

Land Use Effects on Ecological Linkages
between Small Streams and their
Surrounding Terrestrial Habitats

Peter Carlson

*Faculty of Natural Resources and Agricultural Sciences
Department of Aquatic Sciences and Assessment
Uppsala*

Doctoral Thesis
Swedish University of Agricultural Sciences
Uppsala 2014

Acta Universitatis agriculturae Sueciae

2014:18

Cover: Typical forested and agricultural streams of south-central Sweden
(photos: P. Carlson)

ISSN 1652-6880

ISBN (print version) 978-91-576-7984-0

ISBN (electronic version) 978-91-576-7985-7

© 2014 Peter Carlson, Uppsala

Print: SLU Service/Repro, Uppsala 2014

Land Use Effects on Ecological Linkages between Small Streams and their Surrounding Terrestrial Habitats

Abstract

Adult aquatic insects are important vectors for aquatic transfers to terrestrial consumers and an integral component of riparian and terrestrial food webs. Incorporation of aquatic subsidies into terrestrial food webs depends heavily on the dispersal and life history traits of aquatic insects. Agricultural land use often results in the degradation of in-stream and riparian habitats which may affect the efficiency of cross-habitat exchanges.

In this thesis I studied; (i) how land use (forested and agriculture) affects stream invertebrate assemblages, with special focus on aquatic insects, (ii) how riparian habitats differ with land use and how these differences affect dispersal of emerged adult aquatic insects, and (iii) if the distribution of riparian arthropod consumers is related to food resources (aquatic and terrestrial dipterans) and/or riparian habitat (e.g., substratum and microclimate).

Subsidy production (abundances of adult aquatic insects) was over five times greater in agricultural streams, however, most emerging insects dispersed no further than 10m from the stream edge. In contrast, dispersal of adult aquatic insects declined little with distance in the forested sites. Furthermore, the abundance of arthropod consumers was lower at agricultural sites, compared to forested sites. Taken together, these results indicate that agricultural practices result in reduced subsidy resource exchange efficiency, where energy flow to riparian habitats is weakened relative to the productivity of the stream. Specifically, cross-habitat transfers are constrained by factors associated with land use, microhabitat and phenology.

Land use has been largely ignored in studies of aquatic to terrestrial cross-habitat resource exchanges. This thesis illustrates the interdependence of spatial resources and how anthropogenic alterations can disrupt cross-scale linkages. This thesis brings attention to the importance of aquatic-terrestrial linkages in forested and agricultural landscapes, demonstrating that anthropogenic impacts may have deeper consequences for aquatic and terrestrial ecosystems than have been previously identified.

Keywords: land use, habitat, traits, dispersal, subsidies, riparian, streams, arthropods

Author's address: Peter Carlson, SLU, Department of Aquatic Sciences and Assessment, P.O. Box 7050, 750 07 Uppsala, Sweden

E-mail: Peter.Carlson@slu.se

Dedication

To my family...

Contents

List of Publications	7
Abbreviations	9
1 Introduction	11
1.1 Cross-ecosystem resource flows and the importance of aquatic subsidies	11
1.2 In-stream productivity	13
1.3 Aquatic versus terrestrial prey	14
1.4 Timing of emergence	14
1.5 Dispersal	15
1.6 Anthropogenic disturbance	16
1.7 Gaps in current knowledge	17
1.8 Agricultural land use	18
2 Objectives of the thesis	21
3 Materials and methods	23
3.1 Study sites	23
3.2 Sampling of biota	25
3.2.1 Benthic invertebrates (I, II)	25
3.2.1.1 Benthic invertebrate community response variables (I)	26
3.2.1.2 Traits of benthic invertebrates (I, II)	26
3.2.2 Aquatic and terrestrial flying insects (III, IV)	26
3.2.3 Epigeal arthropod consumers (IV)	27
3.3 Sampling of environmental variables	29
3.3.1 Catchment (I)	29
3.3.2 In-stream habitats (I, II)	29
3.3.3 Riparian habitat (I, II, III, IV)	29
3.4 Statistical analyses	31
3.4.1 Environmental gradients (I, IV)	31
3.4.2 Habitat and benthic assemblages (I)	31
3.4.3 Community response variables (I)	32
3.4.4 Invertebrate and stream environment relationships (I)	32
3.4.5 Differences in arthropod assemblage composition (I, IV)	32
3.4.6 Analysis of variance (II, III, IV)	33
3.4.7 Relative importance of different abiotic and biotic predictors (III, IV)	34

4	Results and Discussion	37
5	Conclusions and future research	41
	References	45
	Acknowledgements	55

List of Publications

This thesis is based on the work contained in the following papers, referred to by Roman numerals in the text:

- I Carlson, P.E., Johnson, R.K., McKie, B.G. (2013). Optimizing stream bioassessment: habitat, season, and the impacts of land use on benthic macroinvertebrates. *Hydrobiologia* 704(1), 363-373.
- II Sandin, L., McKie, B.G., Carlson, P.E., Johnson, R.K. Difference in resource transfer potential between stream and terrestrial habitats revealed by dispersal traits. (manuscript).
- III Carlson, P.E., McKie, B.G., Sandin, L., Johnson, R.K. Strong land use effects on the dispersal patterns of emerged stream insects: implications for transfers of aquatic subsidies to terrestrial consumers. (manuscript).
- IV Carlson, P.E., McKie, B.G., Johnson, R.K. Cross-habitat linkages between aquatic insect subsidies and terrestrial arthropods: interacting influences of land use and microhabitat. (manuscript).

Paper I is reproduced with the permission of the publishers.

The contribution of Peter Carlson (PC) to the papers included in this thesis was as follows:

- I All authors conceived the study. PEC planned and conducted the field sampling and much of the laboratory work (sorting and identification). PEC and RKJ analysed the data. PEC wrote the first drafts of the paper, with substantial contribution from RKJ. BGM contributed with interpretation of the results and writing of the manuscript.
- II All authors conceived the study. PEC planned and conducted the field sampling and much of the laboratory work (sorting and identification). BGM and LS analysed the data. All authors contributed to interpretation of the results. PEC and LS wrote first drafts of the paper. All authors contributed to text with significantly large contributions by BGM in later versions of the manuscript.
- III All authors conceived the study. PEC and BGM generated the working hypotheses and the design of the study. PEC conducted the field sampling and laboratory work (sorting and identification). PEC and BGM analysed the data and interpreted the results. PEC wrote the first drafts with substantial contribution from BGM. RKJ contributed with data interpretation and text writing. LS contributed to text.
- IV All authors conceived the study. PEC conducted field sampling and much of the laboratory work (sorting and identification). PEC and BGM analysed the data and interpreted the results with contributions from RKJ. PEC wrote the manuscript with substantial contributions from BGM and RKJ.

Abbreviations

ANOSIM	Analysis of similarity
CPOM	Course particulate matter
FPOM	Fine particulate matter
NMDS	Non-metric multidimensional scaling
SIMPER	Similarity percentage

1 Introduction

1.1 Cross-ecosystem resource flows and the importance of aquatic subsidies

Cross-ecosystem resource flows are increasingly recognized as important links between adjacent ecosystems. Indeed, resource transfers are key components of virtually all ecosystems, since habitats are rarely closed or noninteractive with other habitats (Likens & Bormann, 1974; Polis et al., 1997; Lamberti et al., 2010). When transfers subsidize the functioning of recipient habitats they are known as spatial resource subsidies. Spatial resource subsidies can be further described as any persistent or recurring process in which donor-controlled resources such as nutrients, matter, and organisms cross boundaries and have fundamental impacts on the structure and dynamics of populations, communities and food webs in recipient habitats (Polis et al., 1997). Transfer of spatial resource subsidies, such as organisms, may be accidental (e.g., by winds), or a product of life history (e.g., migration, ontogenetic habitat switches) or interactions (e.g., interference competition inducing dispersal) (Polis et al., 1997).

Boundaries between aquatic and terrestrial ecosystems are important interfaces for spatial resource transfers. Lotic systems offer exceptional models for the study of how resource subsidies affect recipient habitats, not least because of the relatively sharp nature of the aquatic-terrestrial boundary. Although stream systems are small, compared to the surrounding terrestrial landscape, they are also numerous and therefore collectively have the potential to export to the adjacent riparian and terrestrial areas a large subsidy of emerging aquatic insects (e.g., Moldenke & Ver Linden, 2007). These subsidies are important for the life history of riparian and terrestrial consumers; affecting abundance, territoriality, feeding behavior, and reproductive success as well as acting as an integral component of riparian and terrestrial food webs.

Transfer of subsidies from terrestrial to aquatic environments (e.g., as plant litter fall) have been long studied, however, comparatively few studies have addressed reciprocal transfers in the opposite direction (aquatic to terrestrial environments) particularly in the form of emerging aquatic insects. Furthermore, knowledge is lacking of how deliveries and consumption of the adult flying stages of aquatic insects are affected by differing environments within riparian and terrestrial habitats.

The riparian ecotone is the space that can be thought of as the three-dimensional arena where the cyclic processes of aquatic-terrestrial resource exchange occur (Gregory et al., 1991). Riparian zones have been described to extend outward from the wetted edge of the stream channel including the limits of flooding, and extend into the canopy of streamside vegetation (Sedell et al., 1991), and are directly proportional to stream size and site topography (Bilby, 1988). The conditions in riparian zones result in a diverse array of species, habitats, and environmental conditions and processes. In natural riverine systems the most important drivers of riparian microhabitat complexity are disturbance related factors, including flooding regimes (with frequent moderate floods favouring greatest complexity), in combination with characteristics of riparian vegetation and upland influences on the fluvial corridor being the most important. The resulting dynamic environment supports a variety of life-history strategies, biogeochemical cycles and rates, and organisms adapted to disturbance regimes over broad spatial and temporal scales (Naiman & Decamps, 1997). It is the unique physical, chemical, and biological features of this space, which largely mediates characteristics of subsidy and consumer communities along with their associated interactions.

Arthropod generalist predators, such as ground beetles (Carabidae), rove beetles (Staphylinidae), and spiders (Arachne), exploit and benefit from emerging aquatic insects, and are therefore ideal model organisms to study the importance of how different factors affect subsidy utilization. Forested riparian habitats usually contain a greater diversity of microhabitats, which support more species-rich assemblages with a larger number of rare and specialist species (Sadler et al., 2004). On a broad scale, riparian species may be described as euryoecious (species able to tolerate a wide range of environments) and stenoecious (species restricted to specific environmental conditions). Species falling into the latter group are typically hygrophilous (species preferring moist environments) some of which are found only within riparian environments (Matern et al., 2007). In a functionally intact system these taxa typically display lateral distributional patterns from the stream edge correlated with dynamic combinations in strong gradients of temperature,

humidity, and inundation frequency, on top of which can be variations in the degree of vegetation cover, sediment size and sorting, and shading.

The importance of aquatic production to a terrestrial consumer community is moderated by a number of complex and dynamic biotic and abiotic factors, such as spatial and temporal shifts in the relative productivities of habitats (Lynch et al., 2002; Chan et al., 2007) coupled by trophic exchange (Nakano & Murakami, 2001; Wesner, 2010), predator-prey life history traits (Baxter et al., 2005) and features of the riparian ecotone such as boundary permeability (Wiens et al., 1985; Polis et al., 1997; Cadenasso et al., 2003) and microhabitat complexity (Bates et al., 2007). These factors, along with life history trait compatibility of both the subsidy (e.g., delivery, quality, quantity) and consumer community (e.g., mobility, ability to capture and process), can have strong direct and indirect effects on patterns of retention and pathways of use.

In the following sections of the introduction of this thesis I discuss briefly how these components individually influence linkages between aquatic and terrestrial habitats. In three final sections I discuss gaps in current knowledge and how impacts of human disturbance, particularly agricultural practices, influence these components and the potential consequences for resource transfers.

1.2 In-stream productivity

Immature stages of aquatic insects are affected by many interacting biotic (e.g., food webs, trophic relationships) and abiotic (e.g., current, substrate, temperature, oxygen) factors. Most studies and conceptual models pertaining to stream food webs have focused on the quantity of each food web component and the movement of energy and materials from allochthonous and autochthonous food sources to aquatic insects (e.g., Vannote et al., 1980), with much less attention given to the quality of these food sources and seasonal variations in their supply and composition (Feminella & Hawkins, 1995). Seasonal changes and stochastic shifts in food sources of benthic algae and terrestrial matter (Lamberti and Steinman, 1997; Doi et al., 2007) may produce limitation of higher quality resources, and benthic insects track these changes and show dietary shifts as a function of resource availability (Haapala et al., 2001). Limitation and competition for higher quality in-stream basal resources may reflect the relative densities and nutritional quality of the insects as they emerge and become a subsidy for riparian and terrestrial consumers.

1.3 Aquatic versus terrestrial prey

Some studies have demonstrated that aquatic subsidies have the largest effects on recipient food webs when contributions to prey abundance are substantial in comparison to that produced by the recipient habitat alone (Nakano & Murakami, 2001; Marczak et al., 2007b). However, other studies indicate that aquatic insects can provide an important energy subsidy to recipient consumers even when primary productivity of the riparian/terrestrial habitat exceeds that of the stream (e.g., Marczak & Richardson, 2007). Even when riparian in-situ productivity exceeds in-stream productivity these subsidies may have a high impact on consumers by redressing specific nutritional imbalances in terrestrial food webs, particularly in providing proteins and lipids (Mayntz et al., 2005) which are produced within aquatic environments (Gladyshev et al., 2009; Torres-Ruiz & Wehr, 2010) and not easily synthesized or assimilated in terrestrial environments (Muller-Navarra et al., 2000; Arts et al., 2001; Goedkoop et al. 2007). Choice of aquatic or terrestrial prey is influenced by relative prey availability and the ability of a consumer to utilize dynamic resources, and individuals often compete spatially within habitats to be the first recipients of certain subsidy flows (Marczak et al., 2007a).

1.4 Timing of emergence

Timing and rate of aquatic insect emergence can have strong effects on consumer distributions as well as efficiency of subsidy utilization. Aquatic insects often time their emergence based on the physical and biotic environment that adults encounter. For example, seasonal restriction of emergence to the warmer months of the year is a phenomenon typical of insects in colder temperate regions. In addition to seasonality, the rate of emergence is dynamic and taxon specific and may be: continuous with irregular fluctuations in rate; rhythmic, with a lunar period; or sporadic, occurring at irregular intervals of a few days. Timing and rate of emergence is largely based on cues such as light, water temperature and discharge pattern, plus competition and nutrition during the immature stage (Sweeney, 1993; Giberson & Garnett, 1996; Merritt et al., 2008). Variation in climatic conditions and nutrition in the immature stage may also influence the life-cycle, resulting in differences in emergence periods.

1.5 Dispersal

Emergence locality within the stream reach is influenced by geomorphological characteristics and habitat related productivity combined with taxon-specific methods of dispersal. Emergence of most Diptera and Trichoptera occurs through the water column, whereas emergence of others, such as Plecoptera and some Ephemeroptera occurs from the stream bank (Merritt et al., 2008). Dispersal is possible by crawling, swimming, and drift during the aquatic stage and the method of emergence for metamorphosis varies broadly between taxa. Dispersal during the terrestrial stage of aquatic insects occurs mostly by flight, but also by crawling over land and upon available substrate.

Movement of adult aquatic insects among riparian habitats differs broadly among taxa (Huryn et al., 2008). In general most studies have shown that individuals stay close to or above the stream channel, and that densities decline exponentially with increasing distance from the stream (e.g., Jackson & Resh, 1989, Kovats et al., 1996; Collier & Smith, 1998; Winterbourn et al., 2007; Finn & Poff, 2008). Species with longer life spans, especially those that feed as adults, as well as stronger fliers are likely to have a higher capacity for larger dispersal ranges. Longer distance dispersal, including emigration from the natal stream, is typically triggered by environmental cues (e.g., wind speed or direction, light intensity, temperature or moisture gradients, presence or absence of trees or other vegetation) (Ims & Hjermann, 2001). Abundance, relative to in-stream production, also has an effect on maximum dispersal distances along with characteristics of the riparian-terrestrial habitat.

Vegetative related dispersal patterns are often discussed in the context of ‘corridor-barrier’ effects, which suggest that riparian vegetation functions as a ‘corridor’ or as a ‘barrier’ for adults of many aquatic species that require specific vegetation or related physical factors. The importance of the corridor-barrier effect varies between taxa such as stoneflies and caddisflies (Petersen et al., 1999), and chironomid midges (Delettre & Morvan, 2000). For example, longer dispersal distances of up to several kilometers have been reported for stoneflies (Ulfstrand, 1969; Elvang & Madsen, 1973; Kuusela & Huusko, 1996) and caddisflies (Svensson, 1974). Species traits, such as larger overall size, greater thoracic mass, greater wing loading, and greater wing size, have been found to relate to larger population range sizes (Malmqvist, 2000; Hoffsten, 2004; Rundle, et al., 2007) and flight ability (Rankin & Burchsted, 1992; Marden, 2000). In turn, these traits also might be correlated with a greater ability to avoid or tolerate adverse environmental conditions and therefore are potentially less influenced by ‘corridor-barrier’ effects. On the other hand, ‘corridor-barrier’ effects are often particularly important for weak fliers. For example, a study by Delettre and Morvan, (2000) found that

chironomid midges tended to aggregate in vegetated areas rather than open areas near the stream, and as a consequence discouraged dispersal because insects were less likely to move from preferred vegetation into open habitat.

1.6 Anthropogenic disturbance

Anthropogenic disturbance has strong effects on the structure and function of stream ecosystems that may alter benthic communities directly, or alter their basal resources which will have consequences to the value of subsidies for consumers. Likewise, human activity has altered the natural linkages between streams and their surrounding terrestrial environments. Hydromorphological alterations are judged to be one of the most serious human-generated effects affecting the integrity of lotic systems. The most common alterations are channel straightening and removal of riparian vegetation (Allan & Flecker, 1993; Naiman & Décamps, 1997; Ward, 1998). Both have direct effects on organisms in the habitats where they occur, but also have potential to cause indirect effects by interrupting the flux of resources between the two adjacent ecosystems.

Reduction of riparian vegetation (e.g., forest harvesting) can increase solar radiation in the riparian zone as well as wind speed and exposure to air advected from open areas, typically causing increases in air, soil, and stream temperatures and decreases in relative humidity (reviewed by Moore et al., 2005). Furthermore, habitat structure is simplified through the lack of vertical stratification, for example; fewer age classes of trees and shrubs are represented, dead wood is often at a similar stage of decay or totally lacking, and few to no standing dead trees occur. Channelization tends to diminish microhabitat complexity due to interrelated effects from hydropeaking such as increased substrate embeddedness, or washout of vegetation or specific riverine habitats such as sandbars (Allan & Castillo, 2007).

Complete deforestation has had negative impacts on dispersal patterns, and studies have demonstrated greater diversity (Harrison & Harris, 2002) and abundance (Petersen et al., 1999; Smith et al., 2002; Winterbourn et al., 2007) of adult aquatic insects in riparian areas with herbaceous vegetation and trees compared to riparian areas consisting of more open land. Furthermore, exchange of native with non-native riparian forests has been shown to reduce diversity of dispersing adult aquatic insects. For example, in the New Zealand hill country, Collier et al., (1997) found a greater number of adult stream-insect taxa in native than in non-native pine forests. These patterns may be explained by species-specific foraging preferences in vegetation (Harper, 1973) and/or

physical factors related to differences in vegetation such as temperature, humidity, wind, light and shade (Harper, 1973; Sweeney, 1993).

These studies demonstrate that alteration of vegetation differently affects the distribution patterns of adult aquatic insects, compromising the delivery essential resources to consumers of specific subsidies. Moreover, efficient use of subsidies depends largely on the synchronization to specific timing and amount of a resource subsidy relative to life history characteristics of specific consumer taxa (Kato et al., 2004; Paetzold et al., 2005, 2006). The timing of cues to emerge (e.g., temperature and flow patterns) may be altered by reduction of riparian vegetation, channelization, as well as potential impacts from climate change (e.g., Harper & Peckarsky, 2006). Various responses in consumers may be attributed to the degree of specialization for aquatic prey as well as mobility in response to aquatic insect flux.

Habitats with high levels of spatial heterogeneity generally support a diverse assemblage of riparian arthropods, with a range of different life histories capable of responding to availability of different food types (e.g. terrestrial vs. aquatic). Anthropogenic alterations can result in decreased consumer abundance and diversity, and constrain the distribution of sensitive species (e.g., hygrophilous, riparian specialist, forest obligates) inducing shifts towards less specialized euryoecious arthropod assemblages especially those with high dispersal abilities. Negative correlations have been found between alterations to vegetation (e.g., litter depth, structural complexity) and assemblages of spiders (Bultman & Uetz, 1982; Uetz, 1991) and ground beetles (Gunnarsson et al., 2004; Sroka & Finch, 2006). Likewise, riparian arthropod spider and rove beetle abundance and richness are negatively correlated to flow regulation and river channelization (e.g., hydropeaking, substrate embeddedness) (Paetzold et al., 2008).

1.7 Gaps in current knowledge

The total production of potential emergent insects from a stream depends on the number of meters of stream channel with a high or low production of insects with a terrestrial winged stage. Knowledge is lacking of the environmental differences in habitats and resulting changes in biota in relation to resource transfers via emerging aquatic insects. It has been well documented that changes in the dominant habitat types and their environments result in changes to benthic assemblages. However, few studies have specifically focused on impacts to the production of aquatic insects with an adult flying stage, and even fewer studies have addressed how this may impact the specific abilities of the subsidy to infiltrate into the terrestrial environment. Secondly,

in order to give a more holistic insight to the interdependence of factors controlling aquatic resource deliveries, studies are needed that can relate in-stream potential subsidy production to actual dispersal into terrestrial habitats. Studies are lacking that connect dispersal patterns and riparian habitat alterations, especially in the context of the minimum amount needed to maintain efficient transfers of essential resources to consumers that rely on such linkages. Additionally, most studies have considered the role of subsidies only in terms of magnitude, neglecting how structure of the subsidy relative to *in situ* resources may impact subsidy consumption by potential recipients. Thirdly, responses of a broader spectrum of potential consumer taxa need to be studied in order to detect which are keystone taxa in these interactions and which taxa are most sensitive to the weakening or loss of linkages. Certain riparian types have been little studied and we lack information on linkages related to specific microhabitats and other riparian characteristics that are essential to key consumer groups. Studies that include these aspects concurrently will increase our ability to more precisely identify controls of efficiency and retention in transfers of resources across riparian boundaries. Collectively, this would give clearer insight into potential pathways of initial transfers in recipient food webs, how consumers further up the food chain may be impacted, and the ultimate fate of aquatic resources.

1.8 Agricultural land use

The impacts of changes in land use, such as pastoral and crop development and the removal of riparian vegetation on stream ecosystems, are well established (e.g., Quinn, 2000; Allan & Castillo, 2007), but few have considered impacts upon aquatic-terrestrial linkages. Agricultural development often alters the key aspects of stream habitats that influence invertebrate communities, including the type of food available, the physical shape of the stream, flow regime and water quality (Allan & Castillo, 2007). These changes often result in higher in-stream production, compared to forested streams. However, it is important to consider the ability of the donor habitat to export this increase in productivity as subsidies to recipient habitats. Highly eutrophic waterways are often accompanied by changes to benthic assemblage traits that in conjunction with altered riparian habitats may impair their ability to export aquatic derived resources to terrestrial food webs. Furthermore, consumer assemblages in the riparian environment are likely to differ with land use, potentially limiting their capacity to absorb subsidies. Perturbation affecting biota could alter the faunal dynamics and composition of both aquatic and terrestrial food webs by decoupling the natural interaction between riparian and stream habitats. Taken

together, it is likely that agricultural practices ultimately result in reduced subsidy resource exchange efficiency, where energy flow to riparian habitats is weakened relative to productivity of the stream.

2 Objectives of the thesis

The overall objective of this thesis is to increase our understanding of linkages between aquatic and terrestrial ecosystems, with particular focus on how anthropogenic activities in the form of agricultural land use impacts the production and deliveries of aquatic insect resource subsidies, and the responses of terrestrial arthropod consumers. The specific objectives were to:

1. Investigate how land use and habitat interact to affect in-stream benthic invertebrate communities, including abundance, diversity and functional traits. In paper I, the focus was to assess the main environmental drivers of benthic assemblage differences between agricultural and forested streams, and riffle and pool habitats. In paper II, the aim was to assess land use effects on innate dispersal and life history traits of aquatic insects in terms of their potential as vectors of subsidy transfers from streams into terrestrial habitats.

2. Investigate how land use related alterations within the riparian zone affect dispersal patterns of emerging adult aquatic insect subsidies and the capacity of ground-dwelling (epigeal) arthropod consumers to respond to subsidy input. In paper III, the aim was to study how agricultural versus forested riparian environments affect dispersal patterns of flying adult aquatic insects. In paper IV, the aim was to assess how distributions of epigeal arthropod consumers respond to differences in land use, microhabitat complexity and microclimate, and variation in prey type and quantity (e.g., emerging aquatic insects vs. terrestrial insects).

3 Materials and methods

3.1 Study sites

Seasonal samples of benthic invertebrates, aerial insects, and epigeal arthropods as well as environmental variables were collected from eight (Papers II, III, VI) or nine (Paper I) small to medium, lowland boreal streams and their surrounding riparian environments in south-central Sweden (Fig. 1, Table 1). The streams were circumneutral and ranged from nutrient poor to nutrient rich (Table 1). Catchments of four of the streams were predominantly forested, with very little influence of agriculture, while the other four (Papers II, III, IV) or five (Paper I) consisted of landscapes more influenced by agricultural activity, with relatively less forested area. Riparian vegetation differed between the two stream groups. The four forest-dominated streams had catchments consisting almost entirely of mature coniferous and mixed forests, dominated by pine and spruce, with birch also common (Table 1, Fig. 2). Riparian vegetation was more variable among the agricultural sites, consisting either of relatively young broadleaf and mixed forests, including alder and willow, or mainly open grassland and cereal fields with only sparse distributions of brush and trees directly adjacent to the stream bank (Table 1, Fig. 2).

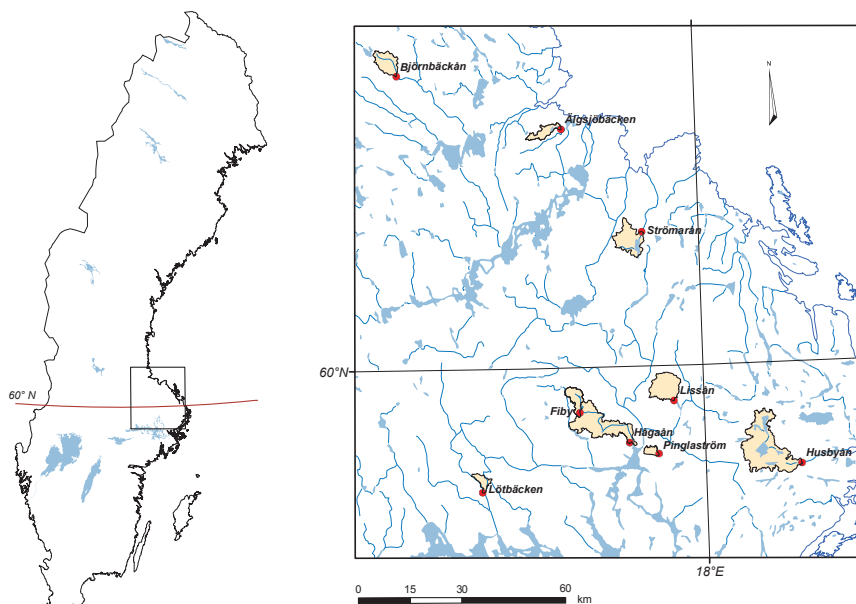


Figure 1. Schematic diagram showing the location of the nine study streams situated in the boreal region of south-central Sweden.



Figure 2. Riparian habitat of (a) an agricultural site (Strömarån), and (b) a forested site (Björnbäcken).

Table 1. Summary of descriptor variables of forested versus agricultural study sites.

Stream *	Paper	Land use	Order	Altitude	Stream chemistry			Catchment			Riparian
					pH	NO ₂ -NO ₃ (µg/L)	TP (µg/L)	Catchment (km ²)	land/pastures	% Arable area	% Forest area
Älgsjö.	I, II, III, IV	For.	2	17.2	8.11	163	17	19.9	0.1	72.7	> 100
Björn.	I, II, III, IV	For.	4	191.1	6.27	18	9	34.8	0	76.4	> 100
Fibyån	I, II, III, IV	For.	3	44.7	6.93	83	53	23.9	0.6	75.9	> 100
Pingla.	I, II, III, IV	For.	2	30.8	6.87	156	72.3	9.1	0.04	98.0	> 100
Hågaån	I, III, IV	Agr.	4	19	8.12	1154	52.5	120.8	28.5	49.1	55.3
Husby.	I, II,	Agr.	4	10.8	7.82	319	45.0	156	25.2	44.5	5.2
Lissån	I, II, III, IV	Agr.	4	15	8.27	1450	112.8	55.3	32.1	50.0	33.5
Löt.	I, II, III, IV	Agr.	3	14.6	7.83	1824	198.2	12.9	42.7	36.3	5.9
Ström.	I, II, III, IV	Agr.	4	28.2	8.08	65.25	24.8	53.9	8.4	60.5	7.4

* Abbreviated stream names in the table are as follows: Älgsjö. = Älgsjöbäcken, Björn. = Björnbäcken, Pingla. = Pinglaström, Husby. = Husbyån, Löt. = Lötbacken, Ström. = Strömarån.

3.2 Sampling of biota

3.2.1 Benthic invertebrates (I, II)

For papers I and II, benthic invertebrate assemblages were quantitatively sampled in autumn 2008 and spring 2009 from pool and riffle habitats. Three replicate samples were collected from each pool and riffle habitat using a 40 cm high, 500 µm mesh Hess sampler covering a bottom area of 0.086 m² (Wildlife Supply Company <http://www.wildco.com>). Collected organisms and detrital material were preserved in the field in 70% ethanol and returned to the laboratory for processing. Organisms were sorted from the debris, identified to

the lowest level of taxonomic resolution possible, and counted. Samples with a relatively high number of organisms (>300/sample) were subsampled by sorting a minimum of 300 individuals in a fraction of the sample, with the remainder of the sample searched for rare taxa not present in the subsample.

3.2.1.1 Benthic invertebrate community response variables (I)

In paper I, mean taxon abundance values from each habitat unit in each season were taken by averaging across the three replicate Hess samples and recalculating to mean abundance per m². Five univariate metrics of assemblage abundance/diversity were used as response variables: (1) total density, (2) taxon richness, (3) evenness, calculated as the square of Shannon diversity divided by the number of taxa, (4) Shannon diversity, and (5) % EPT taxa, calculated as the percentage of Ephemeroptera, Plecoptera, and Trichoptera taxa in a sample.

3.2.1.2 Traits of benthic invertebrates (I, II)

In paper I, biological traits of benthic invertebrates were used to reflect ecological responses of communities to environmental conditions (e.g., Townsend & Hildrew, 1994; Poff, 1997), indirectly describing functional integrity (Dolédéc & Statzner, 2010). Trait information was taken from ASTERICS 3.3 (IRV Software, Vienna, Austria; <http://www.fliessgewaesserbewertung.de/en/download/berechnung/>); 14 trait categories related to functional feeding groups (FFGs) and mode of locomotion were used. The percent of taxa was calculated for each category within the two groups: (i) FFGs were categorized as grazers/ scrapers, miners, xylophagous species, shredders, gatherers/collectors, active filter feeders, passive filter feeders, predators, and parasites; (ii) mode of locomotion traits were categorized as swimming/skating, swimming/diving, burrowing/boring, sprawling/walking, and (semi) sessile.

In paper II, trait information for taxa with an adult winged stage were taken from Poff et al., (2006) regarding: (1) Adult flying strength (weak/strong), (2) Voltinism (semi/uni-, bi- or multivoltine), (3) Size at maturity (small/medium/large), (4) Synchronization of emergence (poorly/well synchronized), and (5) Adult life span (very short/short/long) which give in total 12 states (2 - 3 trait states for each of the five traits).

3.2.2 Aquatic and terrestrial flying insects (III, IV)

Flying insects were sampled for a period of four days in August, September, and October in 2009 and in April 2010. Traps consisted of two clear A4 sized acetate sheets (623.7 cm²) clamped to a 1 m high stand made of an inverted

“plant support” allowing continuous collection of insects on both sides for a total collecting surface area of 1247cm² (Fig. 3) The outermost surface of the acetate sheets were coated with an odorless, non-drying insect coating adhesive (Tanglefoot, The Tanglefoot Company). Traps were placed in transects perpendicular to the stream at distances 1, 5, 10, 50, and 100 m from the stream edge (Fig. 4). On each sample date, acetate sheets were removed from the stands, wrapped in plastic foil, and stored in a freezer for later analysis.

Insects were identified, usually to family level, and classified as either aquatic or terrestrial in origin according to their larval habitats (Nilsson, 2005; Merritt et al., 2008). A few families include aquatic, semi-aquatic and terrestrial species, but these were never abundant, and were classified as aquatic (e.g., Tipulidae). All ephemeropteran, plecopteran, and trichopteran individuals were identified and counted on the entire sheet. For other orders, if a large number of insects (e.g., dipterans) were collected, the following subsampling protocol was used: acetate sheets were placed on white paper, consisting of a grid of 20 5.94 × 5.25 cm squares. Within each sheet, five squares within each row were randomly sampled, resulting in a survey of a minimum of 25% (311.85 cm²) of the total coverage area of both sheets combined. Aquatic and terrestrial dipterans were the dominant group captured among all sites, followed by trichopterans. Thus the primary focus groups in papers III were aquatic dipterans and trichopterans, and in paper IV aquatic and terrestrial dipterans.

3.2.3 Epigeal arthropod consumers (IV)

Carabid and staphylinid beetles (Coleoptera), and ground hunting spiders (Araneae) were collected using pitfall traps, which consisted of glass jars (60 mm diameter × 70 mm deep) sunk into the ground, with the open top of the jar level with the ground surface, and covered by a 15 × 15 mm piece of plywood supported by nails (Fig. 3). Arrays consisting of five jars covering an area of 1 m² were placed at 1, 10, and 50 meters distances perpendicular to the wetted stream edge (Fig. 3, Fig. 4). A mixture of ethanol and glycol was used to fill the bottom half of the jars. Traps were operated over a four day period from summer to autumn 2009 and in spring 2010. Upon collection each group (n = 5 jars) was combined into one sample per distance (e.g., 1, 10, and 50 m), and preserved in 70 % ethanol for subsequent sorting and identification. In the laboratory most individuals were identified to species level, and then sorted into three groups for further analysis: Carabidae beetles, Staphylinidae beetles, and ground-hunting spiders.



Figure 3. Photo of pitfall array and sticky trap.

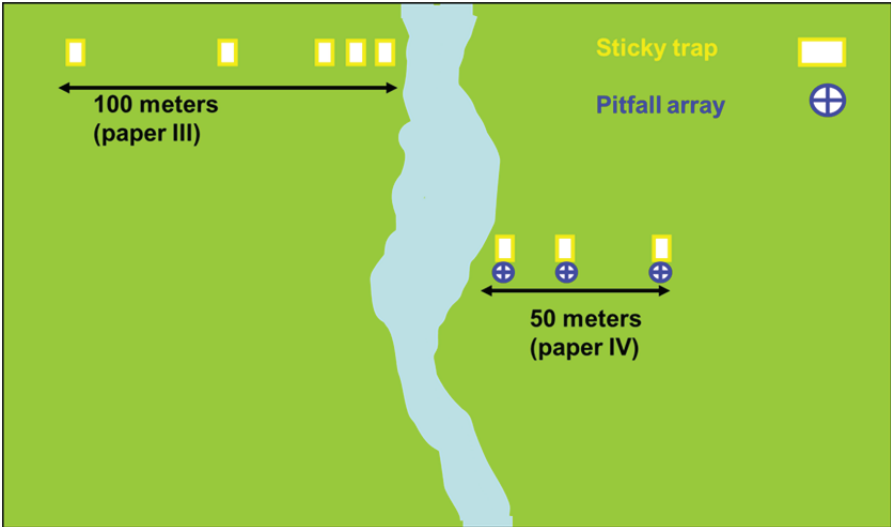


Figure 4. Example of sticky trap and pitfall array set up used in papers III and IV.

3.3 Sampling of environmental variables

3.3.1 Catchment (I)

Data on catchment land use were recorded for all sampling sites from Corine land cover (<http://sia.eionet.europa.eu/CLC2000>). Land use within catchments was delineated according to topographic maps with a scale of 1:100,000 (Swedish Geodata; roadmap from Lantmäteriet) and the delineations were digitized by means of ArcGIS9 (ESRI, Redland, CA; <http://www.esri.com/>). The total area of catchments, as well as the areas of the land use/cover types within the catchments, was then calculated.

3.3.2 In-stream habitats (I, II)

In-stream habitats were characterized in autumn 2009. In-stream habitat types (i.e., pools, riffles) were visually identified and individually surveyed along the 100 m section where benthic invertebrates were sampled. Measurements within each habitat type included length, wetted width, average depth, maximum depth, and flow. Substratum type, occurrences of vegetation, large woody debris, and length of eroding bank were identified visually within individual habitat units. Water samples were analysed for various physicochemical parameters, including nutrients (fractions of N and P) and other relevant variables (e.g., pH, conductivity, and alkalinity) at the Department of Aquatic Sciences and Assessment following international (ISO) or European (EN) standards when available (Wilander et al., 2003). During autumn 2008, coarse particulate organic matter (CPOM) was sampled by taking three additional Hess samples from the same habitat units where benthic invertebrates were collected. CPOM samples were collected once in the autumn after leaf fall to detect the strongest among-stream differences using this variable as a habitat descriptor. The CPOM was placed in plastic bags and frozen upon return to the laboratory. In the laboratory, the thawed CPOM was separated from fine particulate organic matter and invertebrates by rinsing the material in a bucket with a 1 mm mesh screen sieve. The detrital material was sorted into five categories; leaves, needles, grass, woody debris, and other (e.g., cones, seeds, etc.), and each category was oven dried (50°C for 48 h) and weighed to nearest 0.0001 mg (McKie & Malmqvist, 2009). Material from each leaf category was then combusted in a muffle furnace (550°C, 4 h) to determine ash-free dry mass (AFDM).

3.3.3 Riparian habitat (I, II, III, IV)

The riparian zone was classified as a 100 m corridor on both sides of the stream where aerial adult insects and epigeal arthropod consumers were

sampled and adjacent to the 100 m section where benthic invertebrates were sampled. Soil surface temperature at distances 1, 5, 10, and 50 m from the stream and water temperature was measured every four hours during all sampling events.

Slope used in paper III was calculated for two distance categories along each line: “bank” (1-5 m) and “beyond bank” (10-50 m) using ArcGIS (ArcMAP version 10.1) (www.esri.com). Daily average wind speed and direction data for each sampling period were obtained from the nearest weather station in proximity to sampling sites (<http://www.wunderground.com>). Vertical stem structure of trees under the canopy was estimated by point sampling at 25 and 50 m distances from the stream on each line using a Relascope with a gap/chain ratio of 1:50. Relascope measurements result in the sum of the cross sectional area of tree stems at cs. 1.3 m above ground (breast height) within a radius of 56.4 m from the point taken. Values are expressed in square meters of total tree stem area per hectare and commonly referred to as standing stock (SS).

Canopy foliage cover (papers III and IV) was measured using a LI-COR Leaf Area Index (LAI) meter (LAI-2000 model, Lincoln, Nebraska USA). The LAI-2000 measures all light-blocking objects with values expressed in terms of half the square meters of leaf per square meter of ground (m^2 foliage area / m^2 ground area). Four measurements were taken at each “sticky-trap” location (distance and line) at 1.3 m from the ground and then averaged. LAI values range from 0 (bare ground) to over 10 (dense forest). All measurements were made once (on a clear day in early autumn) at peak vegetative production to detect the strongest among-stream differences using this variable as a habitat descriptor.

Soil samples (Paper IV) were taken once in autumn 2009 within each of the 1m^2 pitfall arrays and analyzed for pH and organic content. Soil pH was measured on a soil sample (3 tablespoons) that was mixed with 60 ml of distilled water, shaken for one hour, centrifuged and measured using a pH meter (Radiometer Copenhagen, TIM 800 titration manager) on the clear water phase. Organic matter, as ash-free dry weight, was calculated by weighing approximately 15 mL of soil sample into a ceramic cup to the nearest 0.001 grams and then combusted in an oven for 6 hours at 550°C and reweighed.

Microhabitat descriptors of substrate, ground vegetation, and trees (paper IV) were measured within a plot with a radius of 1.785 from the center of each pitfall array covering a total area of 10m^2 . Within each plot measurements of size and type were classified to categorize substrate and ground vegetation by percent type and trees by number (see Paper IV, Table 1). Within each descriptor group (e.g. substrates) each category (e.g. boulders) was given an

index value where higher values were given to categories contributing more to microhabitat complexity, with the sum of all categories index values within each descriptor group equal to one (see Paper IV). Values were based on previous variables shown important for microhabitat to arthropods in this study and literature (e.g., Uetz, 1975, 1991; Pajunen et al., 1995; Antvogel & Bonn, 2001). Thus, using substrates as an example; sites dominated by cobble and gravel (e.g., Manderbach & Hering, 2001) and/or soil (offering higher moisture and organic material) (e.g., Uetz, 1975; Antvogel & Bonn, 2001) would have a high substrate index score, while a site that is dominated by substrate such as boulder would have a low substrate index score (see Paper IV, Table 1). Likewise, shrubs, ferns and high forbs in the ground vegetation category, and small to medium coniferous trees in the tree category were given a high index value as their relatively higher structural complexity contributes to higher microhabitat complexity and arthropod diversity (e.g., Uetz, 1991) (see Paper IV, Table 1).

3.4 Statistical analyses

3.4.1 Environmental gradients (I, IV)

Principal component analysis (PCA) on centered and standardized variables was done using Canoco 4.5 (ter Braak & Šmilauer, 2002) to assess correlations among the environmental data and to reduce the number of dimensions in the data through linear combinations of the environmental variables (Johnson & Wichern, 1988). In paper I, we used correlation to remove redundant variables ($r > 0.7$) resulting in a parsimonious set of catchment land use/cover, riparian characteristics, and in-stream substratum and water chemistry variables. In paper IV, PCA was used to visually inspect the 12 physicochemical and biological characteristics of the streams and their adjacent riparian habitats. Variables used in the PCA comprised characterization of riparian microhabitat, using 10 different abiotic and biotic (including aquatic and terrestrial dipterans as a measure of food resource availability) variables, stream water total phosphorous concentration as an indicator of eutrophication, and the percentage of coniferous vegetation within the riparian study area (indicative of natural forest vegetation). In papers I and IV, the number of meaningful Principal components (PCs) was determined by examining the eigenvalues of the first few axes.

3.4.2 Habitat and benthic assemblages (I)

Both taxonomic composition and trait data were related to the environment by means of redundancy analysis (RDA) to determine potential predictors of pool

and riffle assemblages. A Monte Carlo permutation test was used to test the significance of the contribution of the variables to the ordination as well as the statistical significance of the relationship between species/traits and environmental variables. Redundancy analysis was done by means of CANOCO version 4.5 (ter Braak & Šmilauer, 2002).

3.4.3 Community response variables (I)

Along with the five univariate metrics of assemblage abundance/diversity used as response variables described in section 3.2.1.1, the first two axes of correspondence analysis based on abundance and presence/absence data were used to describe species turnover. Correspondence analysis was conducted by means of CANOCO version 4.5 (ter Braak & Šmilauer, 2002).

3.4.4 Invertebrate and stream environment relationships (I)

The nine response variables were related to two complex (first two PCA axes) environmental gradients by means of least-squares linear regression. Two metrics were used to compare the response of the taxonomic groups to stress (e.g., Johnson & Hering, 2009):

(1) Precision was calculated as the squared correlation (coefficient of determination, adjusted R^2) between the observed and fitted values as a measure of variance accounted for by the model.

(2) Sensitivity of a taxonomic assemblage to stress was estimated as the magnitude of change (slope) of a predicted stressor–response relationship.

Regression analyses were performed by means of JMP 8.0.1 (SAS Institute Inc. JMP 2009). If necessary, variables were log 10 transformed (continuous environmental data), square root transformed (invertebrate abundance data), or arcsine-square-root transformed (proportional data) to approximate normally distributed random errors.

3.4.5 Differences in arthropod assemblage composition (I, IV)

ANOSIM (analysis of similarities) was used to test for differences in benthic invertebrate assemblage (paper I), and epigeal arthropod (paper IV) composition between habitats and sites. ANOSIM is based on comparing distances between groups (measured as similarity/or dissimilarity in species composition) with distances within groups which are converted to ranks. A large positive R (up to 1) signifies dissimilarity between groups. The significance was computed by permutation of group membership, with 10,000 replicates. SIMPER (similarity percentage) was used for assessing which taxa were primarily responsible for differences between groups based on abundance

(Clarke, 1993). Both analyses were performed by means of PAST version 2.12 (Hammer et al., 2011).

3.4.6 Analysis of variance (II, III, IV)

Paper II trait data were analyzed using a split-plot Analysis of Variance model using the proc mixed routine in SAS Release 9.3 statistical software (SAS Institute Inc., 2011). Land use (forested vs. agriculture), habitat (pool vs. riffle) and season (autumn vs. spring) were fitted as fixed effects. We did not have true temporal replication for season (as invertebrate samples were taken once in autumn and once in spring). However, spatial replication for each season, represented by multiple sampled streams, allowed us to directly assess contrasting habitats and land use between the two sampling periods. We fitted season as a fixed rather than random factor in the REML analyses (see below), while acknowledging that details of these responses may have differed in other years with different seasonal trajectories. Our analysis has multiple error terms, reflecting the hierarchical nature of our sampling design. The “main plots” were the eight streams, fitted as a random block factor and used for testing the effects of land use (four replicates per category). All other fixed factors and interactions were tested against error terms incorporating the stream block factor. The data were analyzed as abundance (individuals/m²) and percentages having a certain trait state (e.g. being semivoltine or having a large size at maturity). Variance estimation was done using the Residual maximum likelihood (REML) method using Type III tests.

In paper III, we used a split plot ANOVA model to test whether response of aquatic insect abundance and richness differed between streams in agricultural versus forested landscapes with distance and time. Land use (forested vs. agriculture), distance (lateral distance from stream bank), and season (high summer, late summer, autumn and spring) were fitted as fixed effects, while stream and transects nested within stream were random factors. Our design has multiple error terms, reflecting the hierarchical nature of our sampling design. Land use was tested using whole streams as replicates, while all other fixed factors and interactions were tested against error terms incorporating the transect block factor. This model was used to assess variation in abundance and richness in total aquatic insects, aquatic Diptera, and Trichoptera. Losses of some replicates caused minor imbalance in our sampling design. Accordingly, we used restricted maximum likelihood (REML) estimation to model our error terms, as this is reliable even when data are unbalanced, unlike traditional ANOVA, denominator df were also modeled separately for each fixed effect test. All ANOVA analyses were conducted using JMP 8.0.1 (SAS Institute Inc., 2009).

In paper IV, we used a split plot ANOVA model to test if the response of Carabidae, Staphylinidae, and ground-hunting spider capture rates differed between streams in agricultural versus forested landscapes with distance and season. Land use (forested vs. agriculture), distance (lateral distance from stream bank), and season (July = high summer, September = early autumn and April = spring) were fitted as fixed effects, while stream was a random factor. Our design has multiple error terms, reflecting the hierarchical nature of our sampling design. Land use was tested using whole streams as replicates; while all other fixed factors and interactions were tested against error terms. This model was used to assess abundance variation in total Carabidae, Staphylinidae, and ground-hunting spiders. All ANOVA analyses were conducted using JMP 8.0.1 (SAS Institute Inc., 2009).

3.4.7 Relative importance of different abiotic and biotic predictors (III, IV)

In paper III, partial least squares regression (PLS) was used to assess the relative importance of different abiotic and biotic predictors for explaining variation in the proportions of individuals reaching at least 50 m from the stream channel (50+100 m sticky traps combined). Thirty-two predictor variables were fitted in our PLS models for paper III. These included variables associated with season, meteorological conditions, topography, canopy foliage, tree stem densities, riparian vegetation with potentially strong influences on insect flight, as well as dominant land use within the catchment, stream identity, and differences in taxa at the family level (see Paper III, Table S-1). Effects of land use on the major variables included in the PLS models were assessed using a mixed model ANOVA with land use fitted as a fixed factor, and streams as random blocks. For variables measured on more than one date (e.g. soil temperature, wind speed), season was also included as a fixed factor.

In paper IV, partial least squares regression (PLS) models were used to assess the relative importance of aquatic dipteran and terrestrial dipteran abundance, eight different abiotic and biotic microhabitat predictors, as well as the eight stream identities, two land use categories (forested vs. agriculture), the three distances from the stream edge, and day in year, for explaining variation in the abundance of different consumer groups. A separate PLS model was constructed for Carabidae, Staphylinidae, and ground-hunting spiders as response variables using the same 24 predictor variables, for a total of three models.

PLS extracts orthogonal components from a set of variables (both dependent and predictor), which maximize explained covariance between the variables (Eriksson et al., 2006). Extracted components were used to construct a predictive model for the response variables, where the variable influence on

projection (VIP) is relative to the importance of predictor variables, which are the squared function of variable loadings across the components (Eriksson et al., 2006). Predictor variables with a VIP greater than 1 are the most important for the model. Eriksson et al. (2006) recommend a cut-off VIP of 0.8 for separating moderately important predictors, whereas those that fall below are less influential.

Prior to all analyses, response variables were natural log, square root, or arcsine transformed as necessary to satisfy parametric assumptions, with predictor variables additional range standardized prior to PLS analyses. Validation of all PLS models was accomplished by a comparing the goodness of fit of the percent of variation of the response (Y) variable explained by the model (R²) and the percent of variation of the response variable predicted by the model according to cross validation (Q²) of the original model with the goodness of fit of several models based on data where the order of the Y-observations has been randomly permuted, while the X-matrix has been kept intact. The statistical significance (*p* value) of the investigated model was than indicated by analysis of variance (ANOVA) in the cross validated residuals of the response variable. Analysis was conducted using SIMCA-P (version 10.0, Umetrics AB, Umeå, Sweden).

4 Results and Discussion

The goal of the first part of this thesis (**Papers I and II**) was to gain insight into how land use may affect in-stream production (quality and quantity) of aquatic insects in relation to their potential to subsidize adjacent riparian and terrestrial habitats. The second part of this thesis (**Papers III and IV**) investigated how land use related alterations to riparian boundaries affect the dispersal of flying aquatic insects, and how the availability of aquatic subsidy interacts with land use to affect the distributions of terrestrial consumers. My results revealed agricultural land use increased overall in-stream production, but altered the composition of dispersal related traits and reduced the extent of spatial dispersal by adult aquatic insects. Furthermore, my studies provide evidence that the capacity of terrestrial consumers to respond to subsidy availability was also reduced in the agricultural landscape.

In **paper I**, I found catchment land use was correlated with reach- and habitat-scale differences related to nutrient levels, sediments, and hydromorphology that resulted in overall higher amounts of basal food resources in agricultural streams and more discrete habitats compared to forested streams. Riffle habitats were characterized by a high percentage of woody debris and cobble substratum covered by mosses and liverworts. Mosses and liverworts were more abundant in agricultural streams, reflecting nutrient enrichment, and indicate higher growth of epiphyton and periphyton (Suren, 1991). Pool habitat characteristics, such as fine sediment particle sizes and high amounts of coarse particulate organic matter (CPOM) were highly amplified in agricultural compared to forested streams. On the catchment scale, riffle habitats were typically greatly reduced in extent in agricultural relative to forested streams (P. Carlson pers. obs.), a finding that corresponds with other studies (e.g., Petersen, 1992; Burcher et al., 2007). Agricultural sites were characterized by dense stands of emergent macrophytes (*Scirpus lacustris*, *Phragmites australis*) in slower flowing stream habitats, and ground vegetation

(largely consisting of herbaceous plants) within the adjacent riparian habitat (P. Carlson pers. obs.). These marked differences in environments were manifested in benthic assemblages, where basal food resources, substratum, and flow had the strongest influence and not physicochemical stressors (e.g., hypoxia). **Paper I** showed that changes in taxonomic composition between forested and agricultural streams were subtle, with losses of only a few sensitive taxa and, with the exception of the proportion of sensitive Ephemeroptera, Plecoptera and Trichoptera (i.e., EPT) taxa, no significant relationships were found between diversity metrics and land use. By contrast, abundances of total benthic assemblages as well as taxa with a winged adult stage were generally higher in agricultural compared to forested streams and in riffles compared to pools (**Papers I and II**), and taxonomic composition of pool and riffle habitats of forested streams was less dissimilar than pool and riffle assemblages of agricultural streams (**Paper I**).

Species traits related to feeding, behavior and locomotion (**Paper I**) differed in occurrence between agricultural and forested streams, and riffle and pool habitats, reflecting differences in basal food resources and substrata in particular. In agricultural streams, traits that enable penetration of fine substrata (e.g., burrowing/boring, miners) and feeding on particulate organic matter (e.g., filter-feeders) were positively correlated with pool habitats, and passive filter feeders (likely related to FPOM) were positively associated with riffle habitats. Conversely, grazers/scrapers, shredders and gatherers/collectors were positively correlated with forested streams, which again can be explained by habitat and food preferences; grazer/scrapper taxa were more prevalent in riffle habitats (likely related to periphyton abundance), while shredders and gatherers/collectors were more common in pool habitats and higher organic content. Higher abundances in agricultural streams likely reflected the high availability of basal food resources; however, changes in assemblage composition related to changes in in-stream habitat (high amounts of organic matter, fine sediments, and slow flow) likely affected the transfer of resources into the terrestrial environment (**Papers I and II**), which was later supported in **paper III**.

Assemblages in agricultural streams were characterized by higher proportions of taxa without a terrestrial stage (e.g., molluscs and oligochaetes), organisms that retain energy within the aquatic system. Furthermore, aquatic insects with an adult flying stage at agricultural sites were characterized by reduced innate dispersal capacities, i.e. weak flying strengths, short adult life spans, and univoltinism. Individuals characterized by these traits will generally stay close to the stream edge following emergence, which, combined with their short adult life span, limits the possibility of extensive dispersal. Furthermore,

such traits were also more characteristic of pool rather than riffle assemblages, a finding that will be magnified at a landscape scale given the dominance of slow flowing habitats in agricultural landscapes. Conversely, traits associated with greater dispersal, such as long adult life spans and strong flying strengths were more associated with forested streams. Although the role of traits was limited to dipterans and trichopterans in **paper III**, the finding that abundances of emerging adult aquatic insects were substantially greater along the agricultural than the forested streams, but that most were caught close to the stream edge at agricultural streams, indicates limited dispersal away from their natal habitat, corroborating findings from **papers I and II**. In contrast, in forested streams the catch of adult aquatic insects declined remarkably little with increasing distance.

Interestingly, results of **paper III** show that characteristics of the terrestrial environment can at least equal the innate dispersal capacities of aquatic insects (**Paper II**) in regulating dispersal. For example, aquatic dipterans and trichopterans differ in traits, particularly in body size; however my results lend no support to the conjecture that the larger size (e.g. of trichopterans) is manifested in a greater ability to avoid or tolerate adverse environmental conditions such as those found at agricultural sites. By contrast, dispersal traits related to feeding in the adult stage were important (e.g. female Ceratopogonidae when searching for a blood meal), but still less so when compared with the environmental characteristics.

Dispersal of dipterans was positively associated with higher densities of both tree stems and foliage, while reduced dispersal was associated with higher soil temperatures, stronger wind speeds, and more pasture and crops (**Paper III**). Significantly, all the factors associated with reduced dispersal were more characteristic of agricultural than forested sites. Despite the steep decline in aquatic insect catch with distance from the stream channel, the much higher production in agricultural streams compared to forested streams resulted in higher densities of subsidies at all distances. Furthermore, the aquatic subsidy remained abundant in early spring and mid-autumn in the agricultural landscape, whereas it was negligible in the forested landscape at these times. However, the spatiotemporal variability of the resource, i.e. high densities near the stream edge in summer, may result in inefficient utilization by terrestrial consumers in agricultural landscapes.

Paper IV revealed that both local habitat features and consumer group assemblages were affected by season, stream edge distance, and their interactions. However, the specific importance of microhabitat complexity and microclimate, and variation in prey type and quantity differed among consumer groups. Seventy-three percent of the arthropod consumers collected (n = 1720

individuals) consisted of staphylinid beetles. Densities of staphylinids were significantly lower at agricultural sites, indicative of the high number of taxa in this group sensitive to riparian conditions at agricultural sites. Nineteen percent of taxa consisted of carabid beetles, and the remaining 8% of ground-hunting spiders, both of whose densities did not differ overall with land use; however there was evidence that sensitive species declined.

The distributions of carabids and ground-hunting spiders were related to availability of aquatic food resources, but whereas carabid densities increased when aquatic subsidy availability was greater, ground-hunting spider densities declined. I found no response of any group to resources of terrestrial dipterans. These results indicate that terrestrial arthropod consumer groups do respond to the availability of aquatic insect subsidies, but that these responses are moderated by factors associated with land use, microhabitat and phenology. These constraining factors likely limit the capacity of epigeal consumers to absorb the higher aquatic (dipteran) production at agricultural sites, particularly near the stream edge.

Taken together, the results of this thesis indicate that agricultural practices do result in reduced subsidy resource exchange efficiency, where energy flow to riparian habitats is weakened relative to productivity of the stream (Fig. 5).

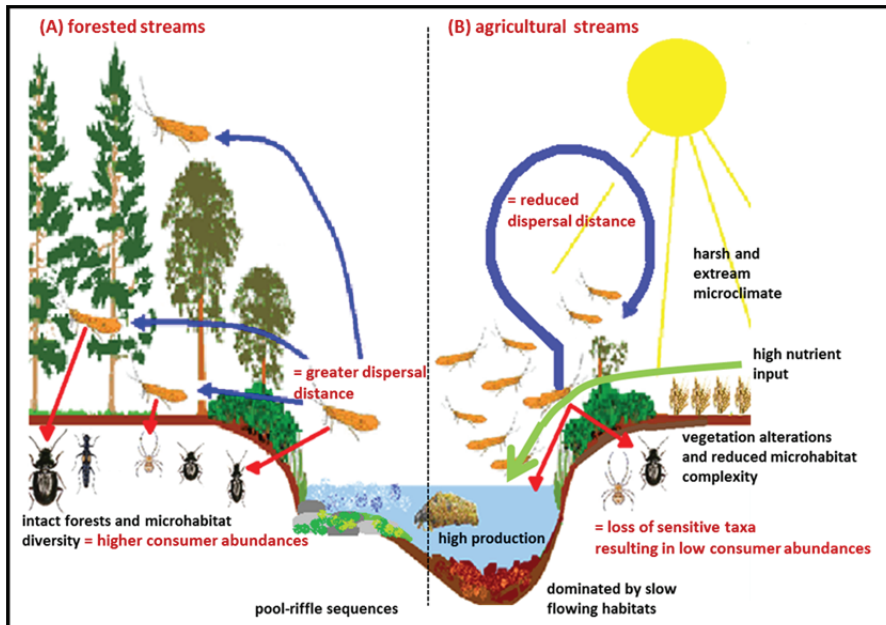


Figure 5. Typical riparian habitats of streams flowing through forested (A) and agricultural (B) landscapes illustrating the likely pathways for subsidy dispersal and consumption, based partly on results of this study.

5 Conclusions and future research

This thesis shows how land use can affect habitats, organisms, and their interactions on multiple scales and specifically the strong impact of anthropogenic degradation in riparian boundaries on exchanges of resource subsidies between terrestrial and stream habitats. I found that agricultural activities can result in increased subsidies to terrestrial habitats as a result of high in-stream production, but that riparian alterations associated with agriculture may decrease the potential to efficiently transfer this production as subsidies into terrestrial environments. Theoretical studies of spatial subsidies have proposed that energy generally flows from more to less productive habitats (e.g., Huxel & McCann, 1998) where the quality and quantity of the subsidy will set the capacity of that subsidy to affect a recipient ecosystem. However, biological effects of subsidies will likely depend upon the nature of the recipient habitat and biota such as foraging behavior, life history, numerical vs. behavioral responses (e.g., Takimoto et al., 2009). Importantly, I found that the strongest effects did not occur in systems of highest contrasting productivity due to land use alterations in the recipient riparian habitat and biota. This emphasizes the importance of considering the ability of the recipient habitat to absorb potential subsidies when modelling resource flows.

Assuming that higher consumer densities equate to increased subsidy incorporation, the findings of this thesis suggest that transfers of aquatic resources to epigeal arthropods are relatively efficient along streams in forested compared to agricultural catchments. It is possible that any reduction in subsidy consumption by epigeal consumers at the agricultural sites might be compensated by other consumers not studied here. Nevertheless, production of the subsidy during summer at agricultural sites was so high that reduced absorption by epigeal consumers will very likely leave significant fractions unutilized. Considering that aquatic systems supply terrestrial systems with lipids essential for maintaining faunal life, and that subsidies into terrestrial ecosystems can be more than three times higher in lotic compared to lentic

systems (Gratton & Vander Zanden, 2009), inefficient transfers might negatively impact terrestrial food webs through losses of essential nutrients (Poulin et al., 2010). The magnitude of consequences of altered subsidy flows into terrestrial habitats has only begun to be realized; however the value of maintaining intact riparian habitats becomes clear when considering the prevalence of streams in agricultural landscapes.

Changes in subsidy deliveries and consumer assemblages revealed in this thesis likely interact altering the pathways aquatic subsidies enter the terrestrial food web. Ecologically intact riparian areas are dynamic ecotones of certain arthropod fauna associated with specific requirements. These requirements may include particular aquatic insect subsidy deliveries in relation to their life histories. However, it is still largely unknown how the assimilation of subsidies differs among species and with life histories. Future studies that address spatiotemporal changes in the characteristics (i.e., body size, nutrient content) of subsidy deliveries with consumption rates (i.e., via fatty acid analysis) would provide insight to which species are dependent on certain subsidy inputs and how they contribute to overall subsidy absorption. Such studies are needed as many terrestrial invertebrate fauna specific to riparian habitats are considered as threatened or are red listed in European countries (e.g., Gärdenfors, 2005). Furthermore, while the results from **paper I** suggest benthic invertebrates were relatively poor indicators of agricultural perturbation in my study streams, results of agricultural effects on riparian arthropods in **paper IV**, particularly staphylinid beetles, indicates their value as sensitive indicators of the ecological effects of riparian alterations. Other studies have suggested the use of riparian spiders and staphylinid beetles as indicators of flow regulation and river channelization (e.g., Paetzold 2008), and Jähnig et al. (2009) found ground beetle assemblages responded more strongly to restoration than aquatic benthic invertebrates.

As agricultural land use increases, an understanding of how to maintain and manage riparian habitats and their adjacent upland habitats for maximal subsidy absorbance capacity becomes more important. In cases where riparian habitats remain intact it may be possible for greater proportions of the aquatic insect subsidy to be absorbed. A useful goal of management might be to increase the quality of the riparian zone itself for terrestrial consumers, as well as to facilitate a more even dispersal of the subsidy across agricultural landscapes (i.e., by providing wind breaks and resting points). However, more studies are needed on how uptake of aquatic subsidies differs among taxa to identify keystone consumers, and the specific habitat conditions they require. Furthermore, there is evidence that fragmented habitats generally support fewer species of habitat specialists (Harrison & Bruna, 1999), thus it may be

important to protect sufficiently large patches along a stream for many riparian fauna to persist. Restoring and maintaining riparian zones for efficient resource transfers does not necessitate widespread reforestation, but implies careful consideration of local environments and the potential benefits of these riparian systems with attention to socioeconomic as well as ecological consequences. Certainly prospects for accurately characterizing larger scale nutrient budgets would be enhanced if these transfers, and their ultimate fate, were better understood.

Land use has been largely ignored in studies of aquatic to terrestrial cross-habitat resource exchanges. This thesis illustrates the interdependence of spatial resources and how anthropogenic alterations can disrupt their linkages. This thesis brings attention to the importance of understanding the strength of aquatic-terrestrial linkages and the mechanisms behind them, while further demonstrating that anthropogenic impacts, particularly resulting from agricultural activity may have deeper consequences for aquatic and terrestrial ecosystems than have been previously identified.

References

- Allan, J.D. & Castillo, M.M. (2007). *Stream ecology: structure and function of running waters*. 2. ed. Oxford: Alden Press.
- Allan, J.D. & Flecker, A.S. (1993). Biodiversity conservation in running waters. *Bioscience*, vol. 43, pp. 32-43.
- Antvogel, H. & Bonn, A. (2001). Environmental parameters and microspatial distribution of insects: a case study of carabids in an alluvial forest. *Ecography*, vol. 24, pp. 470-482.
- Arts, M.T., Ackman, R.G. & Holub, B.J. (2001). "Essential fatty acids" in aquatic ecosystems: a crucial link between diet and human health and evolution. *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 58, pp. 122-137.
- Bates, A.J., Sadler, J.P., Perry, J.N. & Fowles, A.P. (2007). The microspatial distribution of beetles (Coleoptera) on exposed riverine sediments (ERS). *European Journal of Entomology*, vol. 104, pp. 479-487.
- Baxter, C.V., Fausch, K.D. & Saunders, W.C. (2005). Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. *Freshwater Biology*, vol. 50, pp. 201-220.
- Bilby, R.E. (1988). Interactions between Aquatic and Terrestrial Systems. In: Raedeke, Kenneth J. (ed.) *Streamside Management: Riparian Wildlife and Forestry Interactions*. University of Washington. College of Forest Resources. Contribution Number 59, pp. 13-29.
- Bultman, T.L. & Uetz, G.W. (1982). Abundance and community structure of forest floor spiders following litter manipulation. *Oecologia*, vol. 55, pp. 34-41.
- Burcher, C. L. & Benfield, E.F. (2007). The land-cover cascade: Relationships coupling land and water. *Ecology*, vol. 88, pp. 228-242.

- Cadenasso, M.L., Pickett, S.T.A., Weathers, K.C. & Jones, C.G. (2003). A framework for a theory of ecological boundaries. *BioScience*, vol. 53, pp. 750–758.
- Chan, E.K.W., Zhang, Y. & Dudgeon, D. (2007). Contribution of adult aquatic insects to riparian prey availability along tropical forest streams. *Marine and Freshwater Research*, vol. 58, pp. 725-732.
- Clarke, K. R. (1993). Nonparametric multivariate analysis of changes in community structure. *Australian Journal of Ecology*, vol. 18, pp. 117-143.
- Collier, K.J., Smith, B.J. & Baillie B.R.(1997). Summer light-trap catches of adult Trichoptera in hill-country catchments of contrasting land use, Waikato, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, vol. 31, pp. 623-634.
- Collier, K.J., & Smith, B.J. (1998). Dispersal of adult caddisflies (Trichoptera) into forests alongside three New Zealand streams. *Hydrobiologia*, vol. 361, pp. 53-65.
- Delettre, Y.R. & Morvan, N. (2000). Dispersal of adult aquatic Chironomidae (Diptera) in agricultural landscapes. *Freshwater Biology*, vol. 44, pp. 399-411.
- Doi, H., Takemon, Y., Ohta, T., Ishida, Y. & Kikuchi, E. (2007). Effects of reach-scale canopy cover on trophic pathways of caddisfly larvae in a Japanese mountain stream. *Marine and Freshwater Research*, vol. 58, pp. 811-817.
- Dolédec, S. & Statzner, B. (2010). Responses of freshwater biota to human disturbances: contribution of J-NABS to developments in ecological integrity assessments. *Journal of the North American Benthological Society*, vol. 29, pp. 286-311.
- Elvang, O. & Madsen, B.L. (1973). Biological studies on *Taeniopteryx nebulosa* Plecoptera with a note on growth. *Entomologiske Meddelelser*, vol. 41, pp. 49-59.
- Eriksson, L., Johansson, E., Kettaneh-Wold, N., Trygg, J., Wikström, C. & Wold, S. (2006). *Multi- and megavariate data analysis. Part I basic principles and applications*. Second revised and enlarged edition. Umetrics AB. Umeå, SE.
- Feminella, J.W. & Hawkins, C.P. (1995). Interactions between stream herbivores and periphyton: A quantitative analysis of past experiments. *Journal of the North American Benthological Society*, vol. 14, pp. 465-509.
- Finn, D.S. & Poff, N.L.O. (2008). Emergence and flight activity of alpine stream insects in two years with contrasting winter snowpack. *Arctic, Antarctic, and Alpine Research*, vol. 40, pp. 638-646.

- Giberson, D.J. & Garnett, H.L. (1996). Species composition, distribution, and summer emergence phenology of stoneflies (Insecta: Plecoptera) from Catamaran Brook, New Brunswick. *Canadian Journal of Zoology*, vol. 74, pp. 1260-1267.
- Gladyshev, M.I., Sushchik, N.N., Makhutova, O.N., Kalacheva, G.S., Kolmakova, A.A., Kravchuk, E.S. & Dubovskaya, O.P. (2009). Efficiency of transfer of essential polyunsaturated fatty acids along trophic chains in aquatic ecosystems. *Doklady Biochemistry and Biophysics*, vol. 426, pp. 158-160.
- Goedkoop, W., Demandt, M. & Ahlgren, G. (2007). Interactions between food quantity and quality (long-chain polyunsaturated fatty acid concentrations) effects on growth and development of *Chironomus riparius*. *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 64, pp. 425-436.
- Gratton, C. & Vander Zanden, M.J. (2009). Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems. *Ecology*, vol. 90, pp. 2689-2699.
- Gregory, S.V., Swanson, F.J., McKee, W.A. & Cummins, K.W. (1991). An Ecosystem Perspective of Riparian Zones. *Bioscience*, vol. 41, pp. 540-551.
- Gunnarsson, B., Nitterus, K. & Wirdenas, P. (2004). Effects of logging residue removal on ground-active beetles in temperate forests. *Forest Ecology and Management*, vol. 201, pp. 229-239.
- Gärdenfors, U. (2005). Rödlistade arter i Sverige 2005 – The 2005 Red List of Swedish Species. ArtDatbanken, SLU, Uppsala. Available on: <<http://www.artdata.slu.se>> [2014-01-15].
- Haapala, A., Muotka, T. & Markkola, A. (2001). Breakdown and macroinvertebrate and fungal colonization of alder, birch, and willow leaves in a boreal forest stream. *Journal of the North American Benthological Society*, vol. 20, pp. 395-407.
- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2011). PAST: Paleontological Statistics software package for education and data analysis. *Palaeontologia Electronica*, vol. 4: 9pp.
- Harper, M.P. & Peckarsky, B.L. (2006). Emergence cues of a mayfly in a high-altitude stream ecosystem: Potential response to climate change. *Ecological Applications*, vol. 16, pp. 612-621.
- Harper, P.P. (1973). Life histories of Nemouridae in Southern Ontario (Plecoptera). *Hydrobiologia*, vol. 41, pp. 309-356.
- Harrison, S. & Bruna, E. (1999). Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography*, vol. 22, pp. 225-232.

- Harrison, S.S.C. & Harris, I.T. (2002). The effects of bankside management on chalk stream invertebrate communities. *Freshwater biology*, vol. 47, pp. 2233-2245.
- Hoffsten, P.O. (2004). Site-occupancy in relation to flight-morphology in caddisflies. *Freshwater Biology*, vol. 49, pp. 810-817.
- Huryn, A.D., Wallace, J.B. & Anderson, N.H. (2008). Habitat, life history, secondary production, and behavioral adaptations of aquatic insects. In: R.W. Merritt, K.W. Cummins & M.B. Berg (Ed.). *An introduction to the aquatic insects of North America*. 4th edition Kendall/Hunt Publishing Company Dubuque, Iowa, pp. 55-103.
- Huxel, G.R. & McCann, K. (1998). Food web stability: The influence of trophic flows across habitats. *American Naturalist*, vol. 152, pp. 460-469.
- Ims, R.A. & Hjernmann, D.Ø. (2001). Condition-dependent dispersal. In: J. Clobert, E. Danchin, A.A. Dhondt and J.D. Nichols: *Dispersal*. Oxford University Press, pp. 203-216.
- Jackson, J.K. & Resh, V.H. (1989). Distribution and abundance of adult aquatic insects in the forest adjacent to a northern California stream. *Environmental Entomology*, vol. 18, pp. 278-283.
- Johnson, R.A. & Wichern, D.W. (1988). *Applied multivariate statistical analysis*. 2nd edition. Prentice-Hall: Englewood Cliffs, New Jersey.
- Johnson, R.K. & Hering, D. (2009). Response of taxonomic groups in streams to gradients in resource and habitat characteristics. *Journal of Applied Ecology*, vol. 46, pp. 175-186.
- Jähnig, S.C., Brunzel, S., Gacek, S., Lorenz, A.W. & Hering, D. (2009). Effects of re-braiding measures on hydromorphology, floodplain vegetation, ground beetles and benthic invertebrates in mountain rivers. *Journal of Applied Ecology*, vol. 46, pp. 406-416.
- Kato, C., Iwata, T. & Wada, E. (2004). Prey use by web-building spiders: stable isotope analysis of trophic flow at a forest-stream ecotone. *Ecological Research*, vol. 19, pp. 633-643.
- Kovats, Z.E., Ciborowski, J.J.H. & Corkum, L.D. (1996). Inland dispersal of adult aquatic insects. *Freshwater Biology*, vol. 36, pp. 265-276.
- Kuusela, K. & Huusko, A. (1996). Post-emergence migration of stoneflies (Plecoptera) into the nearby forest. *Ecological Entomology*, vol. 21, pp. 171-177.
- Lamberti, G.A., Chaloner, D.T. & Hershey, A.E. (2010). Linkages among aquatic ecosystems. *Journal of the North American Benthological Society*, vol. 29, pp. 245-263.

- Lamberti, G.A. & Steinman, A.D. (1997). A comparison of primary production in stream ecosystems. *Journal of the North American Benthological Society*, vol. 16, pp. 95-104.
- Likens, G.E. & Bormann, F.H. (1974). Linkages between terrestrial and aquatic ecosystems. *BioScience*, vol. 24, pp. 447-456.
- Lynch, R.J., Bunn, S.E. & Catterall, C.P. (2002). Adult aquatic insects: Potential contributors to riparian food webs in Australia's wet-dry tropics. *Austral Ecology*, vol. 27, pp. 515-526.
- Malmqvist, B. (2000). How does wing length relate to distribution patterns of stoneflies (Plecoptera) and mayflies (Ephemeroptera)? *Biological conservation*, vol. 93, pp. 271-276.
- Manderbach, R. & Hering, D. (2001). Typology of riparian ground beetle communities (Coleoptera, Carabidae, Bembidion spec.) in Central Europe and adjacent areas. *Archiv Fur Hydrobiologie*, vol. 152, pp. 583-608.
- Marczak, L.B. & Richardson, J.S. (2007). Spiders and subsidies: results from the riparian zone of a coastal temperate rainforest. *Journal of Animal Ecology*, vol. 76, pp. 687-694.
- Marczak, L.B., Hoover, T.M. & Richardson, J.S. (2007a). Trophic interception: how a boundary-foraging organism influences cross-ecosystem fluxes. *Oikos*, vol. 116, pp. 1651-1662.
- Marczak, L.B., Hoover, T.M. & Richardson, J.S. (2007b). Meta-analysis: trophic level, habitat, and productivity shape the food web effects of resource subsidies. *Ecology*, vol. 88, pp. 140-148.
- Marden, J.H. (2000). Variability in the size, composition, and function of insect flight muscles. *Annual Review of Physiology*, vol. 62, pp. 157-178.
- Matern, A., Drees, C., Kleinwächter, M. & Assmann, T. (2007). Habitat modeling for the conservation of the rare ground beetle species *Carabus variolosus* (Coleoptera, Carabidae) in the riparian zones of headwaters. *Biological Conservation*, vol. 136, pp. 618-627.
- Mayntz, D., Raubenheimer, D., Salomon, M., Toft, S. & Simpson, S.J. (2005). Nutrient-specific foraging in invertebrate predators. *Science*, vol. 307, pp. 111-113.
- McKie, B. G. & Malmqvist, B. (2009). Assessing ecosystem functioning in streams affected by forest management: increased leaf decomposition occurs without changes to the composition of benthic assemblages. *Freshwater Biology*, vol. 10, pp. 2086-2100.
- Merritt, R.W., Cummins, K.W. & Berg, M.B. (2008). *An Introduction to the Aquatic Insects of North America*. Dubuque, IA: Kendall-Hunt.

- Moldenke, A.R. & Ver Linden, C. (2007). Effects of clearcutting and riparian buffers on the yield of adult aquatic macroinvertebrates from headwater streams. *Forest Science*, vol. 53, pp. 308-319.
- Moore, R.D., Spittlehouse, D.L. & Story, A. (2005). Riparian microclimate and stream temperature response to forest harvesting: a review. *Journal of the American Water Resources Association*, vol. 41, pp. 813-834.
- Muller-Navarra, D.C., Brett, M.T., Liston, A.M. & Goldman, C.R. (2000). A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. *Nature*, vol. 403, pp. 74-77.
- Nakano, S. & Murakami, M. (2001). Reciprocal subsidies: Dynamic interdependence between terrestrial and aquatic food webs. *Proceedings of the National Academy of Sciences of the United States of America*, vol. 98, pp. 166-170.
- Naiman, R.J. & Decamps, H. (1997). The Ecology of Interfaces: Riparian Zones. *Annual Review of Ecological Systems*, vol. 28, pp. 621-658.
- Nilsson, A. (2005). *Aquatic insects of North Europe: A taxonomic handbook*. Stenstrup, DK: Apollo Books Aps.
- Paetzold, A., Schubert, C.J. & Tockner, K. (2005). Aquatic terrestrial linkages along a braided-river: Riparian arthropods feeding on aquatic insects. *Ecosystems*, vol. 8, pp. 748-759.
- Paetzold, A., Bernet, J.F. & Tockner, K. (2006). Consumer-specific responses to riverine subsidy pulses in a riparian arthropod assemblage. *Freshwater Biology*, vol. 51, pp. 1103-1115.
- Paetzold, A., Yoshimura, C. & Tockner, K. (2008). Riparian arthropod responses to flow regulation and river channelization. *Journal of Applied Ecology*, vol. 45, pp. 894-903.
- Pajunen, T., Haila, Y., Halme, E., Niemelä, J. & Punttila, P. (1995). Ground-dwelling spiders (Arachnida, Araneae) in fragmented old forests and surrounding managed forests in southern Finland. *Ecography*, vol. 18, pp. 62-72.
- Petersen, I., Winterbottom, J.H., Orton, S., Friberg, N., Hildrew, A.G., Spiers, D.C. & Gurney, W.S.C. (1999). Emergence and lateral dispersal of adult Plecoptera and Trichoptera from Broadstone Stream, UK. *Freshwater Biology*, vol. 42, pp. 401-416.
- Petersen, R.C. (1992). The Rce - a Riparian, Channel, and Environmental Inventory for Small Streams in the Agricultural Landscape. *Freshwater Biology*, vol. 27, pp. 295-306.

- Poff, N.L. (1997). Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. *Journal of the North American Benthological Society*, vol. 6, pp. 391-409.
- Poff, N.L., Olden, J.D., Vieira, N.K.M., Finn, D.S., Simmons, M.P. & Kondratieff, B.C. (2006). Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, vol. 25, pp. 730-755.
- Polis, G.A., Anderson, W.B. & Holt, R.D. (1997). Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, vol. 28, pp. 289-316.
- Poulin, B., Lefebvre, G. & Paz, L. (2010). Red flag for green spray: adverse trophic effects of Bt on breeding birds. *Journal of Applied Ecology*, vol. 47, 884-889.
- Quinn, J.M. (2000). Effects of pastoral development. In: Collier, K.J. & Winterbourn, M.J. (eds) *New Zealand stream invertebrates: ecology and implications for management*. New Zealand Limnological Society pp. 208-229.
- Rankin, M.A. & Burchsted, J.C.A. (1992). The cost of migration in insects. *Annual Review of Entomology*, vol. 37, pp. 533-559.
- Rundle, S.D., Bilton, D.T. & Foggo, A. (2007). By wind, wings or water: body size, dispersal and range size in aquatic invertebrates. In: Hildrew, A.G., Raffaelli, D.G. & Edmonds-Brown, R. (eds) *Body size: The structure and function of aquatic ecosystems (Ecological Reviews)*. Cambridge: Cambridge University Press, pp. 186-209.
- Sadler, J.P., Bell, D. & Fowles, A. (2004). The hydroecological controls and conservation value of beetles on exposed riverine sediments in England and Wales. *Biological Conservation*, vol. 118, pp. 41-56.
- SAS Institute Inc. JMP. (2009). In SAS Institute Inc. 2000 Cary, NC: SAS Institute Inc.
- SAS Institute Inc. (2011). Base SAS® 9.3 Procedures Guide. Cary, NC: SAS Institute Inc.
- Sedell, J.R., Steedman, R.J., Regier, H.A. & Gregory, S.V. (1991). Restoration of Human Impacted Land-Water Ecotones. In: Holland, M.M., Risser, P.G., Naiman, R.J. (eds.) *Ecotones: The Role of Landscape Boundaries in the Management and Restoration of Changing Environments*. Chapman and Hall. New York, NY, pp. 110-129.

- Smith, B.J., Collier, K.J., Halliday, N.J. (2002). Composition and flight periodicity of adult caddisflies in New Zealand hill-country catchments of contrasting land use. *New Zealand Journal of Marine and Freshwater Research*, vol. 36, pp. 863-878.
- Sroka, K. & Finch, O.D. (2006). Ground beetle diversity in ancient woodland remnants in north-western Germany (Coleoptera, Carabidae). *Journal of Insect Conservation*, vol. 10, pp. 335-350.
- Suren, A.M. (1991). Bryophytes as invertebrate habitat in 2 New Zealand alpine streams. *Freshwater Biology*, vol. 26, pp. 399-418.
- Sweeny, B.W. (1993). Effects of streamside vegetation on macroinvertebrate communities of White Clay Creek in eastern North-America. *Proceedings of the Academy of Natural Sciences of Philadelphia*, vol. 144, pp. 291-340.
- Svensson, B.W. (1974). Population movements of adult Trichoptera at a south swedish stream. *Oikos*, vol. 25, pp. 157-175.
- Takimoto, G., Iwata, T. & Murakami, M. (2009). Timescale hierarchy determines the indirect effects of fluctuating subsidy inputs on in situ resources. *American Naturalist*, vol. 173, pp. 200-211.
- ter Braak, C.J.F. & Šmilauer, P. (2002). CANOCO Reference Manual and CanoDraw for Windows User's Guide: Software for Canonical Community Ordination (version 4.5). Ithaca, NY, USA (www.canoco.com): Microcomputer Power [2013-01-02].
- Torres-Ruiz, M. & Wehr, J.D. (2010). Changes in the nutritional quality of decaying leaf litter in a stream based on fatty acid content. *Hydrobiologia*, vol. 651, pp. 265-278.
- Townsend, C.R. & Hildrew, A.G. (1994). Species traits in relation to a habitat template for river systems. *Freshwater Biology*, vol. 31, pp. 265-275.
- Uetz, G.W. (1975). Temporal and spatial variation in species-diversity of wandering spiders (Araneae) in deciduous forest litter. *Environmental Entomology*, vol. 4, pp. 719-724.
- Uetz, G.W. (1991). Habitat structure and spider foraging. In Bell, S.A., McCoy, E.D. & Mushinsky, H.R. (Eds.) *Habitat Structure: The Physical Arrangement of Objects in Space*. Chapman & Hall, London, pp. 325-348.
- Ulfstrand, S. (1969). Ephemeroptera and Plecoptera from River Vindela Èlven in Swedish Lapland. *Entomologisk*, vol. 90, pp. 145-165.

- Vannote, R.L., Minshall, G.W., Cummins, K.W., Sedell, J.R. & Cushing, C.E. (1980). River continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences*, vol. 37, pp. 130-137.
- Ward, J.V. (1998). Riverine landscapes: Biodiversity patterns, disturbance regimes, and aquatic conservation. *Biological Conservation* vol. 83, pp. 269-278.
- Wesner, J.S. (2010). Seasonal variation in the trophic structure of a spatial prey subsidy linking aquatic and terrestrial food webs: adult aquatic insects. *Oikos* vol. 119, pp. 170-178.
- Wiens, J.A., Clifford, S. & Gosz, J.R. (1985). Boundary dynamics: a conceptual framework for studying landscape ecosystems. *Oikos* vol. 45, pp. 421-427.
- Wilander, A., Johnson, R.K. & Goedkoop, W. (2003). Riksinventering 2000 - En synoptisk studie av vattenkemi och bottenfauna i svenska sjöar och vattendrag. Institutionen för Miljöanalys, Uppsala, Sweden.
- Winterbourn, M.J., Chadderton, W.L., Entekin, S.A., Tank, J.L. & Harding, J.S. (2007). Distribution and dispersal of adult stream insects in a heterogeneous montane environment. *Fundamental and Applied Limnology/Archiv für Hydrobiologie*, vol. 168, pp. 127-135.

I would like to thank...

Richard Johnson (main supervisor), for giving me the chance to work on such an interesting and challenging project. I was encouraged by your consistent positive attitude and enthusiasm, it really kept me going. I especially appreciate the time we spent working together on manuscripts and that you were always able to answer questions or help me in other ways, even on short notice. Also thanks for funding my trips to conferences, and giving me an opportunity to see my family, I really appreciate it.

Brendan McKie (co-supervisor). I thank you for the immense amount of time you spent with me developing my ideas and how to think better scientifically. Thanks for sharing your expertise of statistics and teaching me how a good paper should be written. I have enjoyed the time we spent, whether it be in the office, the field, or outside of work.

Leonard Sandin (co-supervisor). Although we didn't meet often, your professional comments and input was useful throughout my PhD experience.

Richard Hopkins for your scientific advice, our discussions were very valuable concerning the terrestrial ecology. Also I thank you for putting me in touch with important authorities and lending me the literature material for identifying my arthropods.

David Angeler and Danny Lau, for always taking the time to answer my questions.

Ulf Grandin for teaching me about forestry field techniques and letting me use your books and equipment.

Micke, Oded, Andre and Emma for all your hard work helping me in the field.

Lars Eriksson, Jonas Sandström and Fredrik Olsson, you guys really helped me out with identification of my invertebrate samples.

Annika, Stina, Maria, Hasse and Herman for helping me with all kinds of practical issues.

Steffi, Emma, Karin J., Oded, Kristina and Amélie for being great room mates.

Mark, my uncle, for igniting my enthusiasm for science. I will always remember the good times we spent together.

Greg and Barb, my parents, for your encouragement and support in pursuing my interests.

My amazing Beatka for sticking through it all, I know it wasn't easy! I really appreciate you and all the support you gave to help me complete this thesis.