*, **64**, 13–29.

APHA. (1995) *Standard Methods for the Examination of Water and Wastewater*, 19th edn. American Public Health Association, Washington.

Battin T.J., Kaplan L.A., Findlay S., Hopkinson C.S., Martí E., Packman A.I., Newbold J.D. & Sabater F. (2008) Biophysical controls on organic carbon fluxes in fluvial networks. *Nature Geoscience*, **1**, 95–100.

Bernhardt E.S. & Palmer M.A. (2007) Restoring streams in an urbanizing world. *Freshwater Biology*, **52**, 738–751.

Bernot M.J., Tank J.L., Royer T.V. & David M.B. (2006) Nutrient uptake in streams draining agricultural catchments of the midwestern United States. *Freshwater Biology*, **51**, 499–509.

Borchard M.A. (1996) Nutrients. In: *Algal Ecology* (Eds R.J. Stevenson, M.L. Bothwell & R.L. Lowe), pp. 183–227. Academic Press, San Diego.

Bott T.L. (2006) Primary productivity and community respiration. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 663–690. Academic Press, San Diego.

Bott T.L., Montgomery D.S., Newbold J.D., Arscott D.B., Dow C.L., Aufdenkampe A.K., Jackson J.K. & Kaplan L.A. (2006) Ecosystem metabolism in streams of the

Catskill Mountains (Delaware and Hudson River watersheds) and Lower Hudson Valley. *Journal of the North American Benthological Society*, **25**, 1018–1044.

Bukaveckas P.A. (2007) Effects of channel restoration on water velocity, transient storage, and nutrient uptake in a channelized stream. *Environmental Science & Technology*, **41**, 1570–1576.

Bunn S.E. & Davies P.M. (2000) Biological processes in running waters and their implications for the assessment of ecological integrity. *Hydrobiologia*, **422/423**, 61–70.

Bunn S.E., Davies P.M. & Mosisch T.D. (1999) Ecosystem measures of river health and their response to riparian and catchment degradation. *Freshwater Biology*, **41**, 333–345.

Dodds W.K. (2007) Trophic state, eutrophication and nutrient criteria in streams. *Trends in Ecology & Evolution*, **22**, 669–676.

Fellows C.S., Clapcott J.E., Udy J.W., Bunn S.E. & Harch B.D. (2006) Benthic metabolism as an indicator of stream ecosystem health. *Hydrobiologia*, **572**, 71–87.

Frissell C.A., Liss W.J., Warren C.E. & Hurley M.D. (1986) A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management*, **10**, 199–214.

Gessner M.O. & Chauvet E. (2002) A case for using litter breakdown to assess functional stream integrity. *Ecological Applications*, **12**, 498–510.

Grimm N.B., Sheibley R.W., Crenshaw C.L., Dahm C.N., Roach W.J. & Zeglin L.H. (2005) N retention and transformation in urban streams. *Journal of the North American Benthological Society*, **24**, 626–642.

Gücker B. & Boëchat I.G. (2004) Stream morphology controls ammonium retention in tropical headwaters. *Ecology*, **85**, 2818–2827.

Gücker B. & Pusch M.T. (2006) Regulation of nutrient uptake in eutrophic lowland streams. *Limnology and Oceanography*, **51**, 1443–1453.

Hall R.O. & Tank J.L. (2003) Ecosystem metabolism controls nitrogen uptake in streams in Grand Teton National Park, Wyoming. *Limnology and Oceanography*, **48**, 1120–1128.

Hall R.O., Bernhardt E.S. & Likens G.E. (2002) Relating nutrient uptake with transient storage in forested mountain streams. *Limnology and Oceanography*, **47**, 255–265.

Hill W.R. (1996) Effects of light. In: *Algal Ecology* (Eds R.J. Stevenson, M.L. Bothwell & R.L. Lowe), pp. 121–148. Academic Press, San Diego.

Houser J.N., Mulholland P.J. & Maloney K.O. (2005) Catchment disturbance and stream metabolism: patterns in ecosystem respiration and gross primary production along a gradient of upland soil and vegetation disturbance. *Journal of the North American Benthological Society*, **24**, 538–552.

Kaplan L.A., Newbold J.D., van Horn D.J., Dow C.L., Aufdenkampe A.K. & Jackson J.K. (2006) Organic matter transport in New York City drinking-water-supply watersheds. *Journal of the North American Benthological Society*, **25**, 912–927.

Lottig N.R., Valett H.M., Schreiber M.E. & Webster J.R. (2007) Flooding and arsenic contamination: influences on ecosystem structure and function in an Appalachian headwater stream. *Limnology and Oceanography*, **52**, 1991–2001.

Martí E., Aumatell J., Godé L., Poch M. & Sabater F. (2004) Nutrient retention efficiency in streams receiving inputs from wastewater treatment plants. *Journal of Environmental Quality*, **33**, 285–293.

Martí E., Sabater F., Riera J.L., Merseburger G.C., von Schiller D., Argerich A., Caille F. & Fonollá P. (2006) Fluvial nutrient dynamics in a humanized landscape. Insights from a hierarchical perspective. *Limnetica*, **25**, 513–526.

McTammany M.E., Benfield E.F. & Webster J.R. (2007) Recovery of stream ecosystem metabolism from historical agriculture. *Journal of the North American Benthological Society*, **26**, 532–545.

Meyer J.L., Paul M.J. & Taulbee W.K. (2005) Stream ecosystem function in urbanizing landscapes. *Journal of the North American Benthological Society*, **24**, 602–612.

Mulholland P.J., Steinman A.D. & Elwood J.W. (1990) Measurement of phosphorus uptake length in streams: comparison of radiotracer and stable PO_4 releases. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 2351–2357.

Mulholland P.J., Marzolf E.R., Webster J.R., Hart D.R. & Hendricks S.P. (1997) Evidence that hyporheic zones increase heterotrophic metabolism and phosphorus uptake in forest Streams. *Limnology and Oceanography*, **42**, 443–451.

Mulholland P.J., Tank J.L., Webster J.R. *et al.* (2002) Can uptake length in streams be determined by nutrient addition experiments? Results from an interbiome comparison study. *Journal of the North American Benthological Society*, **21**, 544–560.

Newbold J.D., Elwood J.W., O'Neill R.V. & van Winkle W. (1981) Measuring nutrient spiralling in streams. *Canadian Journal of Fisheries and Aquatic Sciences*, **38**, 860–863.

Newbold J.D., Bott T.L., Kaplan L.A., Dow C.L., Jackson J.K., Aufdenkampe A.K., Martin L.A., Van Horn D.J. & de Long A.A. (2006) Uptake of nutrients and organic C in streams in New York City drinking-water-supply watersheds. *Journal of the North American Benthological Society*, **25**, 998–1017.

Niyogi D.K., Simon K.S. & Townsend C.R. (2004) Land use and stream ecosystem functioning: nutrient uptake in streams that contrast in agricultural development. *Archiv für Hydrobiologie*, **160**, 471–486.

Palmer M., Bernhardt E., Chornesky E. *et al.* (2004) Ecology for a crowded planet. *Science*, **304**, 1251–1252.

Paul M.J. & Meyer J.L. (2001) Streams in the urban landscape. *Annual Review of Ecology and Systematics*, **32**, 333–365.

Payn R.A., Webster J.R., Mulholland P.J., Valett H.M. & Dodds W.K. (2005) Estimation of stream nutrient uptake from nutrient addition experiments. *Limnology and Oceanography Methods*, **3**, 174–182.

Pellerin B.A., Kaushal S.S. & McDowell W.H. (2006) Does anthropogenic nitrogen enrichment increase organic nitrogen concentrations in runoff from forested and human-dominated watersheds? *Ecosystems*, **9**, 852–864.

Reddy K.R., Kadlec R.H., Flaig E. & Gale P.M. (1999) Phosphorus retention in streams and wetlands: a review. *Critical Reviews in Environmental Science and Technology*, **29**, 83–146.

Roberts B.J., Mulholland P.J. & Houser J.N. (2007) Effects of upland disturbance and instream restoration on hydrodynamics and ammonium uptake in headwater streams. *Journal of the North American Benthological Society*, **26**, 38–53.

Rosemond A.D., Pringle C.M., Ramírez A., Paul M.J. & Meyer J.L. (2002) Landscape variation in phosphorus concentration and effects on detritus-based tropical streams. *Limnology and Oceanography*, **47**, 278–289.

Runkel R.L. (1998) *One Dimensional Transport with Inflow and Storage (OTIS): A Solute Transport Model for Streams and Rivers*. Water Resources Investigations Report 98-4018. U.S. Geological Survey, Denver, CO, U.S.A.

Rysgaard S., Risgaard-Petersen N., Sloth N.P., Jensen K. & Nielsen L.P. (1994) Oxygen regulation of nitrification and denitrification in sediments. *Limnology and Oceanography*, **39**, 1643–1652.

Sabater F., Butturini A., Martí E., Munoz I.., Romani A., Wray J. & Sabater S. (2000) Effects of riparian vegetation removal on nutrient retention in a Mediterranean stream. *Journal of the North American Benthological Society*, **19**, 609–620.

von Schiller D., Martí E., Riera J.L. & Sabater F. (2007) Effects of nutrients and light on periphyton biomass and nitrogen uptake in Mediterranean streams with contrasting land uses. *Freshwater Biology*, **52**, 891–906.

Steinman A.D., Lamberti G.A. & Leavitt P.R. (2006) Biomass and pigments of benthic algae. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 357–379. Academic Press, San Diego.

Strauss E.A. & Lamberti G.A. (2000) Regulation of nitrification in aquatic sediments by organic carbon. *Limnology and Oceanography*, **45**, 1854–1859.

Sweeney B.W., Bott T.L., Jackson J.K., Kaplan L.A., Newbold J.D., Standley L.J., Hession W.C. & Horwitz R.J. (2004) Riparian deforestation, stream narrowing, and loss of stream ecosystem services. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 14132–14137.

Valett H.M., Crenshaw C.L. & Wagner P.F. (2002) Stream nutrient uptake, forest succession and biogeochemical theory. *Ecology*, **83**, 2888–2901.

Vighi M., Finizio A. & Villa S. (2006) The evolution of the environmental quality concept: from the US EPA Red Book to the European Water Framework Directive. *Environmental Science and Pollution Research*, **13**, 9–14.

Webster J.R. & Valett H.M. (2006) Solute dynamics. In: *Methods in Stream Ecology* (Eds F.R. Hauer & G.A. Lamberti), pp. 169–185. Academic Press, San Diego.

Webster J.R., Mulholland P.J., Tank J.L. *et al.* (2003) Factors affecting ammonium uptake in streams - an inter-biome perspective. *Freshwater Biology*, **48**, 1329–1352.

Young R.G. & Huryn A.D. (1996) Interannual variation in discharge controls ecosystem metabolism along a grassland river continuum. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 2199.

Young R.G. & Huryn A.D. (1999) Effects of land use on stream metabolism and organic matter turnover. *Ecological Applications*, **9**, 1359–1376.

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