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Riparian overstory–understory interactions and their potential implications for forest-stream linkages

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ABSTRACT

Despite growing recognition that understory vegetation is an essential component of forest ecosystems, research on forest-stream linkages and the management of riparian zones continues to focus on overstory trees. Streamside herbs, grasses and shrubs have the potential to fulfill several functions upon which adjacent stream ecosystems rely, such as providing detritus and prey to aquatic communities. Here we investigated patterns of riparian understory vegetation and the associated invertebrate community along headwater streams in deciduous broadleaf forest managed under traditional silvicultural practices. We studied eleven sites along a large gradient of overstory canopy openness to assess whether and how resource competition with canopy trees limits the growth of riparian understory vegetation and affects the abundance and community composition of understory invertebrates. We found that the height and above ground biomass of understory vegetation increased steadily with decreasing overstory canopy cover, suggesting that the structure of riparian zones is contingent upon antagonistic interactions between overstory and understory plants. We also observed that invertebrate abundance did not track changes in overstory canopy cover and understory plant biomass although some numerically important invertebrate taxa displayed clear preferences to either closed or open-canopy riparian forest. Our findings demonstrate that riparian understory vegetation can achieve fairly high biomass and, therefore, should help maintain inputs of plant litter to aquatic ecosystems in harvested or naturally disturbed riparian forest. Because understory invertebrates may not fully compensate for reduced inputs of canopy invertebrates to streams, retaining trees along streams may still be the most effective management option for headwater streams.

1. Introduction

Interfaces between land and surface waters are highly productive habitats that are colonized by taxonomically and functionally diverse communities (Gregory et al., 1991; Naiman et al., 2005). The unique features displayed by riparian zones are explained by the presence of a wet and fertile soil and the occurrence of frequent hydrological disturbances. Aquatic ecosystems have thus a powerful influence on riparian plant and animal communities which, in turn, can affect critical properties of the aquatic ecosystems (Naiman and Décamps, 1997; Richardson et al., 2009). The dependence of low-order headwater streams to riparian zones has long been recognized (Hynes, 1975; Gregory et al., 1991). Riparian vegetation stabilizes and protects banks against erosion and interacts with hydraulic factors to shape channel morphology (Gurnell, 2014). Terrestrial woody debris entering streams act as habitat and retention structures (Bilby and Likens, 1980) and leaf litter from surrounding forest represents an important source of carbon and nutrients for stream consumers (Wallace et al., 1997). The canopy of riparian forests, by providing shade to the streams, helps dampen temperature variations (Moore et al., 2005) and limit autochthonous primary production (Kiffney et al., 2004).

Because headwater valleys have been extensively altered by deforestation and a range of other land-use practices, there has been much concern about how best to manage and restore riparian zones (Broadmeadow and Nisbet, 2004; Richardson et al., 2005). Trees and other woody plants that form the overstory canopy are recognized as the primary and most valuable components of riparian communities. Yet, several lines of evidence indicate that, wherever riparian vegetation lacks woody plants (e.g. in agricultural landscapes, and in desert and alpine ecosystems), streamside grasses and herbs have an influence on the aquatic ecosystem

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(e.g. Hession et al., 2003; Menninger and Palmer, 2007; Leberfinger et al., 2011). In forest habitats, the understory vegetation is composed of soft-stem plants (mosses, herbs and grasses) along with seedlings and saplings of canopy trees and various shrubs. This plant community can substantially contribute to terrestrial primary production, nutrient cycling and soil formation (Nilsson and Wardle, 2005). Grasses and herbs can enhance bank stabilization, nutrient retention and sediment trapping by riparian zones (Hession et al., 2003; Mankin et al., 2007). Evidence also suggests that non-woody plants are of equal or higher palatability for aquatic decomposers than leaf litter from trees (Menninger and Palmer, 2007). Invertebrates colonizing understory vegetation may contribute to the fluxes of terrestrial prey fuelling stream predators such as fish (Nakano and Murakami, 2001; Evangelista et al., 2014). In addition, since riparian understory environment displays wet and cool microclimate conditions (Rykken et al., 2007), it may be a favourable habitat for the adult stages of aquatic insects that use riparian vegetation as shelter, reproduction site and feeding site after emergence (Briers and Gee, 2004). It therefore appears that the linkages between ground vegetation, its associated fauna and streams could be tight, but they remain largely unexplored.

Height and aboveground biomass of the understory vegetation are both likely to be relevant features that mediate the effect of vegetation on stream ecosystems. For instance, the levels of shade to the stream are determined by plant height (Broadmeadow and Nisbet, 2004), a feature that may also determine the likelihood that understory plant parts and associated invertebrates fall into streams. Overstory trees may exert strong control on the development of ground vegetation, through resource competition for instance (Barbier et al., 2008). Because soil water and nutrients may be less limiting in riparian zones than in more upland areas, light availability and overstory canopy closure are expected to be key drivers of the growth of riparian understory vegetation (Rykken et al., 2007; Mallik et al., 2013). Overstory canopy may also influence ground plant and invertebrate communities through the formation of a thick ground litter layer and alteration of microclimate conditions (Rykken et al., 2007; Barbier et al., 2008). By creating canopy gap and reducing stand basal area, natural forest disturbance and forestry practices may result in compensatory growth of understory vegetation. It is thus questionable whether and to what extent understory vegetation could take over the role of overstory trees in mediating terrestrial-aquatic linkages.

In this study we aimed (1) to gain insight into the structure and composition of understory plant and invertebrate communities in riparian zones developing along forested headwater streams and (2) to shed light on the control of overstory canopy cover on riparian understory communities. We carried out a field survey of eleven sites selected along a gradient of forest canopy openness determined above small permanent headwater streams. We assessed the height and aboveground standing biomass of the understory vegetation along stream banks and the community structure and composition of understory invertebrates. We hypothesized that, if light availability was the key factor controlling understory vegetation, then its height and aboveground standing biomass would scale positively with forest canopy openness. Because habitat size and resource availability is expected to determine the density and diversity of invertebrates, understory fauna should therefore also respond positively to forest canopy opening.

2. Methods

2.1. Study sites

The Montagne Noire area is a low-elevation mountain area (maximum elevation 1 210 m a.s.l.) located in southern France and covered by native deciduous broadleaf forest and conifer plantations established since the 1960’s. In the study area, the climate is characterized by mild temperatures (mean annual = 10 °C) and abundant precipitations (up to 1700 mm; >150 rainy days per year). The bedrock is primarily composed of schist, gneiss and granit, leading to the formation of acidic soils. The present study was conducted in forested catchments drained by permanent low-order streams and primarily covered by native broadleaf forest dominated by European beech (*Fagus silvatica* L.), native oaks (*Quercus* spp.), chestnut (*Castanea sativa* Mill.), hazelnut (*Corylus avellana* L.), and ash (*Fraxinus excelsior* L.). There, forests were managed under traditional selection systems, even-aged stand for timber production and coppice forest for woodfire production.

Eleven sites were selected within a narrow area of 10 km radius and were distributed across an elevation range of 356–792 m a.s.l. (Table 1). Sites were 80 m long reaches of small low-order streams (channel width: 1.6–3.9 m) naturally bordered by a riparian forest on both sides of the streams. Stream channels and banks were physically similar across sites whereas forest canopy openness differed broadly, ranging from very closed to largely open. Differences in canopy openness were primarily driven by the stages of forest succession and management practices applied in the riparian area. Except forest management, human disturbance of the streams and their banks were negligible. The range of climate conditions across the eleven study sites was evaluated based on temperature and precipitation data collected within the timeframe of the study period (May–September 2012) from two permanent meteorological stations located at contrasting elevations (234 and 760 m a.s.l.) within the study area. Data showed a trend for more abundant precipitation at the higher (Les Marty) than the lower (Dourgne) elevation stations (Fig. 1A). Air temperature was warmer at low vs high elevation as indicated by a 5.6 °C difference in average daily maximum air temperature between the stations (Fig. 1B).

Table 1
Location and environmental characteristics of the 11 studied sites sampled in 2012. Sites are ordered following an increasing level of canopy openness.

Site	Latitude N	Longitude E	Elevation (m a.s.l.)	Channel width (m)	Canopy openness (%)	Dominant life forms
MOUS	43°28’33”	2°14’08”	608	2.6	1.3	Herbs/grasses
FRAI	43°25’15”	2°14’32”	758	2.3	4.3	Herbs/grasses
LAMP	43°25’12”	2°11’22”	715	2.1	6.8	Ferns
PESQ	43°24’54”	2°13’04”	751	2.6	8.2	Ferns
PEYR	43°25’43”	2°13’12”	741	3.1	13.0	Ferns
ORBI	43°26’15”	2°18’20”	792	2.5	21.3	Ferns
BRG1	43°24’29”	2°11’58”	744	1.6	35.8	Ferns/herbs/grasses
SAN	43°28’25”	2°11’57”	558	3.6	40.1	Herbs/grasses/bramble
BRG2	43°23’51”	2°12’01”	701	2.1	44.0	Herbs/grasses/bramble
LINO	43°24’20”	2°15’22”	702	2.3	58.0	Herbs/grasses/bramble
BERN	43°29’07”	2°12’43”	356	3.9	68.3	Herbs/grasses/bramble

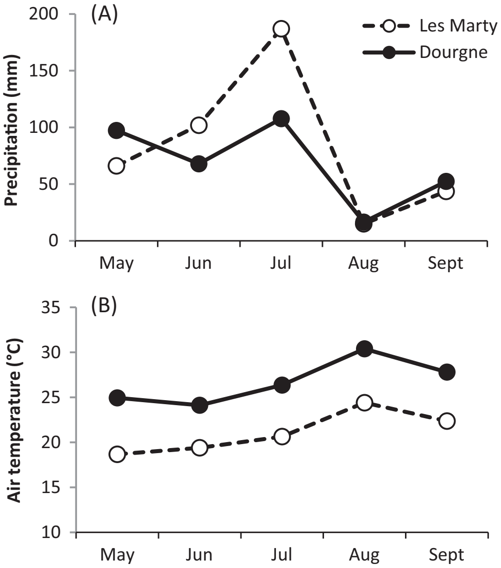

Fig. 1. Precipitation (A) and maximum air temperature (B) at the two permanent meteorological stations situated at contrasting elevation within the study area: Les Marty (760 m a.s.l.) and Dourgne (234 m a.s.l.). Mean monthly values are displayed.

2.2. Sample collection and processing

Overstory canopy openness and the height and aboveground biomass of the understory vegetation were assessed in June 2012 at a fully-foliated forest state. Digital hemispherical pictures were taken vertically upward from the streambed at about one meter above the stream level with a Pentax K-x digital camera fitted with a SIGMA 4.5 mm F2.8 EX DC circular fisheye lens. Pictures were taken under overcast sky condition to minimize flare and reflection problems. Exposure time was set manually following Zhang et al. (2005) to ensure suitable contrast between the sky and the foliage. Gap Light Analyzer v2 software (http://www.ecostudies.org/gla/) was then used to estimate percent gap area, assuming an equisolid angle projection as specified by the lens manufacturer. Because full hemispherical pictures included major topographic features, such in steep sided-valleys (Rutherford et al., 1997), gap area was estimated within a 0–30° zenith range so that non-gap area truly represented overstory tree canopy cover. Four pictures were taken along each site, one every ca. 20 m.

Riparian understory communities (plants and invertebrates) were sampled on both sides of the streams within a one-meter wide strip next to the channel edge. Understory vegetation was dominated by herbaceous (grasses, herbs, ferns) and semi-woody plants (bramble: *Rubus fruticosus* L.) and comprised few seedling and sapling of the overstory trees and shrubs. The height of the understory vegetation was measured from the streambed to the nearest 5 cm every 5 meters on both sides along each site using a grade rod. Total aboveground biomass of the understory vegetation was harvested on four 1 × 0.5 m plots that were equally spaced along each site and taken alternatively on both sides of the streams. The vegetation samples were stored into plastic bags and kept frozen until processing. In the laboratory plant parts were oven-dried (70 °C for 72 h) and weighed to the nearest 0.1 g for biomass determination. Before that, plant-dwelling invertebrates were sorted from the samples under dissecting microscope. Individuals were then identified at the order or (sub-) family level and counted to determine invertebrate densities and richness. Samples of understory invertebrates were also collected in late summer (mid-September 2012) at all sites to evaluate the consistency of invertebrate response to canopy openness. In each site, four sweep net samples were taken along 5-m lines set parallel to the streams.

2.3. Statistics

The Pearson correlation coefficient was used to assess co-variation among environmental factors and response variables. We used linear mixed-effects models (LMM), with the site as a random factor, to infer the effect of overstory canopy openness on the height and aboveground standing biomass of understory vegetation and on the abundance of associated invertebrates. Redundancy analysis (RDA) was performed to assess patterns of invertebrate community structure and composition along environmental gradients. A Hellinger transformation was applied on abundance data to reduce the asymmetry of species distribution (Brocard et al., 2011). LMM and RDA models also included site elevation as explanatory variables to control for cross-site variation in climate conditions. Because much variation (LMM-derived variance component = 75%) in canopy openness was accounted by cross-site difference, the mean values of canopy openness by site were used in the models. All statistical analyses were performed using R (R Core Team, 2015) and the libraries ‘nlme’ (Pinheiro et al., 2015) and ‘lme4’ (Bates et al., 2015), for fitting Gaussian and non-Gaussian LMMs, respectively, and the library “vegan” (Oksanen et al., 2015) for conducting RDA.

3. Results

3.1. Environmental gradients

The eleven sites were distributed over a broad range of overstory canopy openness starting from 1.3% up to 68.3%. Although the most open site was located at the lowest elevation, and had the widest channel (site BERN, Table 1), neither elevation ($R = -0.57$, $P = 0.063$) nor channel width ($R = 0.32$, $P = 0.33$) displayed a significant correlation with canopy openness. The correlation coefficient between canopy openness and elevation was however not negligible, hinting at a potential problem of collinearity. This was alleviated by removing the site BERN from the dataset and analyses (elevation; $R = -0.19$, $P = 0.59$; channel width $R = -0.07$, $P = 0.84$).

3.2. Understory vegetation

The composition of understory vegetation differed among the sites studied. Non-woody plants (herbs, grasses and ferns) were dominant in the least open sites (canopy openness < 40%) whereas semi-woody plants (bramble) were co-dominant in the most open sites (Table 1). Both vegetation height and aboveground standing biomass increased steadily along the gradient of canopy openness (Fig. 2) and these trends were significant ($P = 0.002$ and $P = 0.042$; Table 2). The understory vegetation was as low as 0.17 m (*SE* = 0.02) in the least open site (MOU) and was *ca.* one-order of magnitude taller (1.53 m; *SE* = 0.23; Fig. 2A) in the most open site (BERN). Mean standing biomass ranged from 46 g m^{-2} in the site MOU to 501 g m^{-2} in the site BRG2, one of the most open sites (Fig. 2B).

Site elevation had a negative effect on vegetation height ($P = 0.001$; Fig. 2A) but no significant effect on aboveground standing biomass ($P = 0.51$; Table 2). The model slope estimated for canopy openness was invariant irrespective of whether potential confounding effect of elevation on plant height was alleviated through adding this variable in the LMM model (model 1: slope = +0.0097) or removing an influential point (model 2: slope = +0.0103; Table 2). Slope values here indicated that every 10% increase in canopy openness resulted in a 10 cm taller understory vegetation and an increase of 50 g m^{-2} of aboveground biomass.

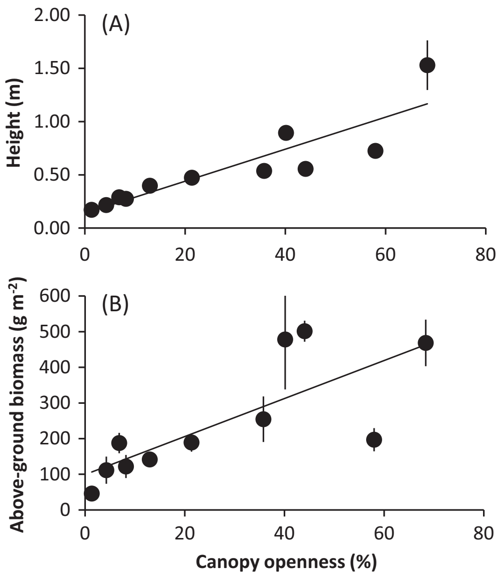

Fig. 2. Relationship between canopy openness (%) and riparian understory vegetation height (A) and above ground standing biomass (B) in the eleven studied sites. Mean values (±SE) and regression lines are displayed.

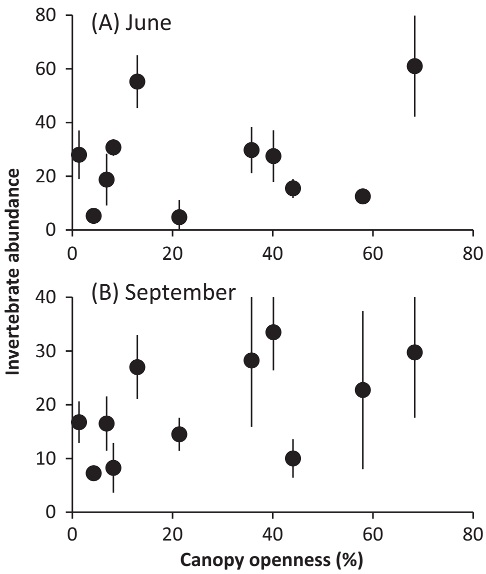

Fig. 3. Invertebrate abundance in riparian understory vegetation in June (A) and September (B) 2012 measured in the eleven studied sites distributed along a gradient of canopy openness (%). Mean values (±SE) are displayed.

3.3. Understory invertebrates

Mean densities of invertebrates from aerial understory plant parts collected in June 2012 ranged from 5 to 61 ind m^{-2}. The highest densities (>50 ind m^{-2}) were observed in two sites with contrasting canopy openness (namely PEYR: 13.0% and BERN: 68.3%). The other sites displayed lower densities of invertebrates of approximately 20 ind m^{-2} (Fig. 3A). There was a good agreement between invertebrate densities measured in June 2012 and in September 2012 ($R = 0.60$, $P = 0.050$). Canopy openness had no effect on the abundance of understory invertebrates collected in June and September 2012 ($P = 0.76$ and $P = 0.45$, respectively; Table 2; Fig. 3B). On both sampling occasions, there was no significant effect of elevation on density ($P > 0.17$; Table 2).

A total of 37 insect and non-insect taxa were found in the riparian vegetation understory (Table 3). Aphids followed by Dipters and Arachnids were numerically dominant in June. In September, Aphids were scarce whereas Dipters and Arachnids made a substantial contribution to the total abundance. The two taxa (Plecoptera and Trichoptera) whose larval stage is strictly aquatic represented less than 10% of the total abundance of understory invertebrates (Table 3). Taxonomic richness by site ranged from 4 to 20 taxa in June and 10 to 24 taxa in September. The greatest number of taxa was always recorded at the site with the largest canopy openness and the lowest elevation (BERN). Although richness of invertebrates tended to increase with canopy openness, these correlations were not significant (June: $R = 0.38$, $P = 0.24$; September: $R = 0.52$; $P = 0.097$). As elevation decreased, invertebrate richness increased in September ($R = -0.87$, $P < 0.001$). There was a similar although not significant ($R = -054$; $P = 0.085$) trend in June.

Redundancy analysis (RDA) showed that linear combinations of canopy openness and elevation explained 15% and 9% of invertebrate community patterns in June and September, respectively. In June, canopy openness and elevation scored quite differently on the two first RDA axes whereas, in September, they both contributed equally to axis 1 and axis 2 (Fig. 4). Although this suggests that independent effects of canopy and elevation were best isolated based on June samples, mixed-effect models of the scores of RDA axis 1 showed that overstory canopy openness had a significant influence on understory invertebrate community at both sampling occasions (Table 2).

Specifically, in June, RDA axis 1 discriminated the five most closed canopy sites (negative scores) vs. the most open sites (positive scores; Fig. 4A). According to axis 1 scores of the taxa (Appendix A), Aphidoidea (+0.47) had the highest affinities to open canopies whereas indicator taxa for closed canopies were Nematocera (−0.42), Collembola (−0.21), Acarina (−0.15), non-identified Araneae (−0.10) and Linyphilidae (−0.09). In September, the four most open sites (BRG2, LINO, SANT, BERN) were spread along a

Table 2
Summary of linear mixed effects models assessing the effects of site elevation and canopy openness on understory plant and invertebrate communities. For each response variable, two models were constructed to tease apart the effects of elevation and canopy openness. The marginal effect of each predictor was assessed in Model 1 fitted to the whole dataset. For model 2, one site was removed from the dataset to suppress collinearity between canopy openness and elevation. Poisson and Gaussian error distributions were assumed for count and non-count data, respectively.

Response variable	Model 1 Elevation Slope	Stat	P	Canopy Slope	Stat	P	Model 2 Canopy Slope	(without BERN) Stat	P
Vegetation height	**−0.0003**	$t = -4.9$	**0.001**	**+0.0097**	**$t = 4.5$**	**0.002**	**+0.0103**	**$t = 5.3$**	**0.001**
Aboveground biomass	−0.24	$t = -0.7$	0.51	**+4.57**	**$t = 2.4$**	**0.042**	**+5.27**	**$t = 2.7$**	**0.028**
Invertebrate abundance in June	−0.0028	$z = -1.3$	0.179	+0.0033	$z = 0.3$	0.76	+0.0045	$z = 0.4$	0.71
Invertebrate abundance in September	80.0017	$z = -1.3$	0.186	+0.0052	$z = 0.7$	0.45	+0.0093	$z = 1.2$	0.23
Invertebrate community structure in June (RDA axis 1)	**+0.0015**	**$t = 2.3$**	**0.010**	**+0.0082**	**$t = 5.6$**	**0.005**	**−0.0084**	**$t = 5.4$**	**0.005**
Invertebrate community structure in September (RDA axis 1)	**+0.0007**	**$t = 1.7$**	**0.028**	**−0.0035**	**$t = 1.6$**	**0.045**	**−0.0083**	**$t = 1.9$**	**0.039**

Table 3
Relative abundance (%) of riparian invertebrate taxa associated to the understory vegetation sampled in June and September 2012.

Phylum/class/order		JUNE											SEPTEMBER										
		MOUS	FRAI	LAMP	PESQ	PEYR	ORBI	BRG1	SANT	BRG2	LINO	BERN	MOUS	FRAI	LAMP	PESQ	PEYR	ORBI	BRG1	SANT	BRG2	LINO	BERN
Arachnida																							
Acari		10.7	14.3	17.3	7.3	10.9		4.2	12.7	6.5	4.0	8.2	13.6				4.7		3.5	0.7			2.5
Araneae	Linyphiidae	9.8	4.8		0.8	0.5			0.9		4.0	0.4	12.1	10.3	22.7	9.1	14.0	10.3	7.1	6.7	27.5	5.5	3.4
	Thomisidae																	3.4			5.0		0.8
	Tetragnathidae		4.8	1.3				0.8							1.5	3.0	0.9			8.2	5.0	4.4	2.5
	Sparassidae												1.5							0.7		2.2	
	other Araneae	26.8						0.8	1.8		2.0		3.0		3.0	9.1			0.9	0.7	10.0		1.7
Opiliones									0.9								1.9						
Pseudoscorpionida		0.9			0.8	0.5							1.5										
Collembola		17.9	4.8	9.3	4.1	6.8		2.5	10.0			6.1	1.5	3.4									1.7
Crustacea	Isopoda	0.9											3.0				0.9			0.7			
Diplopoda		0.9											9.1										1.7
Gasteropoda	Stylommatophora			1.3				1.7	0.9		2.0	0.4		6.9	1.5					2.2			2.5
Insecta																							
Coleoptera	Curculionidae		4.8				5.3				6.0	0.4											
	Chrysomelidae	0.9			0.8				3.6	1.6		3.3							0.9	3.7			1.7
	other Coleoptera				0.8	0.9			1.8						3.0	3.0							1.7
Diptera	Nematocera*	10.7	19.0	30.7	44.7	46.2	5.3	10.1	8.2	14.5	2.0	12.7	18.2	51.7	24.2	21.2	21.5	24.1	23.0	6.7	17.5	23.1	5.9
	Brachycera*	2.7	4.8	5.3	15.4	5.9	15.8	2.5	4.5	4.8	2.0	5.3	19.7	3.4	31.8	33.3	43.0	29.3	19.5	35.8	7.5	34.1	25.2
	other Diptera		4.8			0.5		2.5	2.7											0.7			0.8
Heteroptera	Pentatomidae																		0.9	0.7			2.5
	Lygaeidae																			0.7			0.8
	Nabidae													10.3	1.5			3.4	3.5	2.2	20.0	1.1	
	other Heteroptera				0.8				1.8	12.9		0.4						1.7	0.9	1.5	2.5	3.3	3.4
Hemiptera	Aphidoidea	13.4	19.0	24.0	12.2	17.2	73.7	73.1	41.8	43.5	48.0	44.7		3.4			2.8		0.9	2.2	2.5		17.6
	Cicadelloidea	0.9	4.8		1.6	0.9			1.8		10.0	2.0	1.5	3.4	1.5	6.1	3.7		0.9	4.5	2.5	4.4	14.3
	Fulgoroidea					2.3						0.8											
	Psylloidea		4.8									4.1											
Hymenoptera	Formicidae	1.8			2.4				0.9		8.0	3.3	3.0		1.5	3.0		1.7	0.9				2.5
	Cynipoidea	0.9			1.6	1.4			3.6	1.6	2.0	2.0	6.1			3.0	1.9	6.9	1.8	4.5		4.4	2.5
	Ichneumonoidea				1.6	0.5				4.8		2.5			3.0	3.0		1.7	34.5	3.7		4.4	0.8
	Chalcidoidea			1.3		2.3						0.4	3.0				0.9	1.7		1.5		5.5	
Lepidoptera				1.3		0.9			0.9		2.0	1.2		3.4	4.5	3.0	1.9	1.7		0.7		4.4	1.7
Neuroptera					0.8					1.6													
Orthoptera								0.8				0.4											
Plecoptera*			4.8	2.7	3.3	0.9				3.2	6.0		1.5				0.9	8.6	0.9	10.4			0.8
Psocoptera				1.3						1.6				3.4				1.7				1.1	0.8
Trichoptera*			4.8	4.0		0.9				3.2	2.0					3.0	0.9	3.4				2.2	
Thysanoptera		0.9			0.8	0.9		0.8	0.9			1.2	1.5										
Taxonomic richness		15	13	12	17	18	4	11	18	12	14	20	16	10	12	12	14	14	15	22	10	14	24

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[*] denote taxa whose larvae commonly occur in streams.

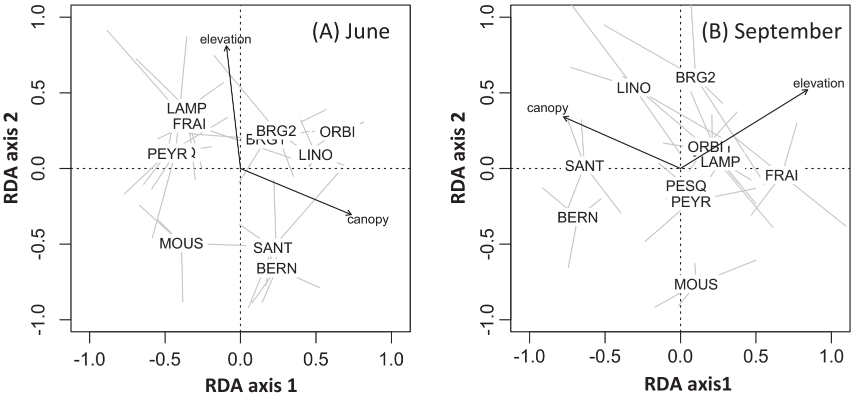

Fig. 4. Redundancy analysis (RDA) biplots showing the relationships between invertebrate taxon abundance in June (A) and September (B) 2012 and environmental variables (overstory canopy openness and site elevation). The grey segments link individual samples to their sites.

curved line crossing the top left area of the ordination plan (Fig. 4B). Nematocera scored in opposite direction (axis 1 and 2 scores: +0.30, −0.11), confirming that this taxon had a low affinity to open canopies.

4. Discussion

4.1. Vegetation

The height and aboveground standing biomass of riparian understory vegetation varied by an order of magnitude across the riparian sites within the relatively small geographic area covered by the current study. This variability was largely explained by variation in overstory canopy openness, which is consistent with the general expectation that understory vegetation is controlled by overstory trees (Barbier et al., 2008; Mallik et al., 2013). In riparian zones, soil moisture and nutrients are likely less limiting than anywhere else in the forest (Naiman and Décamps, 1997), suggesting that light availability was a primary factor controlling understory vegetation production in our study. In addition, past forest disturbance may explain the structure of understory vegetation in the most open sites, which also had the youngest vegetation established following clearcut harvesting operations. Recent (<10 years) forest disturbance may thus have promoted the spread of aggressive ruderal species such as bramble, in the most open sites (Decocq et al., 2004). In contrast, the lack of recent forest disturbance in closed-canopied sites might account for the dominance of smaller and less productive plants such as grass, herbs and ferns. It is worth noting, however, that the increase in plant height and biomass along the gradient of overstory canopy openness was apparent even in mature forest sites and low levels of canopy openness (Fig. 2). It is therefore unlikely that our results on understory vegetation were solely driven by forest age and past disturbance.

The control of riparian zones on the structure and function of adjacent aquatic ecosystems is thought to be directly related to overstory canopy cover (Vannote et al., 1980; Moore et al., 2005; Evangelista et al., 2014). Here we recorded relatively high values of height and above ground biomass achieved by riparian understory vegetation in open sites, which supports the idea that understory vegetation may take over some of the roles played by overstory trees. In five sites, the height equated one quarter of the stream wetted width, indicating that understory vegetation may help maintain shade and a cool microclimate around the streams. The amount of shading by riparian understory may, however, greatly vary according to the orientation of the stream channel relative to the sun as well as local topographic features of sites (Rutherford et al., 1997; Broadmeadow and Nisbet, 2004). A tall vegetation may also ensure that a higher fraction of plant detritus and understory invertebrates reaches the stream. It is important to note that above ground biomass of understory vegetation was up to 500 g m^{-2}, this value being broadly comparable to values of annual litterfall input to mature forest streams (Benfield, 1997). Furthermore, at intermediate and low levels of canopy openness, understory vegetation biomass varied across a range (46–254 g m^{-2}) similar to that reported for overhanging and submerged grasses and herbs along open-canopy streams in agricultural landscape (i.e. 67–276 g m^{-2}, Menninger and Palmer, 2007). Although streams may receive only a fraction of total understory plant biomass, detritus from grasses and herbs may still be important in determining the capacity of the aquatic ecosystem to sustain populations of detritivorous invertebrates and the associated food chains (Menninger and Palmer, 2007; Dangles et al., 2011; Leberfinger et al., 2011).

4.2. Invertebrates

Neither the abundance nor the richness of understory invertebrates change predictably along the gradient of overstory canopy openness. This result differs from those reported by Rykken et al. (2007) that showed greater richness of riparian arthropods along streams in clearcut forest blocks than in closed-canopy mature forest. Nevertheless, this previous study did not establish a clear difference in invertebrate abundance between riparian forest types. In our study, the lack of congruence between understory biomass and invertebrate abundance and richness is intriguing because higher plant biomass is expected to lead to greater abundance and diversity of invertebrates (Haddad et al., 2001). However, plant community composition can also strongly influence invertebrate abundance. For instance, Haddad et al. (2001) demonstrated that, in grassland, C4 grasses weakened the dependence of invertebrate abundance upon plant biomass. It is therefore plausible that the decoupling between plant biomass and invertebrate abundance reported here was, at least partly, driven by a shift in the dominant plant types along the gradient of overstory canopy openness. Another explanation is that cross-ecosystem movements of aquatic insects (Jackson and Resh, 1989; Baxter et al., 2004; Briers and Gee, 2004) have altered the expected relationship between plant biomass and invertebrate abundance. Indeed, the abundance of adult aquatic insects and their terrestrial predators (e.g. spiders) in riparian zones may also be determined by the response of stream insect larvae to riparian forest change (e.g. Lecerf et al., 2012).

The community of understory invertebrates comprised two insect orders, Trichoptera and Plecoptera, whose larval stage lives exclusively in aquatic ecosystems. Overall, these two orders made a fairly small contribution to total invertebrate abundance in the understory vegetation (0–12%). However, the proportion of aquatic insects may exhibit strong day-to-day variations owing to the pulsed nature of emergence events and the short life of adult stages in many taxa (from one day to a week; Briers and Gee, 2004). The coarse taxonomic resolution used in our study is another source of uncertainty in the estimated contribution of adult aquatic insects to riparian invertebrates. For instance, larvae of Diptera, notably Nematocera (e.g. Chironomidae, Simulidae), are numerically abundant in the streams within the study area (e.g. Lecerf et al., 2012), suggesting that these aquatic taxa may have sustained high densities of adult diptera in riparian understory vegetation.

The structure of invertebrate communities was dependent upon overstory canopy openness and site elevation. This result is consistent with previous research suggesting that microclimate conditions are the genuine determinants of invertebrate communities in forested headwater catchments Rykken et al. (2007). In our study, the effect of canopy was quite independent of elevation in June and became apparent through a clear separation between closed (<15% gap area) and open (>20% gap area) canopies. Nematocera was the dominant taxon in understory vegetation below closed canopies and it was gradually replaced by Aphidoidea in open canopy sites. The shift in the dominant invertebrate taxa in riparian zones may have consequences on the fluxes of terrestrial prey to aquatic predators such as stream fish. In a previous study (Evangelista et al., 2014; data not shown), adult Diptera (28%) occurred ten times more often than Aphidoidea (2%) in the gut of brown trout *Salmo trutta* ($n = 273$) sampled in summer in ten of the streams studied here. Moreover, Aphidoidea contributed to less than 5% to total abundance of terrestrial invertebrates collected in pan-trap set on stream banks (Evangelista et al., 2014). These results may indicate that the value of Aphidoidea as terrestrial prey to fish is lower than that of Nematocera, possibly because the former is smaller and less likely to fall into streams than the latter.

4.3. Implication for management

The antagonistic relationship between overstory canopy cover and understory vegetation biomass reported here indicates that herbs, grasses and shrubs may help maintain significant inputs of terrestrial plant litter and restore some shade to streams affected by a decline in riparian tree density. Although natural vegetation dynamics may not always be effective in ensuring the temporal consistency of terrestrial-aquatic linkages, our findings point out the relevance and value of understory vegetation to stream management and restoration. Unlike understory vegetation biomass, the density of understory invertebrates did not exhibit a positive response to overstory canopy openness, suggesting the lack of compensation for the expected reduction of inputs of canopy invertebrates to the streams. Therefore, while having a well-developed ground vegetation along streams is better than having no riparian vegetation at all, a mature riparian forest may still be the desired endpoint if the goal is also to maximize the provision of terrestrial prey to stream fish.

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Appendix A

Species scores for axis 1 and 2 of RDAs of invertebrate taxon abundance in samples collected in June and September. Taxa that contribute the most to discrimination among sites are highlighted in bold.

Taxon	June		September	
	RDA1	RDA2	RDA1	RDA2
Acari	**−0.15**	**−0.06**	−0.05	−0.11
Aphidoidea	**+0.47**	**+0.01**	−0.14	−0.03
Other Araneae	**−0.10**	**−0.05**	+0.01	−0.06
Brachycera	−0.03	−0.09	−0.08	−0.05
Chalcidoidea	−0.02	+0.00	+0.01	−0.01
Chrysomelidae	+0.05	−0.19	−0.11	−0.02
Cicadelloidea	+0.06	−0.09	−0.22	+0.01
Other Coleoptera	−0.01	+0.01	−0.04	−0.01
Collembola	**−0.21**	**−0.17**	−0.04	−0.08
Curculionidae	**+0.06**	**+0.06**		
Cynipoidea	+0.04	−0.09	−0.05	−0.08
Diplopoda	−0.02	−0.01	−0.07	−0.16
Other diptera	−0.10	+0.10	−0.01	−0.02
Formicidae	**+0.09**	**−0.06**	+0.01	−0.08
Fulgoroidea	+0.01	−0.02		
Other Heteroptera	**+0.07**	**−0.02**		
Ichneumonoidea	**+0.08**	**−0.05**	−0.01	+0.09
Isopoda	−0.03	−0.01	+0.01	−0.06
Lepidoptera	+0.03	−0.03	+0.02	+0.08
Linyphiidae	**−0.09**	**−0.05**	+0.02	+0.04
Lygaeidae			−0.05	−0.02
Nabidae			+0.05	+0.16
Nematocera	**−0.43**	**+0.10**	**+0.30**	**−0.11**
Neuroptera	+0.01	+0.01		
Opiliones	+0.00	−0.01	+0.01	+0.01
Orthoptera	+0.03	−0.04		
Pentatomidae			−0.08	−0.01
Plecoptera	+0.05	+0.10	−0.03	+0.00
Pseudoscorpionida	−0.03	+0.01	+0.01	−0.03
Psocoptera	−0.01	+0.01	−0.01	+0.04
Psylloidea	+0.01	−0.09		
Sparassidae			−0.03	+0.06
Stylommatophora	+0.03	−0.02	−0.05	−0.06
Tetragnathidae	−0.02	+0.02	−0.18	+0.02
Thomisidae			−0.02	+0.05
Thysanoptera	−0.04	−0.06	+0.01	−0.03
Trichoptera	+0.03	+0.06	+0.02	+0.07

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