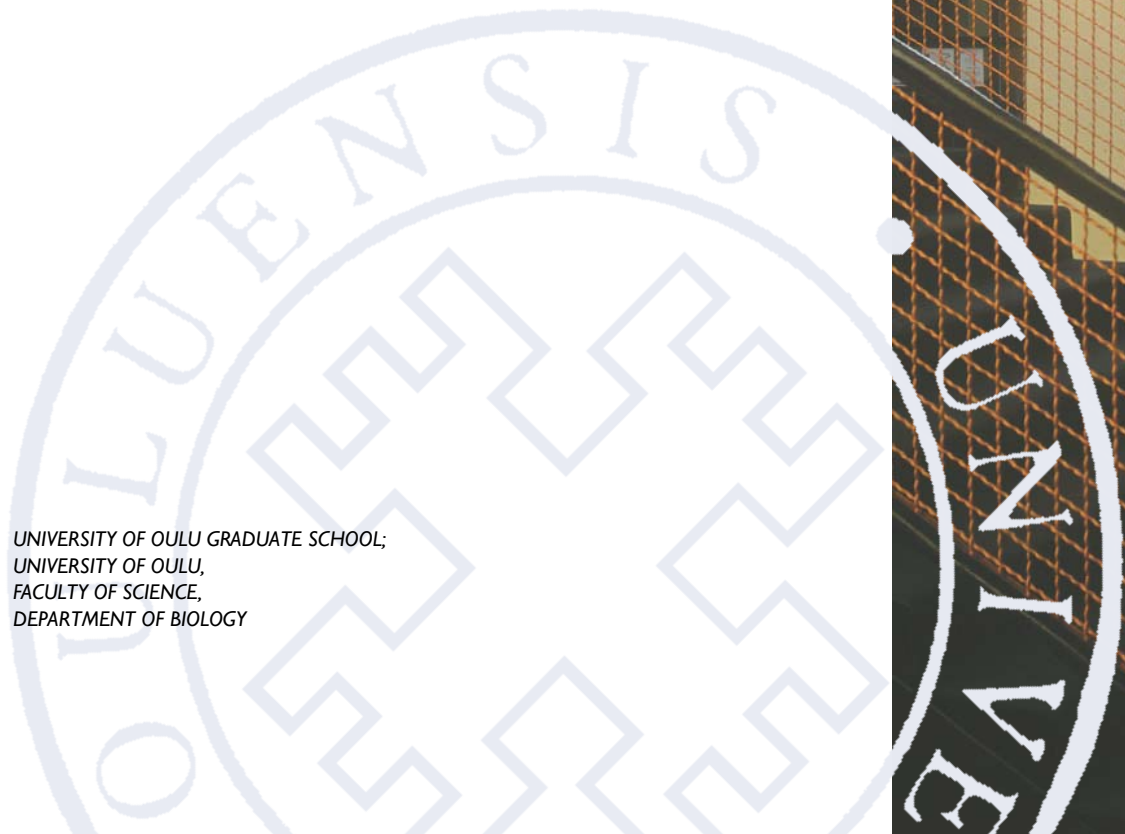*ACTA*

Heli Suurkuukka

SPATIAL AND TEMPORAL VARIABILITY OF FRESHWATER BIODIVERSITY IN NATURAL AND MODIFIED FORESTED LANDSCAPES

UNIVERSITY OF OULU GRADUATE SCHOOL;
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Abstract

Understanding of natural and human induced changes to freshwater biodiversity patterns is critical for efficiently conserving and managing these highly impacted ecosystems. In this doctoral thesis, I study the natural spatial and temporal variability of littoral macroinvertebrate communities, as well as aquatic biodiversity responses (of bryophytes, macroinvertebrates and diatoms) to human impact on forested headwater streams. I also study the temporal variability of natural and human-impacted stream communities. I show that littoral macroinvertebrate communities are most variable between individual samples and to some extent between littorals, and that the diversity patterns of rare and common littoral macroinvertebrates vary at different spatial scales. Temporal (interannual) variability is of minor importance, particularly for the core species of the community. For rare species, however, the temporal component was generally more important than spatial turnover. For headwater streams, I show that most taxonomic groups responded negatively to human impact on the adjacent riparian forest. Nevertheless, pristine riparian forest is not a sufficient surrogate for stream biodiversity as also streams with relatively disturbed riparian forests supported diverse benthic communities. A rapid classification method based on the physical structure of the stream channel and its riparian forest is able to identify the reference-state communities, as well as the most severely altered communities, but a reliable identification of the intermediately-disturbed sites would need more precise information about the key stressors of stream communities. I found that fine sediments originating from forest drainage were the main factor causing reduction of stream biodiversity. I also found that forestry impacted streams varied temporally more than pristine streams, emphasizing the importance of interannual sampling of impacted streams for a reliable status assessment.

Suurkuukka, Heli, Pienvesien biodiversiteetin ajallinen ja paikallinen vaihtelu luonnontilaisessa ja ihmisvaikutteisessa metsämaisemassa.
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Tiivistelmä

Luonnollisen ja ihmisen aiheuttaman biodiversiteettivaihtelun ymmärtäminen hoito- ja suojelutoimissa on tärkeää pienvesien monimuotoisuuden turvaamiseksi. Tarkastelen väitöskirjassani järvien rantavyöhykkeen pohjaeläinten ajallista ja paikallista vaihtelua sekä latvapurojen eliöyhteisöjen (pohjaeläimet, sammalet, piilevät) vasteita ihmisen aiheuttamaan fysikaaliseen muutokseen rantametsässä ja purouomassa. Tarkastelen myös ajallisen vaihtelun eroja luonnontilaisten ja ihmisvaikutteisten latvapurojen eliöyhteisöjen välillä. Osoitan, että järven rantavyöhykkeen pohjaeläinyhteisöt vaihtelevat eniten yksittäisten näytteiden välillä ja pienessä määrin eri rantojen välillä, mutta ajallinen vaihtelu ei heikennä tulosten luotettavuutta muiden kuin harvinaisten lajien osalta yhteen vuoteen rajoittuvassa näytteenotossa. Purotutkimuksissa osoitan, että useiden vesieliöryhmien lajirunsaus muuttuu ihmisen aiheuttaman rantametsän muutoksen seurauksena, mutta luonnontilaista rantametsää ei silti voida pitää yksiselitteisesti myös puron suojelutason mittarina, koska se ei välttämättä turvaa eliöiden lajistollista eheyttä suhteessa alkuperäiseen alueelliseen lajistoon. Rantametsän ja uoman fysikaalisiin rakennepiirteisiin perustuvaa nopeaa luokittelumenetelmää voidaan käyttää eliöyhteisöltään monimuotoisimpien ja metsätalouden voimakkaimmin rasittamien purojen tunnistamisessa. Eliöyhteisöltään lievemmin muutettujen purojen luotettavaan erotteluun luokittelun pitäisi kuitenkin sisältää tarkempaa tietoa metsäojitusten aiheuttamasta liettymisestä, joka on tulosteni perusteella haitallisin metsätaloudesta johtuva puroyhteisöjä rasittava tekijä. Havaitsin myös metsätalouden rasittamien purojen tilanarvioinnin toistettavuuden olevan luonnontilaisia puroja heikompaa, joten metsätalouden rasittamien purojen pidempiaikainen seuraaminen tuntuu välttämättömältä luotettavien tilanarvioiden tuottamiseksi.

Asiasanat: ajallinen mittakaava, betadiversiteetti, biodiversiteetti, järvet, lajirunsaus, piilevät, pohjaeläimet, purot, spatiaalinen mittakaava, vesisammalet

To River Iijoki

Acknowledgements

Abbreviations

ANOVA	Analysis of variance
CAL	calibration
CV	conservation value
RCA	Reference Condition Approach
REF	reference
RIVPACS	River InVertebrate Prediction And Classification System
VLD	validation
WKH	Woodland key habitat

List of original articles

This thesis is based on the following publications, which are referred throughout the text by their Roman numerals:

I   Suurkuukka H, Meissner K & Muotka T (2012) Species turnover in lake littorals: spatial and temporal variation of benthic macroinvertebrate diversity and community composition. Diversity and Distributions 18: 931–941.
II   Suurkuukka H, Virtanen R, Suorsa V, Soininen J, Paasivirta L & Muotka T (2013) Woodland key habitats and stream biodiversity: Does small-scale terrestrial conservation enhance the protection of stream biota? Biological Conservation 170: 10–19.
III Jyväsjärvi J, Suurkuukka H, Virtanen R, Aroviita J & Muotka T (2014) Does the taxonomic completeness of headwater stream assemblages reflect the conservation status of the riparian forest? Forest Ecology and Management 334: 293–300.

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1   Introduction

Freshwater biodiversity is globally threatened, with the trend of biodiversity loss exceeding that in most other ecosystems (Sala *et al*. 2000, Dudgeon *et al*. 2006). Situation in Finland is no different from the global trend. For example, more than 40% of freshwater fishes in Finland are red-listed (Urho *et al*. 2010) and 68% of freshwater habitats in Southern Finland are endangered (Ilmonen *et al*. 2008). The main causes of freshwater species loss are pollution, construction, land use and overexploitation of species and resources, (Abell 2002, Ilmonen *et al*. 2008), and these factors have potentially severe consequences by altering ecosystem functioning. Diminishing resistance and resilience of communities to disturbances such as extreme climate events, and loss of ecological integrity impair also the ecosystem services that freshwaters provide for people. Because of this, a profound understanding of biodiversity patterns is critical for preventing additional biodiversity loss and also to efficiently conserve and manage current freshwater biodiversity. It is of particular importance to know how biodiversity within a region is structured, and what the appropriate spatial and temporal boundaries for conservation as well as for studying the mechanisms that cause the observed diversity patterns are (Zvuloni *et al*. 2010).

Aquatic ecosystems exhibit strong natural fluctuation in environmental conditions at multiple spatial and temporal scales (Allen & Starr 1982). Spatial patterns of freshwater biodiversity such as the species-area relationship (e.g. Rosenweig 1995), relationship between local and regional biodiversity (e.g. Cornell & Lawton 1992, Stendera & Johnson 2005), and the underlying environmental determinants (e.g. Sandin 2003, Mykrä *et al*. 2007) have been studied increasingly during the last two decades, especially in lotic habitats. Variation of freshwater macroinvertebrate communities at the smallest study scales (among and within riffles/littorals) relate to habitat heterogeneity (e.g. Johnson & Goedkoop 2002) and biotic interactions (e.g. Downes *et al*. 1995). The structure of fish communities has been shown to be more dependent on the interaction between flow regime and local geology that define many key abiotic factors (Poff & Allan 1995), whereas diatom (see Soininen 2007) and macrophyte (Paavola *et al*. 2006) communities are largely shaped by chemical properties of the water. Natural variation of freshwater communities at larger scales (i.e. among waterways/regions) is generally associated with geographical position (Mykrä *et al*. 2007, Astorga *et al*. 2011), geology (Richards *et al*. 1997), catchment size (Astorga *et al*. 2011) and dispersal limitation (Astorga *et al*. 2012). On larger

geographic scales, regional factors increase in importance, but habitat and ecosystem-level factors often explain more of the among-site variation in freshwater communities (e.g. Heino *et al.* 2004, Johnson *et al.* 2004). Since so many simultaneous local, regional and historical factors define the habitat conditions determining biological communities (Hildrew & Giller 1994, Poff 1997), observations made at one place or time cannot be readily extrapolated to other scales. Biodiversity patterns may vary also between different freshwater systems (e.g. lakes vs. streams) and thus biodiversity patterns should be studied at multiple freshwater systems across multiple spatial (and temporal) scales.

Despite increasing consensus about investigating ecological patterns and processes at multiple spatial scales, the temporal component of freshwater diversity variation, and its interaction with spatial variation, has remained much less studied (but see Erös & Schmera 2010). This is so even though studies that partition diversity in both space and time would clearly be of high importance to landscape-level management of biodiversity (Magurran *et al.* 2010). A temporally too restricted sampling scale may cause a serious underestimation of freshwater diversity, to the extent of compromising assessment results (Huttunen *et al.* 2012) or any comparison of diversity among sites and habitats (Tylianakis *et al.* 2005). Biodiversity sampling in freshwaters often contains no temporal replication but is conducted over short time-scales. Lack of temporal replication in freshwater systems prone to natural climatic disturbances is particularly disturbing, since it is known that climatic events is one of the main causes of temporal variation in freshwater communities (see Jackson & Füreder 2006 for a review). Moreover, the majority of studies dealing with temporal patterns in running water habitats (e.g. Linke *et al.* 1999, Scarsbrook 2002, Mykrä *et al.* 2012) have focused on only natural biodiversity patterns under pristine environmental conditions while it has been suggested that human-impacted streams may exhibit more inter-annual variability than corresponding pristine streams (see Feio *et al.* 2010).

Many studies have stressed the negative impacts of human induced landscape-scale disturbances on freshwater biodiversity, with a strong focus on benthic macroinvertebrates or fish as the target organism groups (see Allan 2004 for a review). However, few studies have assessed comprehensively the importance of intact riparian forests to wholesale freshwater biodiversity with an effort to identify the most important stressors of the human impact gradient (but see Herbert *et al.* 2010, Sandin 2009). This is so even though riparian forests are generally considered as hot spots of biodiversity and key areas for biodiversity conservation (e.g. Naiman *et al.* 2005). Benefits of terrestrial conservation for

freshwater biodiversity have thus rather been assumed than directly tested for, or have been studied only with a few taxonomic groups.

The two aquatic habitats studied in this thesis, littoral zones of lakes and headwater streams, are characterized by both predictable (snowmelt-induced spring floods) and unpredictable natural disturbances by water level changes, discharge variability and ice dynamics. Their communities differ from larger rivers and lake pelagic areas by their close linkage to terrestrial surroundings. Because of this linkage, headwaters are more prone to land use effects than larger rivers are (Naiman *et al*. 2005). Freshwater bioassessment has been traditionally biased towards large rivers and profundal communities of lakes, while small streams and littorals of lakes have received much less attention. Recently, however, the use of littoral macroinvertebrates in biodiversity surveys and monitoring programs has been increasing (Aroviita & Hämäläinen 2008), and, at the same time, headwater streams have become one of the focus habitats in forest biodiversity conservation (Richardson *et al*. 2010, Timonen *et al*. 2010).

Despite the interest towards headwater streams and lake littorals has increased, studies dealing with spatial and temporal variability of communities in lake littorals (pristine or not) are still relatively rare. The lack of a thorough understanding of the importance of pristine riparian setting to freshwater communities hinders assessment, management and protection of these environments. Freshwater bioassessment has also generally focused on dominant taxa because they are believed to carry the key information about community patterns, whereas rare taxa may not provide a sufficiently strong signal of environmental degradation (e.g. Marchant 2002). In assessing conservation value or wholesale biodiversity, the interest is, by contrast, in total species richness, and particularly in rare and red-listed species. Thus it seems feasible that both dominant and rare species have their place in freshwater assessment and conservation but their distributional patterns and species-environment relationships in lake littorals and headwater streams is poorly known.

2 Aims of the study

The overall objective of this thesis was to study natural and human induced biodiversity variation in communities of two freshwater habitats. The subprojects included several questions with the aim of benefiting forest and freshwater managers and conservation biologists in their work.

Firstly, we assessed spatial and temporal variation of littoral benthic macroinvertebrate diversity and community composition in the absence of human impact (I). We studied whether diversity is mainly generated at the finest sampling scales, that is, individual samples or littorals; or at the scale of different lakes; or whether the interannual dimension is the most important one. We also tested whether rare and dominant taxa exhibit different scale dependent patterns of diversity variation. The outcome is especially important for freshwater assessment, which is usually based on a limited amount of samples and sampling occasions.

Secondly, we studied aquatic biodiversity responses to human impact in forested headwater streams (II, III). We assessed whether total species richness, Shannon diversity and richness of red-listed species of benthic diatoms, bryophytes and macroinvertebrates reflect the gradient of human induced degradation of the riparian forest (II). We also examined whether community composition of each of the three taxonomic groups shows differentiation along the degradation gradient (II) and whether taxonomic completeness (occurrence of native biota) of headwater streams is able to detect different levels of forestry-related human impairment (III). One goal of these subprojects was to test how well a rapid classification method based on the physical structure of the stream channel and its riparian forest mirrors the gradient of forestry-induced habitat degradation and could it thus serve as an environmental surrogate in freshwater conservation prioritization.

Thirdly, we assessed the temporal variation in biodiversity of natural and human impacted stream communities (III) by comparing taxonomic completeness (observed/expected no. of species) of pristine and slightly modified sites. The applied goal was to reveal whether assessment results of small headwaters are consistent through time.

3 Materials and methods

3.1 Study areas

The study was conducted in southern Finland (62° N, 26° E) in three small (< 5 km^2), near-pristine and humic (78– 102 mg Pt l -1) lakes: Ahveninen (Lake 1), Mehtiö (Lake 2) and Pieni-Myhi (Lake 3, Fig 1A). These lakes belong to the same lake type (Finnish lake typology, Vuori *et al*. 2006) and are little impacted by human activities, thus representing natural variation of the reference condition of the small humic lake type.

The effects of human impact on streams (II, III test sites) were studied in the headwaters of River Iijoki (65°200 –65°800 N, 27°080 –28°600 E, Fig 1B). The majority of the River Iijoki catchment is characterized by mixed forests, peatlands and fine-sediment plains. Intensity of land use varies substantially in different parts of the catchment. Remote and inaccessible areas have been left aside of silviculture and 2% of the catchment has been protected as national park, whereas most of the commercial forests on peatlands have been heavily drained by ditching to support forest growth (Korhonen *et al*. 2013). Streams of the study area were classified by the Finnish Forest and Park Services (Metsähallitus) in 1998–2003 to five status classes reflecting the naturalness of the stream channel and the riparian forest. The classification consisted of nearly 2400 sections (200– 1000 m in length) in 257 streams (Hyvönen *et al*. 2005). The classification method is based on six habitat features describing the physical structure of the stream channel and the adjacent riparian forest. Each factor is scored from zero (complete alteration) to five (no human impact) and the overall status class of a site is calculated as the mean of the scores of each of the six factors (rounded to nearest integer). Sites in the severely modified class 1 have been heavily subjected to forest management actions, particularly peatland drainage. Drainage intensity (kilometres of ditches draining into a 500 m long and 25 m wide buffer upstream of a site) in our study sites was highest in the modified class 1 and lowest in the pristine class 5 (GIS-data derived from the Topographical database of National Land Survey of Finland, 2009). Site status improves progressively towards class 5, which consists of unmodified (or nearly so) streams and their riparian forests. A stratified random protocol was used to select 50 independent study reaches (ten replicates in each class of naturalness) (II). In paper III, these sites were further divided into three classes; class 1 (consisting original classes 1

and 2), class 2 (equaling class 3) and class 3 (consisting original classes 4 and 5) and used as test sites in predictive modeling. Four sites representing each of the status classes 2 and 3 were also selected for inter-annual monitoring. The reference (hereafter REF) data in paper III compiled 84 near-pristine streams across northern Finland.
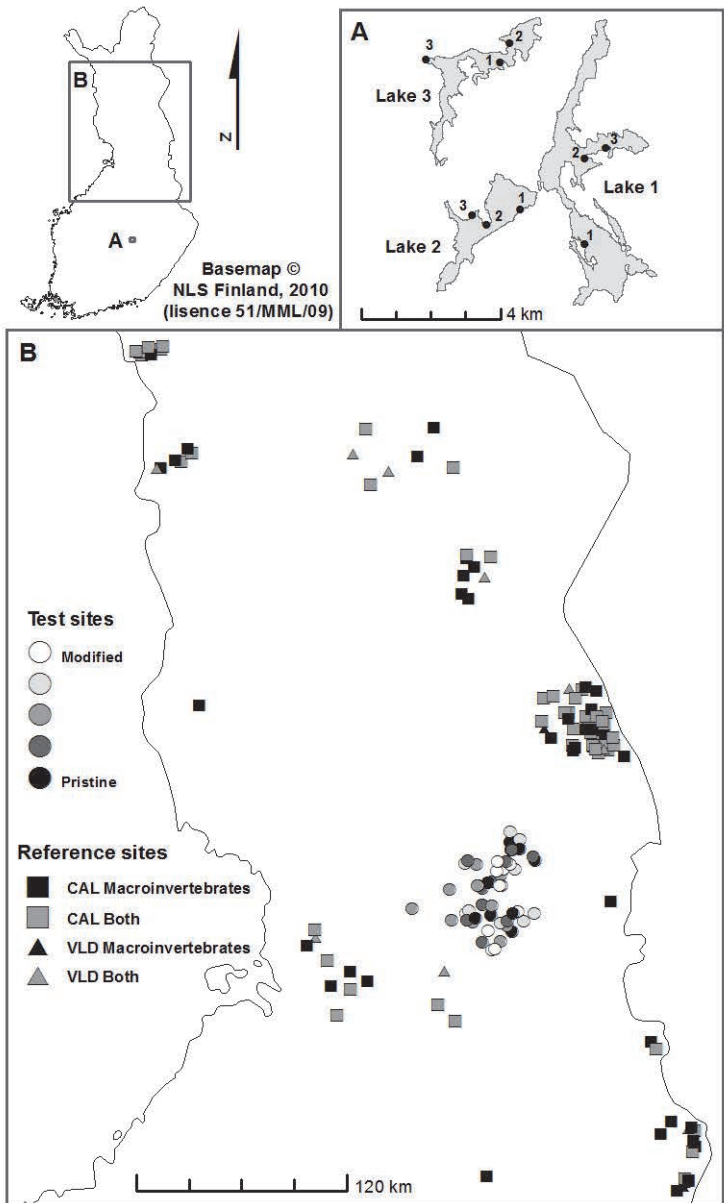
Fig. 1. Location of study sites of article I (A), II and III (B). CAL and VLD in figure B refer to calibration and validation sites, respectively. Black symbols refer to sites where only macroinvertebrate data were available and grey symbols to sites where both macroinvertebrate and bryophyte data were available.

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3.2   Species data

In paper I, species data were obtained by sampling littoral macroinvertebrate communities in each study lake in early September 2005, 2006 and 2007. We collected ten kick samples (hand net 30 x 25 cm, mesh size 0.5 mm) at each site, and three 15–20 m long stony littoral sites were sampled in each lake following the national standard (SFS-EN 28265).

In papers II and III (for the test sites only), biological sampling was conducted between early July and the beginning of September, 40 sites being sampled in 2006 and ten sites in 2007. All classes of naturalness were equally represented in both years. Bryophytes were sampled using ten 0.5 x 0.5 m plots placed across the study section. We estimated the percentage cover of each species in a plot, and the mean cover of a species per site was used in data analyses. After quantitative sampling, a thorough search was conducted to detect rare species not included in the regular plots. These species were given the percentage coverage of 0.1% at the site level.

Diatoms were sampled by randomly picking ten cobble-sized stones at each site. The top surface of a stone was brushed using a template (3 cm x 3 cm) and the ten samples were then pooled to form a composite sample for a site. In the laboratory, samples were cleaned from organic material using wet combustion with hydrogen peroxide, and were then mounted in Naphrax. A total of 500 frustules per sample were identified to species level according to Krammer & Lange-Bertalot (1986–1991) and Lange-Bertalot & Metzeltin (1996) using phase contrast light microscope. Frustules that could not be identified to species level and species with inconsistent identifications (usually <0.5% of total count) were excluded from all analyses.

Macroinvertebrates were sampled in autumn when most aquatic species in boreal streams are in their larval stage (see Nilsson 1996). We took a 2-min kick sample (mesh size 300 μm) at each site, consisting of four 30-s subsamples, aiming to cover most benthic microhabitats present in a riffle section. Samples were preserved in 70% ethanol in the field and identified later in the laboratory, usually to species or genus level. Eight sites selected for inter-annual monitoring were sampled in 2006–2011 (from late September to early October each year) for macroinvertebrates and bryophytes using the same methods as above.

In paper III, the REF data set consisted of macroinvertebrate and bryophyte data sampled between 1992 and 2010 by our research group, Finnish Environment Institute or regional environmental centres. The sampling

procedures of these data complied with those of the test sites. Macroinvertebrate data included 84 REF sites. Bryophyte data were only available for 58 REF sites (Fig 1).

3.3 Environmental data

In paper I, depth and percentage of each particle size (modified Wentworth scale, from 0 = sand to 6 = bedrock) were measured for each sample. Water chemistry variables and catchment land use variables were obtained from the national database OIVA (OIVA 2010).

In paper II, riparian variables included riparian integrity (% riparian zone without human impact), amount of dead wood, number of stumps and riparian tree species composition. All variables were assessed on both sides along the 50-m study reach. The maximum and mean tree heights (roughly corresponding to forest age; e.g. Hökkä & Ojansuu, 2004) were measured with a laser rangefinder (Optilogic 400LH, Tullahoma). Basal area of the tree stand was measured with a relascope as a cross-section area (m^2) of trees at breast height per hectare. In-stream variables in paper II were measured from ten evenly spaced cross-channel transects covering the whole 50-m study site. Depth and current velocity were measured at three locations in each transect, one measurement being taken at the centre of a transect, the other two at 0.25 and 0.75 x the width of the transect. Substratum size was determined as the weighted average of different particle size classes in ten 1-m^2 plots using modified Wentworth scale. Substratum diversity (Simpson diversity index) as well as coefficients of variation for depth and current velocity were used to describe in-stream habitat heterogeneity. Stream slope (cm m^{-1}) was measured using a carpenter's level. The amount of dead wood in the stream channel was quantified by measuring the length and average diameter of each wood particle at least 5 cm in diameter that reached the wetted width of the study site. Water samples were collected simultaneously with macroinvertebrates, and were analysed for pH, conductivity, total phosphorus and colour following national standards (National Board of Waters 1981). Water temperature was measured two to four times during the summer, but because all measurements were strongly correlated, we only used August water temperature which best distinguished between the sites. Channel width was measured in five cross-stream transects. Shading by overhanging vegetation (% canopy cover) was measured with densiometer at 20 locations in evenly spaced cross-channel transects covering the whole study section.

Various environmental variables used for calibrating the predictive models in paper III (geographical position, catchment size, land use and surface geology) were obtained with GIS by using ArcMap 10 Desktop (ESRI 2011) (see Appendix Table 1 for list of variables and source databases). Water pH, conductivity, colour, total phosphorus, riparian disturbance, average tree height and substratum size used for evaluating the relationship between taxonomic completeness and environmental integrity of test sites were obtained from paper II. We also used GIS to evaluate drainage intensity for each site as the overall density of ditches (km km^{-2}) in the upstream catchment and the number of ditches flowing directly into the stream in a 1500-m section upstream of a site.

3.4 Statistical analysis

Biodiversity, here defined as 'variety and abundance of species in a defined unit of study' (Magurran 2004), can be measured in many different ways depending on the perspective of a study. While α diversity measures (e.g. species richness, Simpsons diversity and evenness) emphasise diversity in a defined community or habitat, β diversity stresses the degree to which the diversity of two or more study units differ (Magurran 2004). β diversity measures can be further divided by their use. Here we first measured β diversity in littoral macroinvertebrate communities (paper I) by examining the extent of the difference between spatially defined units of α diversity relative to total species richness (γ diversity; Whittaker 1960). Secondly we measured β diversity as dissimilarity measures (paper I and II) focusing on differences in species composition between units of α diversity. In papers I and II we also measured α diversity as species richness and Shannon diversity, and in paper III we analysed temporal variation in communities of different classes of naturalness, measured as taxonomic completeness (occurrence of native biota).

Table 1 summarizes the statistical methods used in each paper and explains the main objectives of different methods. In paper I, we used a multiplicative partitioning of true diversities (species richness, Shannon diversity) for identifying the most important scale(s) of variation of benthic macroinvertebrate communities across several hierarchical scales, from individual samples to multiple littorals, lakes and years. In this approach, regional species diversity (γ) is partitioned into its within-sample (α) and among-sample diversity (β) multiplicatively where γ is the product of α and β (Whittaker 1960). Multiplicative diversity partitioning results in α that is the mean number of

species across sampling units within a specified scale, γ is the total number of species and β is the number of taxonomically distinct sampling units within the same scale. Most classical diversity indices do not measure diversity per se and must be converted to numbers equivalents ('true diversities' or Hills number) in any approach to diversity partitioning (Jost 2007, Chao *et al*. 2012). Numbers equivalents refer to the number of equally likely elements needed to produce a given value of a diversity index (Jost 2007, Baselga, 2010, Jost *et al*. 2010). We used both species richness (which is its own numbers equivalent) and Shannon's entropy (H') which was converted to numbers equivalents by taking its exponential (exp(H'))(see Jost 2007). We also assessed relative importance of different sampling scales for macroinvertebrate abundance and scale dependent variation in habitat heterogeneity by Nested ANOVA. For studying variation in community composition at each hierarchical scale, we compared the mean within- and between-group distances using mean similarity dendrograms (MSD, Van Sickle 1997, Parsons *et al*. 2003). For assessing whether dominant and rare species exhibited differing patterns of diversity variation through space and time, we formed two non-overlapping species groups, type-specific (dominant) vs. rare taxa. The list of type-specific taxa was defined using the threshold value of ≥ 0.4 for probability of capture in a data set from 57 littoral sites in 23 humic lakes in southeastern Finland (OIVA 2010), and rare species were defined as those with a proportional abundance of $< 0.05\%$ of total community abundance (e.g. Gering *et al*. 2003) across our own data set. Multiplicative diversity partitioning was run separately for both of these species groups.

In paper II, we first confirmed the gradient of environmental degradation by subjecting riparian and in-stream physical environmental variables separately to principal component analysis (PCA). We studied differences among status classes in species diversity, separately for each taxonomic group with one-way ANOVA. We performed ANOVA also for differences among status classes in the number of red-listed species (IUCN categories NT-CR). This could only be done for bryophytes and macroinvertebrates, for which information on the red-list status was available. For bryophytes, we used a regional red-list (Sammaltyöryhmä 2013) whereas for macroinvertebrates, national red-list was used (Rassi *et al*. 2010). Prior to analysis, we combined invertebrates and bryophytes into a single measure of red-listed species number to avoid problems of highly unbalanced data (i.e. many sites lacking red-listed species). We used stepwise multiple linear regression with forward–backward selection to associate species richness to key environmental variables and Non-metric multidimensional scaling (NMDS)

ordinations based on abundance data (Bray–Curtis dissimilarity) to reveal patterns in community composition. For testing significant differences in community structure between status classes we used multivariate analysis of variance for distances (Adonis, Oksanen *et al.* 2010).

In paper III, we measured taxonomic completeness based on the Reference Condition Approach (RCA), in which the current biological status of test sites is compared to a reference status that represents the best attainable condition (Stoddard *et al.* 2006). We used RCA-based modelling technique River InVertebrate Prediction And Classification System (RIVPACS; Moss *et al.* 1987). The technique uses environmental characteristics to predict the species composition of a site in the absence of human impact, and then compares the observed species composition with the predicted one (O/E ratio i.e. taxonomic completeness; Hawkins 2006). An O/E ratio close to 1.0 indicates a high biological integrity of a site. Prior to the development of RIVPACS models, we randomly subdivided the REF data into two subsets: calibration sites (CAL) for model construction (n = 74 and 50 for macroinvertebrates and bryophytes, respectively) and validation sites (VLD) (n = 10 and 8, respectively) for the evaluation of the precision and accuracy of the models. We developed separate predictive models for macroinvertebrates and bryophytes using data from the CAL sites. We also calculated taxonomic completeness values for rare species (as the index of conservation value, CV) (Linke & Norris 2003) by including only locally rare species (probability of capture < 0.5 for macroinvertebrates; p < 0,35 for bryophytes), which were excluded from the original model. Specifics of RIVPACS model construction are described in paper III.

To test for the consistency of the *a priori* status classification method (based on the physical structure of the stream channel and its riparian forest) in relation to taxonomic completeness, we first set boundaries between the high (i.e. reference) and impacted status (procedure similar to Water Framework Directive guidance; see Wallin *et al.* 2003) for macroinvertebrate and bryophyte taxonomic completeness. For that purpose, we calculated the 25th percentile of CAL-site taxonomic completeness and then divided the interval between the 25th percentile and zero into four evenly spaced intervals to create class boundaries between 'good', 'moderate', 'poor' and 'bad' status. All test sites not reaching good status were considered to be impacted in relation to their taxonomic completeness. Last, we calculated the proportion of test sites for which the physically defined class matched the corresponding class defined by taxonomic completeness. We also

used one-way ANOVA, followed by Tukey´s test, to test for differences between taxonomic completeness among the three inventory status classes.

Finally, we evaluated the relationships between taxonomic completeness and variables describing environmental integrity with linear regression models. Prior to that, we summarized environmental variables using Principal Component Analysis (R Core Team 2008).

To examine if the taxonomic completeness of the eight sites monitored through time varied annually, we used linear mixed-effects models fitted by restricted maximum likelihood. Physical status class (2 or 3) was used as a fixed effect and years nested within sites as random effect in the models.

Table 1. Statistical analysis and objectives of each analysis.

Paper	Method	Objective
I	Multiplicative diversity partitioning	To identify the most important scale(s) of variation of benthic macroinvertebrate richness
I	Nested ANOVA	To assess: 1) the relative importance of different sampling scales to macroinvertebrate abundance variation and 2) scale-dependent variation in habitat heterogeneity
I	Mean similarity dendrograms (MSD)	To assess the among-scale variability of benthic macroinvertebrate community composition
II	Principal component analysis (PCA)	To test for gradient of environmental degradation in riparian and in-stream physical variables
II	One-way ANOVA	To test for differences among status classes in species richness and number of red-listed species
II	Stepwise multiple linear regression	To associate species richness to key environmental variables
II	Non metric multidimensional scaling (NMDS)	To graphically understand patterns in community composition
II	Adonis	To test for significant differences in community composition between status classes
III	River InVertebrate Prediction And Classification System (RIVPACS)	To predict native species composition of macroinvertebrates and bryophytes
III	One-way ANOVA	To test for differences between taxonomic completeness among different status of naturalness
III	Principal Component Analysis (PCA)	To identify the main environmental gradients
III	Linear regression	To explore the relationships between taxonomic completeness and environmental stressor gradients
III	Linear mixed effects models (LMM)	To examine if taxonomic completeness monitored through time varied annually

4 Results and Discussion

4.1 Natural biodiversity patterns in lake littorals

A single benthic sample ($\alpha 1$) contained on average 23% of the regional macroinvertebrate species pool of our study lakes across three consecutive years. Within-littoral (i.e. among samples) variation was clearly the major factor comprising regional diversity in our study. Broader spatial scales (between littorals, between lakes) of beta-diversity were less important although littorals within a lake still differed enough to warrant sampling of repeated littorals to capture benthic diversity present in a lake. The interannual ($\beta 4$) component was the smallest of all.

The high within-littoral variation in benthic diversity probably reflects the well-known aggregative distribution of benthic invertebrates in lake littorals (Downing 1991, Stoffels *et al*. 2003). As we found that the greatest contribution by within-littoral variation to overall richness of benthic invertebrates paralleled with greatest variation of substratum heterogeneity at the same scale, it seems that habitat heterogeneity is the key environmental variable shaping sample-scale macroinvertebrate communities also in stony lake littorals as it is known to be in stream riffles (e.g. Johnson *et al*. 2004). Also Stoffels *et al*. (2005) showed in New Zealand that the within-littoral substrate composition was an important driver of spatial patterns in benthic invertebrate community structure, but community structure varied also among lake littorals, reflecting probably the littoral zone topography, wave exposure and allochthonous inputs.

With Shannon's true diversity, which places more emphasis on dominant species, the sample scale alpha diversity ($\alpha 1$) accounted for an even larger proportion (in total 58%) of the regional macroinvertebrate species pool, indicating that the overall diversity variation was largely determined by the same set of common taxa, most of which were found within any one littoral. For type-specific taxa, practically all of the regional diversity was included at the within-littoral ($\alpha 1 * \beta 1$) scale, and no temporal replication was needed to capture almost all type-specific taxa. By contrast, only a very small proportion of the regional species pool of rare taxa was found in an average benthic sample, and all levels of β diversity, including the interannual component, contributed importantly to regional diversity of rare species. Mean similarity dendrograms showed that also community composition varied quite strongly through time, community similarity

being slightly higher at finer spatial scales. The overall level of similarity was 20% higher for type-specific than all taxa.

In a 100-year comparison, water levels in the second sampling year (2006) were record low, while in 2005 and 2007 it did not deviate from the long-term average (OIVA 2010). The low water level decreased sampling depths and affected positively the abundances of macroinvertebrates in year 2006, either because of easier use of the hand net in shallow water or an actual increase in macroinvertebrate abundances. Nevertheless, the amount of temporal community variation was relatively coherent in all lakes, indicating that the record-dry summer conditions affected similarly communities of all lakes. Correspondingly, Huttunen *et al*. (2014) found that temporal variation of boreal stream communities in hydrologically extreme years is coherent, although in their study decreased precipitation led to a drastic decrease in total abundance of stream macroinvertebrates across a broad spatial extent.

Freshwater bioassessment has typically focused only on dominant species, while rare taxa are considered to produce only weak signals of environmental change (Marchant 2002). Core species of the community are thought to have strong association with niche-related processes, while transient species follow a more stochastic pattern (e.g. Magurran & Henderson 2003, Belmaker 2009). These conclusions seem also valid for our benthic communities, as a large proportion of the rare taxa had low affinity to lake littorals and were therefore likely to be regulated by stochastic climatic events and the drought of 2006.

4.2 Human induced biodiversity patterns in headwater streams

The overall taxonomic richness of most aquatic organism groups, as well as the number of red-listed species, responded negatively to environmental degradation of headwater streams and their riparian forest. The main human stressors affecting species richness and changes in community composition were generally related to substratum homogenization following from the accumulation of fine sediments. Also the loss of bryophyte cover (due mainly to sedimentation) shaped the communities and affected negatively the species richness of many macroinvertebrate groups.

Our results correspond well with other studies dealing with the dependence of macroinvertebrate and bryophyte richness on the pristine habitat structure. Intensive silviculture, which is practiced almost throughout Finland, decreases the amount of in-stream large wood, which is an important factor for stream

ecosystem heterogeneity and as a refuge for organisms (Flores *et al*. 2011, Koljonen *et al*. 2012). Cutting of riparian forests also changes canopy shading, which has a direct impact on the productivity and richness of diatoms (Danehy *et al*. 2007). In our study, benthic diatoms showed no clear response to site degradation, either in terms of species richness or community composition, which might be explained by the overriding importance of water chemistry variables for diatoms.

The main reason for the excessive input of fine sediments in the study area is catchment drainage (Hyvönen *et al*. 2005). Catchment drainage is known to cause in-stream habitat impairment (Holden *et al*. 2004). Several other studies have also found negative effects of forestry-induced sedimentation on benthic invertebrates (Vuori & Joensuu 1996, Shaw & Richardson 2001, Pollard & Yuan 2010) and abundance of bryophytes (Englund 1991, Muotka & Virtanen 1995). Because the amount of aquatic bryophytes is an important factor for diatoms through habitat complexity (Soininen & Heino 2007) and for benthic macroinvertebrates via flow refuge and trapping of organic material (Suren & Winterbourn 1992, Muotka & Laasonen 2002), negative effects of sedimentation on stream communities may be particularly severe in headwater systems naturally rich with bryophytes.

We can quite safely conclude that pristine riparian setting indicates higher in-stream species richness and number of red-listed species (II), and we also found corresponding, albeit less strong evidence for taxonomic completeness, which was used to assess the ecological condition of our study sites in relation to independent and geographically more extended reference data set (III). Both macroinvertebrate and bryophyte taxonomic completeness showed differentiation between pristine and strongly modified sites and was negatively related to amount of fine sediments on stream bed. Taxonomic completeness of macroinvertebrates was significantly higher in the pristine sites than in slightly and strongly modified sites, whereas taxonomic completeness of bryophytes was higher in both pristine and slightly modified sites than in strongly modified sites. However, quite a few sites were still classified into incorrect (better or worse) physical status class according to taxonomic completeness. This was particularly true for sites *a priori* classified as slightly modified. Based on taxonomic completeness of macroinvertebrates and bryophytes, respectively 30 and 50% of slightly modified sites were actually in good ecological condition.

The observed differences in taxonomic completeness of the sites *a priori* classified as pristine and strongly modified indicates relatively good performance of physical classification of the rapid habitat classification approach also in terms

of independent and geographically more extended data. Physical status classification was largely able to identify pristine and strongly modified sites according to taxonomic completeness, but reliable classification of slightly modified class was more problematic. There might be multiple explanations for the weaker identification of the slightly modified sites. First, headwater communities may be affected also by land-use impacts that occur at a larger scale than the physical status classification of the riparian forest is focused on. Although some studies show that stream communities are more related to land use on near-stream riparian areas than at the catchment scale land use (e.g. Sponseller *et al*. 2001, Rios & Bailey 2006), others have reported present day catchment variables to be almost equally important (Sandin 2009), or historical catchment land use to be even the most important predictor of macroinvertebrate community structure (Harding *et al*. 1998). Riverine ecosystems are also sensitive to remote land-use changes due to strong reciprocal effects between upstream and downstream habitats (see McCluney *et al.* 2014). However, the physical status class of a stream section was assessed by mainly visually estimated variables of the local stream channel and forest land use in the adjacent riparian area, and thus the method is not suited for detecting possible upstream (or downstream) land-use impacts on metacommunity dynamics of the stream biota. Even though our study sites had a minimum of a 300-m long upstream buffer consisting of the same physical status class, this might be too little in some severely impacted reaches to observe diversity patterns unaffected by upstream or downstream land-use impacts.

Achieving site classification consistent with the diversity patterns for the slightly modified sites might be particularly challenging also because the classification method used sums up different variables that are possibly unequally important stressors for stream organisms. Some of the forestry impacts on biological communities in boreal streams are subtle (Huttunen *et al.* 2012) and may have few direct consequences on biological communities. On the other hand, the classification method may be unable to detect subtle differences in the habitat structure of the slightly modified sites that may, however, be important determinants for the biota (e.g. the actual amount of fine sediments).

Taxonomic completeness of the less common taxa (i.e. the CV index) showed that the pristine riparian setting may provide adequate protection for even the rarest component of the bryophyte flora. For macroinvertebrates, however, also several sites defined *a priori* as degraded contained conservation values in terms of rare taxa occurrence. We also observed several red-listed species in sites

defined *a priori* as slightly modified, albeit the total amount of red-listed species occurrence was higher in pristine streams (II). Results based on species richness, taxonomic completeness, CV index and number of red-listed species all provide a slightly different aspect to the community responses to human land use changes. While species richness gives equal weight to all species, the taxonomic completeness focuses only to common species (probability of capture >50% in CAL data). CV index measures only the rare species, which may not, however, be endangered or vulnerable, but only regionally rare, while the number of red-listed species counts only truly endangered or vulnerable species. Common and rare species often differ in their dispersal abilities, life-history strategies (Kunin & Gaston 1993) and environmental preferences (Magurran & Henderson 2003), which may cause them to respond differently to habitat changes. While the occurrence of transient species may be stochastic, the diversity of truly endangered species may show a stronger response to habitat impairment because of, for example, more specialized environmental requirements and/or because of lower dispersal ability or smaller source populations to re-colonise disturbed sites. In our data, however, all different diversity metrics showed somewhat paralleling relationship with the human disturbance gradient indicating that human-induced land-use changes affect similarly both common and rare species. Reason for finding conservation values and red-listed species also from sites defined *a priory* as degraded, may be that these sites offer secondary habitats for sink populations and may not be adequate for sustaining persistent populations.

The eight streams monitored through time showed little temporal variability in taxonomic completeness. For macroinvertebrates, status classes did not differ in how they varied through time but slightly modified sites had somewhat lower taxonomic completeness than the pristine streams, whereas for bryophytes both status classes showed consistently high taxonomic completeness. The natural sites retained their *a priori* status class nearly always but the two taxonomic groups differed considerably in how they identified the slightly modified sites: one third of the times slight impairment was identified correctly by the macroinvertebrate data, but bryophytes failed consistently in identifying these sites as different from the reference.

In the temporally restricted larger data set, the taxonomic completeness of bryophytes and macroinvertebrates correlated fairly strongly across all sites, but the within-status-class correlations were weaker, being significant only for the slightly modified class. The degree of community concordance of different stream organisms is often rather low, mainly because of deviating environmental

responses (Heino *et al.* 2003, Paavola *et al.* 2006, Padial *et al.* 2012). Our results suggest that even though the diversity patterns of macroinvertebrates and bryophytes were parallel, the sensitivity of these groups to various intensity of human disturbance may differ (see also e.g Mykrä *et al.* 2008). Consequently, our results caution against making conclusions about the performance of pristine riparian setting as a conservation tool for freshwater biota based merely on one taxonomic group.

Our results also caution against making conclusions about stream integrity based on only one year data. Even though the temporal variability in taxonomic completeness was subtle, it was still sufficient to lead to frequent misclassifications. The ecological status of many slightly modified sites may be so close to the status class boundary that even small temporal variation in taxonomic completeness may lead to misclassification, similar to the findings of Huttunen *et al.* (2012). Nevertheless, temporal variation of taxonomic completeness was slightly larger in modified streams and thus temporal monitoring seems even more crucial for modified than pristine sites.

5 Conclusions and implications for management

Understanding the variation of biodiversity in lake and riverine systems is important for providing insight not only into how biotic communities respond to scale-dependent factors, but also into the underlying anthropogenic and natural factors that generate patterns of biodiversity across scales. This is essential for ensuring that conservation, restoration and management actions are targeted efficiently on appropriate scales to preserve the rapidly declining freshwater biodiversity also for future generations.

Natural variation of littoral macroinvertebrate communities is mainly generated at the littoral scale and even spatially restricted (e.g. one littoral within a lake), single-year sampling will detect a great majority of the ubiquitous macroinvertebrate taxa that typically dominate the regional species pool, while most rare species, and therefore a great proportion of gamma-diversity, will remain undetected if interannual sampling is not included. Assessment based on one year data may thus be reliable if the aim is to catch only the dominant species (e.g. type specific taxa), (that is, those commonly used in freshwater assessment), but for comprehensive biodiversity surveys, temporally repeated sampling is essential to capture also the majority of rare species. Our findings stress the importance of detecting patterns caused by rare and common species separately and rigorously assessing the relevance of these patterns for freshwater management and/or conservation programs. Freshwater communities are controlled by different processes at different spatial and temporal scales and these processes affect rare and common species differently. Studies focusing solely on species richness are ultimately weighted towards rare species, whereas bioassessment techniques based on the Reference Condition Approach usually focus on common species. In any case, all bioassessment methods ignoring abundance differences may be blind to environmental stressors that force assemblages to undergo slow compositional changes. It should be noted also that, similar to streams (see Feio *et al*. 2010), human-impacted lakes may exhibit more inter-annual variability than corresponding pristine lakes. This relationship remains untested and should be considered in the future development of assessment-related research and protocols.

Similar to Feio *et al*. (2010), we observed that too restricted a time scale may bias assessment results, particularly for impacted headwater streams. We observed frequent misclassifications on the status-class boundary corresponding the

boundary between classes 'good' and 'moderate' in the EU Water Framework Directive. As this boundary is decisive for management actions, temporal variability in status assessment is particularly problematic, emphasizing the importance of long-term monitoring of impacted running waters. We also observed slightly different responses of bryophyte and macroinvertebrate biodiversity to land-use changes, indicating that these taxonomic groups may provide complementary information about human disturbance and neither one of them should preferably not be used as the only target group in monitoring.

As a rapid conservation or restoration prioritization tool, the physical status classification of the stream channel and its riparian forest was partially successful, by being largely able to separate the clearly impacted sites from the pristine and near-pristine ones, but the identification of slightly modified sites was less reliable. These problems indicate that to be able to effectively detect the most subtle differences in moderately impacted streams, an environmental surrogate method would need to be weighted more towards the most important stressors in each particular situation and be based on more quantitative variables instead of averaged qualitative classes. One such variable might be stream bed stability, although it may be difficult to be measured in rapid inventories. Also information about the age and intensity of catchment-scale land-uses might enhance the performance of the environmental classification as a surrogate method for biological responses, producing a more robust classification especially for the moderately impacted sites. Nevertheless, such rapid classification methods are needed for practical conservation and management of freshwater ecosystems. The physical status classification protocol tested here seems to serve this purpose relatively well.

The strong dependence of freshwater communities on the terrestrial setting is expected given that headwater streams and their riparian forests are tightly interlinked systems that exchange organic and inorganic matter in the form of nutrients, leaves, wood and insects. The degradation of either one of these interlinked systems ultimately affects also the food webs of the other system (see Baxter *et al.* 2005). Thus, the integrated conservation and management of streams and their riparian forests would be necessary but, unfortunately, have been developed in isolation. In forest conservation, riparian corridors are considered mainly as valuable diversity hot spots for forest biodiversity, or as dispersal pathways (Marczak *et al.* 2010), whereas in freshwater conservation, riparian forests act mainly as buffer zones to reduce land-use impacts (Richardson & Danehy 2007, Sweeney *et al.* 2004). Accordingly, streamside forests, as one of

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the woodland key habitats (WKHs) of the Finnish Forest Act (see Pykälä 2007), are designated to protect forest biodiversity, whereas water legislation is focused on protecting solely the aquatic environment.

Our results suggest that streamside WKHs, although initially targeted only at the conservation of the terrestrial biodiversity, may incidentally also preserve part of the headwater biota. However, as we found conservation values also from sites *a priori* classified as degraded, streamside WKHs may need to be complemented by sites that, based on their physical appearance, may seem impacted by, for example, historical forestry effects. Notably, our pristine study sites were not surrounded by forest cuttings and we therefore do not know if the narrow (often only 10 m) streamside WKHs provide any protection for the stream biodiversity if they were surrounded by standard clear cutting of commercial forests. Many studies have stressed that an effective buffer needs to be at least 30 meters on both sides of the channel to retain the biological characteristics of a stream and to prevent chemical and physical changes in stream water after clear cutting (e.g. Castelle *et al.* 1994, Hylander *et al.* 2002).

Nevertheless, our results emphasize the need of controlling the catchment land-use effects in the conservation and management of headwater systems, and urge to study the state of rivers and streams in tight linkage with their catchments. Integrated conservation, management and restoration of streams and their riparian forests would benefit biodiversity conservation of both systems. Thus conservation of aquatic and terrestrial systems should be developed as an entity, and more collaboration between forest and freshwater scientists, as well as managers, is urgently needed.

References

Abell R (2002) Conservation Biology for the Biodiversity Crisis: a Freshwater Follow-up. Conserv Biol 16: 1435–1437.

Allan JD (2004) Landscapes and riverscapes: the influence of land use on stream ecosystems. Annu Rev Ecol Syst 35: 257–284.

Allen TFH & Starr TB (1982) Hierarchy: perspectives for ecological complexity. Chicago, University of Chicago.

Aroviita J & Hämäläinen H (2008) The impact of water-level regulation on littoral macroinvertebrate assemblages in boreal lakes. Hydrobiologia 613: 45–56.

Astorga A, Heino J, Luoto M & Muotka T (2011) Freshwater biodiversity at regional extent: determinants of macroinvertebrate taxonomic richness in headwater streams. Ecography 34: 705–713.

Astorga A, Oksanen J, Luoto M, Soininen J, Virtanen R & Muotka T (2012) Distance decay of similarity in freshwater communities: do macro- and microorganisms follow the same rules? Global Ecol Biogeogr 21: 365–375.

Baxter CV, Fausch KD & Saunders WC (2005) Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biol 50: 201–220.

Baselga A (2010) Multiplicative partition of true diversity yields independent alpha and beta components; additive partition does not. Ecology 91: 1974–1981.

Belmaker J (2009) Species richness of resident and transient coral-dwelling fish responds differentially to regional diversity. Global Ecol Biogeogr 18: 426–436.

Castelle AJ, Johnson AW & Conolly C (1994) Wetland and stream buffer size requirements–a review. J Environ Qual 23: 878–882.

Chao A, Chiu C-H & Hsieh TC (2012) Proposing a resolution to debates on diversity partitioning. Ecology 93: 2037–2051.

Cornell HV & Lawton JH (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. J Anim Ecol 61: 1–12.

Danehy RJ, Chan SS, Lester GT, Langshaw RB & Turner TR (2007) Periphyton and macroinvertebrate assemblage structure in headwaters bordered by mature, thinned, and clearcut douglas-fir stands. Forest Sci 53: 294–307.

Downes BJ, Lake PS & Schreiber SG (1995) Habitat structure and invertebrate assemblages on stream stones: A multivariate view from the riffle. Aust J Ecol 20: 502-514.

Downing JA (1991) Biological and physical heterogeneity in lakes. In: Kolasa J & Pickett S (eds) Ecological heterogeneity New York, Springer-Verlag: 160–180.

Dudgeon D, Arthington AH, Gessner MO, Kawabata Z-I, Knowler DJ, Lévêque C, Naiman RJ, Prieur-Richard, A-H, Soto D, Stiassny MLJ & Sullivan CA (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. Biol Rev 81: 163–182.

Englund G (1991) Effect of disturbance on stream moss and invertebrate community structure. J N Am Benthol Soc 10: 143–153.

Erős T & Schmera D (2010) Spatiotemporal scaling of biodiversity and the species-time relationship in a stream fish assemblage. Freshwater Biol 55: 2391–2400.

ESRI (2011) ArcGIS Desktop: Release 10. Redlands, CA: Environmental Systems Research Institute.

Feio MJ, Coimbra CN, Graça MAS, Nichols SJ and Norris RH (2010) The influence of extreme climatic events and human disturbance on macroinvertebrate community patterns of a Mediterranean stream over 15 y. J N Am Benthol Soc 29: 1397–1409.

Flores L, Larranaga A, Diez J & Elosegi A (2011) Experimental wood addition in streams: effects on organic matter storage and breakdown. Freshwater Biol 56: 2156–2167.

Gering JC, Crist TO & Veech JA (2003) Additive partitioning of species diversity across multiple spatial scales: implications for regional conservation of biodiversity. Conserv Biol 17: 488–499.

Harding JS, Benfield EF, Bolstad PV, Helfman GS & Jones III EBD (1998) Stream biodiversity: The ghost of land use past. Proc Natl Acad Sci USA 95: 14843–14847.

Hawkins CP (2006) Quantifying biological integrity by taxonomic completeness: its utility in regional and global assessments. Ecol Appl 16: 1277–1294.

Heino J, Muotka T, Paavola R & Paasivirta L (2003) Among-taxon congruence in biodiversity patterns: can stream insect diversity be predicted using single taxonomic groups? Can J Fish Aquat Sci 60: 1039–1049.

Heino J, Muotka T, Paavola R, Hämäläinen H & Koskenniemi E (2004) Correspondence between regional delineations and spatial patterns in macroinvertebrate assemblages of boreal headwater streams. J N Am Benthol Soc 21: 397–413.

Herbert ME, McIntyre PB, Doran PJ, Allan JD, Abell R (2010) Terrestrial reserve networks do not adequately represent aquatic ecosystems. Conserv Biol 24: 1002–1011.

Hildrew AG & Giller PS (1994) Patchiness, species interactions and disturbance in the stream benthos. In Giller PS, Hildrew AG & Raffaelli D (eds) Aquatic ecology. Scale, pattern and process. Oxford, Blackwell Science: 21–62.

Holden J, Chapman PJ & Labadz JC (2004) Artificial drainage of peatlands: hydrological and hydrochemical process and wetland restoration. Prog Phys Geog 28: 95–123.

Huttunen K-L, Mykrä H & Muotka T (2012) Temporal variability in taxonomic completeness of stream macroinvertebrate assemblages. Freshwater Sci 31: 423–441.

Huttunen K-L, Mykrä H, Huusko A, Mäki-Petäys A, Vehanen T & Muotka T (2014) Testing for temporal coherence across spatial extents: the roles of climate and local factors in regulating stream macroinvertebrate community dynamics. Ecography 37: 599–608.

Hylander K, Jonsson BG & Nilsson C (2002) Evaluating buffer strips along boreal streams using bryophytes as indicators. Ecol Appl 12: 797–80.

Hyvönen S, Suanto M, Luhta P-L, Yrjänä T & Moilanen E (2005) Puroinventoinnit Iijoen valuma-alueella vuosina 1998–2003. Alueelliset ympäristöjulkaisut 403. Tornio, Tornion kirjapaino (in Finnish, with an English abstract).

Hökkä H & Ojansuu R (2004) Height development of Scots pine on peatlands: describing change in site productivity with a site index model. Can J Forest Res 34: 1081–1092.

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Ilmonen J, Leka J, Kokko A, Lammi A, Lampolahti J, Muotka T, Rintanen T, Sojakka P, Teppo A, Toivonen H, Urho L, Vuori K-M & Vuoristo H (2008) Sisävedet ja rannat. In: Raunio A, Schulman A & Kontula T (eds) Suomen luontotyyppien uhanalaisuus – Osa 1: Tulokset ja arvioinnin perusteet. Suomen ympäristökeskus, Helsinki. Suomen ympäristö 8/2008: 75–109.

Jackson JK & Füreder L (2006) Long-term studies of freshwater macroinvertebrates: a review of the frequency, duration and ecological significance. Freshwater Biol 51: 591–603.

Johnson RK & Goedkoop W (2002) Littoral macroinvertebrate communities: spatial scale and ecological relationships. Freshwater Biol 47: 1840–1854.

Johnson RK, Goedkoop W & Sandin L (2004) Spatial scale and ecological relationships between the macroinvertebrate communities of stony habitats of streams and lakes. Freshwater Biol 49: 1179–1194.

Jost L (2007) Partitioning diversity into independent alpha and beta components. Ecology 88: 2427–2439.

Jost L, DeVries P, Walla T, Greeney H, Chao A & Ricotta C (2010) Partitioning diversity for conservation analyses. Divers Distrib 16: 65–76.

Krammer K. & Lange-Bertalot H (1986–1991) Bacillariophyceae. In: Ettl H, Gerloff J, Heynig H & Mollenhauer D (eds) Freshwater Flora of Central Europe 2. Parts 1–4. Stuttgart, Gustav Fischer-Verlag.

Koljonen S, Louhi P, Mäki-Petäys A, Huusko A & Muotka T (2012) Quantifying the effects of in-stream habitat structure and discharge on leaf retention: implications for stream restoration. Freshwater Sci 31: 1121–1130.

Korhonen K.T, Ihalainen A, Viiri H, Heikkinen J, Henttonen HM, Hotanen J-P, Mäkelä H, Nevalainen S & Pitkänen J (2013) Suomen metsät 2004–2008 ja niiden kehitys 1921–2008. Metsätieteen aikakauskirja 3/2013: 269–608.

Kunin WE & Gaston KJ (1993) The biology of rarity: patterns, causes and consequences. Trends Ecol Evol 8: 298–301.

Linke S, Bailey RC & Schwindt J (1999) Temporal variability of stream bioassessments using benthic macroinvertebrates. Freswater Biol 43: 575–584.

Linke S & Norris RH (2003) Biodiversity: bridging the gap between condition and conservation. Hydrobiologia 500: 203–211.

Naiman RJ, Décamps H & McClain ME (2005) Riparia: Ecology, conservation and management of streamside communities. San Diego, Elsevier.

National Board of Waters (1981) The analytical methods used by National Board of Waters. Report 213. Helsinki, National Board of Waters.

National Land Survey of Finland (2009) The Topographic database. http://www.maanmittauslaitos.fi/en/digituotteet/topographic-database

Nilsson A. (Ed.) 1996. Aquatic Insects of North Europe, vol. 1–2. Stenstrup, Apollo Books

Magurran AE & Henderson PA (2003) Explaining the excess of rare species in natural species abundance distributions. Nature 422: 714–716.

Magurran AE (2004) Measuring biological diversity. Oxford, Blackwell Science.

Magurran AE, Baillie SR, Buckland ST, Dick JMcP, Elston DA, Scott EM, Smith RI, Somerfield PJ & Watt AD (2010) Long-term datasets in biodiversity research and monitoring: assessing change in ecological communities through time. Trends Ecol Evol 25: 574–582.

Marchant R (2002) Do rare species have any place in multivariate analysis for bioassessment? J N Am Bentho Soc 21: 311–313.

Marczak LB, Sakamaki T, Turvey SL, Deguise I, Wood SLR & Richardson JS (2010) Are forested buffers an effective conservation strategy for riparian fauna? An assessment using meta-analysis. Ecol Appl 20: 126–134.

McCluney KE, Poff NL, Palmer MA, Thorp JH, Poole GC, Williams BS, Williams MR & Baron JS (2014) Riverine macrosystems ecology: sensitivity, resistance, and resilience of whole river basins with human alterations. Front Ecol Environ 12: 48–58.

Moss D, Furse MT, Wright JF & Armitage PD (1987) The prediction of the macroinvertebrate fauna of unpolluted running-water sites in Great Britain using environmental data. Freshwater Biol 17: 41–52.

Muotka T & Laasonen P (2002) Ecosystem recovery in restored headwater streams: the role of enhanced leaf retention. J Appl Ecol 39: 145–156.

Muotka T & Virtanen R (1995) The stream as a habitat templet for bryophytes: species' distributions along gradients in disturbance and substratum heterogeneity. Freshwater Biol 33: 141–160.

Mykrä H, Aroviita J, Hämäläinen H, Kotanen J, Vuori K-M & Muotka T. (2008) Assessing stream condition using macroinvertebrates and macrophytes: concordance of community responses to human impact. Fund Appl Limnol 172: 191–203.

Mykrä H, Heino J & Muotka T (2007) Scale-related patterns in the spatial and environmental components of stream macroinvertebrate assemblage variation. Global Ecol Biogeogr 16: 149–159.

Mykrä H, Saarinen T, Tolkkinen M, McFarland B, Hämäläinen H, Martinmäki K & Kløve B (2012) Spatial and temporal variability of diatom and macroinvertebrate communities: How representative are ecological classifications within a river system? Ecol indic 18: 208–217.

OIVA (2010) Available at: http://wwwp2.ymparisto.fi/ (accessed 25 February 2010).

Oksanen J, Blanchet FG, Kindt R, Legendre P, O'Hara RG, Simpson GL, Solymos P, Stevens MHM & Wagner H (2010) vegan: Community Ecology Package. R package version 1.17-1. Available at: http://CRAN.R-project.org/package=vegan (accessed 10 March 2010).

Paavola R, Muotka T, Virtanen R, Heino J, Jackson D & Mäki-Petäys A (2006) Spatial scale affects community concordance among fishes, benthic macroinvertebrates and bryophytes in streams. Ecol Appl 16: 368–379.

Padial AA, Declerck SAJ, De Meester L, Bonecker CC, Lansac-Tôha FA, Rodrigues LC, Takeda A, Train S, Velho LFM & Bini LM (2012) Evidence against the use of surrogates for biomonitoring of Neotropical floodplains. Freshwater Biol 57: 2411–2423.

Parsons M, Thoms MC & Norris RH (2003) Scales of macroinvertebrate distribution in relation to the hierarchical organization of river systems. J N Am Benthol Soc 22: 105–122.

Pykälä J (2007) Implementation of Forest Act habitats in Finland: Does it protect the right habitats for threatened species? Forest Ecol Manag 242: 281–287.

Poff NL (1997) Landscape filters and species traits: towards mechanistic understanding and prediction in stream ecology. J N Am Benthol Soc 16: 391–409.

Poff NL & Allan JD (1995) Functional organization of stream fish assemblages in relation to hydrological variability. Ecology 76: 606–627.

Pollard AI & Yuan LL (2010) Assessing the consistency of response metrics of the invertebrate benthos: a comparison of trait- and identity-based measures. Freshwater Biol 55: 1420–1429.

Rassi P, Hyvärinen E, Juslén A & Mannerkoski I (2010) The 2010 Red List of Finnish Species. Helsinki, Ympäristöministeriö & Suomen ympäristökeskus.

R Development Core Team (2008) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at: http://www.R-project.org

Richards C, Haro RJ, Johnson LB & Host GE (1997) Catchment and reach-scale properties as indicators of macroinvertebrate species traits. Freshwater Biol 37: 219–230.

Richardson JS & Danehy RJ (2007) A synthesis of the ecology of headwater streams and their riparian zones in temperate forests. Forest Sci 53: 131–147.

Richardson JS, Tylor E, Schluter D, Pearson M & Hatfield T (2010) Do riparian zones qualify as critical habitat for endangered freshwater fishes? Can J Fish Aquat Sci 67: 1197–1204.

Rios SL & Bailey RC (2006) Relationship between Riparian Vegetation and Stream Benthic Communities at Three Spatial Scales. Hydrobiologia 553: 153–160.

Rosenzweig ML (1995) Species diversity in space and time. Cambridge, Cambridge University Press.

Sala OE, Chapin FS, Armesto JJ, Berlow E, Bloomfield J, Dirzo R, Huber-Sanwald E, Huenneke LF, Jackson RB, Kinzig A, Leemans R, Lodge DM, Mooney HA, Oesterheld M, Poff NL, Sykes MT, Walker BH, Walker M & Wall DH (2000) Global biodiversity scenarios for the year 2100. Science 287: 1770–1774.

Sammaltyöryhmä 2013. The distribution of bryophytes in forest vegetation and regional environmental districts in Finland (in Finnish). http://www.ymparisto.fi/fi-FI/Luonto/Lajit/Lajiensuojelutyo/Eliotyoryhmat/Sammaltyoryhma/Suomen_sammalet

Sandin L (2003) Benthic macroinvertebrates in Swedish streams: community structure, taxon richness, and environmental relations. Ecography 26: 269–282.

Sandin L (2009) The effects of catchment land-use, near-stream vegetation, and river hydromorphology on benthic macroinvertebrate communities in a south-Swedish catchment. Fund Appl Limnol 174: 75–87.

Scarsbrook MR (2002) Persistence and stability of lotic invertebrate communities in New Zealand. Freshwater Biol 47: 417–431.

Shaw EA & Richardson JS (2001) Direct and indirect effects of sediment pulse duration on stream invertebrate assemblages and rainbow trout (*Oncorhynchus mykiss*) growth and survival. Can J Fish Aquat Sci 58: 2213–2221.

Sweeney BW, Bott TL, Jackson JK, Kaplan LA, Newbold JD, Standley LJ, Hession WC & Horwitz RJ (2004) Riparian deforestation, stream narrowing, and loss of stream ecosystem services. Proc Natl Acad Sci USA 101: 14132–14137.

Soininen J (2007) Environmental and spatial control of freshwater diatoms—a review. Diatom research 22: 473–490.

Soininen J & Heino J (2007) Variation in niche parameters along the diversity gradient of unicellular eukaryote assemblages. Protist 158: 181–191.

Suren AM & Winterbourn MJ (1992) The influence of periphyton, detritus and shelter on invertebrate colonization of aquatic bryophytes. Freshwater Biol 27: 327–339.

Sponseller RA, Benfield EF & Valett HM (2001) Relationship between land use, spatial scale and stream macroinvertebrate communities. Freshwater Biol 46: 1409–1424.

Stendera SES & Johnson RK (2005) Additive partitioning of aquatic invertebrate species diversity across multiple spatial scales. Freshwater Biol 50: 1360–1375.

Stoddard J, Larsen D, Hawkins C, Johnson R & Norris R (2006) Setting expectations for the ecological condition of streams: the concept of reference condition. Ecol Appl 16: 1267–1276.

Stoffels RJ, Closs GP & Burns CW (2003) Multiple scales and the relationship between density and spatial aggregation in littoral zone communities. Oikos 103: 81–92.

Stoffels RJ, Clarke KR & Closs GP (2005) Spatial scale and benthic community organisation in the littoral zones of large oligotrophic lakes: potential for cross-scale interactions. Freshwater Biol 50: 1131–1145.

Timonen J, Siitonen J, Gustafsson L, Kotiaho JS, Stokland JN, Sverdrup-Thygeson A & Mönkkönen M (2010) Woodland key habitats in northern Europe: concepts, inventory and protection. Scand J Forest Res 25: 309–324.

Tylianakis JM, Klein A-M & Tscharntke T (2005) Spatiotemporal variation in the diversity of Hymenoptera across a tropical habitat gradient. Ecology 86: 3296–3302.

Urho L, Pennanen JT & Koljonen ML (2010) Fish. In: Rassi P, Hyvärinen E, Juslén A & Mannerkoski I (eds) The 2010 Red List of Finnish Species. Helsinki, Ympäristöministeriö & Suomen ympäristökeskus: 336–343.

Van Sickle J (1997) Using mean similarity dendrograms to evaluate classifications. J Agr Biol Envir S 2: 370–388.

Vuori KM, Bäck S, Helsten S, Karjalainen SM, Kauppila P, Lax HG, Lepistö L & Londesborough S (2006) The basis for typology and ecological classification of waterbodies in Finland. Finnish Environment 807: 1–151 (in Finnish with English summary).

Vuori K-M & Joensuu I (1996) Impact of forest drainage on the macroinvertebrates of a small boreal headwater stream: Do buffer zones protect lotic biodiversity? Biol Conserv 77: 87–95.

Wallin M, Wiederholm T & Johnson RK (2003) Guidance on establishing reference conditions and ecological status class boundaries for inland surface waters. CIS Working group 2.3 – REFCOND, 7.0, 93 p.

Whittaker RH (1960) Vegetation of the Siskiyou mountains, Oregon and California. Ecol Monogr 30: 279–338.

Zvuloni A, van Woesik R & Loya Y (2010) Diversity partitioning of stony corals across multiple spatial scales around Zanaibar island, Tanzania. PLoS One, 5: e9941.

Appendix

Table 1. Description of the GIS variables used in paper III.

Variable	Specification of the measurements and data source
Slope	For 500 m up- and downstream of a site; Digital elevation model, 10m x 10m, 2009. (National Land Survey of Finland, 2009; http://www.maanmittauslaitos.fi/en/digituotteet/ elevation-model-25-m)
Drainege intensity	Overall density of ditches (km km^{-2}) in the upstream catchment; Topographical database, 1:10 000, 2009. (National Land Survey of Finland, 2009; http://www.maanmittauslaitos.fi/en/ digituotteet/topographic-database)
Number of ditches	Number of ditches flowing directly into the stream (50m buffer) in a 1500-m section upstream of a site; Topographical database, 1:10 000, 2009.
Distance to upstream lake (m)	Topographical database, 1:10 000, 2009.
Catchment area (km2)	Digital elevation model, 10m x 10m, 2009.
Peatland	% of topsoil in the drainage area; CORINE Land Cover 2006. (Finnish Environment Insitute, 2006; http://sia.eionet.europa.eu/ CLC2006)
Lakes	% in the drainage area; CORINE Land Cover 2006.
Agriculture	% in the drainage area; CORINE Land Cover 2006.
Pasture	% in the drainage area; CORINE Land Cover 2006.
Open bogs	% in the drainage area; CORINE Land Cover 2006.
Deciduos forests	% in the drainage area; CORINE Land Cover 2006.
Coniferous forests	% in the drainage area; CORINE Land Cover 2006.
Mixed forests	% in the drainage area; CORINE Land Cover 2006.
Logged forests	% in the drainage area; CORINE Land Cover 2006.
Ultrabasic bedrock	% of bedrock in the drainage area; Bedrock Map 1:1 000 000, 1997. (Geological Survey of Finland, 1997; https://sui.csc.fi/applications/paituli/meta/dokumentit/gtk/kp_milj/SKTSHP.pdf)
Basic bedrock	% of bedrock in the drainage area; Bedrock Map 1:1 000 000, 1997.
Neutral bedrock	% of bedrock in the drainage area; Bedrock Map 1:1 000 000, 1997.
Acidic bedrock	% of bedrock in the drainage area; Bedrock Map 1:1 000 000, 1997.
Mineral deposition	% of subsoil in the drainage area; Superficial Litholigy, 1: 1 000 000, 2010. (Geological Survey of Finland, 2010; http://arkisto.gtk.fi/metatieto/onegeologywp3-dataspecv5.pdf)
Peatland deposition	% of subsoil in the drainage area; Superficial Litholigy, 1: 1 000 000, 2010.

Original articles

I   Suurkuukka H, Meissner K & Muotka T (2012) Species turnover in lake littorals: spatial and temporal variation of benthic macroinvertebrate diversity and community composition. Diversity and Distributions 18: 931–941.

II   Suurkuukka H, Virtanen R, Suorsa V, Soininen J, Paasivirta L & Muotka T (2013) Woodland key habitats and stream biodiversity: Does small-scale terrestrial conservation enhance the protection of stream biota? Biological Conservation 170: 10–19.

III Jyväsjärvi J, Suurkuukka H, Virtanen R, Aroviita J & Muotka T (2014) Does the taxonomic completeness of headwater stream assemblages reflect the conservation status of the riparian forest? Forest Ecology and Management 334: 293–300.

630.   Stibe, Agnis (2014) Socially influencing systems : persuading people to engage with publicly displayed Twitter-based systems

631.   Sutor, Stephan R. (2014) Large-scale high-performance video surveillance

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645.   Väisänen, Maria (2014) Ecosystem-level consequences of climate warming in tundra under differing grazing pressures by reindeer

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