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What predicts the use by brook trout (*Salvelinus fontinalis*) of terrestrial invertebrate subsidies in headwater streams?

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SUMMARY

1. Spatial subsidies are important resources for organisms in receiving habitats, particularly when production in those habitats is low. Terrestrial invertebrates provide a critical subsidy for trout, including eastern brook trout (*Salvelinus fontinalis*), but we have limited understanding of what causes input and use of these subsidies to vary among streams.
2. We predicted that forest successional stage would be an especially important driver of variation in terrestrial invertebrate subsidies to brook trout in headwater streams due to differences in terrestrial invertebrate biomass in early and late successional habitats. Specifically, we expected biomass of aerial invertebrates, those capable of dispersal to the stream, to be greater in early successional habitat than late successional habitat due to the nutrient-rich, herbaceous vegetation typical of early successional habitat.
3. We measured aerial terrestrial invertebrate biomass in early and late successional habitats, input to streams and use by resident brook trout in 12 first- and second-order catchments in northern New Hampshire, U.S.A. The study catchments represented a range of early successional habitat coverage (0–51.5%). We also measured a suite of reach-scale variables that might influence terrestrial invertebrate input and use by brook trout, including riparian forest conditions and benthic invertebrate biomass.
4. Within study catchments, aerial terrestrial invertebrate biomass and abundance were significantly higher in early successional habitats than late successional habitats. However, terrestrial invertebrate input to streams and use by brook trout were unrelated to per cent early successional habitat in the catchment, and to other catchment and riparian forest characteristics. These results indicate that the management for upland early successional habitat has little effect on terrestrial invertebrate subsidies to headwater streams and fish.
5. Surprisingly, benthic invertebrate biomass was the one significant predictor of per cent terrestrial invertebrates in brook trout diets. Use of terrestrial invertebrate subsidies declined with increasing benthic invertebrate biomass, suggesting that productivity in the aquatic environment influences the degree to which brook trout use terrestrial subsidies. Although subsidy inputs are controlled by the donor system, this study shows that use of these subsidies by consumers can be determined by conditions in the recipient habitat.

Keywords: forest succession, headwater streams, invertebrate, *Salvelinus fontinalis*, spatial subsidy

Introduction

Spatial subsidies can provide critical resources for organisms in receiving habitats, influencing both population and community dynamics. Changes in subsidy supply can cause changes in the behaviour and biomass of receiving consumers (Nakano, Miyasaka & Kuhara, 1999b; Kawaguchi, Taniguchi & Nakano, 2003; Marczak, Thompson & Richardson, 2007) and in the strength of predation and competition in food webs of receiving

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habitats (Polis, Anderson & Holt, 1997; Baxter *et al.*, 2007). Because subsidy inputs are controlled by the donor system (Polis *et al.*, 1997), the magnitude of their contribution and strengths of related individual, population and community-level effects vary with conditions in the donor system (Wipfli, 1997; Allan *et al.*, 2003). The role that *in situ* production plays in regulating consumer use of resource subsidies is less well understood, although it is reasonable to expect that availability of *in situ* resources should influence the use of subsidies (Marczak *et al.*, 2007).

Due to their high edge-to-area ratio, headwater streams can be strongly influenced by terrestrial subsidies (Vannote *et al.*, 1980). In headwater streams flowing through deciduous forests, allochthonous inputs in the form of plant material and terrestrial invertebrates provide the necessary energy to support higher trophic levels (Likens & Bormann, 1974). The importance of terrestrial invertebrates as a subsidy for fishes in small streams was first considered when Allen (1951) noted that aquatic invertebrate production was insufficient to support brown trout (*Salmo trutta*) production in a New Zealand stream. This observation, which has been corroborated by studies of production budgets for trout streams (Waters, 1988), has become known as the 'Allen paradox' (Hynes, 1970). Since then, there has been growing evidence that terrestrial invertebrate inputs are a critical resource for stream-dwelling salmonids (e.g. Nakano *et al.*, 1999b; Kawaguchi & Nakano, 2001; Baxter *et al.*, 2007). However, we have limited the understanding of the factors causing natural variation in terrestrial invertebrate inputs to streams and use of these subsidies by fish.

Terrestrial invertebrates are a high-energy spatial subsidy to streams. On average, terrestrial invertebrates have a greater mass and lower C/N ratio than aquatic invertebrates (Nakano *et al.*, 1999a). In addition, they are seasonally important because their summertime peak in production often coincides with a seasonal reduction in aquatic invertebrate production (Needham, 1928; Hynes, 1970; Hunt, 1975; Garman, 1991). Terrestrial invertebrates often make up a substantial portion of the summer diet of headwater stream salmonids (e.g. 50–86%; Garman, 1991; Wipfli, 1997; Nakano *et al.*, 1999b) and as much as 53% of the total annual energy budget (Kawaguchi & Nakano, 2001; Nakano & Murakami, 2001). Even in systems where terrestrial invertebrates comprise only 10–15% of the invertebrate drift biomass, they can make up more than 33% of fish diet, suggesting that stream fish often prey selectively on terrestrial invertebrates (Elliot, 1973; Hubert & Rhodes, 1989; Garman, 1991; Young, Rader & Belish, 1997; Nakano *et al.*, 1999a).

Brook trout (*Salvelinus fontinalis*), a salmonid native to eastern North America, are heavily subsidised by terrestrial invertebrates. In the Appalachian mountains of eastern North America, brook trout occupy low-order headwater streams where aquatic invertebrate production is generally low, especially during the late summer and autumn (Cada, Loar & Cox, 1987; Ensign, Strange & Moore, 1990). Sweka & Hartman (2008) showed that terrestrial invertebrate consumption can make up for this low aquatic invertebrate production, accounting for 38–47% of the biomass consumed and 51–63% of the energy consumed annually by brook trout. Therefore, in the absence of terrestrial invertebrates, brook trout would have to have more than double their aquatic invertebrate consumption to maintain the same growth rates.

Our understanding of how changes in terrestrial invertebrate inputs affect stream communities comes from manipulative experiments and reach-scale observational studies. Manipulative field experiments have demonstrated that fish respond behaviourally and numerically to experimental reductions in terrestrial invertebrates (Nakano *et al.*, 1999a; Kawaguchi *et al.*, 2003). However, experimental reductions in terrestrial invertebrate inputs in these studies are dramatic and probably exceed variation caused by natural factors and management activities (e.g. forest stand composition, timber harvest). Reach-scale observational studies have measured variation in terrestrial insect abundance that results from differences in riparian forest structure and composition (Wipfli, 1997; Allan *et al.*, 2003; Greene, Lowe & Likens, 2008). For example, Allan *et al.* (2003) reported that biomass of terrestrial invertebrates collected 1 m from the stream bank on deciduous trees in early successional forests was greater than on coniferous trees in old-growth forests in Alaska. However, the increased output from deciduous forests did not result in higher biomass of terrestrial invertebrates entering streams or higher percentages of terrestrial invertebrates in fish diets. The authors hypothesised that this was the result of aerial dispersal and mixing of terrestrial invertebrates beyond the riparian zone, suggesting that a catchment-level approach would be useful for understanding the input and use of terrestrial invertebrate subsidies.

No study has measured how forest characteristics at the catchment-scale influence terrestrial invertebrate subsidies to streams, although determining whether this relationship exists can inform forest management beyond riparian buffers. We know that catchment-scale forest conditions influence inputs of coarse particulate organic matter and nutrients to streams (England & Rosemond, 2004). Catchment-scale forest conditions may also influence inputs of aerial terrestrial invertebrates. Studies using harmonic radar transponders to track insect flight have documented dispersal distances of more than 600 m (Riley *et al.*, 1998; Osborne *et al.*, 1999), and both winged and wingless terrestrial invertebrates enter headwater streams (Edwards & Huryn, 1996). These findings suggest that subsidies by aerial invertebrates originating beyond the riparian zone may be significant. While reviews have emphasised the importance of understanding effects of land use on terrestrial–aquatic linkages at appropriate scales (Fausch *et al.*, 2002; Allan, 2004; Baxter, Fausch & Saunders, 2005), studies of terrestrial invertebrate subsidies have focused on riparian zones without explicitly testing whether this is the appropriate scale.

Among the catchment-scale variables likely to influence terrestrial invertebrate subsidies to headwater streams, early successional habitat, characterised by dense, short-statured woody vegetation, abundant and diverse herbaceous vegetation, and a high productivity/biomass ratio, may be especially important (Brown, 1984). Terrestrial invertebrate abundance is predicted to be greater in early successional habitat than late successional habitat because insect herbivores seek more nutrient-rich, herbaceous vegetation that is typical of early successional habitat (Brown, 1984; Mattson & Scriber, 1987; Ohgushi, 1992). Invertebrate biomass is generally greater in early successional habitat than late successional habitat (Manley *et al.*, 1995; Schowalter, Zhang & Progar, 2005; Schultz & De Santo, 2006; Ober & Hayes, 2008). However, studies have also reported reduced invertebrate biomass in early successional habitat (e.g. Duguay, Wood & Miller, 2000) or no differences in biomass in early and late successional habitat (e.g. Grindal & Brigham, 1998). In addition, insects targeting early successional habitat are highly mobile, with rapid colonisation rates and high reproductive potential (Brown, 1984; Hetrick *et al.*, 1998). This increase in biomass of mobile invertebrates may cause heavier invertebrate traffic over streams in catchments with high percentages of early successional habitat, leading to increased stream subsidies. Sweka (2003) proposed that inputs of terrestrial invertebrates to streams would be highest in catchments with a mosaic of early successional habitat and late successional habitat, providing a mixture of structural diversity and high productivity vegetation. However, the influence of upland early successional habitat coverage on terrestrial invertebrate subsidies to streams has not been tested.

We examined the influence of catchment-scale forest structure on terrestrial invertebrate inputs to headwater streams and use of these subsidies by brook trout in 12 catchments in northern New Hampshire, U.S.A. (Fig. 1). Specifically, we tested two interrelated predictions: (i) biomass of aerial terrestrial invertebrates would be greater in upland early successional habitat than upland late successional habitat in the study catchments and (ii) per cent terrestrial invertebrate biomass in brook trout diets would increase with per cent upland early successional habitat in the study catchments. We first assessed differences in biomass of aerial terrestrial invertebrates in upland early successional habitat and late successional habitat in the study catchments. We then tested whether per cent terrestrial invertebrate biomass in diets of brook trout was related to six independent variables: (i) per cent early successional habitat in the catchment, (ii) mean distance of early successional habitat patches to the stream, (iii) per cent riparian vegetation cover over the stream, (iv) biomass input of terrestrial invertebrates to the stream, (v) per cent terrestrial invertebrate biomass in stream drift and (vi) biomass of benthic aquatic invertebrates within the stream. By examining correlations among these independent variables, we were also able to assess how catchment-scale and reach-scale forest characteristics influenced inputs of terrestrial invertebrates to streams, independent of use by brook trout.

Methods

Study area and forest habitat assessment

Twelve study catchments encompassing first- or second-order streams (Fig. 1) were selected in the Dead Diamond River drainage of New Hampshire, U.S.A. Brook trout are the only fish species in these headwater streams. Catchments were selected to maximise range in per cent cover of early successional habitat (ESH from here on) while minimising variability in potentially confounding forest and stream characteristics (Table 1). Fifty-metre study reaches were chosen for invertebrate collection and brook trout sampling, where the downstream end of the reach was at least 50 m upstream of the confluence of the study stream and another stream. Riparian buffers surrounding the stream were a minimum of 40 m wide, which minimised variability in canopy cover over the streams.

The entire Dead Diamond drainage experienced heavy timber harvest in the late 1800's and early 1900's, and its headwater drainage has experienced varying degrees of clear-cut and selective harvest since the 1930's (Kevin Evans, Dartmouth College Woodlands Office, pers. comm). Within these catchments, stand ages ranged from 0 to approximately 70 years old. In this study, ESH

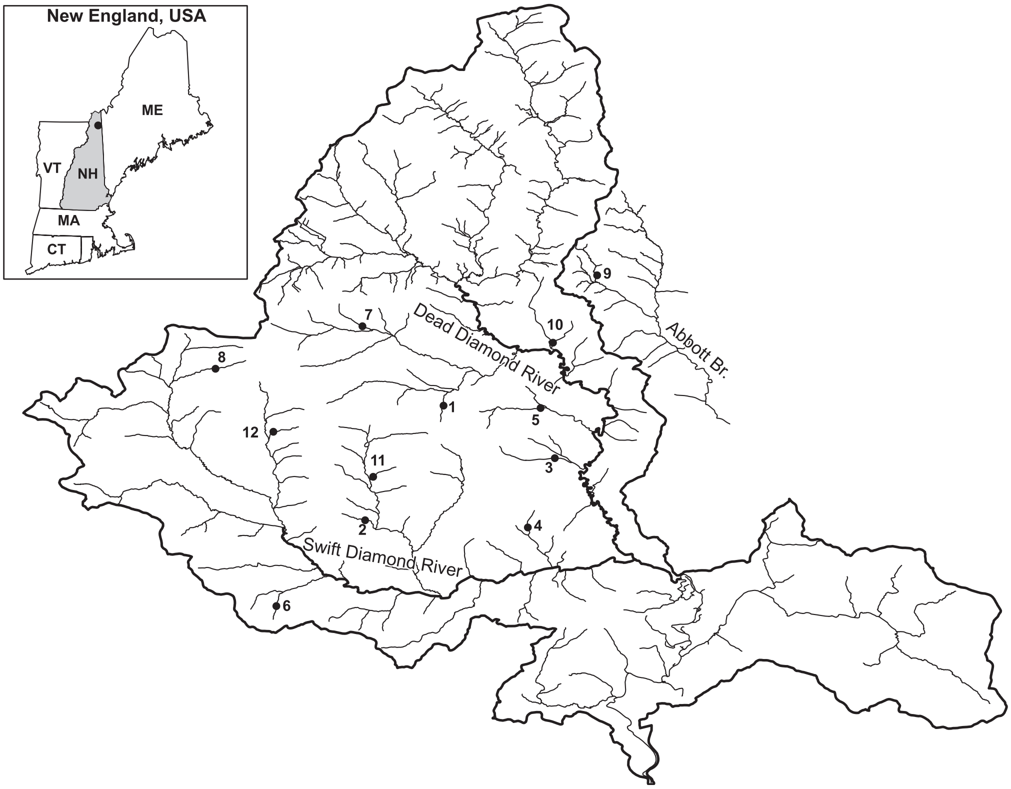

Fig. 1 Map of study stream locations (1–12 in order from lowest to highest per cent early successional habitat in the catchment; Table 1) in the Dead Diamond River drainage in New Hampshire, U.S.A.

consisted of clear-cut patches ranging from 3 to 7 years old; late successional habitat (LSH from here on) consisted of intact forest more than 50 years old. LSH was composed of mixed coniferous and deciduous vegetation, and ESH was composed of shrubs and short-statured deciduous trees. Tree species include red maple (*Acer rubrum*), sugar maple (*Acer Saccharum*), speckled alder (*Alnus rugosa*), balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), yellow birch (*Betula alleghaniensis*), spruce (*Picea*) and red ash (*Fraxinus pennsylvanica*). ESH is dominated by wild raspberry (*Rubus* sp.) and mapleleaf viburnum (*Viburnum acerifolium*).

The catchment coverage of ESH was quantified using high-resolution, colour aerial photographs of the study catchments (1 m resolution, U.S. Department of Agriculture, National Agricultural Imagery Program, September 2009). Catchment boundaries were delineated using a digital elevation model (U.S. Geological Survey, 2009) and the WATERSHED function in IDRISI Taiga (Clark Labs, Worcester, MA, U.S.A.). Early and late successional forest boundaries were delineated manually, which resulted in a thematic raster layer from which percentages of the two cover types were determined.

For each catchment, we also measured mean distance from the centres of ESH patches to the centre of the study reach because we expected that the spatial proximity of ESH patches might influence terrestrial inputs, independent of total ESH coverage (Table 1). Across the twelve study streams, ESH coverage was uncorrelated with the mean distance of ESH patches to the study reach (Pearson's product-moment correlation analysis, $r = -0.31$, $P = 0.34$). In addition, to test whether variation in riparian cover influenced terrestrial invertebrate inputs to the stream, we measured riparian cover over the stream with a densitometer. Densitometer readings were recorded every 5 m along the 50 m long study reaches. At each location, mean per cent forest cover was calculated from one reading taken facing upstream, one facing downstream, one facing the left bank and one facing the right bank. Because within-group variability was smaller than between-group variability (ANOVA, $F_{1,10} = 2.03$, $P = 0.042$), we included riparian canopy cover in the regression model to test for the influence of small differences in canopy cover on brook trout diet. All field data were collected during summer 2010.

Table 1 Stream and catchment characteristics for study sites in the Dead Diamond Drainage, New Hampshire, U.S.A. Streams are ordered left to right by the quantity of early successional habitat (ESH) in the catchment. Mean width, depth and substrate size (±1 SE) are based on 11, 50 and 50 measurements, respectively

	Stream											
	1	2	3	4	5	6	7	8	9	10	11	12
Stream characteristics												
Mean width (m)	2.4	1.8	3	2	3	2.2	3.1	1.8	2.6	1.5	1.1	1.9
SE	0.25	0.14	0.31	0.06	0.09	0.03	0.13	0.20	0.24	0.15	0.18	0.20
Mean depth (m)	0.06	0.07	0.07	0.06	0.09	0.04	0.05	0.07	0.08	0.03	0.06	0.06
SE	0.006	0.007	0.009	0.011	0.045	0.024	0.025	0.014	0.009	0.003	0.008	0.005
Mean substrate Size (cm)	10.3	8.5	10.1	8.5	6.1	7	9.1	9.5	12.1	6.4	5.7	7.5
SE	1.41	1.53	1.36	1.07	9.31	1.21	2.06	1.35	1.69	0.07	1.25	1.16
Mean daily Temperature (ºC)	14.5	14.4	14.9	15	14.9	14.3	14.4	14.1	14.9	14.9	14.2	14.3
SE	0.20	0.21	0.25	0.23	0.24	0.18	0.22	0.21	0.23	0.30	0.25	0.21
Stream canopy Cover (%)	98.8	99.7	95.4	99.4	95.7	99.7	98.6	96.3	95.1	99.4	97.4	95.6
SE	0.1	0.2	0.4	0.3	3.3	0.2	1.0	2.3	1.9	0.2	1.1	3.3
PH	7.2	6.4	7.3	6.4	7.2	6.8	7.2	7.7	7.4	7.2	7.4	7.3
Conductivity (μs cm^{-1})	20.3	12.8	30.8	15.2	24.4	11.9	22.7	40.1	37.5	21.3	37.3	25.9
Site characteristics												
Elevation (m)	579	565	456	535	497	721	591	701	572	438	588	700
Catchment Area (km^2)	1.29	1.30	3.84	2.25	4.03	1.50	4.06	3.48	2.08	1.77	1.05	1.65
Catchment forest characteristics												
Age of ESH (yrs)	N/A	6	4	4	5	3	4	7	3	3	4	6
ESH (%)	0	1.6	2	2.4	5.7	9.2	11.1	16.8	19.1	24.2	36.7	51.5
Mean distance ESH to stream (m)	N/A	125	1192	395	570	123	789	370	137	480	147	340

Upland terrestrial invertebrate biomass

To assess biomass of aerial terrestrial invertebrates in upland ESH and LSH, we collected invertebrates from each habitat type in each of 10 study catchments in July and August. Two of the 12 study catchments lacked patches of ESH large enough for sampling (Catchments 1 and 2; Table 1, Fig. 1). ESH and LSH sampling sites were separated from the stream and from each other by a minimum of 100 m. To minimise the influence of edge effects on aerial terrestrial invertebrate samples, all traps were placed at least 30 m from the forest edge. In each habitat type, five replicates of three coloured pan traps (white, yellow and blue) were set out at a height of 0.5 m above ground (Leather, 2005). Pan traps were randomly placed inside ESH and LSH patches within an area of about 4.5 ha and left open for two 48-h, rain-free, low-wind periods beginning on 4 July and 19 August. Each pan trap was filled with water to a depth of 3 cm, and a drop of soap was introduced to break the water's surface tension.

These traps were intended to capture aerial terrestrial invertebrates capable of dispersal to the stream. No terrestrial invertebrate trap is completely without bias (Southwood, 1978; Edwards & Huryn, 1995; Wipfli, 1997; Leather, 2005). For example, we cannot exclude the possibility that visibility of pan traps by aerial invertebrates is greater in open ESH. However, pan trap sampling is the method with the least bias that allowed for sufficient replication in this study (Leather, 2005).

Trapped invertebrates were preserved in vials containing 70% ethanol. All adult invertebrates were identified to the family level with the exception of the order Araneae. Invertebrate body lengths were measured to the nearest 0.5 mm, and dry masses (mg) were calculated using taxon-specific length-mass conversion equations (Sage, 1982; Sample *et al.*, 1993). This method of measuring biomass for trapped invertebrates has been recommended in place of direct weighing because it provides more accurate measurements and because specimens may have lost mass due to partial decomposition while in traps (Wipfli, 1997).

Terrestrial invertebrate inputs to streams

To quantify terrestrial invertebrate inputs to the study streams, we measured the biomass of terrestrial invertebrates in stream-surface pan traps and stream drift nets along the 50 m study reaches. While stream-surface pan traps allow measurement of surface inputs directly at the study reach, drift samples integrate invertebrate inputs from a larger scale. Surface and drift samples were collected on two occasions during the summer: once in July and once in August.

Three clear plastic pan traps (1100 cm^2 surface area with sides 10 cm high) were elevated on steel posts 10 cm above the surface of pools within the study reaches. Traps were filled with water and 5 mL of dish soap to a depth of 5 cm and left open on 48-h, rain-free, low-wind periods beginning on 4 July and 19 August. Collection, transportation of samples and biomass measurement methods were the same as those for the upland terrestrial invertebrate sampling. Invertebrates were categorised as terrestrial if their larval origin is terrestrial. Invertebrate families that include members with aquatic and terrestrial larval stages were assigned to the habitat where larvae most commonly develop, based on recommendations of McAlpine *et al.* (1981) and Merritt, Cummins & Berg (2008).

Drift nets (45 cm width, 350 μm net mesh size) were set in riffles at a depth of 10 cm and left open for 24 h on 13 July and 22 August. Mean flow velocity was calculated from ten measurements taken when nets were set and retrieved. In the field, samples were transported to the laboratory in 70% ethanol, where all aquatic and terrestrial invertebrates were identified to the family level. Invertebrate biomass (g m^{-3} discharge, dry mass) was determined by body length measurements and taxon-specific length-mass conversion equations (Smock, 1980; Sage, 1982; Sample *et al.*, 1993; Benke *et al.*, 1999).

Benthic invertebrate biomass

Because brook trout are generalist feeders that forage at the stream surface, in the drift and on benthic invertebrates (McNicol, Scherer & Murkin, 1985; Bechara, Moreau & Hare, 1993), the per cent terrestrial invertebrates in brook trout diets could be influenced by the availability of benthic invertebrates. Therefore, we collected benthic invertebrate samples on 2–3 July and again on 17–18 August. For collection, the 50 m study reaches were divided into three 16.6 m long sections. In each of the three sections, three randomly chosen riffles and three randomly chosen pools were sampled with a Surber sampler (0.09 m^2, 350 μm net mesh size) and composited into one sample each for riffles and pools. This resulted in three composite samples for riffles and pools in each reach, each covering a total area of 0.27 m^2. Methods for transportation, identification and biomass measurements were the same as described for drift samples.

Brook trout diet

To quantify the use of terrestrial invertebrates by brook trout, we measured the percentage by mass of terrestrial items in brook trout diets. Fifteen brook trout individuals in each stream were sampled with electroshocking between 0800 and 1300 hr on 12–14 July and 23–26 August using a backpack electrofishing unit (Model LR – 24, Smith-Root Inc., Vancouver, WA, U.S.A.). All individuals were between 80 and 120 mm, which represent brook trout 1 and 2 years of age based on size frequency distributions (M.K. Wilson, unpubl. data). Fish were anaesthetised with tricaine methanesulphonate, and stomach contents were removed by flushing water into fish stomachs using a 30-mL spray bottle with a narrow nozzle (Hyslop, 1980). Stomach contents were collected in an 80-μm nylon mesh filter and transferred to plastic bags containing 95% ethanol for transportation.

Diet items were identified to the family level for all prey except the order Araneae and orders of immature terrestrial invertebrates. If total body measurements were not possible, we estimated lengths of partially digested prey based on intact individuals of the same taxon that was similar in size. Invertebrate dry mass was determined by body length measurements and the taxon-specific length-mass conversion equations (Sage, 1982; Sample *et al.*, 1993). Per cent terrestrial invertebrate biomass in the diet of an individual brook trout was calculated as the mass of terrestrial invertebrates divided by the mass of all prey items, multiplied by 100. The mean per cent terrestrial invertebrate biomass was then taken across all fish in each stream to represent the average contribution of terrestrial invertebrates to the brook trout population.

Because trout feeding behaviour may also be influenced by stream temperature, fish density and size of fish sampled (Baldwin, 1957; Marchand & Boisclair, 1998; Utz & Hartman, 2009), we measured these three variables to assess their influence on the per cent terrestrial invertebrate biomass in brook trout diet. Mean daily stream temperatures were calculated from recordings taken every 10 min from 1 July to 29 August. Despite small differences in means, within-stream variation in mean daily temperature was smaller than between-stream variation (ANOVA, $F_{1,11} = 4.22$, $P < 0.0001$). Fish density within the 50 m study reach was estimated from three-pass removal surveys, during which study reach boundaries were blocked with 1-cm mesh seines. Mean fish length was calculated from measurements of thirty brook trout sampled for diet analysis.

Data analysis

We used a linear mixed effects model, implemented in program R (version 2.13.1; R Development Core Team, Vienna, Austria), to test whether biomass of aerial terrestrial invertebrates differed between upland ESH and LSH. Habitat type (early or late successional) was modelled as a fixed factor nested within the catchment, which was modelled as a random factor to account for variation among catchments in invertebrate abundance in both ESH and LSH. A likelihood ratio test was used to assess the contribution of catchment as a random factor (Bolker *et al.*, 2009). We used the same set of analyses to test whether abundance of aerial terrestrial invertebrates differed between upland habitat types. Biomass and abundance data were log-transformed for these analyses.

We used stepwise multiple regression analyses (forward and backward selection, $P = 0.05$ to enter and remove), implemented in JMP version 9.0 (SAS Institute Inc., Cary, NC, U.S.A.), to assess catchment-scale, riparian and in-stream predictors of per cent terrestrial invertebrate biomass in brook trout diets. The six independent variables were as follows: (i) per cent ESH in the catchment, (ii) mean distance of ESH patches to the stream, (iii) per cent riparian vegetation cover over the stream, (iv) biomass input of terrestrial invertebrates to the stream, (v) per cent terrestrial invertebrate biomass in stream drift and (vi) biomass of benthic aquatic invertebrates within the stream.

Before running the stepwise multiple regression analysis, we tested for correlations among these independent variables. These correlation analyses were used to assess multicollinearity among independent variables, which can undermine multiple regression analyses (Graham, 2003). However, they also allowed us to test whether catchment and riparian forest variables were related to biomass of terrestrial invertebrate input, per cent terrestrial invertebrate biomass in drift and benthic invertebrate biomass (variables 4, 5 and 6 above). Additionally, they allowed us to test whether biomass of terrestrial invertebrates collected in stream pan traps was related to per cent terrestrial invertebrate biomass in drift and thereby determine whether these measures of input should both be included in the multiple regression model (variables 4 and 5 above). Finally, correlation analysis of forest characteristics allowed us to determine whether timber harvest in upland habitats caused variation in canopy cover within riparian buffers (1 and 3 above). This could occur due to increased light input through upland clearings, increasing riparian canopy cover, or because upland clearings make riparian trees more susceptible to blow down, decreasing riparian canopy cover.

To assess the influence on brook trout diet of stream temperature, fish density and size of fish sampled for diet analysis, we used multiple linear regression analysis. These three independent variables were regressed against per cent terrestrial invertebrate biomass in fish diet.

Results

Forest habitat assessment

Per cent early successional habitat (ESH) in the 12 study catchments ranged from 0 to 51.5% (Table 1). Mean distance of ESH patches to the study reach ranged from 125 to 1192 m and was uncorrelated with per cent ESH in the catchment ($P > 0.05$). Over-stream riparian canopy cover was consistently high (range = 95.1–99.7%, Table 1).

Upland terrestrial invertebrate biomass

Aerial terrestrial invertebrate biomass was greater in upland ESH than in upland late successional habitat (LSH) ($F_{1,18} = 45.94$, $P < 0.0001$, Fig. 2). In addition, abundance of aerial terrestrial invertebrates was greater in ESH than LSH ($F_{1,18} = 3.65$, $P = 0.057$). To determine whether aerial terrestrial invertebrate biomass in ESH and LSH varied with per cent ESH in the catchment, we conducted a likelihood ratio test comparing the mixed effects model to a general linear model in which the per cent ESH in the catchment was excluded (i.e. excluding catchment as a random effect). This test showed that per cent ESH in the catchment had no influence on aerial

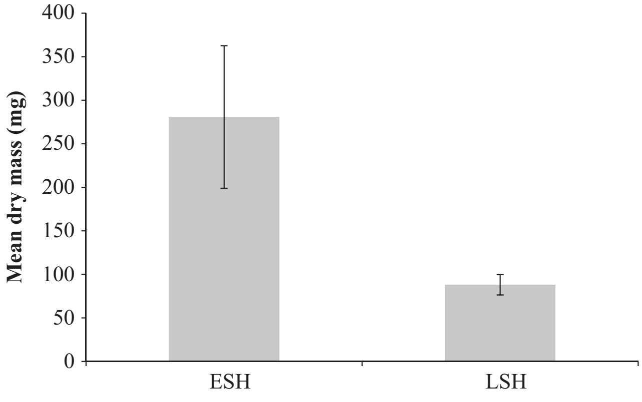

Fig. 2 Mean biomass (mg, dry mass) of aerial terrestrial invertebrates collected from pan traps in focal patches of early successional habitat (ESH) and late successional habitat (LSH) in 10 catchments of the Dead Diamond River drainage. Error bars represent 95% confidence intervals.

Table 2 Mean values (±1 SE) for terrestrial invertebrate (TI) biomass (mg) in stream-surface pan traps, per cent TI biomass in the stream drift, biomass (g m^{-2}) of benthic aquatic invertebrates and per cent TI biomass in brook trout diets

Stream	Pan trap TI biomass (mg ± 1 SE)	% TI biomass in drift (± 1 SE)	Benthic invertebrate biomass (g m^{-2} ± 1 SE)	% TI biomass in brook trout diet (± 1 SE)
1	48.6 (±13.8)	47.4 (±14.8)	0.92 (± 0.1)	53.3 (± 7.6)
2	43.4 (±8.3)	34.4 (±10.5)	0.74 (± 0.0)	54.5 (± 7.9)
3	40.7 (±13.0)	50.5 (±4.0)	1.90 (± 0.6)	46.8 (± 8.1)
4	42.7 (±10.8)	14.8 (±3.6)	0.85 (± 0.2)	60.4 (± 8.1)
5	135.3 (±40.8)	55.3 (±7.1)	1.54 (± 0.3)	43.9 (± 7.9)
6	72.3 (±22.7)	72.9 (±4.0)	1.71 (± 0.4)	47.5 (± 7.2)
7	50.1 (±14.2)	66.0 (±4.0)	1.67 (± 0.2)	51.8 (± 7.8)
8	49.3 (±16.6)	56.0 (±4.0)	1.52 (± 0.3)	51.9 (± 8.3)
9	63.1 (±13.5)	56.7 (±4.4)	1.17 (± 0.3)	49.6 (± 7.2)
10	61.3 (±23.3)	74.1 (±4.6)	0.60 (± 0.2)	65.2 (± 8.3)
11	53.2 (±17.6)	26.8 (±4.9)	1.27 (± 0.3)	59.3 (± 8.0)
12	49.3 (±14.5)	59.7 (±1.7)	1.29 (± 0.3)	54.9 (± 5.1)

terrestrial invertebrate biomass at ESH and LSH sites ($\chi^2 = 0.0028$, $P = 0.96$, d.f. = 1).

Terrestrial invertebrate subsidies and brook trout diets

Table 2 summarises our data on terrestrial invertebrate subsidies, benthic invertebrate biomass and brook trout diet composition in the study streams. All independent variables in the multiple regression analysis were uncorrelated (Table 3). This eliminated the potential problem of multicollinearity, allowing us to distinguish among predictors of variation in terrestrial invertebrate use by brook trout with multiple regression analysis. Measures of terrestrial invertebrate biomass in stream pan traps and drift nets were unrelated to forest habitat characteristics at both riparian and catchment scales. In addition, biomass of terrestrial invertebrates in pan traps was unrelated to the biomass (g m^{-3} discharge) of terrestrial invertebrates in drift samples, indicating that these methods of assessing terrestrial invertebrate input were not interchangeable. Finally, catchment and riparian forest characteristics were unrelated, indicating that timber harvest in upland habitats did not cause variation in canopy cover within riparian buffers.

Stepwise multiple regression analysis retained only benthic invertebrate biomass as a significant predictor of per cent terrestrial biomass in brook trout diet. Per cent terrestrial invertebrate biomass in brook trout diets declined with increasing biomass of benthic invertebrates in streams ($F_{1,10} = 12.18$, $P = 0.006$, $r^2 = 0.55$; Fig. 3, Table 2). Per cent terrestrial invertebrate biomass in brook trout diets was unrelated to stream temperature, fish density within the study reach or length of fish sampled for diet analysis ($P > 0.5$). Mean fish density within the 50 m study reaches ranged from 18 to 55 individuals and mean fish length ranged from 86 to 104 mm (Table 4).

To determine whether the relationship between benthic invertebrate biomass and brook trout diet composition differed in July and August, we used ANCOVA to test for direct and interactive effects of month and benthic invertebrate biomass on per cent terrestrial invertebrate biomass in brook trout gut contents. We found no significant interactive effect of month and benthic invertebrate biomass ($P > 0.5$), but significant direct effects of month and benthic invertebrate biomass ($P < 0.04$). These results indicate that per cent terrestrial invertebrate biomass in brook trout gut contents was higher in July than August, but the negative relationship with benthic invertebrate biomass (Fig. 3) did not differ between months.

Table 3 Correlation matrix for the six independent variables in the stepwise regression analysis, based on the data collected from twelve catchments in the Dead Diamond River drainage (Tables 1 and 2). All correlations are non-significant at the level of $P = 0.05$ (Pearson's product-moment correlation)

	% Early successional habitat	Mean patch distance	% Riparian vegetation cover	Benthic invertebrate biomass	Terrestrial invertebrate biomass input	% Terrestrial invertebrate biomass in drift samples
% ESH	1					
Mean patch distance	−0.42	1				
% Riparian vegetation cover	0.18	−0.15	1			
Benthic invertebrate biomass	−0.03	0.05	−0.27	1		
Terrestrial invertebrate biomass input	0.04	−0.03	0.25	−0.54	1	
% Terrestrial invertebrate biomass in drift samples	0.17	−0.19	0.10	0.29	0.41	1

Table 4 Mean brook trout density within the 50 m study reach, estimated from 3-pass removal surveys and mean length (±1 SE) of fish sampled for diet analysis. Mean fish density was calculated from estimates made for July and August populations, and mean fish length was calculated from thirty fish sampled for diet analysis

Stream	Mean fish density	Mean fish length (mm ± 1 SE)
1	48	95.5 (± 1.6)
2	28	97.7 (± 1.6)
3	40	95.8 (± 2.4)
4	27	86.0 (± 2.8)
5	47	95.6 (± 3.9)
6	18	99.5 (± 1.4)
7	58	99.6 (± 2.8)
8	26	101.7 (± 1.3)
9	39	93.4 (± 1.9)
10	54	95.3 (± 2.7)
11	21	104.3 (± 3.5)
12	55	104.1 (± 2.9)

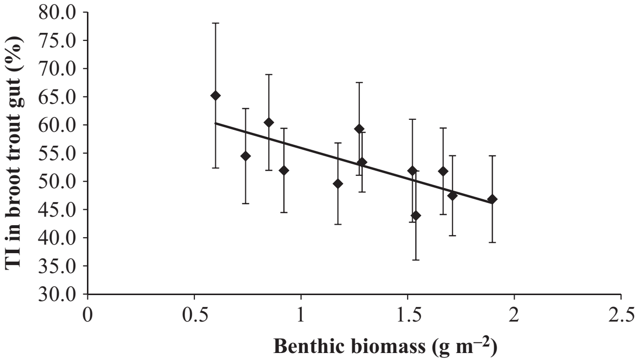

Fig. 3 Linear regression result showing that the percentage by mass of terrestrial invertebrates (TI) in brook trout diets was negatively related to biomass of benthic invertebrates in the study streams ($P = 0.006$, $F_{1,10} = 12.18$, $r^2 = 0.55$; Table 2). Error bars represent 95% confidence intervals.

Discussion

This study provides novel insights into the importance of early successional habitat for forest invertebrate production and the mechanisms influencing terrestrial invertebrate use by brook trout. Aerial terrestrial invertebrate biomass was greater in early successional habitat than late successional habitat, indicating that early successional habitat can contribute valuable resources to higher trophic levels in forests of the north-eastern U.S.A. However, inputs of terrestrial invertebrates to headwater streams and use of these subsidies by brook trout did not increase with per cent early successional habitat in catchments. Surprisingly, our results suggest that benthic invertebrate biomass in streams, not the magnitude of terrestrial invertebrate inputs, determines the proportional use of terrestrial and aquatic invertebrates by brook trout during summer months. *In situ* production may, therefore, be more important in mediating use of terrestrial invertebrate subsidies than previously thought.

While theory predicts greater biomass of terrestrial invertebrates in early successional habitat than late successional habitat (Brown, 1984; Mattson & Scriber, 1987; Ohgushi, 1992), effects of forest age on invertebrate abundance and biomass are not well understood, particularly in the north-eastern U.S.A. (Schowalter *et al.*, 2005). Our data indicate that the summertime biomass of aerial terrestrial invertebrates is greater in early successional habitat than late successional habitat in north-eastern forests. Forest ownership in north-eastern forests has recently shifted from large-scale timber companies to diverse, smaller landowners, resulting in reductions in parcel size, in the amount of land under active management and in the extent and frequency of forest clearings (Brooks, 2003; Hagan, Irland & Whitman, 2005). Our data suggest that the inclusion of upland early successional habitat in forest management plans may increase the secondary production that supports terrestrial vertebrates at higher trophic levels (Dessecker & McAuley, 2001; Litvaitis, 2001; Degraaf & Yamasaki, 2003; Fuller & Destefano, 2003).

Despite increased biomass of aerial terrestrial invertebrates in early successional habitat, our data do not support the hypothesis that catchments with more early successional habitat contribute greater terrestrial invertebrate subsidies to headwater streams. The response variable in our multiple regression analysis was per cent terrestrial invertebrate biomass in brook trout diet, representing the relative importance of terrestrial versus aquatic prey to this consumer. However, the lack of correlation among predictor variables also shows that per cent early successional habitat in the catchment had no influence on the biomass of terrestrial invertebrates entering the stream or in the stream drift. Riparian vegetation cover over the stream also did not predict terrestrial invertebrate input, although this result was expected due to wide buffers (≥40 m) and consistently high riparian cover of study streams. To confirm that variation in riparian vegetation did not influence terrestrial invertebrate input and use by brook trout, we conducted *a posteriori* stepwise multiple regression using data on mean tree diameter at breast height, stand density and understory cover from two 50 m long, 2 m wide riparian transects along each study reach. These variables were also unrelated to terrestrial invertebrate use by brook trout, terrestrial invertebrate biomass in stream-surface pan traps and terrestrial invertebrate biomass in the stream drift.

Our results are consistent with Allan *et al.* (2003), who found greater biomass of terrestrial invertebrates on early successional vegetation in the riparian zone, but that streams flowing through early successional habitat did not receive greater inputs of terrestrial invertebrate biomass compared with streams flowing through late successional habitat. There are several possible explanations for these concordant findings. First, it may be that aerial terrestrial invertebrates remain in early successional habitat patches for the duration of their life and do not disperse away from these high-quality habitats. Alternatively, aerial invertebrates may disperse away from and between early successional habitat patches without falling into headwater streams, which represent a small area within the catchment. Finally, aerial mixing by wind and dispersal may render current sampling methods insufficient for detecting inputs (Macneale, Peckarsky & Likens, 2004). Because trees interfere with insect tracking methods, understanding of invertebrate dispersal in forest ecosystems is still poor (Riley & Smith, 2002). Better understanding of the mechanisms of terrestrial invertebrate subsidies to streams requires better methods for tracking invertebrate movement in forests.

Surprisingly, biomass density of benthic aquatic invertebrates was the best predictor of per cent terrestrial invertebrates in brook trout diets. *A posteriori* analysis revealed the same negative relationship between abundance of aquatic invertebrates and per cent terrestrial invertebrate biomass in brook trout diets. Together, these results suggest that use of terrestrial invertebrate subsidies by brook trout depends on availability of *in situ* diet items, namely aquatic invertebrates. Previous studies have shown that per cent terrestrial invertebrates in trout diets often exceeds per cent terrestrial invertebrates in the drift, suggesting that trout selectively feed on this terrestrial resource (Elliot, 1973; Hubert & Rhodes, 1989; Garman, 1991; Nakano *et al.*, 1999a). However, unlike here, these studies do not report relationships between terrestrial invertebrate inputs and per cent terrestrial invertebrates in trout diets, which would provide direct evidence that terrestrial invertebrate input determines use.

In our study, per cent terrestrial invertebrate biomass in the drift (mean = 49.9%, SD = 18.5%) was similar to that found in brook trout diet (mean = 53.0%, SD = 6.1%), suggesting that trout are not selectively feeding on terrestrial invertebrates. Aquatic adult invertebrates comprised less than 3% of total invertebrate drift biomass and therefore comprised a small proportion of the aerial contribution to stream drift. Terrestrial invertebrate inputs (both in surface pan traps and drift nets) were unrelated to per cent terrestrial invertebrates in brook trout diet and, importantly, all measures of invertebrate input, availability and use exhibited significant variability across study streams. Clearly, terrestrial invertebrates are an important component of brook trout diet during the summer. But, in our study streams, terrestrial invertebrate use by brook trout appears to be determined by availability of benthic invertebrates, rather than inputs of terrestrial invertebrates.

Feeding behaviour of brook trout may be influenced by biotic and abiotic conditions in streams, including prey abundance, stream temperature, trout density, trout size and visibility (Baldwin, 1957; Griffeth, 1974; Allan, 1981; Sweka & Hartman, 2001; Utz & Hartman, 2009). Biomass density of benthic invertebrates in our study streams (mean = 1.3 g m^{-2}) was comparable with that of forested, headwater streams in other regions (e.g. Nakano *et al.*, 1999b; mean = 1.2 g m^{-2}; Smock, 1985 mean = 2.14 g m^{-2}). Therefore, the response of brook trout to benthic invertebrate biomass in this system does not appear to be related to abnormally high levels of in-stream productivity. Additionally, per cent terrestrial invertebrate biomass in brook trout diets was unrelated to trout density, size or stream temperature, suggesting that these factors did not influence brook trout feeding behaviour. However, it is important to note that the size range of our sampled fish was limited to 80–120 mm. It has been shown that size class can determine the extent to which brown trout (*Salmo trutta*) use terrestrial invertebrate subsidies (Gustaffson, Bergman & Greenberg, 2010). We may have seen a similar pattern if the size range of brook trout in our streams was broader. More generally, it is important to recognise that different species of fish vary in their use of terrestrial invertebrate subsidies (Sullivan, Zhang & Bonner, 2012).

To date, stream subsidy studies have focused on the land-to-water flow of resources as the driver of subsidy consumption by stream predators, but little attention has been given to the influence of stream invertebrate production. With manipulative experiments, studies have shown that changes in the magnitude of terrestrial subsidies to streams influence the abundance of *in situ* resources via changes in density and behaviour of consumers that feed on both resources (Nakano *et al.*, 1999a, b). However, the extreme variation in terrestrial inputs created in these experiments (e.g. 20-fold experimental decrease in mean input; Nakano *et al.*, 1999a) is probably much larger than variation under non-experimental conditions (e.g. less than threefold difference between maximum and minimum mean input; Mason & Macdonald, 1982; Wipfli, 1997; Kawaguchi & Nakano, 2001; Allan *et al.*, 2003). Consequently, effects documented in these experiments may overshadow factors mediating inputs and use of subsidies in natural and managed catchments, including availability of aquatic prey.

Benthic invertebrate production has been heavily studied and is influenced by a wide variety of factors, including primary productivity, leaf litter input, stream chemistry, solar radiation, sedimentation and pollution, predator species composition and life history of resident invertebrate species (reviewed in Benke & Huryn, 2010). Variation in these factors can be caused by natural features of the catchment (Likens & Bormann, 1995) and human activities, including timber harvest and development (Resh *et al.*, 1988; Whiles & Wallace, 1995; Sponseller, Benfield & Valett, 2001; Allan, 2004). Our results suggest that understanding the causes and consequences of variation in terrestrial subsidies to streams will require more explicit consideration of the natural and anthropogenic factors influencing in-stream habitat conditions and the resulting variation in aquatic prey resources. More broadly, while subsidy inputs are donor-controlled, this study shows that use of these subsidies by consumers can be determined by conditions in the recipient habitat.

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