2012

WHAT PREDICTS TERRESTRIAL INVERTEBRATE SUBSIDY USE BY BROOK TROUT (SALVELINUS FONTINALIS) IN HEADWATER STREAMS?

Matthew Kestrel Wilson
The University of Montana

WHAT PREDICTS TERRESTRIAL INVERTEBRATE SUBSIDY USE BY BROOK TROUT
(*SALVELINUS FONTINALIS*) IN HEADWATER STREAMS?

By

MATTHEW KESTREL WILSON

B.S., University of California, Santa Barbara, 2006

Thesis

Presented in partial fulfillment of the requirements
for the degree of

Master of Science
in Wildlife Biology

The University of Montana
Missoula, MT

Spring 2012

Approved by:

_____
Sandy Ross, Associate Dean of
The Graduate School

_____
Dr. Winsor H. Lowe, Chair
Wildlife Biology

_____
Dr. Lisa A. Eby
Wildlife Biology

_____
Dr. Laurie B. Marczak
Wildlife Biology

_____
Dr. Keith H. Nislow
Environmental Conservation
University of Massachusetts

ABSTRACT

Wilson, Matthew, M.S., Spring 2012   Wildlife Biology

WHAT PREDICTS TERRESTRIAL INVERTEBRATE SUBSIDY USE BY BROOK TROUT (*SALVELINUS FONTINALIS*) IN HEADWATER STREAMS?

Chairperson: Dr. Winsor H. Lowe

Spatial subsidies provide critical resources for organisms in receiving habitats, particularly when production in those habitats is low. While it is clear that terrestrial invertebrates provide a critical subsidy for trout, including eastern brook trout (*Salvelinus fontinalis*), we have limited understanding of what causes input and use of these subsidies to vary among streams. Among the watershed characteristics that may influence input and use of terrestrial invertebrates, I predicted that forest succession stage would be especially important due to differences in terrestrial invertebrate biomass in early and late successional habitats. To test this prediction, I measured terrestrial invertebrate biomass, input to streams, and use by resident brook trout in 12 first and second-order watersheds in northern New Hampshire, USA, representing a range of early successional habitat coverage (0-52%). I also measured invertebrate diversity and abundance in early and late successional habitats to assess the importance of habitat heterogeneity for forest invertebrate communities. Within the study watersheds, terrestrial invertebrate biomass, diversity, and abundance were significantly higher in early successional habitats than late successional habitats. However, biomass of terrestrial invertebrate inputs to streams was unrelated to the percent early successional habitat in the watershed, and both watershed and reach-scale forest characteristics were unrelated to percent terrestrial invertebrates in brook trout diets. Surprisingly, benthic invertebrate biomass was strongly, negatively related to the percent terrestrial invertebrates in brook trout diets, suggesting that productivity in the aquatic environment may influence the degree to which brook trout use terrestrial invertebrate subsidies. Overall, these results show that terrestrial invertebrate biomass is greater in early successional forest habitats, but that increasing the percent early successional habitat in watersheds does not influence the magnitude of this subsidy, or use by brook trout. While more research is needed on the factors influencing dietary preferences of salmonids, these results highlight the influence of *in situ* invertebrate production on use of terrestrial resources. Although terrestrial invertebrates may be an important food resource for salmonids, my results show that in-stream productivity can influence the relative importance of these allochthonous resources to aquatic consumers.

TABLE OF CONTENTS

LIST OF FIGURES AND TABLES

Figures

Tables

ACKNOWLEDGMENTS

CHAPTER 1: WHAT PREDICTS TERRESTRIAL INVERTEBRATE SUBSIDY USE BY BROOK TROUT (*SALVELINUS FONTINALIS*) IN HEADWATER STREAMS?

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 behavior and biomass of receiving consumers (Nakano et al. 1999a, Kawaguchi et al. 2003, Marczak et al. 2007a) and in the strength of predation and competition in food webs of receiving habitats (Polis et al. 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 (Nakano et al. 1999a, Anderson and Polis 2004). 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 use of subsidies (Marczak 2007b).

Due to their high edge-to-area ratio, headwater streams are 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 energy necessary to support higher trophic levels (Likens and Bormann 1974, Nakano et. al. 1999b, Sweeka and Hartman 2008). 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 (e.g., 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

subsidy for stream-dwelling salmonids (e.g., Nakano et. al. 1999b, Kawaguchi et. al. 2001, Baxter et. al. 2007). However, we still have limited understanding of the factors causing natural variation in terrestrial invertebrate inputs to streams and use by fish.

Terrestrial invertebrates are a high-energy spatial subsidy to streams. On average, terrestrial invertebrates have a greater mass and a lower C:N ratio than aquatic invertebrates (Nakano et al. 1999b). 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% in Garman 1991, Wipfli 1997, Nakano et al. 1999a), and as much as 53% of the total annual energy budget (Kawaguchi and Nakano 2001, Nakano and Murakami 2001). Even in systems where terrestrial invertebrates comprise only 10 - 15% of the invertebrate drift biomass, they can make up >33% of fish diet, suggesting that stream fish often prey selectively on terrestrial invertebrates (Elliot 1973, Hubert and Rhodes 1989, Garman 1991, Young et al. 1997, Nakano et al. 1999a).

Brook trout (*Salvelinus fontinalis*), a salmonid native to eastern North America, are heavily subsidized by terrestrial invertebrates. In the Appalachian mountains of eastern North America, brook trout occupy low-order headwater streams where aquatic invertebrate production is generally thought to be low, especially during the late summer and fall (Cada et al. 1987, Ensign et al. 1990). Sweka and Hartman (2008a) 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 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 behaviorally and numerically to experimental reductions in terrestrial invertebrates (Nakano et al. 1999b, Kawaguchi et al. 2003). However, experimental reductions in terrestrial invertebrate inputs in these studies are dramatic, and likely 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 result from differences in riparian forest structure and composition (Wipfli 1997, Allan et al. 2003, Greene et al. 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. They hypothesized that this could have been the result of aerial dispersal and mixing of terrestrial invertebrates beyond the riparian zone. These studies limit measurement of forest characteristics to the riparian zone, and therefore do not address watershed-level influence on terrestrial invertebrate supply to streams.

No study has measured how watershed-scale forest characteristics influence terrestrial invertebrate subsidies to streams, although determining whether this relationship exists can inform forest management beyond riparian buffers. We know that watershed-scale forest conditions influence inputs of coarse particulate organic matter and nutrients to streams (Likens

and Bormann 1995, Johnson and Covich 1997, England and Rosemond 2004). Watershed-scale

forest conditions may also influence inputs of winged terrestrial invertebrates. Studies using

harmonic radar transponders to track insect flight documented dispersal distances of over 600 m

(Riley et al. 1998, Osborne et al. 1999), and both winged and wingless terrestrial invertebrates

enter headwater streams (Edwards and Huryn 1996). These findings suggest that subsidies by

winged invertebrates originating beyond the riparian zone may be significant. While reviews

have emphasized the importance of understanding effects of land use on terrestrial-aquatic

linkages at appropriate scales (Fausch et al. 2002, Allan 2004, Baxter et al. 2005), studies of

terrestrial invertebrate subsidies have focused on riparian zones without explicitly testing

whether this is the appropriate scale

Among the watershed-scale variables likely to influence terrestrial invertebrate subsidies

to headwater streams, early successional habitat (ESH from here on) – characterized by dense,

short-statured woody vegetation, abundant and diverse herbaceous vegetation, and a high

productivity:biomass ratio – may be especially important (Brown 1984, Brooks et. al. 2012).

Terrestrial invertebrate abundance is predicted to be greater in ESH than late successional habitat

(LSH from here on) because insect herbivores seek more nutrient rich, herbaceous vegetation

typical of ESH (Brown 1984, Mattson and Scribner 1987, Ohgushi 1992). Invertebrate biomass

is generally found to be greater in ESH than LSH (Manley et. al. 1995, Schowalter et. al. 2005,

Shultz and DeSanto 2006, Ober and Hayes 2008). However, studies have also reported reduced

invertebrate biomass in ESH (e.g., Duguay et. al. 2000), or no differences in biomass in ESH and

LSH (e.g., Grindal and Brigham 1998). In addition, insects targeting ESH are highly mobile,

with rapid colonization 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 watersheds with high percentages of ESH, leading to increased stream subsidies. Sweka (2003) proposed that inputs of terrestrial invertebrates to streams would be highest in watersheds with a mosaic of ESH and LSH, providing a mixture of structural diversity and high productivity vegetation. However, the influence of small watershed ESH coverage on terrestrial invertebrate subsidies to streams has not been tested.

I examined the influence of watershed-scale forest structure on terrestrial invertebrate inputs to headwater streams and use of these subsidies by brook trout in 12 watersheds in northern New Hampshire, USA (Figure 1-1). Specifically, I tested two interrelated predictions: (1) biomass of terrestrial invertebrates would be greater in upland ESH than upland LSH in the study watersheds, and (2) percent terrestrial invertebrate biomass in brook trout diets would increase with percent upland ESH in the study watersheds. I first assessed differences in biomass of terrestrial invertebrates in upland ESH and LSH in the study watersheds, using biomass as an index of terrestrial invertebrate productivity. I then tested whether percent terrestrial invertebrate biomass in diets of brook trout was related to six independent variables: (1) percent ESH in the watershed, (2) mean distance of ESH patches to the stream, (3) percent riparian vegetation cover over the stream, (4) biomass input of terrestrial invertebrates to the stream, (5) percent terrestrial invertebrate biomass in stream drift, and (6) biomass of benthic aquatic invertebrates within the stream. By examining correlations among these independent variables, I was also able to assess how watershed and reach-scale forest characteristics influenced inputs of terrestrial invertebrates to streams and their use by brook trout.

Materials and Methods

Study Area and Forest Habitat Assessment

Twelve study watersheds encompassing first or second order streams (Figure 1-1) were selected in the Dead Diamond River drainage of New Hampshire, USA. Brook trout are the only fish species in these headwater streams. Watersheds were selected to maximize range in percent cover of ESH while minimizing variability in a suite of potentially confounding forest and stream characteristics (Table 1-1). Fifty meter 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 minimized variability in canopy cover over the streams.

The entire Dead Diamond drainage experienced heavy timber harvest in the late 1800s and early 1900s, and its headwater drainages have experienced varying degrees of clearcut and selective harvest since the 1930s (personal communication, Kevin Evans, Dartmouth College Woodlands Office). Within these watersheds, stand ages ranged from 0 to approximately 70 years old. In this study, ESH consisted of clearcut patches ranging from 3 - 7 years old; LSH consisted of intact forest >50 years old. LSH was composed of mixed conifer 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*).
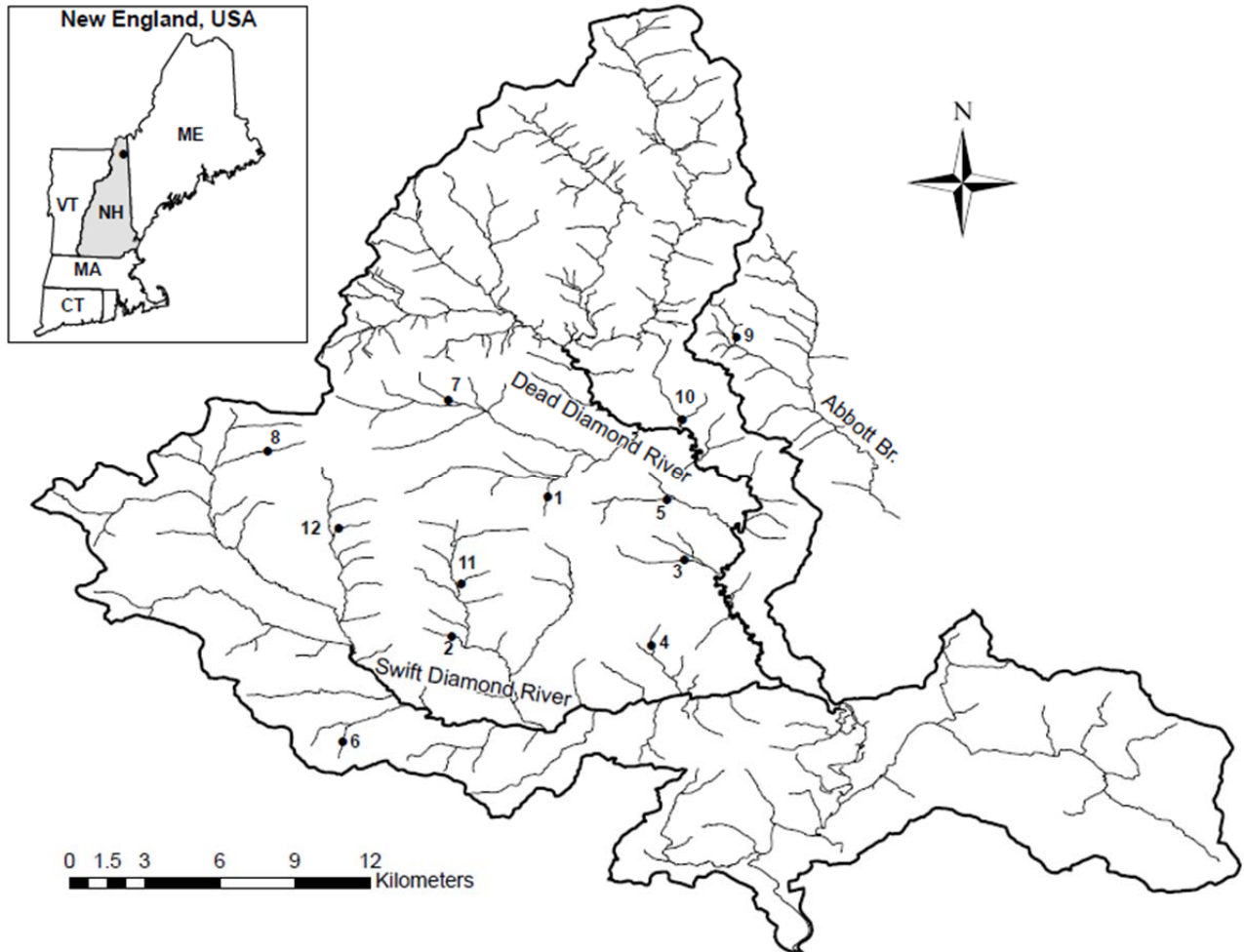
Figure 1-1. Map of study stream locations (1 - 12 in order from lowest to highest percent ESH in the watershed) in the Dead Diamond River drainage in New Hampshire, USA.

Table 1-1. Stream and watershed-scale forest characteristics for sites in the Dead Diamond Drainage, NH, U.S.A. Streams are ordered left to right by the quantity of ESH in the watershed. Mean width, depth, and substrate size (±1 SE) are based on 11, 50, and 50 measurements, respectively.

Forest and Stream Characteristics	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 (^{o}C)	14.5	14.4	14.9	15	14.9	14.3	14.4	14.1	14.9	14.9	14.2	14.3
SE	.20	.21	.25	.23	.24	.18	.22	.21	.23	.30	.25	.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)	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
Watershed 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

The watershed coverage of ESH was quantified using high resolution, color aerial photographs of the study watersheds (1 m resolution, USDA National Agricultural Imagery Program, taken September 2009). Watershed boundaries were delineated using a digital elevation model (USGS 2009) and the WATERSHED function in IDRISI Taiga © 2009. 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 watershed, I also measured mean distance from the centers of ESH patches to the center of the study reach because I expected that the spatial proximity of ESH patches might influence terrestrial inputs, independent of total ESH coverage (Table 1-1). Across the twelve study streams, ESH coverage was uncorrelated with the mean distance of ESH patches to the study reach (Pearson's product moment, $r = -0.31$, $P = 0.34$). In addition, to be sure that small changes in riparian cover did not influence terrestrial invertebrate inputs to the stream, I measured riparian cover over the stream with a densiometer. Densiometer readings were recorded every 5 m along the 50 m–long study reaches. At each location, mean percent forest cover was calculated from one reading taken facing upstream, one facing downstream, one facing the left bank, and one facing the right bank. Since within-group variability was smaller than between-group variability (ANOVA, $F_{1,10} = 2.03$, $P = 0.042$), I 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 the summer of 2010.

Upland Terrestrial Invertebrate Biomass

To assess biomass of terrestrial invertebrates in upland ESH and LSH, I collected invertebrates from each habitat type in each of 10 study watersheds in July and August. Two of

the 12 study watersheds lacked patches of ESH large enough for sampling (Watersheds 1 and 2, Table 1-1 and Figure 1-1). ESH and LSH sites were separated from the stream and from each other by a minimum distance of 100 m. To minimize the influence of edge effects on terrestrial invertebrate samples, all traps were placed at least 30 m from the forest edge. In each habitat type, five replicates of three colored 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 of ESH and LSH patches within an area of ~4.5 ha and left open for two 48-hour, rain-free, low-wind periods beginning on July 4 and August 19. Each pan trap was filled with water to a depth of 3 cm and a drop of soap to break the water's surface tension.

These traps were intended to capture winged invertebrates capable of dispersal to the stream. No terrestrial invertebrate trap is completely without bias (Southwood 1978, Edwards and Huryn1995, Wipfli 1997, Leather 2005). For example, I cannot exclude the possibility that visibility of pan traps by winged 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% EtOH. All adult invertebrates were identified to the family level with the exception of the order Aranae. Larval invertebrates were identified to order. Invertebrate body lengths were measured to the nearest 0.5 mm and dry masses were calculated with 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, I 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 stream 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 sides10 cm high) were elevated on rebar 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-hour, rain-free, low-wind periods beginning on July 4 and August 19. Collection, transportation of samples, and biomass measurement methods were the same as those for the upland terrestrial invertebrate sampling. Invertebrates were categorized as terrestrial if their larval origin is terrestrial. Invertebrate families that include members with aquatic and terrestrial larval stages were assigned to the habitat in which their larvae most commonly develop, based on the recommendations of McAlpine et al. (1981) and Merritt et. al. (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 hours on July 13 and August 22. Mean flow velocity was calculated from ten measurements taken when nets were set and retrieved. In the field, samples were transported to the lab in 70% EtOH, where all aquatic and terrestrial invertebrates were identified to the family level. Invertebrate dry mass (g/m^3 discharge) was determined by body length measurements and taxon-specific length-mass conversion equations (Smock 1980, Sage 1982, Sample et al. 1993, Benke 1999).

Benthic Invertebrate Biomass

Because brook trout are generalist feeders that forage at the stream surface, in the drift, and on benthic invertebrates (Mcnicol et al. 1985, Bechara et al. 1993), the percent terrestrial invertebrates in brook trout diets could be influenced by the availability of benthic invertebrates. Therefore, I collected benthic invertebrate samples on July 2 - 3 and again on August 17 - 18. 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 use of terrestrial invertebrates by brook trout, I 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 July 12 - 14 and August 23 - 26 using a backpack electrofishing unit (Model LR - 24, Smith-Root Inc., Vancouver, WA, USA). All individuals were between 80 and 120 mm, which represent brook trout 1 and 2 years of age based on size frequency distributions (MK Wilson, unpublished data). Fish were anesthetized with tricaine methanesulfonate and stomach contents were removed by flushing water into fish stomachs using a 30 mL spray bottle with a narrow nozzle (Hyslop et. al. 1980). Stomach contents were collected in an 80 µm nylon mesh filter and transferred to plastic bags containing 95% EtOH for transportation to the lab. Diet items were identified to the family level for all prey

except the order Aranae and orders of immature terrestrial invertebrates. If total body measurements were not possible, I estimated lengths of partially digested prey based on intact individuals of the same taxon that were 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). Percent 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 percent 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 behavior may also be influenced by stream temperature, fish density, and size of fish sampled for diet analysis (Baldwin 1957, Marchand and Boisclair 1998, Utz and Hartman 2009), I measured these three variables to assess their influence on the percent terrestrial invertebrate biomass in brook trout diet. Mean daily stream temperatures were calculated from recordings taken every 10 minutes from July 1 to August 29. 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

I used a linear mixed effects model, implemented in Program R (version 2.13.1), to test whether biomass of terrestrial invertebrates differed between upland ESH and LSH. Habitat type

(early or late successional) was modeled as a fixed factor nested within the watershed, which was modeled as a random factor to account for variation among watersheds in invertebrate abundance in both ESH and LSH. A likelihood ratio test was used to assess the contribution of watershed as a random factor (Bolker et. al. 2009). I used the same set of analyses to test whether abundance of terrestrial invertebrates differed between upland habitat types. Biomass and abundance data were log transformed for these analyses.

I used stepwise multiple regression analyses (forward and backward selection, $P = 0.05$ to enter and remove), implemented in JMP version 9 (SAS 2009), to assess watershed-scale, riparian, and in-stream predictors of the percent terrestrial invertebrate biomass in brook trout diets. The six independent variables were: (1) percent ESH in the watershed, (2) mean distance of ESH patches to the stream, (3) percent riparian vegetation cover over the stream, (4) biomass input of terrestrial invertebrates to the stream, (5) percent terrestrial invertebrate biomass in stream drift, and (6) biomass of benthic aquatic invertebrates within the stream.

Before running the stepwise multiple regression analysis, I 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 me to test whether watershed and riparian forest variables were related to biomass of terrestrial invertebrate input, percent terrestrial invertebrate biomass in drift, and benthic invertebrate biomass (variables 4, 5, and 6 above). Additionally, they allowed me to test whether biomass of terrestrial invertebrates collected in stream pan traps was related to percent 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 me to determine whether

timber harvest in upland habitats caused variation in canopy cover within riparian buffers (1 and 3 above).

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

Results

Forest Habitat Assessment

The percent ESH in the 12 study watersheds ranged from 0 to 51.5% (Table 1-1). Mean distance of ESH patches to the study reach ranged 125 to 1192 m and was uncorrelated with the percent ESH in the watershed (Table 1-2). Over-stream riparian canopy cover was consistently high (range = 95.1 - 99.7%, Table 1-1).

Upland Terrestrial Invertebrate Biomass

Terrestrial invertebrate biomass was greater in upland ESH than in upland LSH ($F_{1,18}$ = 45.94, P < 0.0001, Figure 1-2). In addition, abundance of terrestrial invertebrates was greater in ESH than LSH ($F_{1,18}$ = 3.65, P = 0.057). To determine whether terrestrial invertebrate biomass in ESH and LSH varied with percent ESH in the watershed, I conducted a likelihood ratio test comparing the mixed effects model to a general linear model in which the percent ESH in the watershed was excluded (i.e., excluding watershed as a random effect). This test showed that the percent ESH in the watershed had no influence on terrestrial invertebrate biomass at ESH and LSH sites (χ^2 = 0.0028, P = 0.96, df=1).

Table 1-2. Correlation matrix for the six independent variables in the stepwise regression analysis, based on data collected from twelve watersheds in the Dead Diamond River drainage in northern New Hampshire, U.S.A. All correlations are not significant at the level of P = 0.05 (Pearson product moment correlation). TI = Terrestrial Invertebrate. ESH = Early Successional Habitat.

	% ESH	Mean Patch Distance	% Riparian Vegetation Cover	Benthic Biomass	TI Biomass	% TI in Drift
% ESH	1					
Mean Patch Distance	-0.42	1				
% Riparian Vegetation Cover	0.18	-0.15	1			
Benthic Biomass	-0.03	0.05	-0.27	1		
TI Biomass	0.04	-0.03	0.25	-0.54	1	
% TI in Drift	0.17	-0.19	0.10	0.29	0.41	1
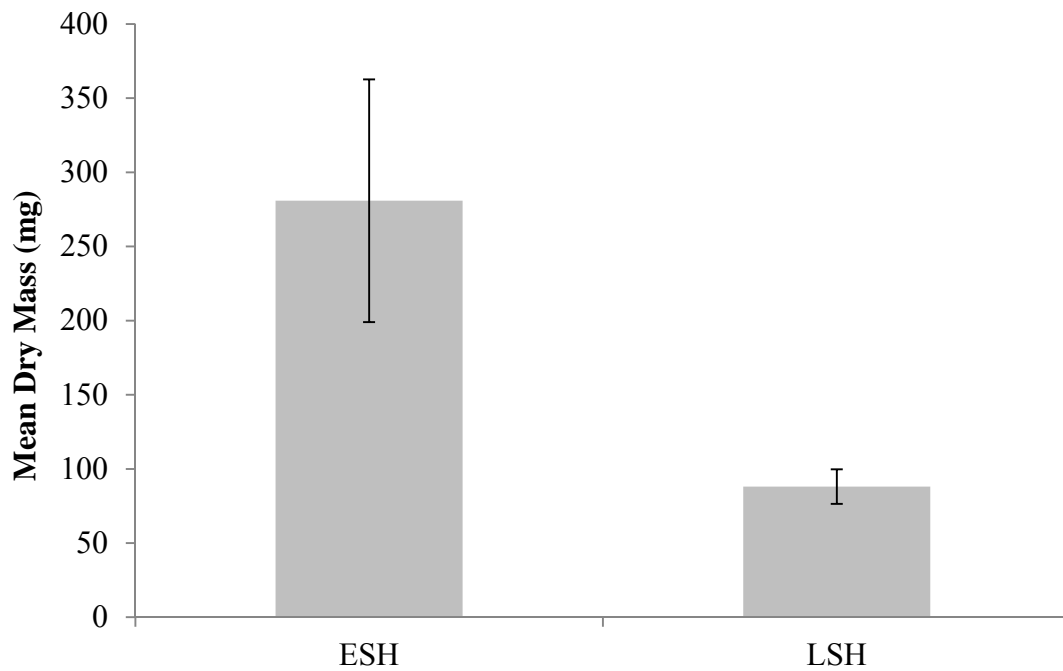
Figure 1-2. Mean dry mass (mg) of terrestrial invertebrates collected from pan traps in early successional habitat (ESH) and and late successional habitat (LSH) focal patches in 10 watersheds of the Dead Diamond River drainage in northern New Hampshire U.S.A. Error bars represent 95% confidence intervals.

Terrestrial Invertebrate Subsidies to Streams and Brook Trout Diets

All independent variables in the multiple regression analysis were uncorrelated (Table 1-2). This eliminated the potential problem of multicollinearity in multiple regression analysis and allowed me to distinguish among these predictors of variation in terrestrial invertebrate use by brook trout. Measures of terrestrial invertebrate biomass in stream pan traps and drift nets were unrelated to forest habitat characteristics at both riparian and watershed 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, which indicates that these methods of assessing terrestrial invertebrate input were not interchangeable. Finally, watershed 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 the percent terrestrial biomass in brook trout diet. Percent terrestrial invertebrate biomass in brook trout diets was negatively related to biomass of benthic invertebrates in streams ($F_{1,10}$=12.18, $P = 0.006$, r^2= 0.55, Figure 1-3, Table 1-3). Percent terrestrial invertebrate biomass in brook trout diets was unrelated to stream temperature, fish density within the stream study reach, and length of fish sampled for diet analysis ($F_{1,7}$=0.72, $P = 0.57$). 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 1-4).
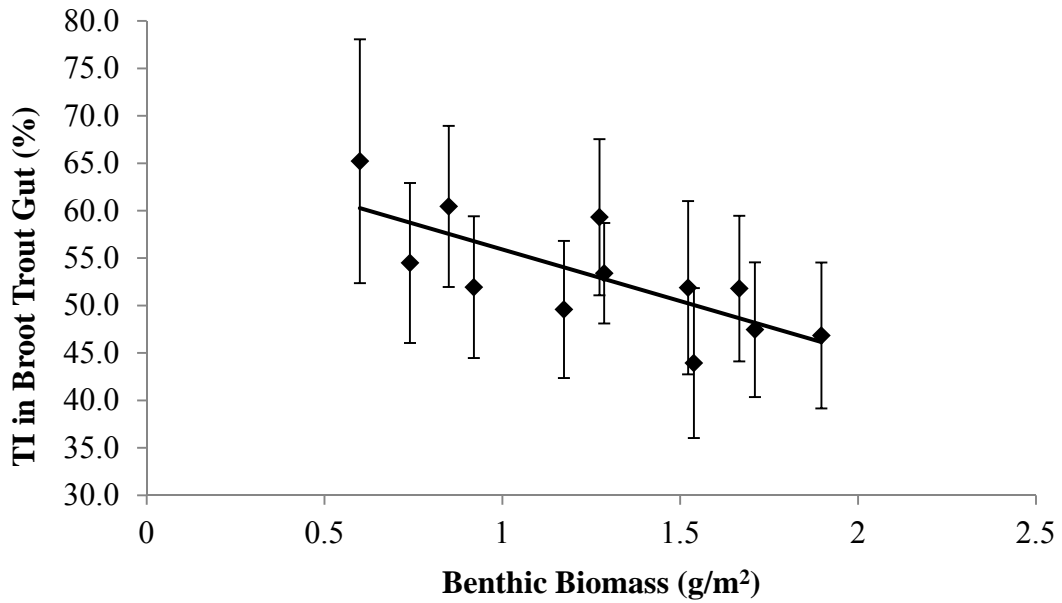
Figure 1-3. Linear regression result showing that the percentage by mass of terrestrial invertebrates (TI) in brook trout diet was negatively related to biomass of benthic invertebrates (P = 0.006, $F_{1,10}$ = 12.18, r^2 = 0.55). Data is from twelve streams in the Dead Diamond River drainage in northern New Hampshire, U.S.A. Error bars represent 95% confidence intervals.

Table 1-3. Mean values (± 1 SE) for terrestrial invertebrate (TI) dry mass (mg) in stream-surface pan traps, percent TI in the stream drift, dry mass (g/m^2) of benthic aquatic invertebrates, and percent TI in brook trout diet. Data are from 12 streams in the Dead Diamond River drainage in northern New Hampshire, U.S.A.

Stream	Pan Trap TI Dry Mass in mg (± 1 SE)	% TI in Drift (± 1 SE)	Benthic Invertebrate Dry Mass in g/m^2 (± 1 SE)	% TI 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)

Table 1-4. Mean brook trout density within the 50 m study reach, estimated from 3-pass removal surveys, and mean length (± 1 SE) in mm of fish sampled for diet analysis from 12 streams in the Dead Diamond River drainage in northern New Hampshire, U.S.A. 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 (± 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)

To determine if the relationship between benthic invertebrate biomass and brook trout diet composition differed in July and August I used ANCOVA to test for direct and interactive effects of month and benthic invertebrate biomass on percent terrestrial invertebrate biomass in brook trout gut contents. I 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 percent terrestrial invertebrate biomass in brook trout gut contents was higher in July than August, but the relationship with benthic invertebrate biomass (Fig. 1-3) did not differ between months.

Discussion

This study provides novel insight on the importance of ESH for forest invertebrate production, and the mechanisms influencing terrestrial invertebrate use by brook trout. Terrestrial invertebrate biomass was greater in ESH than LSH, indicating that ESH habitat can contribute valuable resources to higher trophic levels in northeastern forests. However, inputs of terrestrial invertebrates to headwater streams and use of these subsidies by brook trout did not increase with percent ESH in watersheds. Surprisingly, my 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 invertebrates subsidies than previously thought.

While theory predicts greater biomass of terrestrial invertebrates in ESH than LSH (Brown 1984), effects of forest age on overall invertebrate abundance and biomass is not well

understood, particularly in the northeastern United States (Schowalter et. al. 2005). My data from ten between-habitat comparisons indicate that the summertime biomass of winged terrestrial invertebrates is greater in ESH than LSH in northeastern forests. This result can be explained by the higher productivity to biomass ratio, more nutrient rich leaves (in particular a lower C:N ratio), and lower production of defense compounds in early successional vegetation (Schowalter et al. 1986, Ohgushi, 1992), all of which make early successional leaves a more valuable resource for terrestrial invertebrates (Mattson and Scriber 1987, Chapin III et. al. 2002). As invertebrates are a common diet item for terrestrial vertebrates, this finding may provide a partial explanation for the preference for ESH of many species of birds (Litvaitis 1993, Dessecker and McAuley 2001, DeGraaf and Yamasaki 2003) and small mammals (Litvaitis 2001, Fuller and DeStefano 2003).

Forest ownership in northeastern forests has recently shifted from large-scale timber companies to diverse, smaller landowners, resulting in reductions in parcel size and in the amount of land currently under active management (Brooks 2003). This has had major consequences for forest ecosystems in the northeastern U.S.A. (Hagan et al. 2005). Specifically, a reduction in the scale of timber management, along with the succession of abandoned agricultural fields to mature forest, has reduced the extent and frequency of forest clearings. My data suggest that including upland ESH in forest management plans may increase the secondary production that supports vertebrates at higher trophic levels.

Despite increased terrestrial invertebrate biomass in ESH, my data do not support the hypothesis that watersheds containing a greater percent ESH contribute greater terrestrial invertebrate subsidies to headwater streams. In this study, the focal response variable was percent terrestrial to aquatic invertebrate biomass in brook trout diet, representing the relative

23

importance of terrestrial invertebrates to this consumer. However, my results also show that the percent ESH in the watershed had no influence on the biomass of terrestrial invertebrates entering the stream and in the stream drift. In addition, riparian vegetation cover over the stream did not predict terrestrial invertebrate input, but this result was expected due to wide buffers (min = 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, I conducted *a posteriori* stepwise multiple regression using data on mean tree diameter at breast height (dbh), stand density, and understory cover along two 50 m long, 2 m wide riparian transects adjacent to the stream bank of 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.

My results are consistent with the findings of Allan et al. (2003), who measured greater biomass of terrestrial invertebrates on early successional vegetation in the riparian zone, but did not find that streams flowing through ESH received greater inputs of terrestrial invertebrate biomass than streams flowing through LSH. There are several possible explanations for my findings and those of Allan et. al. (2003). First, it may be that winged terrestrial invertebrates remain in ESH patches for the duration of their life and do not disperse away from these high-quality habitats. If this is true, the increased invertebrate biomass found in ESH benefits only those consumers found in ESH and has no influence on consumers found in LSH or streams buffered by riparian zones. Alternatively, winged invertebrates may disperse away from and between ESH patches without falling into headwater streams, which represent a small area within the watershed. Finally, aerial mixing by wind and dispersal may render current sampling methods insufficient for detecting inputs (Macneale et. al. 2004). Because trees interfere with

insect tracking methods, understanding of invertebrate dispersal in forest ecosystems is still poor (Riley and 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 percent terrestrial invertebrates in brook trout diets (Figure 1-3). *A posteriori* analysis revealed the same negative relationship between abundance of aquatic invertebrates and percent terrestrial invertebrate biomass in brook trout diets. Together, these results suggest that use of terrestrial invertebrate subsidies by brook trout depends primarily on availability of *in situ* diet items – aquatic invertebrates. Previous studies have shown that the percent terrestrial invertebrates found in trout diets often exceeds the percent terrestrial invertebrates found in the drift, suggesting that trout selectively feed on this terrestrial resource (Elliot 1973, Hubert and Rhodes 1989, Garman 1991, Nakano et. al. 1999b). However, these studies do not report relationships between terrestrial invertebrate inputs and percent terrestrial invertebrates in trout diets, which would provide direct evidence that terrestrial invertebrate input determines use of this allochthonous resource. In my study, percent 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 < 3% of the total invertebrate drift biomass, and therefore comprised a small proportion of the aerial contribution to stream drift. In addition, terrestrial invertebrate inputs (both in surface pan traps and drift nets) were unrelated to percent terrestrial invertebrates in brook trout diet. Therefore, while it is clear that terrestrial invertebrates are an important component of brook trout diet during the summer, my results indicate that terrestrial invertebrate

use by brook trout is determined by availability of benthic invertebrates, rather than terrestrial invertebrates.

Feeding behavior 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 Jr. 1974, Allan 1981, Sweka and Hartman 2008b, Utz and Hartman 2009). Biomass density of benthic invertebrates in my study streams (mean = 1.3 g / m^2) was comparable to that of forested, headwater streams in other regions (e.g., Nakano et. al. 1999b: mean = 1.2 g/m^2; Smock et. al. 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, the percent terrestrial invertebrate biomass in brook trout diets was unrelated to trout density, size, and stream temperature, suggesting that these factors did not influence brook trout feeding behavior.

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 on subsidy use. With manipulative experiments, studies have shown that changes in the magnitude of terrestrial subsidies to streams influences the abundance of *in situ* resources via changes in density and behavior of consumers that feed on both resources (Nakano et. al. 1999a, Nakano et. al. 1999b). 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 likely much larger than variation resulting from natural and anthropogenic factors in unmanipulated watersheds (e.g., < 3-fold difference between maximum and minimum mean input, Mason and MacDonald 1984, Wipfli 1997, Kawaguchi and Nakano 2001, Allan et. al. 2003). Consequently, effects documented in these experiments may

overshadow factors mediating subsidy inputs and use in natural systems – including availability of aquatic prey. The importance of terrestrial invertebrate inputs to streams for stream consumers, therefore, may vary with in situ production.

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 and Huryn 2010). Variation in these factors can be determined by natural features of the watershed (Likens and Bormann 1995) and anthropogenic impacts, including timber harvest and development (Resh et. al. 1988, Whiles and Wallace 1995, Sponseller et. al. 2001, Allan et. al. 2004). My 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 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.

Literature Cited

Allan, J.D. 1981. Determinants of diet of brook trout (*Salvelinus fontinalis*) in a mountain stream. Canadian Journal of Fisheries and Aquatic Sciences **38**:184-192.

Allan, J. D., M. S. Wipfli, J. P. Caouette, A. Prussian, and J. Rodgers. 2003. Influence of streamside vegetation on inputs of terrestrial invertebrates to salmonid food webs. Canadian Journal of Fisheries and Aquatic Sciences **60**:309-320.

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

Allen, K. R. 1951. Horokiwi stream: a study of a trout population. New Zealand Marine Department of Fisheries Bulletin 10. Wellington, New Zealand.

Anderson, W. B., and G. A. Polis. 2004. Allochthonous nutrient and food inputs: consequences for temporal stability. Pages 82–95 in G. A. Polis, M. E. Power, and G. R. Huxel (eds.). Food webs at the landscape level. University of Chicago Press, Chicago, Illinois.

Baldwin, N.S. 1957. Food consumption and growth of brook trout at different temperatures. Transactions of the American Fisheries Society **86**:323-328.

Baxter, C. V., K. D. Fausch, M. Murakami, and P. L. Chapman. 2007. Invading rainbow trout usurp a terrestrial prey subsidy from native charr and reduce their growth and abundance. Oecologia **153**:461-470.

Baxter, C. V., K. D. Fausch, and W. C. Saunders. 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biology **50**:201-220.

Bechara, J.A., G. Moreau, and L. Hare. 1993. The impact of brook trout (*Salvelinus fontinalis*) on an experimental stream benthic community – the role of spatial and size refugia. Journal of Animal Ecology **62**:451-464.

Benke, A.C., A.D. Huryn, L.A. Smock, and J.B. Wallace. 1999. Length-mass relationships for freshwater macroinvertebrates in North America with particular reference to the southeastern United States. Journal of the North American Benthological Society **18**:308-343.

Benke, A.C., and A.D. Huryn. 2010. Benthic invertebrate production – facilitating answers to ecological riddles in freshwater ecosystems. Journal of the North American Benthological Society **29**:264-285.

Bolker, B.M., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J.S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution **46**:590-599.

Brooks, R. T. 2003. Abundance, distribution, trends, and ownership patterns of early-successional forests in the northeastern United States. Forest Ecology and Management **185**:65-74.

Brooks, R.T., K.H. Nislow, W.H. Lowe, M.K. Wilson, and D.I. King. 2012. Forest succession and terrestrial-aquatic biodiversity in small forested watersheds: a literature review of principles, relationships, and implications for management. Forestry: An International Journal of Forest Research doi: 10.1093/forestry/cps031.

Brown, V. K. 1984. Secondary succession: insect-plant relationships. Bioscience **34**:710-716.

Cada, G. F., J. M. Loar, and D. K. Cox. 1987. Food and feeding preferences of rainbow and brown trout in southern Appalachian streams. American Midland Naturalist **117**:374-385.

Chapin III, F.S., H.A. Mooney, M.C. Chapin, and P. Matson. 2002. Principles of terrestrial ecosystem ecology. Springer, New York.

DeGraaf, R.M., and M.Yamasaki. 2003. Options for managing early-successional forest and shrubland bird habitats in the northeastern United States. Forest Ecology and Management **185**:197-191.

Dessecker, D.R., and D.G. McAuley. 2001. Importance of early successional habitat to ruffed grouse and American woodcock. Wildlife Society Bulletin **29**:456-465.

Duguay, J.P., P. Bohall-Wood, and G.W. Miller. 2000. Effects of timber harvests on invertebrate biomass and avian nest success. Wildlife Society Bulletin **28**:1123-1131.

Edwards, E. D., and A. D. Huryn. 1995. Annual contribution of terrestrial invertebrates to a New Zealand trout stream. New Zealand Journal of Marine and Freshwater Research **29**:467-477.

Elliot, J. M. 1973. The food of brown and rainbow trout (*Salmo trutta* and *S. gairdneri*) in relation to the abundance of drifting invertebrates in a mountain stream. Oecologia **12**:329-347.

England, L. E., and A. D. Rosemond. 2004. Small reductions in forest cover weaken terrestrial-aquatic linkages in headwater streams. Freshwater Biology **49**:721-734.

Ensign, W. E., R. J. Strange, and S. E. Moore. 1990. Summer food limitation reduces brook and rainbow-trout biomass in a southern Appalachian stream. Transactions of the American Fisheries Society **119**:894-901.

Fausch, K. D., C. E. Torgersen, C. V. Baxter, and H. W. Li. 2002. Landscapes to riverscapes: bridging the gap between research and conservation of stream fishes. Bioscience **52**:483-498.

Fuller, T.K., and S. DeStefano. 2003. Relative importance of early-successional forests and shrubland habitats to mammals in the northeastern United States. Forest Ecology and Management **185**:75-79.

Garman, G. C. 1991. Use of terrestrial arthropod prey by a stream-dwelling cyprinid fish. Environmental Biology of Fishes **30**:325-331.

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology **84**:2809-2815.

Greene, B. T., W. H. Lowe, and G. E. Likens. 2008. Forest succession and prey availability influence the strength and scale of terrestrial-aquatic linkages in a headwater salamander system. Freshwater Biology **53**:2234-2243.

Griffeth Jr., J.S. 1974. Utilization of invertebrate drift by brook trout (*Salvelinus fontinalis*) and cutthroat trout (*Salmo clarki*) in small streams in Idaho. Transactions of the American Fisheries Society **103**:440-447.

Grindal, S.D., and R.M. Brigham. 1998. Short-term effects of small-scale habitat disturbance on activity by insectivorous bats. The Journal of Wildlife Management **62**:996-1003.

Hagan, J. M., L. C. Irland, and A. A. Whitman. 2005. Changing timberland ownership in the Northern Forest and implications for biodiversity. Report # MCCS-FCP-2005-1, Manomet Center for Conservation Sciences. Brunswick, Maine.

Hetrick, N. J., M. A. Brusven, T. C. Bjornn, R. M. Keith, and W. R. Meehan. 1998. Effects of canopy removal on invertebrates and diet of juvenile coho salmon in a small stream in southeast Alaska. Transactions of the American Fisheries Society **127**:876-888.

Hubert, W. A., and H. A. Rhodes. 1989. Food selection by brook trout in a subalpine stream. Hydrobiologia **178**:225-231.

Hunt, R. L. 1975. Use of terrestrial invertebrates as food by salmonids. A. D. Hasler, (ed.). Coupling of land and water systems. Springer-Verlag, New York.

Hynes, H. B. N. 1970. The ecology of running waters. University of Toronto Press, Toronto, Ontario.

Hyslop, E. J. 1980. Stomach contents analysis – a review of methods and their application. Journal of Fish Biology **17**:411-429.

Johnson, S. L., and A. P. Covich. 1997. Scales of observation of riparian forests and distributions of suspended detritus in a prairie river. Freshwater Biology **37**:163-175.

JMP, Version 9. SAS Institute Inc., Cary, NC, 1989-2012.

Kawaguchi, Y., and S. Nakano. 2001. Contribution of terrestrial invertebrates to the annual resource budget for salmonids in forest and grassland reaches of a headwater stream. Freshwater Biology **46**:303-316.

Kawaguchi, Y., Y. Taniguchi, and S. Nakano. 2003. Terrestrial invertebrate inputs determine the local abundance of stream fishes in a forested stream. Ecology **84**:701-708.

Leather, S.R. (ed.). 2005. Insect sampling in forest ecosystems. Wiley-Blackwell, Malden, Massachusetts.

Litvaitis, J.A. 1993. Response of early successional vertebrates to historic changes in land use. Conservation Biology **7**:866-873.

Litvaitis, J.A. 2001. Importance of early successional habitats to mammals in eastern forests. Wildlife Society Bulletin **29**:466-473.

Likens, G. E., and F. H. Bormann. 1974. Linkages between terrestrial and aquatic ecosystems. Bioscience **24**:447-456.

Likens, G.E., and F.H. Bormann. 1995. Biogeochemistry of a forested ecosystem. Second Edition. Springer-Verlag, New York.

Macneale, K.H., B.L. Peckarsky, and G.E. Likens. 2004. Contradictory results from different methods for measuring direction of insect flight. Freshwater Biology **49**:1260-1268.

Manley, S.W., R.S. Fuller, J.M. Lee, L.A. Brennan. 1995. Arthropod response to strip disking in old fields managed for northern bobwhites. Proceedings of the Southeastern Association of Fish and Wildlife Agencies Conference. **48**:227-235.

Marchand, F., and D. Boisclair. 1998. Influence of fish density on the energy allocation pattern of juvenile brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **55**:796-805.

Marczak, L. B., T. M. Hoover, and J. S. Richardson. 2007a. Trophic interception: how a boundary-foraging organism influences cross-ecosystem fluxes. Oikos **116**:1651-1662.

Marczak, L.B., M.T. Ross, and J.S. Richardson. 2007b. Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. Ecology **88**:140-148.

Mason, C. F., and S. M. Macdonald. 1982. The input of terrestrial invertebrates from tree canopies to a stream. Freshwater Biology **12**:305-311.

Mattson, W.J., J.M. Scriber. 1987. Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral considerations. In: Slansky, Jr., F., and J. Rodriguez (eds.), Nutritional Ecology of Insects, Mites, Spiders, and Related Invertebrates. Wiley, New York, pp. 105–146.

McAlpine, J. F., B.V. Peterson, G.E. Shewell, H.J. Teskey, J.R. Vockeroth, and D.M. Wood (ed.). 1981. Manual of nearctic diptera. Ottowa: Research Branch Agriculture Canada.

Mcnicol, R. E., E. Scherer, and E. J. Murkin. 1985. Quantitative field investigations of feeding and territorial behavior of young-of-the-year brook charr, *Salvelinus fontinalis*. Environmental Biology of Fishes **12**:219-229.

Merritt, R.W., K.W. Cummins, and M.B. Berg. 2008. An introduction to the aquatic insects of north america, Fourth Edition. Kendall/Hunt Publishing Company, Dubuque, Iowa.

Nakano, S., Y. Kawaguchi, Y. Taniguchi, H. Miyasaka, Y. Shibata, H. Urabe, and N. Kuhara. 1999a. Selective foraging on terrestrial invertebrates by rainbow trout in a forested headwater stream in northern Japan. Ecological Research **14**:351-360.

Nakano, S., H. Miyasaka, and N. Kuhara. 1999b. Terrestrial-aquatic linkages: riparian arthropod inputs alter trophic cascades in a stream food web. Ecology **80**:2435-2441.

Nakano, S., and M. Murakami. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proceedings of the National Academy of Sciences of the United States of America **98**:166-170.

Needham, P. R. 1928. A net for the capture of stream drift organisms. Ecology **9**:339-342.

Ober, H.K., and J.P. Hayes. Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. Forest Ecology and Management **256**:1124-1132.

Ohgushi, T. 1992. Resource limitation on insect herbivore populations. In: Hunter, M.D., T. Ohgushi, and P.W. Price (eds.). Effects of resource distribution on animal-plant interactions. Academic Press, San Diego, CA, pp. 199-241.

Osborne, J. L., S. J. Clark, R. J. Morris, I. H. Williams, J. R. Riley, A. D. Smith, D. R. Reynolds, and A. S. Edwards. 1999. A landscape-scale study of bumble bee foraging range and constancy, using harmonic radar. Journal of Applied Ecology **36**:519-533.

Polis, G. A., W. B. Anderson, and R. D. Holt. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annual Review of Ecology and Systematics **28**:289-316.

Resh, V.H., A.V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar. The role of disturbance in stream ecology. Journal of the North American Benthological Society **7**:433-455.

Riley, J. R., P. Valeur, A. D. Smith, D. R. Reynolds, G. M. Poppy, and C. Lofstedt. 1998. Harmonic radar as a means of tracking the pheromone-finding and pheromone-following flight of male moths. Journal of Insect Behavior **11**:287-296.

Riley, J.R., and A.D. Smith. 2002. Design considerations for an harmonic radar to investigate the flight of insects at low altitude. Computers and Electronics in Agriculture **35**:151-169.

Sage, R.D. 1982. Wet and dry-weight estimates of insects and spiders based on length. American Naturalist **108**: 407-411.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist **129**:234-240.

Schowalter, T.D., W.W. Hargrove, and D.A. Crossley Jr.1986. Herbivory in forested ecosystems. Annual Review of Entomology **31**:177–196.

Schowalter, T. D., Y. L. Zhang, and R. A. Progar. 2005. Canopy arthropod response to density and distribution of green trees retained after partial harvest. Ecological Applications **15**:1594-1603.

Schultz, M.E., and T.L. DeSanto. 2006. Comparison of terrestrial invertebrate biomass and richness in young mixed red alder-conifer, young conifer, and old conifer stands of southeast Alaska. Northwest Science **80**:120-132.

Smock, L.A. 1980. Relationships between body size and biomass of aquatic insects. Freshwater Biology **10**:375-383.

Smock, L.A. 1985. Macroinvertebrate production in a southeastern United States blackwater stream. Ecology **66**:1491-1503.

Southwood, T.R.E. 1978. Ecological methods: with special reference to the study of insect populations. 2nd ed. Chapman and Hall, London.

Sponseller, R.A., E.F. Benfield, and H.M. Valett. 2001. Relationships between land use, spatial scale and stream macroinvertebrate communities. **46**:1409-1424.

Sweka, J. A. 2003. Aquatic-terrestrial linkages in Appalachian streams: influence of riparian inputs on stream habitat, brook trout populations, and trophic dynamics. Dissertation. West Virginia University, Morgantown, West Virginia, USA.

Sweka, J. A., and K. J. Hartman. 2008a. Contribution of terrestrial invertebrates to yearly brook trout prey consumption and growth. Transactions of the American Fisheries Society **137**:224-235.

Sweka, J. A., and K. J. Hartman. 2008b. Influence of turbidity on brook trout reactive distance and foraging success. Transactions of the American Fisheries Society **130**:1548-8659.

Utz, R.M., and K.J. Hartman. 2009. Density-dependent individual growth and size dynamics of central Appalachian brook trout (*Salvelinus fontinalis*). Canadian Journal of Fisheries and Aquatic Sciences **66**:1072-1080.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. River continuum concept. Canadian Journal of Fisheries and Aquatic Sciences **37**:130-137.

Waters, T. F. 1988. Fish production - benthos production relationships in trout streams. Polskie Archiwum Hydrobilogii **35**:545-561.

Whiles, M.R., and J.B. Wallace. 1995. Macroinvertebrate production in a headwater stream during recovery from anthropogenic disturbance and hydrologic extremes. Canadian Journal of Fisheries and Aquatic Sciences **52**:2402-2422.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. Canadian Journal of Fisheries and Aquatic Sciences **54**:1259-1269.

Young, M. K., R. B. Rader, and T. A. Belish. 1997. Influence of macroinvertebrate drift and light on the activity and movement of Colorado River cutthroat trout. Transactions of the American Fisheries Society **126**:428-437.

CHAPTER 2: THE CONTRIBUTION OF EARLY SUCCESSIONAL HABITAT TO INVERTEBRATE DIVERSITY AND BIOMASS IN NORTHEASTERN FORESTS

Introduction

Habitat heterogeneity across landscapes is important for supporting plant and animal diversity (Kerr and Packer 1997, Tews et. al. 2004, Kreft and Jetz 2007) and disturbance is often critical for maintaining this heterogeneity (Connell 1978, Rogers 1996). In the northeastern U.S.A., early successional habitat (ESH), characterized by abundant short-statured woody vegetation, abundant and diverse herbaceous vegetation and a high productivity:biomass ratio, results from natural and anthropogenic disturbances and contributes heterogeneity to forested landscapes. ESH in this region is maintained by timber harvest and naturally by windstorms, ice storms, fires, drought, and insect and disease infestations, although large-scale, stand-replacing events are infrequent (Lorimer 2001).

ESH is critical to many species of vertebrates in northeastern forests, including birds, bats, and small mammals (DeGraaf and Yamasaki 2001, Hunter et. al. 2001, King et. al. 2012). For example, DeGraaf and Yamasaki (2001) list 40 New England wildlife species (12% of the regional wildlife fauna of 338 species) that are restricted to ESH and only 32 species (10%) as not using ESH in combination with other forest size classes. A common explanation for the frequent use of ESH by vertebrates is higher abundances of invertebrate prey relative to surrounding forests (e.g., Vega-Rivera et. al. 1998, Greenberg et. al. 2011, Chandler et. al. 2012). However, studies evaluating differences in invertebrate richness and biomass in early and late successional habitats (LSH) are rare (Loeb and Okeefe 2011). Furthermore, although steady decline of ESH in the northeastern U.S.A. over recent decades has led to special-status designations of plants and vertebrates that rely on this habitat (DeGraaf and Yamasaki 2001)

(Litvaitis 1993, Trani et. al. 2001), the implications of decreasing ESH for invertebrate taxa have received little consideration.

Several characteristics of ESH vegetation in northern mixed conifer-deciduous forests suggest that invertebrate diversity and biomass should be greater in ESH than LSH. First, increased sunlight and nutrient availability in ESH supports high plant diversity and floral abundance (Elliot et. al. 2011, Greenberg et. al. 2011). This increase in plant diversity and floral abundance should attract pollinators and phytophagous insects that specialize on ESH plant species (Greenberg et. al. 2011). Second, ESHs have a high productivity:biomass ratio (Horn 1974), resulting in greater abundance of resources for secondary consumers, including invertebrates. Finally, regenerating plants in ESH have higher concentrations of nitrogen (a limiting nutrient for many herbivorous invertebrates), lower concentrations of secondary defense compounds (inhibitory to many herbivorous invertebrates), and thinner cell walls with less lignin than plants in LSH (Ball et. al. 2002), making ESH vegetation a higher quality food resource (Mattson and Scribner 1987, Ohgushi 1994). This increase in plant diversity, nutrient content, and palatability should benefit invertebrate growth and reproduction, and improve invertebrate resistance to parasites and disease (Loader and Damman 2008).

To date, most studies comparing invertebrate richness and biomass in ESH and LSH limit the breadth of sampling to one order or family (reviewed in Lewinsohn et. al. 2005). For example, ESH in New England is critical for many rare moth and butterfly species. Wagner et. al. (2003) reported 56 Lepidopteran species of conservation concern that use ESH vegetation as a larval host, and they proposed that invertebrates in other orders, including rare species, also require ESH habitat. However, I am aware of no study comparing community richness and biomass of multiple orders of invertebrates in ESH and LSH of the northeastern U.S.A. Studies

from elsewhere suggest that community-level responses to ESH of invertebrates vary with region (e.g., Summerville and Crist 2002, Ulyshen et. al. 2005, Jeffries et. al. 2006), ESH type and size (Shure and Phillips 1991), and target taxa (Kaoru and Hiroshi 1999, Schowalter et. al. 2005), highlighting the importance of collecting region-specific data (Lewinsohn et. al. 2005).

Understanding invertebrate response to ESH in northeastern forests is especially important given the declining trajectory of ESH cover in the northeastern U.S.A. (Trani et. al. 2001). Maintenance of wildlife openings and ESH habitat by means of timber harvest in the northeast has been proposed to mitigate this decline (Askins 2001, Litvaitis 2003, Wagner et. al. 2003), but the influence of these actions on diversity and biomass of terrestrial invertebrates has not been evaluated. In addition, invertebrate pollinators – species with a particularly important ecosystem function – are experiencing large-scale declines in abundance and diversity (Cane and Tepedino 2001, Biesmeijer et. al. 2006, Potts et. al. 2010). Although ESH is likely to be important for native pollinators in northeastern forests due to the richness of flowering plants it supports (Steffan-Dewenter and Tscharntke 2001, Elliot et. al. 2011), we have little data on associated pollinator communities.

My goal was to measure how family-level invertebrate richness, community composition, biomass, and abundance differ between ESH and LSH in northeastern forests. To meet this goal, I used colored pan traps to sample invertebrates in ESH and LSH focal patches in 12 small watersheds in northern New Hampshire, U.S.A. Using these trap data, I then quantified family-level invertebrate richness, biomass and abundance in the two habitat types, as well as dissimilarity in community composition between the two habitats. Finally, to address the potential influence of total watershed coverage of ESH and focal ESH patch size on invertebrate

communities, I tested whether these landscape-level variables were related to invertebrate richness and biomass in focal ESH patches.

Materials and Methods

Study Area and Watershed Characteristics

Study sites were located in twelve first and second order watersheds of the Dead Diamond River drainage of New Hampshire, U.S.A. (Figure 2-1). ESH and LSH focal patches were paired within eight of these watersheds. The four remaining watersheds did not have patches of both ESH and LSH large enough to meet invertebrate sampling criteria, but did have sufficiently large patches of one habitat type (ESH in two watersheds, LSH in two watersheds). Watersheds differed in their total percent coverage of ESH and focal patches of ESH differed in size (Table 2-1). I measured both of these characteristics from aerial photographs in IDRISI Taiga © 2009 to assess their potential influence on invertebrate communities. ESH and LSH patches paired within watersheds differed in elevation by no more than 30m and all focal patches ranged 582 m to 683 m (Table 2-1).

The entire Dead Diamond drainage experienced heavy timber harvest in the late 1800s and early 1900s, and its headwater drainages have experienced varying degrees of clearcut and selective harvest since the 1930s (personal communication, Kevin Evans, Dartmouth College Woodlands Office). Within these watersheds, stand ages ranged from 0 to approximately 70 years old. In this study, ESH consisted of clearcut patches ranging from 3 - 7 years old; LSH consisted of intact forest > 50 years old. LSH was composed of mixed conifer 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*

38

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*).

Figure 2-1. Map of study watershed locations (1 – 12, corresponding to labels in Table 2-1) in the Dead Diamond River drainage, New Hampshire, U.S.A.

Table 2-1. Descriptive characteristics (watershed area (ha), elevation (m), and %ESH) of the 12 study watersheds and their focal ESH patch size (ha). Mean focal patch elevation is the mean of the elevations of ESH and LSH focal patches within the watershed, which differed by no more than 30 m in elevation in all watersheds. Focal ESH patch size (ha) and % ESH in the watershed were used to assess their influence on ESH invertebrate richness and biomass.

Watershed and Focal Patch Characteristics	Watershed											
	1	2	3	4	5	6	7	8	9	10	11	12
Watershed area (ha)	129	130	384	225	403	150	406	348	208	177	105	165
Mean focal patch elevation (m)	742	672	618	677	653	825	812	775	637	582	695	836
% ESH in the watershed	0	1.6	2	2.4	5.7	9.2	11.1	16.8	19.1	24.2	36.7	51.5
Focal ESH patch size (ha)	NA	NA	4.1	4.5	3.9	11.7	5.6	23.1	10.1	5.4	25.7	5

Invertebrate Collection

To assess richness, community composition, biomass, and abundance of terrestrial invertebrates in upland ESH and LSH, I sampled invertebrates from ESH and LSH focal patches in the 12 study watersheds in July and August of 2010. ESH and LSH patches were separated from each other by a minimum distance of 100 m. In each patch, five replicate arrays of three colored pan traps (white, yellow, and blue) were set out at a height of 0.5 m above ground (Leather 2005, Campbell et. al. 2007). To minimize the influence of edge effects on terrestrial invertebrate samples (Deans et. al. 2005), all traps were placed at least 30 m from the ESH-LSH transition. Pan trap arrays were randomly placed ~35 m apart inside of focal patches and left open for two 48-hour, rain-free, low-wind periods beginning on July 4 and August 19. Each pan trap was filled with water to a depth of 3 cm and a drop of soap to break the water's surface tension. Pan traps target pollinating invertebrates, but they may also collect phytophagous and predatory invertebrates (Campbell et. al. 2007).

For each pan trap array, trapped invertebrates were pooled into a single composite sample and preserved in 70% EtOH. All invertebrates were identified to the family level with the exception of larval invertebrates and all Aranae, which were low in abundance (combined, < 1% of sampled individuals). In addition, two families of aquatic invertebrates (Nemouridae and Perlidae) were found in low abundance in some traps. Body lengths were measured to the nearest 0.5 mm and dry masses were calculated with taxon-specific length-mass conversion equations (Sage 1982, Sample et. al. 1993). This method of measuring biomass for trapped invertebrates is 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).

No terrestrial invertebrate trap is completely without bias (Southwood 1978, Edwards and Huryn 1995, Wipfli 1997, Leather 2005), and I cannot exclude the possibility that visibility of pan traps by winged invertebrates is greater in open ESH. However, pan trap sampling provided the least bias while allowing for sufficient replication in this study (Leather 2005, Campbell et. al. 2007). Although family-level identification prevented pollinator-specific analyses, pan traps target pollinators, and are known to be effective in capturing pollinators (Leather 2005, Campbell et. al. 2007). Therefore, I assumed that overall community-level responses to ESH and LSH documented with this method were consistent with responses of the pollinator community.

To quantify family-level richness, community composition, biomass and abundance, I calculated mean abundances of each family from the ten replicate trap arrays (5 arrays per sampling session, 2 sampling sessions) for each of the 10 ESH and LSH focal patches across the 12 study watersheds. Differences in richness between ESH and LSH habitats were assessed based on these estimates of mean family-level invertebrate abundance from replicate watersheds across the Dead Diamond River drainage, so they represent the contribution of ESH and LSH within watersheds to overall invertebrate richness across the landscape or region.

Data Analysis

To assess differences in richness in ESH and LSH at sampling intensities ranging 1-10 watersheds, I estimated the richness of the family pool from the sample distribution of each habitat type using non-parametric Mao tau estimators (Colwell et al., 2004) with EstimateS version 8.2 (Colwell 2011). This resulted in sample-based accumulation curves with 95% confidence intervals (CI) calculated from 5000 reshufflings of the sample order. Accumulation curves did not reach an asymptote, so I used the first order jackknife method (Burnham and

Overton 1979) in EstimateS to estimate asymptotic family richness in ESH and LSH habitats; this method adjusts for bias due to taxa being missed during sampling (Nichols et. al. 1998). Confidence intervals (95%) were calculated from 5000 reshufflings of the sample order.

I used non-metric multidimensional scaling (NMDS) implemented by an analysis of similarities (ANOSIM; Clarke 1993) to display and test for dissimilarities in invertebrate family composition between habitat types using the Jaccard (for presence/absence data) and Bray-Curtis (for abundance data) indices of dissimilarity (MASS and vegan packages in Program R, Venables and Ripley 2002, Oksanen et. al. 2011, R Development Core Team 2011). Two axes of ordination in this NMDS analysis allowed for easy interpretation while maintaining acceptable stress (<15%) and goodness of fit values (Kruskal 1964, MacCallum 1981, Kenkel and Orloci 1986).

I used a linear mixed effects model to test whether biomass and abundance of terrestrial invertebrates differed between upland ESH and LSH (nlme package in Program R, Pinheiro et. al. 2011). Habitat type (ESH vs. LSH) was modeled as a fixed factor nested within the watershed, which was modeled as a random factor to account for variation among watersheds in invertebrate biomass and abundance in both ESH and LSH. A likelihood ratio test was used to assess the contribution of watershed as a random factor (Bolker et. al. 2009, Zuur et. al. 2009). I used the same analyses to test whether abundance of terrestrial invertebrates differed between upland habitat types. Biomass and abundance data were log transformed for these analyses.

Finally, to better understand differences among watersheds in ESH invertebrate communities, I used linear regression analysis to assess the influence of focal patch size and total percent ESH in the watershed on ESH invertebrate richness and biomass. Log-transformed, first order jackknifed estimates of family richness for each focal patch were used in this analysis.

44

These estimates were based on a sampling intensity of ten replicates within each focal patch. Prior analyses indicated that focal patch size and total percent ESH in the watershed were not correlated (Person product moment correlation, r = 0.30, P = 0.39; Graham 2003).

Results

Altogether, 11,347 invertebrates belonging to 11 orders and 115 families were collected (Appendix 2A-1). In addition to Aranae, twenty eight families from the orders Coleoptera, Diptera, Hemiptera, Hymenoptera, and Thysanoptera were present at all sites. While Dipteran families were the most commonly found families in traps, no single order appeared to dominate diversity across sites. Muscidae was the most abundant family at ESH sites and wasps of the family Diapiidae were most abundant at LSH sites. The grasshopper family Romaleidae had the greatest biomass in ESH sites and the family Muscidae had the greatest biomass in LSH sites.

Rarefaction curves estimated 112 families for the whole group of ESH sites and 80 families for the whole group of LSH sites (Figure 2-2). Non-overlapping bootstrapped 95% CI indicate differences in family richness between the two habitat types. The slopes (m) of the curves at a sampling intensity of 10 watersheds (m = 2.8 for ESH, 1.5 for LSH) indicate that the curves did not reach an asymptote and that additional families may be detected with greater sampling intensity. The higher slope of the ESH curve indicates that the gap in family richness between ESH and LSH habitats would increase with sampling intensity. Asymptotic family richness (mean ± bootstrapped 95% CI) was estimated to be 137.2 ± 18.2 families for ESH and 93.5 ± 6.7 families for LSH (Figure 2-3). Again, non-overlapping bootstrapped 95% CI indicate differences in family richness between the two habitat types.
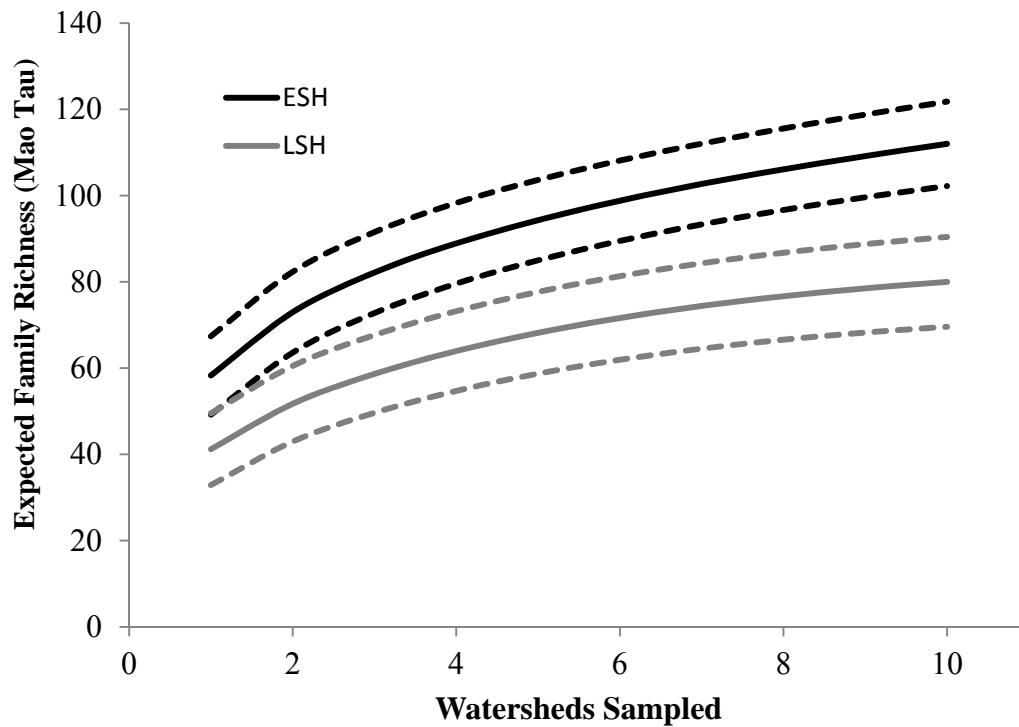
Figure 2-2. Expected invertebrate family richness (Mao Tau) as a function of number of watersheds sampled, based on data from pan traps in patches of early successional habitat (ESH) and late successional habitat (LSH) in 12 watersheds in northern New Hampshire, U.S.A. Dashed lines represent 95% confidence bands.

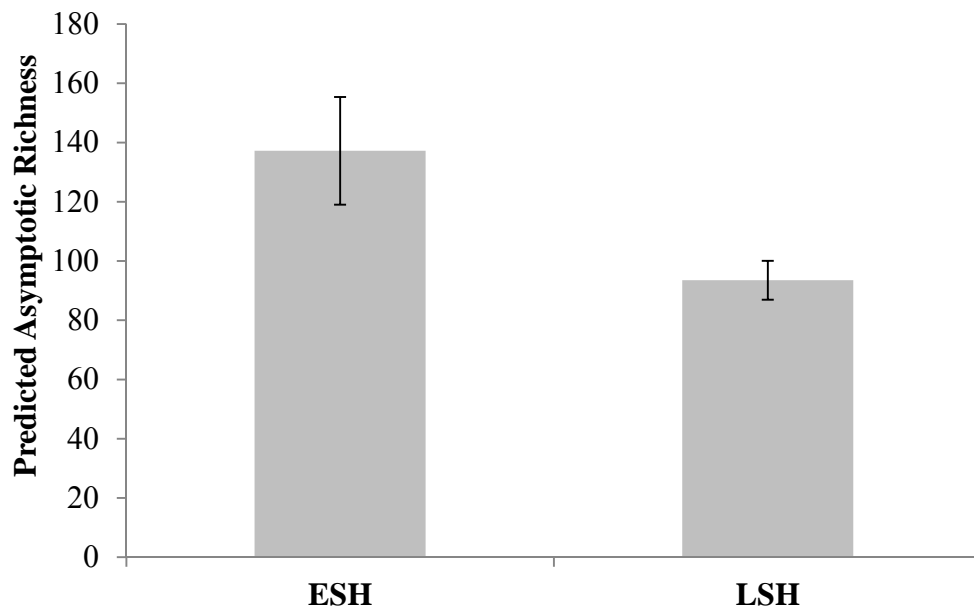**Figure 2-3.** Predicted asymptotic invertebrate family richness, based on data from pan traps in patches of early successional habitat (ESH) and late successional habitat (LSH) in 12 watersheds in northern New Hampshire, U.S.A. Richness values are first order jackknife estimates calculated in the program EstimateS. Error bars represent bootstrapped 95% CI.

The results of non-metric multidimensional scaling with two axes of ordination showed a clear difference in community composition related to habitat type (Figure 2-4). Dissimilarity in community composition between the two habitat types was statistically significant, based on both occurrence ($R = 0.70$, $P < 0.001$; 100,000 permutations) and abundance ($R = 0.80$, $p < 0.001$, 100,000 permutations). In the NMDS analysis of abundance data, the stress value was 11.81% and the nonmetric R^2 was 0.99. In the NMDS analysis of occurrence data, the stress value was 14.74% and the nonmetric R^2 was 0.98. While 36 families were detected exclusively in ESH, only 5 families were detected exclusively in LSH (Appendix 2A-2).

Linear mixed model analysis indicated that terrestrial invertebrate biomass was greater in ESH than LSH ($F_{1,8} = 45.94$, $P < 0.0001$, Figure 2-5). Mean invertebrate biomass ($\pm$ 95% CI) was 281 ± 82 mg dry mass in ESH and 88 ± 12 mg dry mass in LSH (Table 2-2). In addition, abundance of terrestrial invertebrates was greater in ESH than LSH ($F_{1,8} = 3.65$, $P = 0.057$, Figure 2-5). Mean invertebrate abundance ($\pm$ 95% CI) was 62.9 ± 8 in ESH and 50.6 ± 14 in LSH (Table 2-2). To determine whether terrestrial invertebrate biomass or abundance in ESH and LSH varied with percent ESH in the watershed, I conducted a likelihood ratio test comparing the mixed effects model to a general linear model in which the percent ESH in the watershed was excluded (i.e., excluding watershed as a random effect). This test showed that percent ESH in the watershed had no influence on terrestrial invertebrate biomass or abundance in focal patches of ESH and LSH ($\chi^2 = 0.0028$, $P = 0.96$, df $= 1$).

Regression analysis indicated that family richness was not related to ESH focal patch size ($F_{1,8} = 2.55$, $P = 0.14$) or percent ESH in the watershed ($F_{1,8} = 0.05$, $P = 0.83$). Biomass was also unrelated to patch size ($F_{1,8} = 0.10$, $P = 0.76$, Figure 2-6) and percent ESH in the watershed (see LRT above).
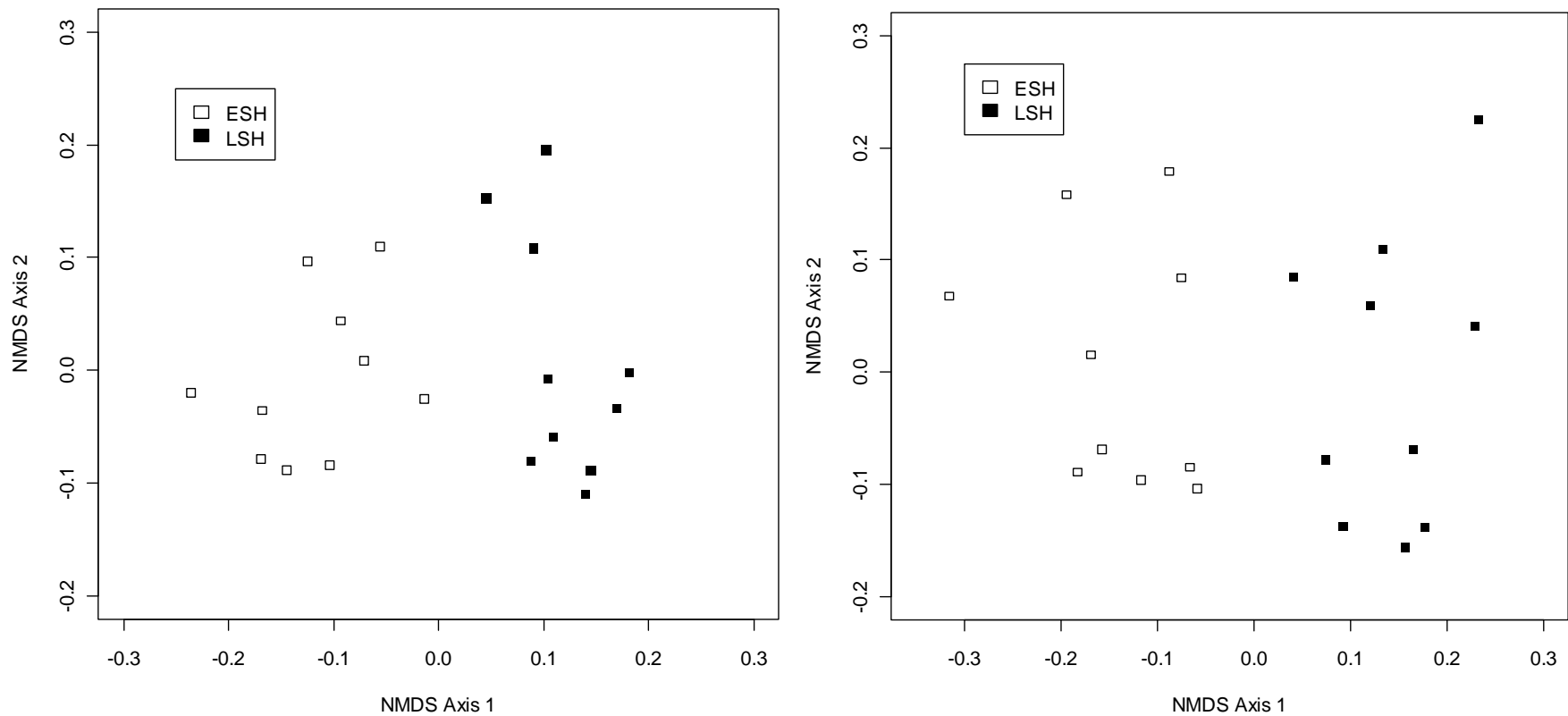
Figure 2-4. Ordination scores from the non-metric multidimensional scaling for invertebrate family abundance data (A) and occurrence data (B) from pan traps in patches of early successional habitat (ESH) and late successional habitat (LSH) in 12 watersheds in northern New Hampshire, U.S.A. Each point represents the community composition of invertebrates ESH (open) or LSH (filled) patches, where points close in ordination space are compositionally more similar than points that are distant, thus axes are unit-less. Community composition is dissimilar between habitat types.
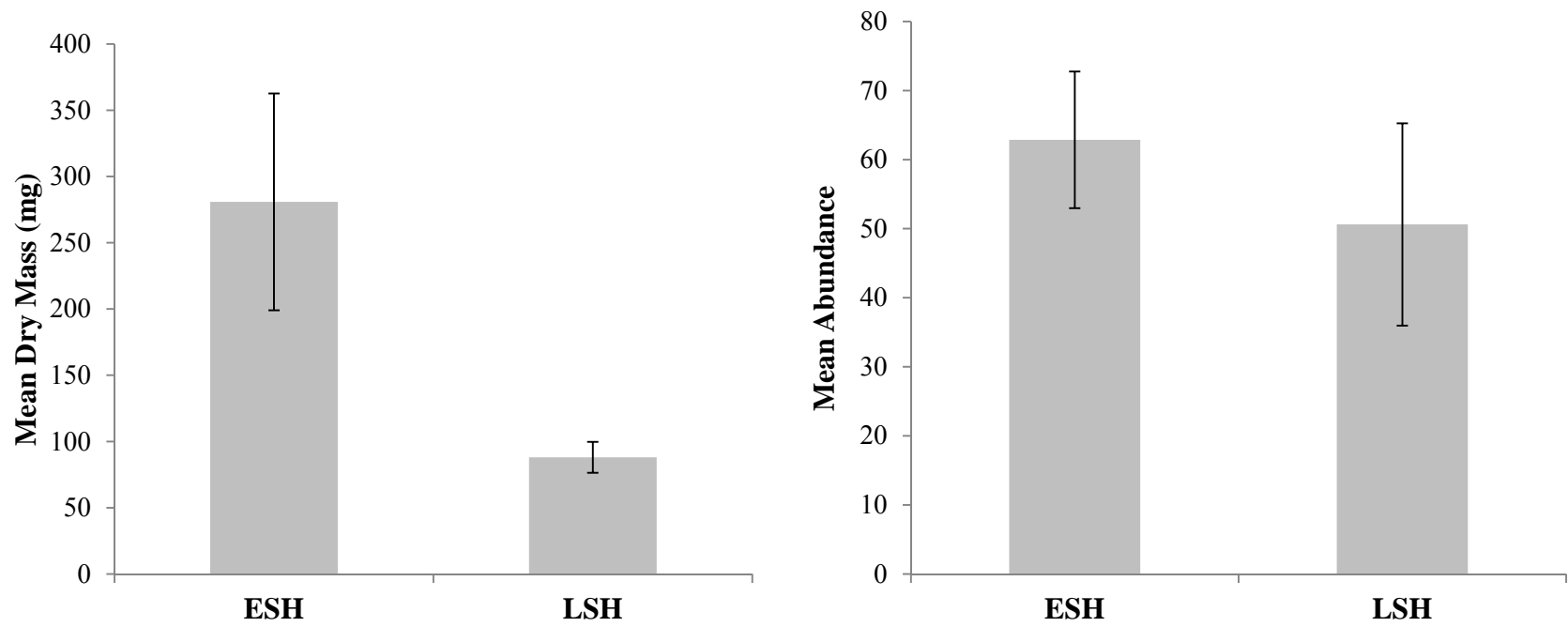
Figure 2-5. Mean dry mass (mg) and abundance of invertebrates, based on data from pan traps in patches of early successional habitat (ESH) and late successional habitat (LSH) in 12 watersheds in northern New Hampshire, U.S.A. Error bars represent 95% CI.

Table 2-2. Mean invertebrate abundance, biomass, and estimated richness (first order jacknife), based on data from pan traps in patches of early successional habitat (ESH) and late successional habitat (LSH) in 12 watersheds in northern New Hampshire, U.S.A. Focal patch-specific richness was estimated from ten replicate samples (five from each site in two sampling sessions). Total asymptotic richness estimates (*) for ESH and LSH are based on ten replicates of watershed means and standard deviations were calculated from bootstrapping. Two watersheds did not have large enough ESH habitat and two additional watersheds did not have large enough LSH habitat to meet criteria for invertebrate collection.

Site	Abundance		Biomass (mg)		Estimated Richness	
	ESH	LSH	ESH	LSH	ESH	LSH
1	NA	42	NA	94	NA	52
2	NA	37	NA	83	NA	49
3	76	28	483	85	73	44
4	50	33	251	88	76	52
5	65	48	330	130	61	50
6	58	96	143	102	75	59
7	51	43	149	84	68	48
8	66	64	222	72	73	51
9	80	36	389	57	106	53
10	41	NA	133	NA	53	NA
11	75	80	474	86	80	63
12	67	NA	234	NA	57	NA
Mean (± 95% CI)	63 (± 8)	51 (± 14)	281(± 82)	88 (± 12)	137 (± 18)*	94 (± 6)*

Figure 2-6. Expected family richness (Mao Tau) in early successional habitat (ESH) patches as a function of ESH patch size ($F_{1,8} = 2.59$, $P = 0.15$), based on data from pan traps in ESH patches in 10 watersheds in northern New Hampshire, U.S.A. Error bars represent 95% CI.

Discussion

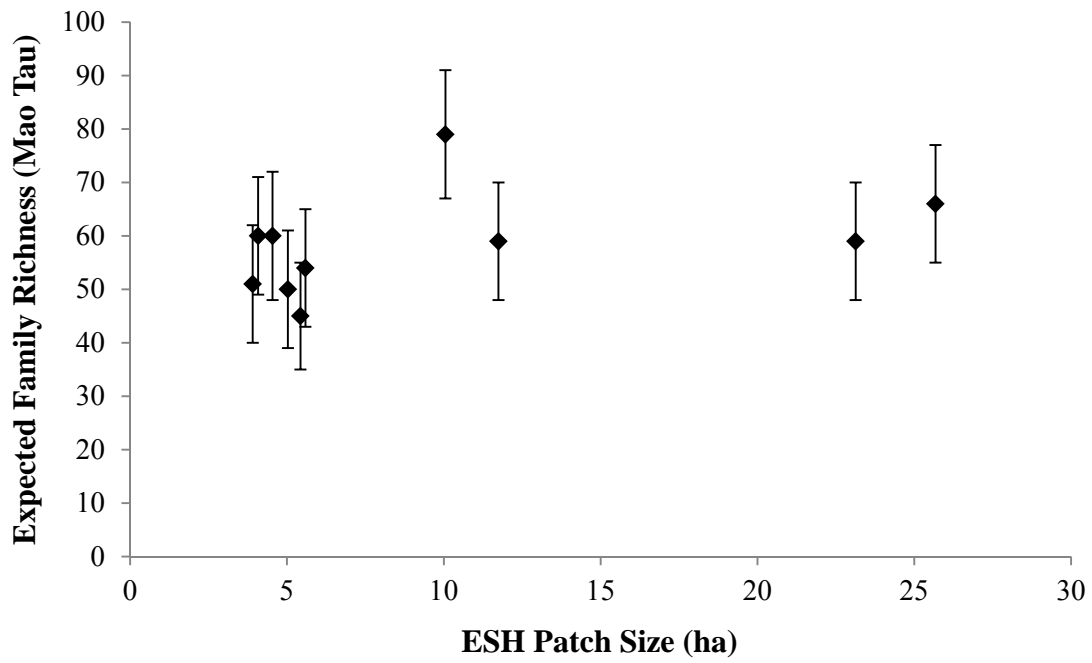I found that ESH patches in northeastern forests support greater richness, biomass, and abundance of invertebrates than LSH patches. Furthermore, I found dramatic dissimilarity in invertebrate community composition between ESH and LSH habitats. General patterns of terrestrial invertebrate response to harvest-induced ESH are likely region-specific (Lewinsohn et. al. 2005) and these are the first data on community-level responses for the northeastern U.S.A. Along with previous studies showing the importance of ESH for plants and vertebrates, these data show that including ESH in northeastern landscapes is critical for maintaining overall biodiversity.

Mean biomass of invertebrates was 3.2 times greater in ESH than LSH. This result may be explained by higher floral abundance (Elliot et. al. 2011, Greenberg et. al. 2011) and greater productivity:biomass ratio (Horn 1974), higher nitrogen concentration, and lower concentration of defense compounds in ESH vegetation (Mattson and Scribner 1987, Ohgushi 1992). Regardless of the cause, this result is consistent with the strong association with ESH of many insectivorous vertebrate species (e.g., Vega-Rivera et. al. 1998, Greenberg et. al. 2011, Chandler et. al. 2012). For example, Chandler et. al. (2012) found that seven of nine mature forest-nesting birds were more abundant in ESH during the post-fledgling stage, and suggest that this is likely due to greater abundance of insect prey. Most bird species in temperate deciduous forests are primarily insectivorous during the breeding season, and reproductive output may be limited by low food abundance (Holmes et. al. 1986). Bat foraging activity is greater in ESH (Ober and Hayes 2008, Brooks 2009), and abundance of small mammals, many of which are insectivorous (Boutin 1989), often increases with creation of ESH by timber harvest (Healy and Brooks 1988,

Kirkland 1990). Also, predators of small mammals, including gray fox, bobcat, and snakes, use young forest habitats, likely due to increased prey abundance (e.g., Haroldson and Fritzell 1984, Kjoss and Litvaitis 2001, Litvaitis 2001). The greater invertebrate productivity in ESH than LSH shown here may help explain the reliance of many vertebrate species on ESH in northeastern forests.

Mean family richness was 1.5 times greater in ESH than LSH. In addition to factors mentioned above, this result may be explained by the greater floral abundance and understory plant diversity found in ESH (Elliot et. al. 2011, Greenberg et. al. 2011). This result is consistent with studies in other regions, including windthrow gaps in Europe and harvest-induced ESH in the southeastern U.S.A. and Alaska (e.g., Bouget and Duelli 2004, Ulyshen et. al. 2005, Schultz and DeSanto 2006, respectively). However, studies have also reported reduced invertebrate richness in ESH (e.g., Summerville and Crist 2002), or no differences in richness of ESH and LSH (e.g., Jeffries et. al. 2006).

A major part of the variation among studies in response of terrestrial invertebrates to harvest-induced ESH is likely associated with regional differences in logging practices, forest dynamics and environmental characteristics. For example, logging in the New England region is generally associated with small-scale selection or group cuts (Miller et. al. 1998, Lowe and Bolger 2002, Kittredge et. al. 2003), as opposed to the extensive even-aged management characteristic of Pacific Northwest forests (Anderson 1992, Bisson et. al. 1992, Grialou et. al. 2000). Similarly, natural regeneration of logged stands is rapid in New England and leads to increased plant diversity (Askins 2001, Elliot 2011), while drier, high-relief, conifer-dominated forests in the western U.S.A. experience slower regeneration and moderate changes in plant diversity (Barrett 1995).

I found that invertebrate richness and biomass were unrelated to focal patch size and the percent ESH in the study watersheds. This result suggests that even small patches of ESH in an otherwise forested watershed will increase watershed-level invertebrate diversity. However, minimum ESH patch size (3.9 ha) was relatively large compared with studies that have observed correlations between patch size and invertebrate communities (e.g., Shure and Phillips 1991, Bouget and Duelli 2004). For example, Shure and Phillips (1991) found that invertebrate biomass and richness was greater in small (0.016 ha) and large (10 ha) forest openings than in mid-sized openings one year after harvest. They attribute this to surface heat build-ups in mid-sized openings, which experienced exposure to sunlight but had not yet developed regenerating vegetation. My results suggest that no additional increase in richness is gained in patch sizes greater than 4 ha, but this study does not address the importance of very small canopy gaps (~0.01 ha) created by natural disturbance for invertebrate diversity (Seymour et. al. 2002).

Results of my study suggests that including ESH in northeastern landscapes will maintain high levels of invertebrate diversity and reduce extinctions of species that specialize on these habitats (Wagner et. al. 2003). Furthermore, the dissimilarity in community composition between ESH and LSH show that different taxa are reliant on these two habitat types, and that including both habitat types on the landscape will benefit regional invertebrate diversity. However, further research targeting non-pollinator taxa and using additional sampling techniques (e.g., pitfall traps, sweep-netting, malaise traps, and blacklight traps) is clearly needed to identify broader patterns of invertebrate response to ESH in this region.

The results of this study are especially important in light of two current trends in the northeastern U.S.A. First, each decadal national forest assessment documents a decline in the area of ESH in this region due to reductions in the scale and intensity of timber management, and

succession of previously abandoned agricultural fields to mature forest (Trani et. al. 2001). Coverage of ESH in New England prior to European settlement (~13%) is within the estimated range of current coverage (4 - 18%). However, while efforts to restore pre-settlement ESH conditions and natural disturbance processes are desirable, forest management may be necessary to maintain sufficient ESH coverage to sustain populations of species dependent on these habitats (Lorimer 2001, Lorimer and White 2003, Brooks et. al. 2012). Recent decline in ESH has already caused federal and state special-status designations of a large number of New England flora and fauna that rely on ESH (DeGraaf and Yamasaki 2001). My data suggest that continued loss of this habitat type will lead to regional extinctions of invertebrate taxa as well. Second, there has recently been a decline in the abundance and diversity of native insect pollinators in the northeastern U.S.A. and elsewhere (Cane and Tepedino 2001, Biesmeijer et. al. 2006, Potts et. al. 2010). While family-level identification in this study prevented pollinator-specific analyses, it is likely that my pan trap data reflect trends in pollinator communities (Leather 2005, Campbell et. al. 2007). If this is correct, then my results suggest that maintaining ESH on the landscape will help to minimize regional losses of pollinators.

Literature Cited

Anderson, N.H. 1992. Influence of disturbance on insect communities in Pacific-Northwest streams. Hydrobiologia **248**:79-92.

Askins, R.A. 2001. Sustaining biological diversity in early successional communities: the challenge of managing unpopular habitats. Wildlife Society Bulletin **29**:407-412.

Ball, D.M., C.S. Hoveland, and G.D. Lacefield. 2002. Southern forages: modern concepts for forage crop management. Potash and Phosphate Institute, Norcross.

Barrett, J.W. 1995. Regional silviculture of the United States. John Wiley and Sons, New York.

Biesmeijer, J. C, S. P. M. Roberts, M. Reemer, R. Ohlemuller, M. Edwards, T. Peeters, A. P. Schaffers, S. G. Potts, R. Kleukers, C. D. Thomas, J. Settele, and W. E. Kunin. 2006. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science **313**:351-354.

Bisson, P.A., T.P. Quinn, G.H. Reeves, and S.V. Gregory. 1992. Best-management practices, cumulative effects, and long-term trends in fish abundance in Pacific Northwest river systems. In: Naiman, R.J. (ed.). Watershed management: balancing sustainability and environmental change. Springer-Verlag, New York. pp. 189-233.

Bolker, B.B., M.E. Brooks, C.J. Clark, S.W. Geange, J.R. Poulsen, M.H.H. Stevens, and J.S. White. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology and Evolution **24**:127-135.

Bouget, C., and P. Duelli. 2004. The effects of windthrow on forest insect communities: a literature review. Forest Ecology and Management **118**:281-299.

Boutin, S. 1989. Food supplementation experiments with terrestrial vertebrates: patterns, problems, and the future. Canadian Journal of Zoology **68**:203-220.

Burnham, K. P., and W. S. Overton. 1979. Robust estimation of population size when capture probabilities vary among animals. Ecology **60**:927-936.

Brooks, R.T. 2009 Habitat-associated and temporal patterns of bat activity in a diverse forest landscape of southern New England, USA. Biodiversity Conservation **18**:529-545.

Brooks, R.T., K.H. Nislow, W.H. Lowe, M.K. Wilson, and D.I. King. 2012. Forest succession and terrestrial-aquatic biodiversity in small forested watersheds: a literature review of principles, relationships, and implications for management. Forestry: An International Journal of Forest Research doi: 10.1093/forestry/cps031.

Campbell, J.W., and J. L. Hanula. 2007. Efficiency of Malaise traps and colored pan traps for collecting flower visiting insects from three forested ecosystems. Journal of Insect Conservation **11**:399-408.

Cane, J. H., and V. J. Tepedino. 2001. Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. Conservation Ecology **5**: article 1.

Chandler, C.C., D.I. King, and R.B. Chandler. 2012. Do mature forest birds prefer early-successional habitat during the post-fledging period? Forest Ecology and Management **264**:1-9.

Clarke, K.R., 1993. Non-parametric multivariate analysis of changes in community structure. Australian Journal of Ecology **18**:117-143.

Colwell, R.K., C.X. Mao, and J. Chang. 2004. Interpolating, extrapolating, and comparing incidence-based species accumulation curves. Ecology **85**:2717-2727.

Colwell, R. K. 2011. EstimateS: statistical estimation of species richness and shared species from samples. Version 8.2. Department of Ecology and Evolutionary Biology, University of Connecticut, Storrs, USA. (accessed 1 December 2011).

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science **199**:1302-1310.

Deans, A.M., J.R. Malcolm, S.M. Smith, and M.I. Bellocq. 2005. Edge effects and the responses of aerial insect assemblages to structural-retention harvesting in Canadian boreal peatland forests. Forest Ecology and Management **204**:249-266.

DeGraaf, R.M., and M. Yamasaki. 2001. New England wildlife: habitat, natural history and distribution. University Press of New England, Hanover, NH.

Edwards, E. D., and A. D. Huryn. 1995. Annual contribution of terrestrial invertebrates to a New Zealand trout stream. New Zealand Journal of Marine and Freshwater Research **29**:467-477.

Elliott, K.J., C.A. Harper, and B. Collins. 2011. Herbaceous response to type and severity of disturbance. In: Greenberg, C.G., G. Collins, and F. Thompson III (eds.). Sustaining young forest communities: ecology and management of early successional habitats in the central hardwood region, USA. Springer, New York, pp. 97-119.

Graham, M.H. 2003. Confronting multicollinearity in ecological multiple regression. Ecology **84**:2809-2815.

Greenberg, C.H., R.W. Perry, C.A. Harper, D.J. Levey, and J.M. McCord. 2011. The role of young, recently disturbed upland hardwood forest as high quality food patches. In: Greenberg, C.G., G. Collins, and F. Thompson III (eds.). Sustaining young forest communities: ecology and management of early successional habitats in the central hardwood region, USA. Springer, New York, pp. 121-141.

Grialou, J.A., S.D. West, and R.N. Wilkins. 2000. The effects of forest clearcut harvesting and thinning on terrestrial salamanders. Journal of Wildlife Management **64**:105-113.

Haroldson, K.J., and Fritzell, E.K. 1984. Home ranges, activity, and habitat use by gray foxes in an oak-hickory forest. Journal of Wildlife Management **48**:222-227.

Healy, W.M., and Brooks, R.T. 1988. Small mammal abundance in northern hardwood forest stands in West Virginia. Journal of Wildlife Management **52**:491-496.

Holmes R.T., T.W. Sherry, and F.W. Sturges. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecolological Monographs **56**:201-220.

Horn, H.S. 1974. The ecology of secondary succession. Annual review of ecology and systematics **5**:25-37.

Hunter, W.C., D.A. Buehler, R.A. Canterbury, J.L. Confer, and P.B. Hamel. 2001. Conservation of disturbance-dependent birds in eastern North America. Wildlife Society Bulletin **29**:440-455.

Jeffries, J.M., R.J. Marquis, and R.E. Forkner. 2006. Forest age influences oak insect herbivore community structure, richness, and density. Ecological Applications **16**:901-912.

Kaoru, M., and M. Hiroshi. 1999. Changes in insect assemblages with secondary succession of temperate deciduous forests after clear-cutting. Japanese Journal of Entomology New Series **2**:11-26.

Kenkel, N.C. and L. Orloci. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. Ecology **67**:919-928.

Kerr, J.T. and L. Packer. 1997. Habitat heterogeneity as a determinant of mammal species richness in high-energy regions. Nature **385**:252-254.

King, D.I., K.H. Nislow, R.T. Brooks, R.M. DeGraaf, and M. Yamasaki. 2012. Early-successional forest ecosystems: far from "forgotten". Frontiers in Ecology and the Environment **9**:319-320.

Kirkland, G.L. Jr. 1990. Patterns of small mammal community change after clearcutting in temperate North American forests. Oikos **59**:313-320.

Kittredge, D.B., A.O. Finley, and D.R. Foster. 2003. Timber harvesting as ongoing disturbance in a landscape of diverse ownership. Forest Ecology and Management **180**:425-442.

Kjoss, V.A., and Litvaitis J.A. 2001. Community structure of snakes in a human-dominated landscape. Biological Conservation **98**:285-292.

Kreft, H., and W. Jetz. 2007. Global patterns and determinants of vascular plant diversity. Proceedings of the National Academy of Sciences. **104**:5925-5930.

Kruskal, J. B. 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. Psychometrika **29**:1-27.

Leather, S.R. (ed.). 2005. Insect sampling in forest ecosystems. Wiley-Blackwell, Malden, Massachusetts.

Lewinsohn, T.M., V. Novotny, and Y. Basset. 2005. Insects on plants: diversity of herbivore assemblages revisited. Annual Review of Ecology and Systematics **36**:597-620.

Litvaitis, J.A., 1993. Response of early-successional vertebrates to historic changes in land use. Conservation Biology. **7**:866-873

Litvaitis, J.A. 2001. Importance of early successional habitats to mammals in eastern forests. Wildlife Society Bulletin **29**:466-473.

Litvaitis, J.A. 2003 Are pre-Columbian conditions relevant baselines for managed forests in the northeastern United States. Forest Ecology and Management **185**:113-126.

Loader, C. and H. Damman. 1991. Nitrogen content of food plants and vulnerability of *Pieris rapae* to natural enemies. Ecology **72**:1586-1590.

Loeb, S.C., and J.M. O'Keefe. 2011. Bats and gaps: the role of early successional patches in the roosting and foraging ecology of bats. . In: Greenberg, C.G., G. Collins, and F. Thompson III (eds.). Sustaining young forest communities: ecology and management of early successional habitats in the central hardwood region, USA. Springer, New York, pp. 167-189.

Lorimer, C.G. 2001. Historical and ecological roles of disturbance in eastern North American forests: 9,000 years of change. Wildlife Society Bulletin **29**:425-439.

Lorimer, C.G. and A.S. White. 2003. Scale and frequency of natural disturbance in the northeastern US: implications for early successional forest habitats and regional age distributions. Forest Ecology and Management **185**:41-64.

Lowe W.H., and D.T. Bolger. 2002. Local and landscape-scale predictors of salamander abundance in New Hampshire headwater streams. Conservation Biology **16**:183-193.

MacCallum, R. 1981. Evaluating the goodness of fit in nonmetric multidimensional scaling in ALSCAL. Applied Psychological Measurement **5**:377-382.

Mattson, W.J., and J.M. Scriber. 1987. Nutritional ecology of insect folivores of woody plants: nitrogen, water, fiber, and mineral considerations. In: Slansky, Jr., F., and J. Rodriguez (eds.). Nutritional ecology of insects, mites, spiders, and related invertebrates. Wiley, New York, pp. 105-146.

Miller, A.B., E.S. Bryant, and R.W. Birnie. 1998. An analysis of land cover changes in the northern forest of New England using multitemporal landsat mss data. International Journal of Remote Sensing **19**:245-265.

Nichols, J. D., T. Boulinier, J. E. Hines, K. H. Pollock, and J. R. Sauer. 1998. Inference methods for spatial variation in species richness and community composition when not all species are detected. Conservation Biology **12**:1390-1398.

Ober, H.K., and J.P. Hayes. Influence of forest riparian vegetation on abundance and biomass of nocturnal flying insects. Forest Ecology and Management **256**:1124-1132.

Ohgushi, T., 1992. Resource limitation on insect herbivore populations. In: Hunter, M.D., T. Ohgushi, and P.W. Price (eds.). Effects of resource distribution on animal-plant interactions. Academic Press, San Diego, pp. 199-241.

Oksanen, J., F. G. Blanchet, R. Kindt, P. Legendre, P. R. Minchin, R. B. O'Hara, G. L. Simpson, P. Solymos, M.H.H. Stevens, and H. Wagner. 2011. vegan: Community Ecology Package. R package version 2.0-0. http://CRAN.Rproject.org/package=vegan.

Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar and the R Development Core Team. 2011. nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-101.

Potts, S.G., J.C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and William E. Kunin. 2010. Global   pollinator declines: trends, impacts and drivers. Trends in Ecology and Evolution **25**:345-353.

Rogers, P. 1996. Disturbance ecology and forest management: a review of the literature. Washington (DC): USDA Forest Service General Technical Report INT-GTR-336.

R Development Core Team. 2011. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org/.

Sage, R.D. 1982. Wet and dry-weight estimates of insects and spiders based on length. American Naturalist **108**:407-411.

Sample, B. E., R. J. Cooper, R. D. Greer, and R. C. Whitmore. 1993. Estimation of insect biomass by length and width. American Midland Naturalist **129**:234-240.

Schowalter, T. D., Y. L. Zhang, and R. A. Progar. 2005. Canopy arthropod response to density and distribution of green trees retained after partial harvest. Ecological Applications **15**:1594-1603.

Schultz, M.E., and T.L. DeSanto. 2006. Comparison of terrestrial invertebrate biomass and richness in young mixed red alder-conifer, young conifer, and old conifer stands of southeast Alaska. Northwest Science **80**:120-132.

Seymour, R.S., A.S. White, and P.G. deMaynadier. 2002. Natural disturbance regimes in northeastern North America - evaluating silvicultural systems using natural scales and frequencies. Forest Ecology and Management **155**:357-367.

Shure, D.J., and D.J. Phillips. 1991. Patch size of forest openings and arthropod populations. Oecologia **86**:325-334.

Southwood, T.R.E. 1978. Ecological methods: with special reference to the study of insect populations. 2nd ed. Chapman and Hall, London.

Steffan-Dewenter, I., and T. Tscharntke. 2001. Succession of bee communities on fallows. Ecography **24**:83-93.

Summerville, K.S., and T.O. Crist. 2002. Effects of timber harvest on forest Lepidoptera: community, guild, and species responses. Ecological Applications **12**:820-835.

Tews, J., U. Brose, B. Grimm, K. Tielborger, M.C. Wichmann, M. Schwager, and F. Jeltsch. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography. **31**:79-92.

Trani, M.K., R.T. Brooks, T.L. Schmidt, V.A. Rudis, and C.M. Gabbard. 2001. Patterns and trends of early-successional forests in the eastern United States. Wildlife Society Bulletin **29**:413-424.

Ulyshen, M.D., J.L. Hanula, S. Horn, J.C. Kilgo, and C.E. Moorman. Herbivorous insect response to group selection cutting in a southeastern bottomland hardwood forest. Environmental Entomology **34**:395-402.

Vega Rivera, J.H., J.H. Rappole, J.H. McShea, and C.A. Has. 1998. Wood thrush post fledgling movements and habitat use in northern Virginia. Condor **100**:69-78.

Venables, W.N., and B.D. Ripley. 2002. Modern applied statistics with S. Springer-Verlag, Berlin.

Wagner, D.L., M.W. Nelson, and D.F. Schweitzer. 2003. Shrubland Lepidoptera of southern New England and southeastern New York: ecology, conservation, and management. Forest Ecology and Management. **185**:95-112.

Wipfli, M. S. 1997. Terrestrial invertebrates as salmonid prey and nitrogen sources in streams: contrasting old-growth and young-growth riparian forests in southeastern Alaska, USA. Canadian Journal of Fisheries and Aquatic Sciences **54**:1259-1269.

Zuur, A.F., E.N. Ieno, N.J.Walker, A.A. Saveliev, and G.M. Smith. 2009. Mixed effects models and extensions in ecology with R. Springer, New York.

Appendix Table 2A-1. Mean abundance and biomass (mg) of invertebrate families, based on data from pan traps in patches of early successional habitat (ESH) and late successional habitat (LSH) in 12 watersheds in northern New Hampshire, U.S.A.

Family/Order	Mean Abundance		Mean Biomass (mg)	
	ESH	LSH	ESH	LSH
Acrididae	0.35	0.00	66.48	0.00
Anthomyiidae	1.90	1.09	10.54	6.15
Aphelinidae	0.15	0.00	0.03	0.65
Aphididae	1.67	0.72	1.15	0.00
Apidae	0.42	0.00	58.29	0.00
Asilidae	0.57	0.17	19.94	14.12
Aulacigastridae	0.15	0.05	1.39	0.18
Berytidae	0.10	0.00	0.78	0.00
Bombylidae	0.05	0.00	7.87	0.00
Braconidae	0.93	1.06	6.06	2.56
Buprestidae	0.40	0.05	8.79	3.56
Caeciliusidae	0.30	0.91	9.41	1.38
Calliphoridae	0.86	0.00	17.28	0.00
Camillidae	3.87	0.98	3.20	0.75
Cecidomyiidae	2.35	4.08	0.29	0.38
Cerambycidae	0.45	0.25	11.05	8.93
Ceraphronidae	1.19	1.10	0.13	0.16
Ceratopogonidae	0.39	0.15	0.16	0.12
Cercopidae	0.25	0.05	5.25	3.59
Chamaemyiidae	0.05	0.00	0.12	0.00
Charipidae	0.10	0.00	0.15	0.00
Chironomidae	6.02	4.96	0.49	0.47
Chloropidae	0.73	0.55	1.00	0.87

Chrysomelidae	0.10	0.00	2.39	0.00
Cicadellidae	2.15	1.69	5.86	0.00
Cicadidae	0.20	0.10	4.76	2.90
Coccinellidae	0.10	0.00	16.71	4.24
Coleophoridae	0.15	0.10	1.88	0.48
Conopidae	0.25	0.10	10.92	4.39
Crabronidae	0.25	0.00	37.22	1.37
Curculionidae	0.65	0.35	3.07	0.00
Cydnidae	0.98	0.00	19.78	0.00
Dermestidae	0.17	0.05	1.53	0.73
Diapriidae	2.19	6.28	0.41	1.12
Diptera (Larvae)	2.00	0.00	5.58	0.00
Dolichopodidae	5.26	1.84	14.46	5.33
Drosophilidae	0.43	0.15	0.88	0.74
Dryomyzidae	0.10	0.23	2.57	6.67
Elateridae	0.20	0.10	10.69	8.02
Empididae	1.72	2.54	7.24	7.60
Encyrtidae	1.04	0.05	0.18	0.11
Eucinetidae	0.05	0.00	0.24	0.00
Eucoilidae	0.58	0.80	0.12	0.12
Eulophidae	0.45	0.18	0.12	0.22
Eupelmidae	0.90	0.25	0.40	0.68
Figitidae	0.00	0.10	0.00	0.02
Formicidae	0.10	0.15	3.63	1.71
Glaphyridae	1.12	0.00	58.27	0.00
Halictidae	1.92	0.35	19.54	8.05
Heleomyzidae	0.20	0.30	3.59	3.67

Hesperiidae	0.53	0.15	128.97	11.69
Ichneumonidae	1.93	3.09	12.39	11.95
Lampyridae	0.20	0.00	88.80	0.00
Lauxaniidae	0.30	0.30	2.82	3.70
Lepidoptera (Larvae)	0.25	0.53	10.54	11.03
Leuctridae	0.05	0.05	2.90	1.75
Lycidae	0.05	0.00	5.68	0.00
Megaspilidae	0.15	0.18	0.25	0.18
Melyridae	0.05	0.00	6.44	0.00
Membracidae	0.76	0.05	9.38	1.05
Milichiidae	0.05	0.00	0.21	0.00
Miridae	2.17	0.48	5.70	2.23
Mordellidae	0.66	0.05	7.49	7.62
Muscidae	6.88	4.62	56.51	30.47
Mycetophagidae	0.05	0.00	0.32	0.00
Mycetophilidae	0.76	1.15	3.01	1.77
Mymaridae	2.48	0.89	0.08	0.02
Mymarommatidae	0.35	0.10	0.06	0.03
Nemouridae	0.00	0.15	0.00	1.76
Nitidulidae	0.30	0.15	1.23	14.12
Noctuidae	1.36	1.05	16.67	10.71
Nymphalidae	0.05	0.00	132.48	0.00
Pamphiliidae	1.22	0.65	15.81	10.90
Panorpodidae	0.43	0.70	60.14	29.95
Pentatomidae	0.05	0.10	0.05	0.34
Perlidae	0.00	0.10	0.00	4.56
Pholcidae	0.05	0.00	1.59	0.00

Phoridae	1.98	3.64	2.34	3.82
Piophilidae	0.05	0.05	1.02	0.67
Pipunculidae	0.28	0.10	2.84	1.07
Platygastridae	0.05	0.10	0.05	0.04
Platypezidae	0.10	0.05	5.33	11.43
Pompilidae	1.10	0.10	16.42	12.48
Psychodidae	0.64	0.62	0.55	0.58
Pteromalidae	0.05	0.00	0.05	0.00
Ptiliidae	0.05	0.00	0.05	0.00
Ptychopteridae	0.05	0.00	4.16	0.00
Rhagionidae	0.05	0.00	1.11	0.00
Romaleidae	0.15	0.00	152.98	0.00
Salticidae	0.25	0.00	3.95	0.00
Scarabaeidae	0.05	0.05	6.77	24.24
Scatopsidae	6.15	5.09	0.43	0.41
Scelionidae	0.05	0.10	0.08	0.05
Sciaridae	1.40	2.12	0.73	0.81
Sciomyzidae	0.05	0.05	3.29	6.09
Sepsidae	1.09	0.15	5.65	3.39
Signiphoridae	0.00	0.05	0.00	0.00
Simuliidae	0.86	0.15	0.51	0.39
Sphaeroceridae	0.30	0.38	1.07	0.80
Sphecidae	0.05	0.00	2.93	0.00
Aranae	1.17	1.35	3.51	3.48
Staphylinidae	1.44	4.79	4.07	4.86
Stratiomyidae	0.15	0.00	17.91	0.00
Syrphidae	3.12	0.79	32.82	9.62

Tabanidae	0.53	0.10	19.43	11.77
Tachinidae	2.25	0.96	24.51	12.33
Tanaostigmatidae	0.10	0.00	0.02	0.00
Tenthredinidae	0.05	0.00	9.75	0.00
Tephritidae	0.10	0.00	5.67	0.00
Therevidae	0.13	0.00	25.56	0.00
Thripidae	1.61	0.93	0.31	0.19
Thyreocoridae	0.05	0.00	1.47	0.00
Tingidae	0.00	0.10	0.00	1.09
Tipulidae	1.59	3.03	3.63	6.51
Vespidae	0.84	0.00	31.00	0.00

Appendix 2A-2. List of families that were detected exclusively in early successional habitat (ESH) and late successional habitat (LSH) in pan traps in 12 watersheds in northern New Hampshire, U.S.A.

ESH	LSH
Acrididae	Figitidae
Aphelinidae	Nemouridae
Apidae	Perlidae
Berytidae	Signiphoridae
Bombylidae	Tingidae
Calliphoridae	
Chamaemyiidae	
Charipidae	
Chrysomelidae	
Coccinellidae	
Crabronidae	
Cydnidae	
Diptera (Larva)	
Eucinetidae	
Glaphyridae	
Lampyridae	
Lycidae	
Melyridae	
Milichiidae	
Mycetophagidae	
Nymphalidae	
Pholcidae	
Pteromalidae	
Ptiliidae	
Ptychopteridae	
Rhagionidae	
Romaleidae	
Salticidae	
Sphecidae	
Stratiomyidae	
Tanaostigmatidae	
Tenthredinidae	
Tephritidae	
Therevidae	
Thyreocoridae	