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Summary of results: Headwater streams (Fig. 1) represent important habitats within forest landscapes, providing multiple ecosystem services (e.g., maintenance of water quality), and contributing to broad-scale patterns of aquatic biodiversity. The ecological characteristics of small woodland streams are closely linked to the terrestrial landscapes they drain, and are known to be sensitive to land use activities, including forest management and other drivers of forest change. In this study, we evaluated the factors that influence **macroinvertebrate biodiversity** and **biofilm activity** among boreal headwater streams draining forests at different stages of ‘post-logging recovery’ – from recently clear-felled stands to older (> 100 year) forests. Our goal was identify key environmental factors that influence variation in these ecological variables among streams draining landscapes that are subject to a history of forestry activities. To

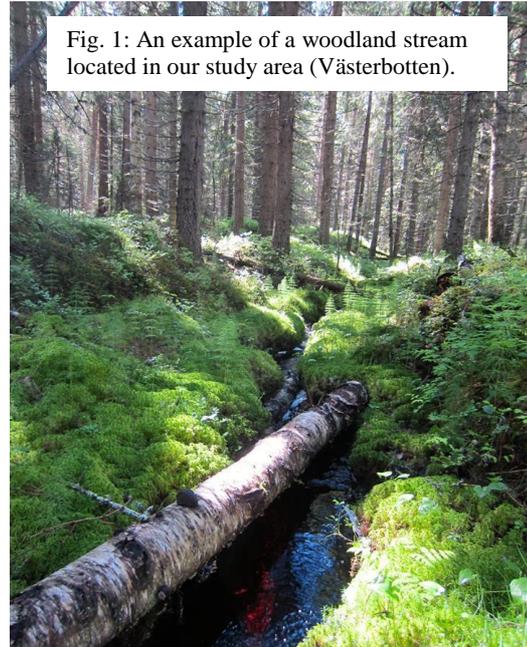


Fig. 1: An example of a woodland stream located in our study area (Västerbotten).

this end, we focused on the potential significance of stream habitat conditions (e.g., temperature, light, and benthic substrate), inorganic nutrient availability, and forest stand age and composition in surrounding catchment and in adjacent riparian zones. Below we provide a summary of the three main components of this project.

1. Benthic algae

While most woodland streams are strongly ‘heterotrophic’, meaning that the bulk of energy available to the ecosystem comes from terrestrial sources (e.g., leaf litter), the growth of benthic algae is known to be disproportionately important to aquatic food webs because it represents a high quality food source to benthic consumers. For this reason, there is much interest in understanding how light, nutrients, flow regimes, and land use interact to govern the production of benthic algae in woodland streams. However, very little is known about the relative importance of these different environmental controls in humic rich, boreal waters. Given this knowledge gap, we measured the accumulation of benthic algae on ceramic tiles placed in 17 streams during the summer of 2103. At the same time, we quantified a suite of habitat variables, including canopy cover, light, temperature, and stream chemistry.

Local riparian vegetation differed among sites from almost entirely open (clear-felled), to stands dominated by early successional birch forests, to those represented by older (100+

years) pine and spruce trees. Canopy cover of channels ranged from 13 to 96% across this gradient of streams and these estimates of cover correlated closely with our direct measurements of incident light reaching benthic surfaces. Variation in incident light in turn influenced the growth of benthic algae during the summer, which differed by more than 20-fold among sites, and was highest for the streams draining the recent clear cut. Light was not the only important determinant, however. A preliminary multiple regression model aimed at predicting benthic algae identified stream inorganic nitrogen (N) concentration (+ relationship), temperature (+), light (+), depth (-), and dissolved organic carbon (-) as key predictors ($r^2 = 0.81$, $p < 0.001$, $n = 45$ tile pairs). Thus, while incident light does influence observed variation in stream algal growth, the availability of key limiting nutrients (inorganic N), as well as other habitat factors (e.g., temperature) act as important constraints. Overall, these results suggest that the short-term effects of clear-felling (e.g., within the first decade), which include both elevated light and higher nutrient availability, will result in greater algal productivity in most cases. However, results also indicate that elevated light conditions are required – but not sufficient to support this autotrophic response. Thus, in the context of forest disturbance and recovery, the duration of elevated nutrient loading from clear-felled lands appears to play a major role in shaping this stream ecosystem response over longer time-scales.

We are currently conducting follow up experiments to more directly evaluate how light and nutrients interact to govern autotrophic production in boreal streams influenced by forestry, and a manuscript on the controls over algal growth in boreal streams will be completed in the autumn of 2014.

2. *Heterotrophic biofilms*

Heterotrophic biofilms, composed of bacteria and fungi developing on rocks, leaves, and wood play critical roles in the ecology and biogeochemistry of stream ecosystems everywhere. There are very few studies of the factors that drive biofilm activity in boreal streams, however, and basic information regarding nutrient limitation and the potential role(s) of landscape structure and vegetation cover remain poorly understood. In the autumn of 2013, we deployed nutrient diffusing substrata (NDS; Fig. 2) to measure the activity associated with stream biofilm communities across the gradient of study sites described above ($n = 20$ sites). Briefly, NDS are constructed using small plastic cups filled with agar that includes nitrogen (N), phosphorus (P), nitrogen and phosphorus in combination (NP), or nothing (as a control). Organic substrate (cellulose) is affixed to the surface of the cups and they are placed in the stream for two weeks, during which nutrients diffuse out of the agar and enrich the biofilm community growing on the overlying cellulose.



Fig. 2: NDS cups ready to deploy at a study site

Cellulose surfaces are then incubated in the laboratory (in the dark) and respiration is measured from the consumption of oxygen.

As was observed with benthic algae, we found that the respiration of stream biofilms differed by as much as 25-fold among sites (comparing rates in ‘control cups’), was highest at the

recently clear-felled site, and increased among the 20 streams with background concentrations of inorganic nitrogen. Furthermore, experimental enrichment of biofilms with N resulted in significantly greater rates of respiration relative to controls. In contrast, P addition alone had no significant effects on microbial activity. Overall these results point to strong N limitation of boreal stream biofilm communities (Fig. 3a). In addition to respiration, we analyzed NDS surfaces for phospholipid fatty acids (PLFA), which provide information about the composition of microbial communities present and serve as a proxy for total microbial biomass. As observed with respiration, PLFA biomass was greater for NDS cups receiving N enrichment. However, unlike the respiration results, the highest levels of biomass were observed when N and P were added together (suggesting co-limitation, Fig 3b). The subtle differences in the respiratory versus biomass responses to experimental nutrient addition suggest variation in biofilm growth efficiency and energy allocation (e.g., investment into growth vs. exoenzyme production) when N is enriched alone or in combination with P. **Current and future experiments are seeking to better understand the microbial mechanisms and stoichiometric constraints that underlie these dynamics at the base of boreal stream food webs.**

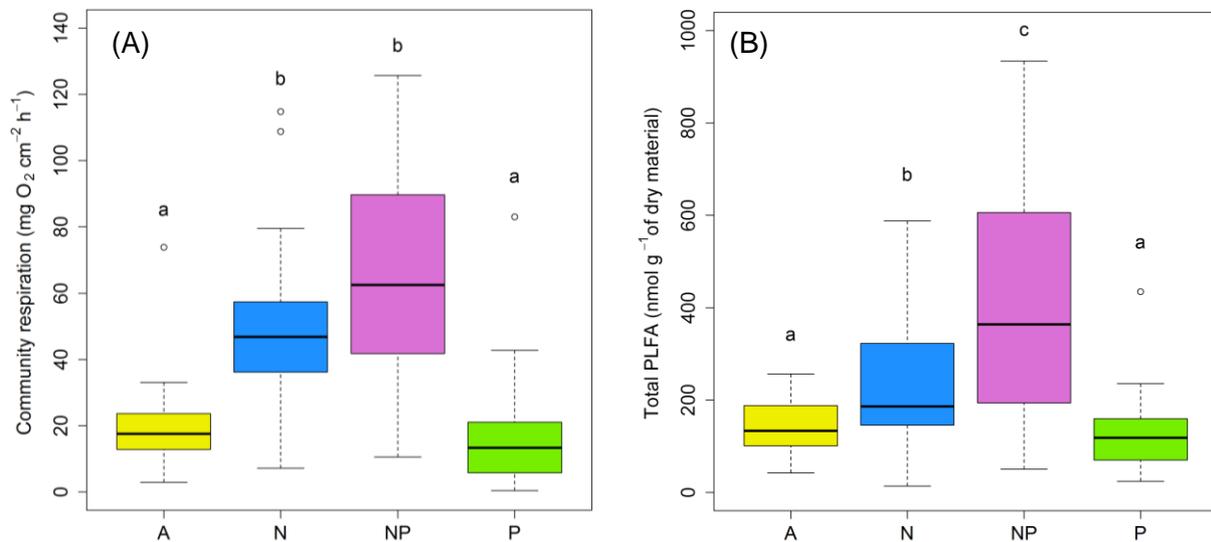


Fig. 3: Biofilm respiration (A) and phospholipid fatty acid biomass (B) for NDS cups following a three-week incubation in 20 headwater streams located in northern Sweden. Box-plots show the distribution of respiration and biomass for control cups (agar only, A), as well as cups receiving nitrogen (N), phosphorus (P), and nitrogen and phosphorus together (NP). Boxes with shared overlying letters are not significantly different ($p > 0.05$).

3. Macroinvertebrate communities

We sampled benthic macroinvertebrates and associated physical, chemical, and biological habitat variables at 18 streams in the fall of 2013 (Fig 4). Invertebrate richness varied among sites from 12 to 38 taxa. For most sites, benthic communities were numerically dominated by **Dipteran** larvae (families Simuliidae and Chironomidae); **Plecopteran** larvae from the family Nemouridae were the next most abundant group. The clear-felled catchment had fairly low taxonomic richness (only 15 taxa), yet the highest overall invertebrate abundance.

Overall, results suggest that forest clear-felling and recovery may induce changes in the composition and biodiversity of macroinvertebrate communities, but that other aspects of stream habitat and landscape structure are important as well. More specifically, preliminary results indicate significant positive correlations between taxonomic richness and water depth (Spearman $r = +0.62$, $p = 0.005$, $n = 18$) and catchment area ($r = +0.69$, $p = 0.001$), indicating that even small changes in stream size influence local community composition. In addition, several physical and chemical habitat variables were correlated with variation in taxonomic richness among sites, including average substrate size ($r = +0.53$, $p = 0.02$) and pH ($r = +0.60$, $p = 0.007$), which are both key variables known to influence the structure of stream communities.



Fig. 4: Students sampling stream invertebrates at one the study sites

Finally, preliminary results do suggest that variation in macroinvertebrate richness among sites may be related to changes in the age distribution of forests in the surrounding catchments. For example, taxonomic richness tended to increase among sites with greater coverage by forest stands within 5-10 and 11-50 year old age classes (Spearman $r = +0.46$, $p = 0.05$ and $r = +0.58$, $p = 0.01$, respectively). At the same time, richness tended to decline among sites with greater coverage of the oldest forest age class (101 – 300 year old stands; $r = -0.69$, $p = 0.001$). It is important to note that the potential causal mechanisms underlying relationships between taxonomic richness and forest age are not yet clear. Such correlations need to be interpreted with caution, and could indeed be spurious.

Current multivariate and multiple regression analyses are seeking to better understand and resolve how long-term changes in forest composition interact with other drainage characteristics and habitats features to influence patterns of macroinvertebrate richness, community composition, and distribution of key life history traits.

Communication: Results from this research project have been presented 1) as part of an undergraduate thesis project at Umeå University (Johan Lidman, 2012) and 2) at two major international conferences (Society for Freshwater Sciences and the Joint Aquatic Sciences Meeting). We are currently finalizing data analysis and are working on three manuscripts that will address: 1) patterns of invertebrate biodiversity, 2) the controls over benthic algal growth, 3) the factor that govern heterotrophic biofilms development. The current hope is to submit these manuscripts for peer review in 2014.

Citations:

1. Lidman, J. *Hur påverkas bentiska funktionella födogrupper av kalavverkning? Effekt på abundans, samt återhämtning, av funktionella födogrupper efter kalavverkning kring små vattendrag. Examensarbete i Biologi*, 15 hp, institutionen för Ekologi, miljö och geovetenskap, Umeå universitet. Rapporten godkänd 2012-11-06.
2. Jonsson, M., Sponseller, R.A., and Laudon, H. *Long-term recovery patterns of headwater stream macroinvertebrate communities following clearcutting -*

substituting space for time. **Society for Freshwater Science (SFS) Annual Meeting**, May 19-23 2013, Jacksonville, Florida, USA

3. Burrows, R.M., Hotchkiss, E. R., Jonsson, M., Laudon, H., McKie, B. G., Sponseller, R. A. 2014. *Heterotrophic biofilms in boreal streams exhibit strong nitrogen limitation during autumn.* **Joint Aquatic Sciences Meeting (JASM)**, 18-23 May, Portland, Oregon USA.

Manuscripts in preparation

1. Jonsson, M., Burrows, R.M., Laudon, H., and Sponseller, R.S. Effects of forest management on macroinvertebrate biodiversity in boreal headwater streams.
2. Sponseller, R.A., R.M. Burrows, E. Fältström, J. Andersson, and M. Jonsson. Light availability, nutrient limitation, and patterns of periphyton growth in boreal streams.
3. Burrows, R.M., Hotchkiss, E. R., Jonsson, M., Laudon, H., McKie, B. G., Sponseller, R. A. Nutrient limitation of heterotrophic biofilms in boreal headwater streams.

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