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Forest canopy cover determines invertebrate diversity and ecosystem process rates in depositional zones of headwater streams

EVE DE NADAÏ-MONOURY*,†, FRANCK GILBERT*,† AND ANTOINE LECERF*,†
*Université de Toulouse; INP, UPS; EcoLab (Laboratoire Ecologie Fonctionnelle et Environnement); 118 Route de Narbonne, 31062 Toulouse, France
†CNRS; EcoLab; 31062 Toulouse, France

SUMMARY

1. Previous studies of the ecological linkages between forest and headwater streams have focussed primarily on patterns and processes in erosional habitats, typically riffles. Depositional zones trap large amounts of sediments and particulate organic matter, suggesting that they may be important for forest–stream linkages.
2. We studied the invertebrate benthos and two key ecological processes, surface sediment reworking and leaf litter breakdown, in the depositional zones of streams bordered by contrasting riparian vegetation. We compared three stream reaches, draining open canopy forest regenerating after recent clearcut harvesting, with reaches on three different streams bordered by older forests with closed canopies. We also assessed whether, and to what extent, forest canopy cover determined abiotic factors at the reach scale (physicochemistry of stream water) and patch scale (sediment properties).
3. Depositional zones in both types of stream harboured a taxonomically and functionally diverse invertebrate community, including efficient sediment reworkers and specialised shredders. Higher diversity was found in open canopy than in closed canopy streams, despite similarities in habitat morphology and sediment properties.
4. Water temperature and sediment reworking rate were higher in open canopy forest than in closed canopy forest. As rates of sediment reworking, adjusted for temperature, did not differ between forest types, temperature was probably a key factor linking the forest canopy to stream depositional zones. The rates of leaf litter breakdown sometimes varied substantially between streams, but no consistent forest effect was detected for this process.
5. Temperature-adjusted rates of surface sediment reworking and litter breakdown were positively correlated with the density of invertebrates that rework sediments and shredders, respectively. A relationship between these two ecological processes was found across depositional zones in closed canopy forest, but not in open canopy forest.
6. This study on depositional zones provides new evidence of the strong linkage between forest and headwater streams. By moderating stream summer temperature, riparian canopy cover has the potential to affect invertebrate metabolic rates and, indirectly, the intensity of surface sediment reworking. However, other factors, such as the quality and diversity of basal trophic resources, may also account for invertebrate diversity pattern across streams and the positive relationship between litter breakdown and sediment reworking in closed canopy forest.

Keywords: benthic invertebrates, bioturbation, ecosystem functioning, litter breakdown, sediment reworking

Correspondence: Université de Toulouse; INP, UPS; EcoLab (Laboratoire Ecologie Fonctionnelle et Environnement); 118 Route de Narbonne, 31062 Toulouse, France. E-mail: eve.monoury@gmail.com

Introduction

Stream ecologists have long recognised the powerful influence of land on aquatic ecosystems (e.g. Cummins, 1974). The River Continuum Concept (RCC), a pivotal theory in stream ecology for the last three decades, proposes that channel morphology and riparian vegetation concomitantly determine the structural and functional attributes of lotic communities along river networks (Vannote *et al.*, 1980). In low-order headwater streams, riparian forest canopy regulates water temperature (Moore, Spittlehouse & Story, 2005) and instream primary production (Kiffney, Richardson & Bull, 2004) through light interception and provides allochthonous organic matter used as food and habitat by aquatic consumers (Bilby & Likens, 1980; Wallace *et al.*, 1997). Forest also controls stream hydrology, water chemistry, channel morphology and substratum particle size (Naiman & Decamps, 1997). Thus, by affecting habitat features and trophic resources, changes in forest age, canopy structure and plant communities have the potential to modify substantially the composition of stream communities and the functional role they play in ecosystems (e.g. Stout, Benfield & Webster, 1993; Stone & Wallace, 1998).

Based on the RCC, it would be expected that the local influence of riparian forest on stream ecosystems would decrease as we move downstream to wider channels. Empirical evidence further indicates that the strength of forest–stream linkages may also depend on the type of habitat in headwater streams. In the 'Coweeta litter exclusion experiment', a strong treatment effect was found for invertebrate assemblages on mixed substrata, but not on moss-covered bedrock (Wallace *et al.*, 1997). Similarly, Stone & Wallace (1998) found that, compared to bedrock, riffles and depositional areas are more sensitive to long-term effects of forest disturbance and plant succession on stream invertebrates. By determining the storage and export of allochthonous organic matter and sediments, and by acting as a filter on species traits, local geomorphological and hydraulic factors may alter the dependence of benthic communities upon riparian zones. However, because streambed erosion and sediment transport dominate geomorphological processes in low-order headwater streams, knowledge of forest–stream linkages has relied primarily on empirical data from samples taken in erosional habitats such as riffles. In contrast, little effort has been made to investigate ecological effects of forest changes on depositional zones characterised by low shear stress, a fine substratum and a high standing stock of particulate organic matter (Metzler & Smock, 1990).

Depositional zones contribute to stream biodiversity by hosting specialised invertebrate taxa such as burrowers and shredders (Wagner, 1991; Lloyd & Ormerod, 1992; Dangles, 2002b) and by offering refuges to rheophilic animals during spates (Lancaster & Hildrew, 1993). Stream invertebrates drive many key ecosystem-level processes (Covich, Palmer & Crowl, 1999; Wallace & Hutchens, 2000). Studies on leaf litter breakdown have shed light on the major contribution of shredders to the conversion of leaf litter into finer particles and biomass (Cuffney, Wallace & Lugthart, 1990). Leaf consumption by shredders can account for more than 50% of leaf mass loss (Hieber & Gessner, 2002), and some investigators have reported that depositional zones are hotspots of leaf breakdown when the density of efficient shredders peaks (Kobayashi & Kagaya, 2005). Benthic fauna are also geomorphological agents in these habitats due to low current velocity outside flood events, soft sediment and the abundance of interstitial and burrowing invertebrates (Moore, 2006). Invertebrates can displace particles (sediment reworking) and facilitate the transport of solutes and dissolved gases (ventilation) at the surface and within sediments (Mermillod-Blondin & Rosenberg, 2006; Kristensen *et al.*, 2012). Sediment reworking has been shown to influence indirectly benthic community structure and the rates of carbon and nutrient flows and transformation in ecosystems (Mermillod-Blondin *et al.*, 2003; Covich *et al.*, 2004; Creed, Taylor & Pflaum, 2010; Mermillod-Blondin, 2011; Statzner, 2012).

The rates of sediment bioturbation and litter breakdown should be related when shredders are also capable of sediment reworking. For instance, Creed *et al.* (2010) reported that the excavation behaviour of the limnephilid caddis *Pycnopsyche gentilis* substantially increases the breakdown of buried leaf litter in sand. The two processes are also potentially mutually linked through nutrient and energy flows. Bioturbation can promote the conditioning and mineralisation of leaf litter by microbial decomposers through enhanced nutrient transfer from sediment to leaf litter (Mermillod-Blondin, 2011; Hunting *et al.*, 2012). Conversely, as stream invertebrates meet their energy needs by the consumption of leaf litter, litter-derived FPOM or detritivorous prey (Wallace *et al.*, 1997), the abundance and activity of reworkers may be limited by the rate at which energy is released from leaf litter during breakdown.

Sediment reworking is not easy to quantify in lotic ecosystems, explaining why its ecological importance remains poorly appreciated in streams (Statzner, 2012). To overcome methodological barriers, we developed a procedure to assess the rate of surface sediment

reworking by benthic fauna in the shallow and soft sediments of stream depositional zones (De Nadaï-Monoury *et al*., 2013). This method is based on optical quantification of the area covered by tracers added to the bed. It can be applied *in situ* to examine the biotic (e.g. density, diversity and community structure of benthic invertebrates) and abiotic (e.g. temperature and sediment properties) factors controlling sediment bioturbation in ecosystems (Ouellette *et al*., 2004; Duport *et al*., 2006; Statzner, 2012).

Here, we attempted a fresh approach to the study of forest–stream linkages by focussing on patterns and processes in depositional zones in streams draining forests of contrasting age and riparian canopy cover. Specifically, we compared streams in closed canopy forests with others running through young forests regenerating after recent clearcut harvesting. Benthic invertebrate were expected to differ between stream categories in response to contrasting chemical and physical environment. In turn, biotic and abiotic factors may mediate forest effect on sediment bioturbation and litter breakdown. While we predicted that process rates would be greater in open than in closed canopy streams, notably due to differences in water temperature, this expectation could be confounded by the response of invertebrate reworkers and/or shredders to other abiotic factors (e.g. sediment properties). We also hypothesised that rates of sediment reworking and litter breakdown would be positively related as these processes may be regulated by the same ecological factors and/or they may influence each other.

Methods

Study streams

This study was carried out in the Montagne Noire, a forested area drained by a dense network of headwater streams *c*. 50 km east of Toulouse, south-western France (43°33′N, 1°29′E). Three stream reaches running through open canopy forest were compared with three paired control streams bordered exclusively by closed canopy (>30-year-old) broadleaf forests (closed canopy forest) (Table 1). Open canopy forests have been established by recent (*c*. 5-year-old) clearcut harvesting in both upland and riparian areas on both banks of the stream. Stream length affected by logging ranged from 250 to 550 m. Harvesting operations were carried out to limit both streambed destruction by harvesting machines and fine sediment transported by surface water. Since no forested buffer strips were left along either side of the streams, the riparian vegetation along open streams comprised early-successional species, that is, herbaceous vegetation, young trees (*Salix* spp., *Populus* spp., *Fraxinus* sp., *Alnus glutinosa*), coppice (*Corylus avellana*) and an understorey

Table 1 Description of the three pairs of stream reaches included in this study. Each pair consisted of a stream running in closed canopy forest (CCF) and a similar stream running in open canopy forest (OCF). Mean and SE are given for canopy cover (n = 5 depositional zones), water temperature (n = 15 daily mean values) and water chemistry (n = 5 sampling occasions). Concentrations of dissolved carbon and nutrients were all above the detection limits of analytical methods

Parameter	Pair 1		Pair 2		Pair 3	
Code	P1-CCF	P1-OCF	P2-CCF	P2-OCF	P3-CCF	P3-OCF
Name	Lampy	Bergnassonne	Sant	Bernazobre	Orival	Montaud
Riparian vegetation type	Closed canopy	Open canopy	Closed canopy	Open canopy	Closed canopy	Open canopy
Stream attributes						
Latitude N	43°25′07″	43°23′50″	43°27′48″	43°29′07″	43°26′18″	43°29′52″
Longitude E	2°11′15″	2°12′01″	2°12′06″	2°12′40″	2°05′41″	2°15′58″
Altitude (m. a.s.l.)	705	630	565	320	475	330
Catchment area (km²)	1.2	2.1	3.4	5.6	2.3	4.0
Forested area cut (km²)	–	0.07	–	0.04	–	0.05
Width (m)	1.6–2.4	1.4–2.8	2.6–5.3	2.1–4.6	1.5–5.5	2.3–3.6
Canopy cover (% open)	12.4 ± 1.1	45.2 ± 6.6	10.7 ± 2.5	38.9 ± 9.1	3.5 ± 0.7	38.4 ± 4.5
Water characteristics						
Temperature (°C)	12.5 ± 0.04	14.6 ± 0.07	14.5 ± 0.04	14.7 ± 0.05	12.8 ± 0.05	15.4 ± 0.05
pH	6.9 ± 0.1	7.1 ± 0.1	7.8 ± 0.2	7.9 ± 0.1	7.6 ± 0.1	7.2 ± 0.1
Conductivity (μS cm^{-1})	48.2 ± 0.9	40.2 ± 1.8	116.5 ± 8.9	114.6 ± 4.0	72.9 ± 1.6	49.2 ± 1.4
[NO_3] (μg N L^{-1})	2002 ± 241	796 ± 98	1729 ± 93	1166 ± 64	1547 ± 98	1186 ± 108
[PO_4] (μg P L^{-1})	1.41 ± 0.50	1.22 ± 0.51	8.14 ± 2.39	8.14 ± 3.17	4.76 ± 1.20	7.63 ± 2.75
[DOC] (μg C L^{-1})	1438 ± 331	2007 ± 430	1146 ± 273	677 ± 83	3713 ± 1250	1922 ± 315

(*Rubus* spp.). Our surveys were carried out along a 50-m reach of each stream, on the lower third section of the harvested reach in each case. Each open reach was paired with a reach on a nearby (<10 km) stream with similar chemical and physical attributes but running exclusively through closed canopy forest. These stream reaches were heavily shaded during growing season, predominantly by deciduous beech (*Fagus sylvatica*) and oak (*Quercus* spp.) (Lecerf *et al.*, 2005).

Water chemistry and temperature

Water chemistry was determined on five occasions in 2011. Specific conductivity (μS cm^{-1} at 25 °C) and pH were measured in the field using multiparameter probes (Multi 340i, WTW). Filtered (Whatman GF/F glass fibre filter) water samples were returned to the laboratory to determine concentrations of nitrate (liquid chromatography; Dionex®; Thermo Fisher Scientific Inc., Waltham, MA, U.S.A.), soluble reactive phosphorus (automated continuous-flow colorimetric analyser; ALPKEM Corporation, Clackamas, OR, U.S.A.) and dissolved organic carbon (DOC analyser TOC 5000; Shimadzu Scientific Instruments, Inc., Columbia, MD, U.S.A.). Throughout the sediment reworking and litter breakdown experiments, water temperature was recorded every 30 min using HOBO Pendant® (Onset Computer Corporation, Cape Cod, MA, U.S.A.) data loggers.

Habitat description

Along each of the six streams, we selected five benthic habitat patches larger than 0.04 m^2 composed primarily of fine-grain sediments (typically sands) with very low water velocity (typically <0.05 m s^{-1}) outside flood events. The canopy cover over these depositional zones, their morphology (total area and mean water depth) and sediment characteristics (granulometry, organic matter and chlorophyll-*a* content) were determined at the end of the study (July 2011). Canopy cover was quantified from hemispherical images taken vertically upwards from depositional zones using a digital camera equipped with a SIGMA 4.5 mm F2.8 EX DC circular fisheye lens (Lecerf *et al.*, 2012). Gap Light Analyser v2 (http://www.ecostudies.org/gla/) software was used to assess percentage gap area, our estimate of cover, over a zenith angle range of 0–45°. In each depositional zone, three sediment samples were collected using a 5-cm-long corer (a 14-cm-internal-diameter PVC pipe). Sediment grain size distribution was determined following Wentworth (1922): 0–62.5 μm = 'silt', 62.5–125 μm = 'very fine', 125–250 μm = 'fine', 250–500 μm = 'medium', 500–1000 μm = 'coarse', >1000 μm = 'very coarse'. Sediments were first passed through a 1-mm mesh sieve, and the sizes of both fractions (i.e. passing through the sieve or not) were quantified on a volumetric basis. The finest (<1 mm) fraction was then analysed using a laser diffraction particle size analyser (Master sizer 2000, Malvern, U.K.). Organic matter content in sediment samples was determined in the laboratory using the loss-on-ignition method (550 °C for 6 h). The cover of a 55-mm Petri dish was used for sampling surface sediment (71.2 cm^2, 1 cm deep, three replicates) in the field. These samples were later analysed for chlorophyll-*a* content with a spectrophotometric method after freeze drying and pigment extraction in 90% acetone (Steinman, Lamberti & Leavitt, 2006).

Surface sediment reworking

The rate of surface sediment reworking in depositional zones was determined using inert particulate fluorescent tracers (luminophores; Partrac Ltd., Glasgow, UK) added onto the stream bottom following the method of De Nadaï-Monoury *et al.* (2013). Tracer size range (300–800 μm) was chosen to match the grain size distribution of natural sediments. A fraction (283.5 cm^2, 1–70%) of the area covered by each depositional zone (n = 30) was isolated from the rest of the stream using a PVC pipe (20 cm outer diameter and 30 cm length) set upright and inserted *c.* 7 cm deep into the sediment. The top of each pipe was 10–15 cm above the water surface so as to prevent overflow and to facilitate digital image capture. A large opening (21 cm long, 3.5 cm height) in the side of the pipe, covered by a 250-μm nylon mesh net, was made at mid-height of the submerged part of the pipes to ensure water renewal while limiting the exchange of macroinvertebrates. These 'arenas' were secured by iron stakes driven into the stream bed.

Surface sediment reworking was quantified as the rate at which luminophores disappeared from the sediment surface assuming that tracers undergo the same fauna-induced movements as sediment particles. Results from a laboratory microcosm experiments indicated that, in the absence of fauna, disappearance of the tracer from the sediment surface was negligible. Although this assumption might not be fully verified under natural conditions, bioturbation determination was conducted during low flow, when the contribution of physical forces to particle displacement is minimal. A thin (*c.* 2 mm) and uniform layer of orange luminophores was added into arenas at the beginning of the experiment, and the surface

occupied by optical tracers was determined from digital images taken on days 0, 4, 8, 11 and 15 (De Nadaï-Monoury *et al.*, 2013). Pictures were taken under ultraviolet light (λ: 365 nm) using an 8.2 Mpixel digital camera (Canon EOS 20D, Tokyo, Japan) mounted on a tripod. The dark condition required for the use of portable UV light was ensured by wrapping an opaque cloth over the microcosm and camera. Image-Pro Plus (MediaCybernetics Inc., Rockville, MD, U.S.A.) was used to quantify the areas occupied by luminophores and stream sediments after extraction of the red channel and thresholding of each picture.

At the end of this experiment, the sediments and associated fauna within arenas were sampled to a depth of 10 cm, and the organic fraction composed of particulate organic matter and macroinvertebrates were elutriated and preserved in 70% ethanol. In the laboratory, invertebrates were counted and identified to the lowest practicable level under a dissecting microscope. Invertebrates with strong sediment reworking abilities (burrowers or crawlers with an interstitial habit) were distinguished from others (maximal aquatic stage size <10 mm with low mobility and/or weak association with fine sediments) based on functional traits (Tachet *et al.*, 2010). In our streams, *Ephemera* sp., *Odontocerum albicorne*, *Sericostoma* sp., *Cordulegaster* sp., *Sialis* sp., *Dicranota* sp., *Hexatoma* sp., *Glossiphonia* sp. and Bivalvia met these criteria and were subsequently classified as sediment reworkers. Other invertebrates with strong affinities with interstitial habitats, typically Chironomidae which were numerically dominant in our samples, were assumed to contribute little to surface sediment reworking due to their small size (Chironomidae body length <2 mm) and a high proportion of coarse and very coarse sand in the depositional zones studied here (Table 2).

Litter breakdown

A leaf litter breakdown experiment was conducted in parallel to the sediment reworking experiment. We constructed 10-mm plastic mesh bags filled with 5.00 ± 0.01 g (mean ± min-max) of air-dried leaves of alder (*Alnus glutinosa*) collected at abscission. Litter bags, one per depositional zone (n = 30), were deployed in the stream sites at the beginning of the sediment reworking experiment and recovered 15 days later. Litter bags were stored individually in plastic zip-lock bags and kept (<6 h) at stream temperature until processing. In the laboratory, the leaves were rinsed with tap water to remove sediment and dried at 60 °C for 72 h. Remaining leaf material was weighed to the nearest 0.01 g. Leaf mass remaining in the bags was expressed as the ratio of final to initial litter dry mass corrected for mass loss due to handling (determined using five extra litter bags).

Leaf-colonising invertebrates were collected onto a 500-μm mesh sieve and preserved in 90% ethanol. After counting and identification, the invertebrates were assigned to shredder and non-shredder groups based on the literature (Tachet *et al.*, 2010).

Statistical analyses

Habitat features determined in each depositional zone (zone area, water depth, organic matter content, chlorophyll-*a* content and the relative contributions of each sediment size class) were summarised using a normalised principal component analysis (PCA). Variable weights were set to give equal importance to sediment granulometry determined based on six classes (weights = 1/6) and to other habitat attributes, each based on a single quantitative variable (weight = 1).

Table 2 Description of depositional zones of streams in closed canopy forest (CCF) and open canopy forest (OCF). The range of values (n = 5) for each stream is given

	Pair 1		Pair 2		Pair 3	
Parameter	P1-CCF	P1-OCF	P2-CCF	P2-OCF	P3-CCF	P3-OCF
Water depth (m)	0.1–0.5	0.1–0.2	0.1–0.4	0.1–0.3	0.2–0.5	0.1–0.3
Area (m²)	0.04–3.00	0.24–1.98	0.40–2.10	0.24–1.95	1.00–2.28	0.44–0.91
Chlorophyll-*a* (mg m^{-2})	42.7–72.5	38.8–84.6	30.1–119.5	32.5–115.2	7.4–30.0	23.8–39.5
Organic matter (kg m^{-3})	14.8–26.3	14.3–18.6	35.9–57.7	34.8–60.8	15.5–30.0	13.9–34.2
Silt (%)	4.8–8.2	2.8–4.9	12.7–16.0	12.3–25.0	3.8–7.6	8.2–9.3
Very fine (%)	2.9–6.1	2.1–4.4	8.0–13.4	5.7–15.8	2.3–4.8	9.3–13.3
Fine (%)	5.5–11.2	3.1–5.9	10.7–17.6	5.7–17.8	2.8–7.1	13.8–22.6
Medium (%)	18.7–23.9	13.4–20.4	10.6–19.9	12.2–22.1	9.3–18.8	17.3–25.9
Coarse (%)	17.8–23.9	19.7–30.6	8.3–16.0	10.2–19.4	9.0–21.5	10.6–19.7
Very coarse (%)	28.2–46.2	36.5–58.9	18.6–47.1	8.3–43.5	45.1–63.3	12.5–36.0

The fraction of surface area occupied by tracers declined exponentially throughout the surface sediment reworking experiment. Surface sediment reworking rate (*SSR*) in each depositional zone was thus estimated as the slope of the linear regression of the ln-transformed fraction of area occupied by tracers *versus* time (days) with the intercept forced to ln (1). Values of R^2 ranged from 0.77 to 0.87, indicating a good model fit across all depositional zones. The breakdown rate of alder litter was calculated as follows: $k = -\ln(R)/t$, where R is the fraction of litter mass remaining at bag retrieval and t the incubation time (=15 days). Temperature-corrected rates for both processes (*SSR* and *k*) were also calculated by replacing days by degree-days (sum of mean daily temperature over time) in equations.

The diversity and composition of the invertebrate benthos in depositional zones were assessed based on benthic fauna taken from each arena at the end of the sediment reworking experiment. Invertebrate diversity was assessed as taxon richness (S) and Pielou's evenness index (J) (Magurran, 2004). Taxon richness was corrected for differences in invertebrate abundance across samples using the rarefaction method (Magurran, 2004). Multidimensional scaling was used to assess community structure based on the Bray–Curtis dissimilarity index. Assemblages of sediment reworkers and shredders were examined from arena and litter bag samples, respectively.

Wilcoxon tests were conducted on data paired by sampling date to test for differences in water chemistry parameters ($n = 5$) and mean daily temperature ($n = 15$) between the open- and closed-canopied streams within each pair. The effect of forest type on habitat characteristics, benthic invertebrates and process rates was assessed using linear mixed-effect models (LMM). 'Stream pair' was considered as a random factor to compare depositional zones within each stream pair simultaneously. We also used linear regression and Pearson's correlation to examine relationships between selected response variables. Statistics were performed with the libraries: base, ade4 (Dray & Dufour, 2007), vegan (Oksanen *et al.*, 2012) and nlme (Pinheiro *et al.*, 2011) in R software (R Development Core Team, 2011).

Results

Habitat characteristics

Riparian canopy cover (measured as the percentage of the sky visible) ranged from 3.5 to 12.4% at closed streams and 38.4–45.2% at open streams. Stream water was circumneutral (pH 6.9–7.9) and of low conductivity (40.2–116.5 μS cm^{-1}). Open streams had significantly higher water temperature and lower nitrate concentration than closed streams (Wilcoxon paired tests: $P < 0.001$; Table 1). In contrast, the forest type did not affect the concentrations of dissolved phosphorus (1.22–8.14 μg P L^{-1}) or dissolved organic carbon (677–3713 μg C L^{-1}).

A PCA on the abiotic characteristics of depositional zones condensed 60.2% of the information into the first two axes (Fig. 1). The first axis represents a gradient of increasing shear stress from left to right. The organic matter and chlorophyll-*a* contents of sediments increased as substratum grain size decreased (Fig. 1a). The second axis corresponded to a gradient of habitat volume determined by the depth and area of the depositional zones (Fig. 1a). The ordination map of depositional zones and the projection of mean scores by stream highlighted differences among the three stream pairs. Depositional zones in streams within pair two had finer sediments and higher organic matter content than in other stream pairs (Fig. 1b; Table 2). PCA axis 1 did not discriminate closed and open streams (LMM of axis 1 score: $F_{1,26} = 0.54$, $P = 0.469$). PCA axis 2 showed that depositional zones were on average larger and deeper in closed than in open streams within pairs one and three (Fig. 1b; Table 2). However, as this trend was not observed in stream pair two, and it was largely due to two influential points with the lowest PCA axis 2 scores in stream pairs one and three, there was no significant difference between closed and open streams overall (LMM of axis 2 score: $F_{1,26} = 3.52$, $P = 0.071$; Fig. 1b).

Macroinvertebrates

The diversity of benthic macroinvertebrates in arenas was always greater in open than in closed streams (Fig. 2). Differences in taxonomic richness were substantial (+1 to 4 taxa in open streams; Fig. 2a; LMM: $F_{1,26} = 1.32$, $P = 0.001$). Evenness was significantly higher in open than in closed stream communities (Fig. 2b; LMM: $F_{1,26} = 8.65$, $P = 0.007$). Forest type also determined community structure and composition but the direction of the shift between closed stream and open stream communities differed among pairs on the ordination plane (Fig. 3). This variable response was particularly evident in the functional groups of sediment reworkers and shredders (Table 3). None of the 10 reworker taxa showed a consistent directional difference between closed and open streams. For instance, *Sericostoma* (Trichoptera) was twice as abundant in open as in closed streams of pairs one and three, whereas no such large difference

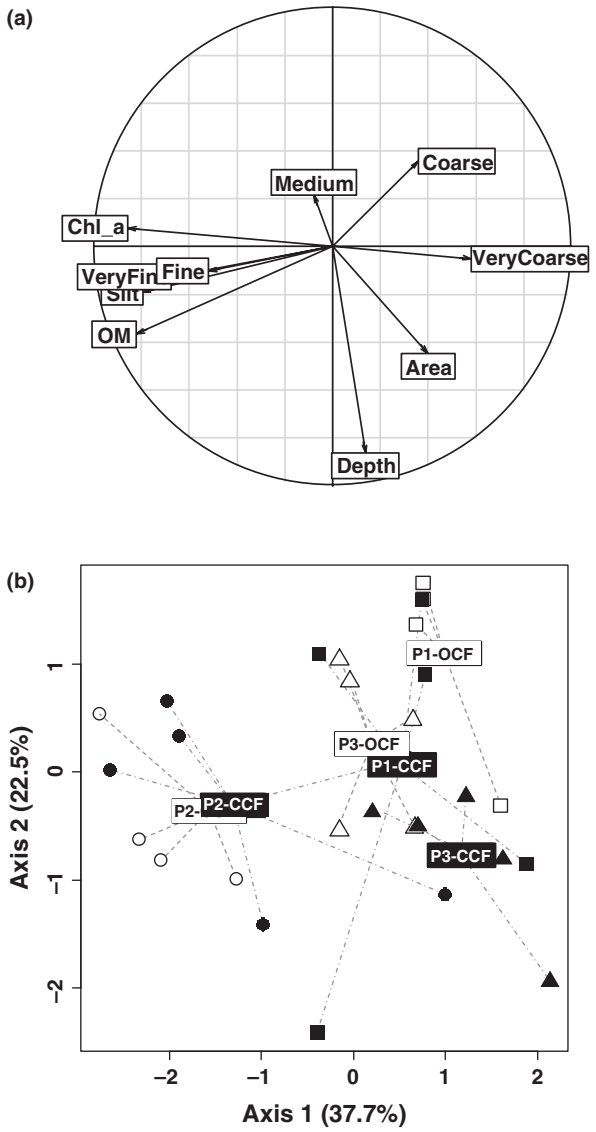

Fig. 1 Principal component analysis of 10 abiotic variables (see Table 2) determined in 30 depositional zones. Correlation circle (a) and ordination plot of the samples (b) were drawn for the two-first principal components that condensed 60.2% of total variation in the data set. Points represent depositional zones sampled in streams in closed canopy forest (CCF; solid symbols) and open canopy forest (OCF; open symbols). Each point is linked to the average position of the stream site to which it belongs.

was observed for pair two. Moreover, total reworker density was higher in open than in closed streams of pairs two and three, whereas it was lower in the closed than in the open streams of pair one (Table 3). Two (*Potamophylax* and *Sericostoma*) of the six invertebrate shredders collected in leaf bags were more abundant in open than in closed streams across all three stream pairs, whereas effect of forest on other shredders was variable. *Gammarus* (Amphipoda) was restricted to the closed

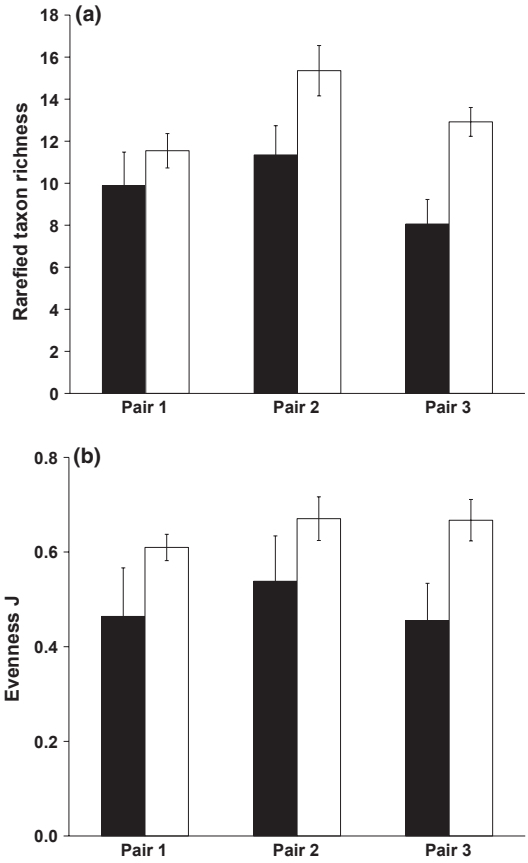

Fig. 2 Diversity of benthic invertebrates from arenas assessed through rarefied taxon richness estimated for 79 individuals per sample (a) and Pielou's evenness index (b). Solid and open bars represent means (±SE) for streams in closed canopy forest and open canopy forest, respectively.

streams of pairs one and two, but was extremely abundant in the open stream of pair three (Table 3). Total shredder density in litter bags was not statistically different between forest types (LMM: $F_{1,26} = 0.22$, $P = 0.642$).

Ecosystem processes

Surface sediment reworking rate (*SSR*) ranged from 0.2 to 0.5 day^{-1}. It was significantly higher in open than in closed streams (Fig. 4a; LMM: $F_{1,26} = 7.72$, $P = 0.010$). However, after degree-day correction, this difference was no longer significant (LMM: $F_{1,26} = 1.87$, $P = 0.183$). Forest type effect on *SSR* was smallest in pair two (Fig. 4a,b). Litter breakdown rate varied widely among streams (0.09–0.35 day^{-1}; Fig. 4c,d), and differences between closed and open streams were inconsistent across the three pairs (LMM on daily k: $F_{1,26} = 3.55$, $P = 0.071$; k in degree-days^{-1}: $F_{1,26} = 2.09$, $P = 0.160$). Specifically, pair two behaved quite differently from pairs one and three.

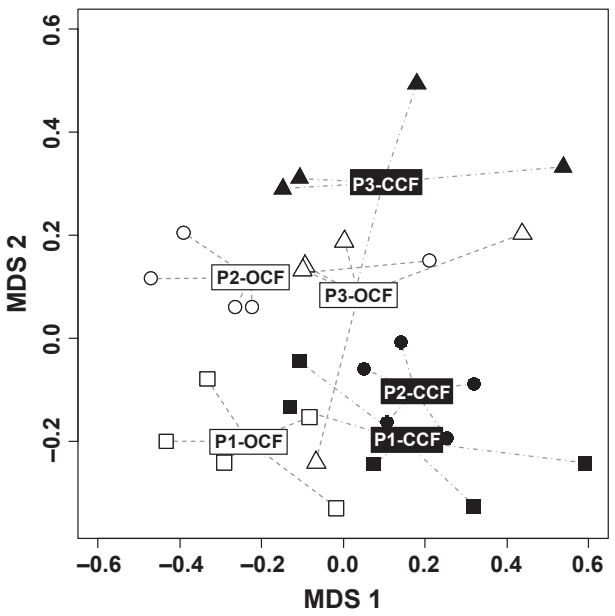

Fig. 3 Structure of the invertebrate benthos from arenas assessed through non-metric multidimensional scaling based on Bray–Curtis dissimilarity index (2D-stress = 0.22). Points represent depositional zones sampled in streams in closed canopy forest (CCF; solid symbols) and open canopy forest (OCF; open symbols). Each point is linked to the average position of the stream site to which it belongs.

Linear regressions were used to test whether the rates of surface sediment reworking and litter breakdown were controlled by the density and diversity of invertebrates, notably sediment reworkers and shredders (Table 4). Temperature-corrected *SSR* was not related to total invertebrate (including Chironomidae) density ($P = 0.33$), but it increased with reworker density ($P = 0.007$) and richness ($P = 0.009$). Temperature-corrected breakdown rate increased with shredder density ($P < 0.001$), but not with shredder richness ($P = 0.400$; Table 4). We also evaluated the agreement between surface sediment reworking and litter breakdown rate (Fig. 5). There was a positive relationship over all data points ($F_{1,28} = 14.71$, $P < 0.001$, $R^2 = 0.32$); however, a separate regression for depositional zones in closed or open streams revealed quite a strong relationship between process rates in closed streams ($F_{1,13} = 18.60$, $P < 0.001$, $R^2 = 0.59$; Fig. 5), but no significant relationship for open streams ($F_{1,13} = 1.72$, $P = 0.212$, $R^2 = 0.12$).

Discussion

Moderation of water temperature by riparian forest canopy is a key mechanism by which land influences stream ecosystems (Vannote *et al.*, 1980; Moore *et al.*,

Table 3 Assemblages of invertebrate reworkers and shredders in streams in closed canopy forest (CCF) and open canopy forest (OCF). Values are mean and SE ($n = 5$ depositional zones) determined based on either benthic samples (number of reworkers m^{-2}) or litter bags (number of shredders g^{-1} leaf dry mass)

	Pair 1		Pair 2		Pair 3	
	P1-CCF	P1-OCF	P2-CCF	P2-OCF	P3-CCF	P3-OCF
Sediment reworkers						
Ephemera			63.5 ± 34.2	169.3 ± 57.3	91.7 ± 30.7	148.1 ± 55.1
Odontocerum albicorne	98.8 ± 40.8	70.5 ± 37.0	91.7 ± 23.9	35.3 ± 11.2		225.7 ± 217.0
Sericostoma	28.2 ± 13.2	49.4 ± 14.1	77.6 ± 23.4	70.5 ± 11.2	134.0 ± 39.3	296.3 ± 80.9
Cordulegaster	14.1 ± 8.6	7.1 ± 7.1	7.1 ± 7.1	21.2 ± 21.2		42.3 ± 7.1
Sialis	35.3 ± 22.3			14.1 ± 8.6		
Dicranota	42.3 ± 20.6	7.1 ± 7.1			91.7 ± 91.7	105.8 ± 51.1
Hexatoma	345.6 ± 177.5	338.6 ± 89.6	56.4 ± 28.7	14.1 ± 14.1	21.2 ± 14.1	98.8 ± 40.8
Glossiphonia				42.3 ± 25.9		
Bivalvia	7.1 ± 7.1	0.0 ± 0.0	28.2 ± 7.1	7.1 ± 7.1	70.5 ± 44.6	77.6 ± 30.3
Total sediment reworkers	571.4 ± 218.4	472.6 ± 124.5	324.5 ± 70.9	373.9 ± 93.7	409.1 ± 149.9	994.6 ± 248.5
Shredders						
Gammmarus	197.2 ± 47.1		1275.8 ± 553.4		34.1 ± 16.3	8090.0 ± 5476.4
Leutridae	2.3 ± 2.3	1.1 ± 0.7	9.5 ± 9.5	104.7 ± 98.9		300.0 ± 300.0
Nemouridae	11.7 ± 6.8	0.4 ± 0.4		7.1 ± 6.3	24.1 ± 16.0	410.0 ± 397.6
Potamophylax	97.1 ± 74.7	201.2 ± 137.0	1348.3 ± 744.9	1454.0 ± 1454.0	140.6 ± 74.4	600.0 ± 284.6
Halesus		2.7 ± 1.2	36.4 ± 36.4	18.3 ± 16.3	0.5 ± 0.5	100.0 ± 100.0
Sericostoma		0.4 ± 0.4	4.8 ± 4.8	116.7 ± 97.2	14.0 ± 7.7	1000.0 ± 880.3
Total shredders	308.2 ± 65.4	205.7 ± 135.5	2674.8 ± 962.1	1700.8 ± 1334.8	213.3 ± 92.6	10500.0 ± 7376.6

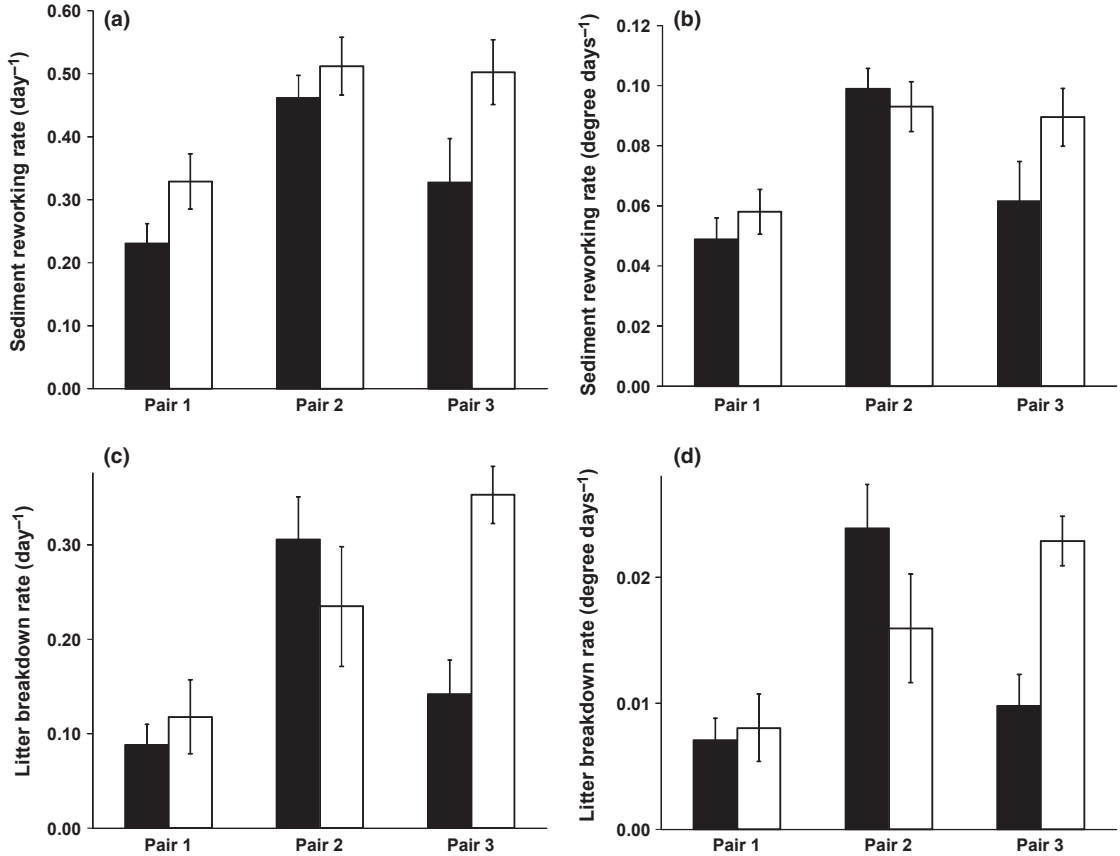

Fig. 4 Ecosystem processes assessed by surface sediment reworking rate (a, b) and litter breakdown rate (c, d) in depositional zones. Rates were expressed either day^{-1} (a, c) or degree-days^{-1} (b, d). Solid and open bars represent means (±SE) for streams in closed canopy forest and open canopy forest, respectively.

2005). In this study, water temperature determined in summer was on average 1.6 °C higher in open canopy than in closed canopy streams, which is within the range of post-harvest temperature increase reported in the literature (Moore *et al.*, 2005). In addition to moderating stream temperature in summer, shade from riparian forest limits instream benthic algal biomass (Kiffney *et al.*, 2004). This effect was not detected here, at least based on chlorophyll-*a* analyses of surface sediment in depositional zones. However, these habitats may not provide ideal conditions for algal development, due to fine substratum, sediment deposition and slow flow (Biggs, 1996). High water temperature provides conditions for faster N uptake and immobilisation by microbial decomposers, algae and moss in open canopy forest streams than in closed canopy streams (Mulholland, 1992; Sabater *et al.*, 2000). Furthermore, it is plausible that N-immobilisation by fast-growing plants in young forest resulted in lower N inputs to streams (Vitousek & Reiners, 1975; Silsbee & Larson, 1983). These two mechanisms are likely to explain why nitrate concentrations in stream water were lower in open canopy forest.

Our findings suggest that depositional zones are important habitats in the context of forest–stream linkages. Invertebrate diversity and bioturbation rate were consistently greater in open streams than in closed canopy ones. As depositional zones were physically similar between stream categories, the influence of terrestrial vegetation on invertebrate diversity and functions was probably determined at the reach scale. The differences in surface sediment reworking rates between closed and open streams were minimal in stream pair two, which had the smallest differences in mean water temperature (+0.2 °C). Furthermore, as surface sediment reworking no longer discriminated between stream categories after temperature correction, water temperature was certainly involved in modulating bioturbation (Ouellette *et al.*, 2004). Similarly, metabolic constrains on biodiversity (Petchey *et al.*, 1999; Allen, Brown & Gillooly, 2002) may also account for the greater species richness and evenness in the warmer streams (open canopy).

The role of invertebrates in sediment bioturbation was indicated by the significant correlations between surface

Table 4 Results of linear regression assessing the effect of invertebrates on ecosystem process rates. Sediment reworking rate (*SSR*) was tested against total invertebrate density and the density and richness of reworkers, and litter breakdown rate (*k*) against the density and richness of shredders

Linear regression	Slope	*t*-value	*P*-value	R^2
Sediment reworking rate (degree-days^{-1})				
SRR versus total invertebrates density	<0.001	0.99	0.330	0.01
SRR versus sediment reworkers density	0.019	2.91	0.007*	0.21
SRR versus sediment reworkers richness	0.008	2.80	0.009*	0.19
Litter breakdown (degree-days^{-1})				
k versus shredders density	0.004	9.26	<0.001*	0.74
k versus shredders richness	−0.001	−0.85	0.400	0

Asterisks denote significance at 0.05.

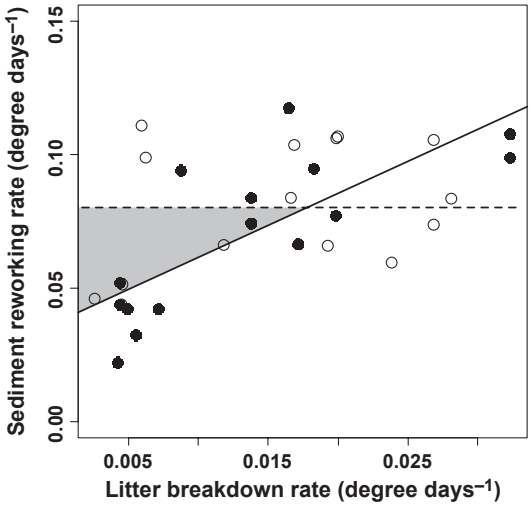

Fig. 5 Surface sediment reworking rate plotted against litter breakdown rate (both expressed degree-days^{-1}). Points represent depositional zones sampled in streams in closed canopy forest (solid symbols) and in open canopy forest (open symbols). Solid lines represent the linear regression model between processes in closed-canopied streams ($P < 0.001$. $R^2 = 0.59$), and dotted lines represent the grand mean of surface sediment reworking rate for open streams in the absence of significance for linear regression ($P = 0.212$. $R^2 = 0.12$). The shaded area corresponds to the gap between open and closed canopy streams at low values of litter breakdown.

sediment reworking rate and reworker density and richness (Table 4). Reworkers are taxa with the potential to cause significant disturbance to the sediments through burrowing. As such, the rate of sediment reworking should increase with reworker density until a maximum rate is reached, as already described for specific taxa (Duport *et al.*, 2006). For natural communities, the link between sediment reworking and faunal density is certainly more complex (*e.g.* Gerino *et al.*, 2007). As reworkers differ in size, mobility and burrowing capacity, their diversity can also positively influence sediment reworking through more extensive exploration of sediment volume (*i.e.* complementarity effects; Solan *et al.*, 2004). Lastly, it is plausible that species interactions modulate sediment bioturbation. For instance, Maire *et al.* (2010) reported that bioturbation rate in soft sediment increased in the presence of benthic predators due to predator avoidance behaviour by the burrowing prey. Such a trait-mediated indirect effect of predators on sediments may be important in stream depositional zones, which are colonised by numerous predatory invertebrates (e.g. *Glossiphonia*, *Cordulegaster*, *Odontocerum albicorne*, *Sialis*, *Dicranota* and *Hexatoma*).

The reworker group did not include all invertebrate taxa believed to affect sediment distribution and properties (e.g. Statzner, 2012). Rather, reworkers were defined as the largest invertebrates with the strongest abilities to rework sediment in the depositional zones investigated here. Due to the predominance of coarse-grained sediments, small burrowers, mostly Chironomidae, were expected to contribute little to sediment bioturbation and, thus, were not assigned as reworkers. Irrespective of sediment size, Chironomidae should be expected to affect sediment properties primarily through bioventilation (Svensson & Leonardson, 1996; Biswasa *et al.*, 2009; Nogaro & Steinman, 2013). The assumption that Chironomidae did not behave as reworkers in our study was verified by controlled laboratory experiments (see Fig. S1 in Supporting Information). Experimental data demonstrated that, when at natural density (*c.* 4600 m^{-2}), Chironomidae were one order of magnitude less efficient in reworking surface sediment than common larger-bodied reworkers (*Sericostoma* and *Cordulegaster*, Table S1).

Litter breakdown rate did not respond consistently to the difference in the forest canopy, and thus, water temperature may not be the main explanation for differences between streams. Our findings are consistent with those of two previous studies which indicated that, in this study region, the rate of breakdown of alder in riffles may vary nonlinearly with riparian canopy cover (Lagrue *et al.*, 2011; Lecerf *et al.*, 2012). The strong coupling between litter breakdown rate and shredder density (Table 4) suggests that invertebrates were directly involved in determining the variation in litter breakdown rate. Invertebrate assemblages in litter bags included facultative shredders (*Gammarus.* Leuctridae, Nemouridae), known to consume resources other than leaf litter, and specialised shredders (*Potamophylax* and *Sericostoma*) that rely more heavily on leaf litter as their primary food resource (Dangles, 2002a). The regular occurrence of

specialised shredders in our samples suggests that leaf litter was present in the depositional zones during the study period. In summer, the detritus pool was composed of unbroken litter, notably beech leaves shed the previous autumn, and of freshly fallen leaves (vertical litter inputs determined on three closed and three open canopy streams in Montagne Noire in July 2011: 34 g litter dry mass m^{-2} and 7 g litter dry mass m^{-2}, respectively; A. Lecerf, unpublished data). The importance of summer litterfall in deciduous forest for shredders has also been proposed by other investigators (e.g. Hoover, Pinto & Richardson, 2011).

Litter breakdown in streams is most often measured in erosional zones, such as riffles, whereas depositional zones are generally avoided due to the risk of burial of leaf bags. However, as noted by previous investigators, depositional zones can be hotspots of litter breakdown (e.g. Kobayashi & Kagaya, 2005). This idea is supported by the extremely high breakdown rates reported in this study (mean by stream: 0.04 to 0.41 day^{-1}). In comparison, exponential breakdown rates for alder leaf litter exposed in coarse mesh bags set in riffles are generally lower than 0.1 day^{-1} (e.g. Gessner & Chauvet, 2002; Hladyz *et al.*, 2010). Aggregation of large-bodied shredders in depositional zones may account for fast breakdown of leaf litter in these habitats (Dangles, 2002b; Kobayashi & Kagaya, 2005). In addition, sediment reworkers may indirectly stimulate organic matter processing, as suggested here by the partial agreement between surface sediment reworking rate and litter breakdown rate (Fig. 5). There are at least of two mechanisms accounting for this correlation between the two processes. First, fine particle reworking and excavation behaviour can reduce the adverse effect of sedimentation on litter breakdown by making leaf litter more accessible to consumers (Creed *et al.*, 2010; Sanpera-Calbet, Chauvet & Richardson, 2012). Second, bioturbation in lentic habitats could promote the conditioning and mineralisation of leaf litter by microbial decomposers through enhanced nutrient transfer from sediment to leaf litter (Mermillod-Blondin, 2011; Hunting *et al.*, 2012).

Additionally or alternatively, surface sediment reworking may be influenced indirectly by litter breakdown in closed canopy streams. Leaf litter is the main source of energy introduced to food webs in these ecosystems (Wallace *et al.*, 1997) and, thus, sediment reworking by invertebrates must be fuelled by energy released from leaf litter and incorporated into detritivore biomass. Moreover, the disruption of the relationship between the rates of surface sediment reworking and litter breakdown in open canopy forest may indicate that invertebrate reworkers rely on alternative energy sources. In such streams, autochthonous primary production is often substantial and can contribute significantly to energy flow in food webs (Vannote *et al.*, 1980; Finlay, 2001). Accordingly, the consumption of herbivorous invertebrate prey by predatory reworkers (e.g. *Glossiphonia*, *Cordulegaster*, *Odontocerum albicorne*, *Sialis*, *Dicranota* and *Hexatoma*) may explain why the temperature-corrected rates of surface sediment reworking were higher in open than in closed canopy streams when litter breakdown was slow (i.e. shaded area on Fig. 5; $k < 0.01$ degree-$days^{-1}$).

To conclude, this study on depositional zones provides new empirical confirmation of the tight linkage between forest and streams. By moderating stream summer temperature, riparian canopy cover potentially affects invertebrate metabolic rate and, indirectly, the intensity of surface sediment reworking. Even though we did not detect physical differences (morphology, sediment properties) between depositional zones in closed and open canopy streams, it is unlikely that water temperature was the sole factor underpinning forest effect on streams. For instance, previous studies have shown that young forest delivers larger amount of high-quality leaf litter to streams than older forest, thus providing an alternative explanation for the greater invertebrate diversity in open canopy streams in the present study (Stout *et al.*, 1993). Lastly, an interesting finding from the present study is that forest modulates the coupling between ecosystem processes. Further studies are warranted to determine whether the two-way feedback mechanisms suggested here really account for positive relationship between sediment reworking rate and litter breakdown rate. As hotspots of organic matter retention and breakdown, depositional zones are ideal habitats in which to further our mechanistic understanding about factors affecting ecosystem process rates.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Surface sediment reworked (cm^2) against time (d) determined in microcosms containing Chironomidae inoculated at a density of 4600 ind m^{-2}.

Table S1. Surface sediment reworking coefficients for some stream invertebrates.

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