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## Partitioning spatial, environmental, and community drivers of ecosystem functioning

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# Partitioning spatial, environmental, and community drivers of ecosystem functioning

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## Abstract

**Context** Community composition, environmental variation, and spatial structuring can influence ecosystem functioning, and ecosystem service delivery. While the role of space in regulating ecosystem functioning is well recognised in theory, it is rarely considered explicitly in empirical studies.

**Objectives** We evaluated the role of spatial structuring within and between regions in explaining the functioning of 36 reference and human-impacted streams.

**Methods** We gathered information on regional and local environmental variables, communities

(taxonomy and traits), and used variance partitioning analysis to explain seven indicators of ecosystem functioning.

**Results** Variation in functional indicators was explained not only by environmental variables and community composition, but also by geographic position, with sometimes high joint variation among the explanatory factors. This suggests spatial structuring in ecosystem functioning beyond that attributable to species sorting along environmental gradients. Spatial structuring at the within-region scale potentially arose from movements of species and materials among habitat patches. Spatial structuring at the between-region scale was more pervasive, occurring both in analyses of individual ecosystem processes and of the full functional matrix, and is likely to partly reflect phenotypic variation in the traits of

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functionally important species. Characterising communities by their traits rather than taxonomy did not increase the total variation explained, but did allow for a better discrimination of the role of space.

**Conclusions** These results demonstrate the value of accounting for the role of spatial structuring to increase explanatory power in studies of ecosystem processes, and underpin more robust management of the ecosystem services supported by those processes.

**Keywords** Spatial structuring · Community ecology · Ecosystem processes · Species traits · Variance partitioning

## Introduction

Biological processes that regulate the retention and flux of energy and nutrients are central to the functioning of ecosystems, and the services ecosystems provide society (Truchy et al. 2015). Ecosystem functioning can be defined as “the joint effects of all processes [fluxes of energy and matter] that sustain an ecosystem” (Naeem and Wright 2003) over time and space through biological activities. Concern that environmental degradation is compromising important ecosystem processes and the services they support has stimulated research into the factors regulating ecosystem functioning along both natural and anthropogenic gradients (Von Schiller et al. 2008; Frainer et al. 2017). Usually, functioning is quantified as one or more ecosystem-level process rates, such as primary production or litter decomposition (Gessner and Chauvet 2002; Srivastava and Vellend 2005), with variation in these processes often explained by abiotic (e.g. temperature, moisture, soil chemistry) and biotic (e.g. community composition, biodiversity) variables, all quantified at local scales. In contrast, although well recognised in theory, the role of spatial structure, arising from the spatial distribution of key species or habitats (Schmitz 2010), the movements of organisms among habitat patches (Loreau et al. 2005), or larger scale variation in species phenotypes (Ashton et al. 2000), as a regulator of ecosystem functioning at local scales is rarely considered explicitly in empirical studies (Pringle et al. 2010). This is a key shortcoming, given the extent to which human activities are currently altering the distribution of species and

linkages between habitats and ecosystems at multiple spatial scales (Heffernan et al. 2014).

Multiple forms of structuring in the spatial distribution of species and habitats, species characteristics, and behaviours have the potential to influence ecosystem functioning at local scales. Firstly, species and the processes they regulate are often sorted at local scales along gradients in key environmental factors, which both influence the suitability of habitat patches for different species and regulate organism activity rates (Leibold et al. 2004; Venail et al. 2010). For example, the key ecosystem process of litter decomposition often varies along gradients in pH, since low pH not only reduces diversity of decomposer organisms, but also suppresses the activity of key fungi that drive the enzymatic hydrolysis of leaf litter (McKie et al. 2006). Secondly, as posited by meta-ecosystem theory, the movements of species, nutrients, and materials among habitat patches might also impose spatial structure on ecosystem functioning (Loreau et al. 2005). For instance, source-sink dynamics underpinning “mass-effects” in organism movements might contribute to maintenance of ecosystem functioning in a local “sink” habitat patch through ongoing immigration of essential species for particular ecosystem processes. Similarly, transfers of nutrients and energy across habitat boundaries or within ecological networks can result in spatial subsidization of ecosystem processes in recipient ecosystem, as seen in the patchy subsidization of terrestrial food webs by the emerging adult stages of aquatic insects (Burdon and Harding 2008; Carlson et al. 2016). Thirdly, the model of “self-organized systems” posits that organization in the spatial distribution of keystone or foundational species arising from interspecific interactions can also drive predictable spatial structuring in ecosystem functioning (Schmitz 2010; Dong and Fisher 2019). This is seen in African savannah habitats, where the evenly spaced distribution of termite mounds creates a spatial matrix in soil humidity, aeration, and nutrient content, which are all enhanced in the vicinity of termite mounds, and which in turn promote predictable structuring in biodiversity and productivity of both plants and invertebrates (Pringle et al. 2010). Finally, variation in species phenotypes might drive substantial spatiotemporal variability in the importance of particular species and communities for ecosystem functioning (Lecerf and Chauvet 2008; Des Roches et al. 2018). Latitudinal variation in intraspecific body

size (Ashton et al. 2000; McKie and Cranston 2005) is particularly likely to alter the importance of particular species for functioning over large scales, given the importance of biomass as a key driver of ecosystem processes (Brown et al. 2004; Hildrew et al. 2007; Perkins et al. 2010).

In practice, most studies investigating spatial variation in ecosystem functioning evaluate the joint variation of ecosystem processes and biodiversity along easily quantified environmental gradients in, for example, nutrients, temperature and habitat structures (Young and Collier 2009; Frainer et al. 2017). Accordingly, the environmental sorting model is, by default, the dominant paradigm through which spatial structuring in ecosystem functioning is understood. In contrast, isolating how spatial patterns in functioning are shaped by biotic interactions, meta-ecosystem processes, and phenotypical variation in species behaviour is a major practical challenge. Such efforts are most likely to occur in studies focused on small scale impacts of key species and interactions, movements of organisms and materials, and intraspecific variability in traits (Pringle et al. 2010; Logue et al. 2011). However, even where more detailed investigations into the particular mechanisms underlying spatial structuring of ecosystem functioning are not logistically feasible, as is often the case in routine biomonitoring, quantification of the portion of variation attributable to spatial structuring might still yield insights relevant for management. For example, management that targets the impacts of an anthropogenic stressor on local-scale ecosystem functioning might only be partially effective if a significant portion of variation in functioning is attributable to the interactions and movements of organisms and materials among habitat patches, and/or phenotypic variation in species phenotypes. In such cases, further research into the mechanisms underpinning spatial structuring, and the interplay between spatial structuring and environmental and biotic variation at local scales, is needed to underpin the development of more efficient management.

Here we ask how much of the variability in ecosystem functioning among 36 boreal streams distributed across three regions in Sweden can be attributed to their spatial location (i.e. geographic position) relative to environmental characteristics and community composition. The three regions spanned a distance of 770 km between the southernmost

(boreonemoural ecoregion, mean annual temperature 6.6 °C) and the northernmost (in the middle boreal ecoregion, mean annual temperature 1.5 °C) sites. We further evaluate whether spatial structuring occurs predominantly within or between regions. Our study systems ranged from forested reference sites to streams strongly impacted by human activities, allowing an assessment of the importance of spatial structuring when environmental parameters vary under anthropogenic influence. We used variance partitioning analysis to assess how much variation in a matrix of seven functional metrics was explained by the unique and joint effects of (i) environmental variables and (ii) the community composition of four organism groups (invertebrates, diatoms, macrophytes, and fish), as well as geographic position of the streams, which were used to evaluate the role of spatial structuring separated into (iii) within- and (iv) between-region spatial components. We conducted additional analyses where key organism groups were scored according to their functional traits rather than taxonomic identities. Such traits represent the phenotypic attributes of an organism that regulate its responses to environmental factors (e.g. thermal tolerances, life history strategies) and its influences on ecosystem processes (e.g. feeding rates, feeding mode) (Naeem and Wright 2003; Violle et al. 2007; Truchy et al. 2015). According to Grime's mass-ratio hypothesis (Grimes et al. 1998), ecosystem functioning is likely to vary according to the dominant traits in an assemblage, and as such characterisation of species according to their traits is posited to increase explanatory power in studies relating communities and ecosystem functioning (Enquist et al. 2015; Gagic et al. 2015). We assessed the following general hypotheses.

- (1) The unique and shared effects of environmental and community composition variables together explain more variation in ecosystem functioning than geographic position, reflecting the sorting of species according to environmental characteristics, and the role of environment and community characteristics in regulating ecosystem processes.
- (2) Additionally, some variation in ecosystem functioning is also attributable to geographic position, reflecting the potential for spatial

structuring to arise from mechanisms other than species sorting along environmental gradients.

- (3) We expect strong spatial structuring at the between region scale, due to the likelihood that differences in species phenotypes across regions alter the impacts of communities on functioning. We further expect that spatial structuring of ecosystem functioning occurs within-regions, due to the potential for both meta-ecosystem and self-organisation mechanisms to influence functioning at this scale.
- (4) The use of species traits will increase explanatory power, compared to the characterisation of communities by their taxonomic identities alone, in line with Grime’s hypothesis that the effects of biota on functioning are driven by the dominant traits in the community.

## Methods

### Study sites

We quantified biodiversity, ecosystem functioning and environmental variables in 36 streams across three distinct regions in Sweden (Appendix 1, Fig. S1.1) using identical protocols across all regions and stream reaches. Within each region, we sampled 2nd–3rd order stream reaches that drain forested ‘reference’ catchments, as well as streams that are more heavily impacted by human activities. This design insured inclusion of strong environmental gradients within and among regions (Appendix S1, Fig. S1.1). The major anthropogenic pressure in each region varied, with agriculture, hydropower, and forestry activities dominating in the southern, central, and northern regions, respectively.

### Ecosystem functioning

We quantified a set of seven indicators of ecosystem functioning using well-defined and recognised methods (Lamberti and Resh 1983; Benfield 1996; Gessner 2005; Dietrich et al. 2013) (see Appendix S2 for detailed descriptions). Five were direct measures of basal ecosystem processes in freshwater food webs: (1) the biomass accrual of primary producers in algal biofilms, (2) the decomposition of terrestrial detritus

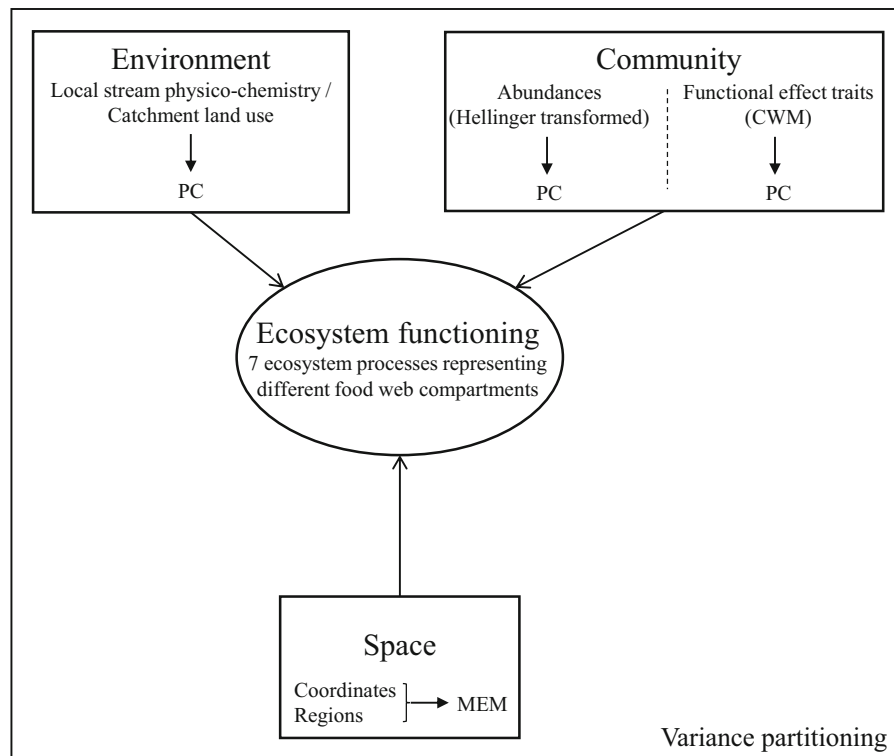
by the full decomposer assemblage and (3) by microbial decomposers only, and (4) the biomass accrual of aquatic fungi on litter in the presence and (5) absence of invertebrate detritivores (i.e. coarse vs. fine meshed litterbags). We quantified two further variables to capture the functioning of additional food web compartments: (6) the biomass accrual of an aquatic bryophyte (*Fontinalis dalecarlica*), as a macrophyte “phytometer”, and a measure of (7) fine particulate organic matter (FPOM) deposition (Appendix S2). Each indicator captures distinct aspects of stream food webs that can be differently affected by local and regional scale community and environmental variation. For instance, decomposition of terrestrial detritus and algal productivity are regulated not only by community composition and stream flow characteristics at local scale, but also potentially by subsidies of nutrients and other materials (including leaf litter) from surrounding catchments (McKie et al. 2008; Von Schiller et al. 2008). These processes may be additionally influenced by the presence of barriers (e.g. dams) which might hinder the free movement of key organisms contributing directly to the process itself (e.g. detritivores or algal species) or impacting those organisms (e.g. predators).

### Biotic sampling and environmental predictors

Primary producers (benthic diatoms and macrophytes) and consumers (benthic invertebrates and fish) were sampled once in each stream reach following European/Swedish standard methods (Naturvårdsverket 2003, 2010) (see Appendix S3 for a detailed description of the sampling methods). We also compiled a comprehensive dataset on potential environmental drivers of community composition and stream ecosystem functioning, including catchment land use (a strong driver of local habitat conditions), and stream physical and chemical variables quantified during our field study at each stream reach (Fig. 1; see Appendix S1, Table S1.1 for a detailed list of the parameters included in the study).

### Species traits

Trait information was retrieved for two taxonomic groups: fish traits were extracted from the “Freshwater ecology.info” database (Schmidt-Kloiber and Herzig 2015), while invertebrate traits came from Tachet



**Fig. 1** Conceptual figure summarizing the types of explanatory variables (boxes) that were included in our analyses to explain variation in ecosystem functioning (the response depicted as a circle). Ecosystem functioning of 36 streams was assessed by measuring seven different ecosystem processes. Environmental variables consisted of properties quantified at each sampled stream reach (e.g. water chemistry) together with information on catchment land use, which strongly impacts local environmental conditions. Community composition encompassed data on benthic diatoms, macrophytes, macroinvertebrates and fish,

represented either as species abundances or functional traits in our different analyses. Environmental and community variables were collapsed to fewer dimensions (principal component (PC)) through principal component analysis (PCA). Space was accounted for using the geographical coordinates of the sampling sites and the regions to which the site belong to (3 distinct regions were included in the study). Spatial scales were represented as Moran’s eigenvector maps (MEM). Significant PC and MEM were selected with a forward selection procedure before being used in the variance partitioning analysis

et al. (2010). For both groups, we focused on traits that are closest in their definition to true functional effect traits (Truchy et al. 2015) (Appendix S2, Table S2.1), i.e. most likely to be correlated with the effects of organisms on ecosystem processes (Hooper et al. 2002; Lavorel and Garnier 2002; Naeem and Wright 2003). We compiled a set of traits that represents not only the likely direct influences of organisms on our functional measures (e.g. feeding preferences, body size), but also habitat-use and phenological traits regulating where and when different species are likely to be most active in their influences on function (Frainer et al. 2014) (Appendix S2, Table S2.1). Additionally, we quantified the body lengths of litter-consuming invertebrates (a functional guild known as “shredders”) found colonising our litter bags to the

nearest mm, and converted these length measures into biomass estimates, based on formulae from Meyer (1989).

#### Data analyses

All analyses were performed in the R environment (R Core Team 2018).

We used Moran’s Eigenvector Maps (MEM) to model spatial structuring of our ecosystem functioning data (Borcard and Legendre 2002; Legendre and Legendre 2012). Our spatial model consisted of two components (Fig. 1): (i) a B-component, representing region identity using a dummy variable, and (ii) a W-component, consisting of MEM describing the spatial structuring among streams within a region,

based on Euclidean distances (i.e. geographical distances). Euclidean distances were the most appropriate to represent our study design, which comprised streams situated in three distinct regions that were not strongly connected hydrologically (i.e. no sampling station was situated downstream of another). MEM analyses produce a set of orthogonal spatial variables derived from the geographical coordinates of the study sites (Dray et al. 2006). The approach used here was a sophisticated version of the MEM analysis using the function “create.MEM.model” developed by Declerck et al. (2011), for which we specified the site coordinates and the region. The within-region spatial structures in the dataset were taken into account using this approach, as the sites in the other two regions get zero values when the spatial structure within a given region is considered (Declerck et al. 2011). This analysis results in a staggered matrix of MEM eigenvectors. We then selected the significant MEM with a forward selection procedure (Blanchet et al. 2008) (function “forward.sel” in the R package packfor (Dray et al. 2013)).

To account for environmental variation and community effects on ecosystem functioning, environmental and community variables (i.e. abundances or traits) were first collapsed to fewer dimensions using principal component analysis (PCA) in which the variables were centred and standardised, using the R package ade4 (Dray and Dufour 2007) (Fig. 1). The species abundance matrices were Hellinger-transformed prior to running the PCA (Legendre and Gallagher 2001) while the trait matrices for fish and invertebrates were represented by community weighted means (CWM) calculated as:  $\sum_{i=1}^n \text{relative abundance}_i \times \text{trait}_i$  (for a species  $i$ , Lavorel et al. (2008)). Therefore, final matrices of environmental and community variables consisted of site scores along principal components (PC) that were also selected using a forward selection procedure (Fig. 1). This procedure ensured that all explanatory variables were given equal weights in our variance partitioning analyses (see below).

We used variance partitioning (VP) analyses to separate variation in ecosystem functioning explained by spatial structuring at the between- and within-region scales (B- and W-components), from that explained by our environment (E) and community composition (C; as abundances or traits) matrices. The

VP method allows partitioning the variation attributable purely to single sets of variables from the shared variation of two or more sets of variables (Borcard and Legendre 2002). We used the function “varpart” from the R package vegan (Oksanen et al. 2015).

We conducted four types of variance partitioning analysis, denoted hereafter as VP sets 1–4. In sets 1–2, we systematically assessed variation in the entire functional matrix when accounting for all organism groups together (VP1), followed by analyses for each functional indicator separately (VP2), since different indicators may vary in the degree to which they are regulated by environmental, biotic and spatial factors:

- VP1: a single analysis that partitioned spatial variation associated with the between- (B), within-region (W) scales from that associated with the abiotic environment (E) and community composition ( $C_c$ ), on the complete ecosystem functioning matrix (i.e. including all seven functional indicators), and conducted using community data for all four biological groups combined. The variables in the ecosystem functioning matrix were standardized to mean = 0 and SD = 1 prior to analysis.
- VP2: comprised seven analyses that were identical to the VP1 analyses, except they were conducted for each functional indicator separately rather than the complete functional matrix. As only one response variable was analysed at a time, no standardization was applied in these analyses.

In sets 3–4, we analysed variation in the entire functional matrix, but with each organism group fitted separately, since particular organism groups might differ in their importance for combined functioning (VP3). We further evaluated the explanatory power of species traits as a substitute for taxonomic identities in the community matrices for two organism groups (VP4). In all these analyses, variables in the ecosystem functioning matrix were standardized to mean = 0 and SD = 1.

- VP3: comprised four analyses identical to that of VP1, except that they were conducted for each biological group (i.e. diatoms, macrophytes, macroinvertebrates and fish) separately.
- VP4: comprised two analyses that were identical to VP3 analyses, except that community composition was quantified on the basis of species traits ( $C_t$ ) rather than species abundances, separately for the



two biological indicators for which adequate trait information was available, viz. fish and invertebrate traits.

We tested for the significance of our global models that include the explanatory variables selected with the forward selection procedure; and then tested for the significance of the unique fractions B, W, C and E using the function “rda” from the package *vegan* (Oksanen et al. 2015). It is not possible to test the significance of shared variation.

## Results

### VP1: importance of spatial scales for stream ecosystem functioning

In our partitioning of the entire functional matrix and including information on all organism groups, spatial structuring at two spatial scales (B- and W-components), communities and environment together explained 52% of the total variation ( $P < 0.001$ ). The within-region spatial component, community composition, as well as environment explained significant unique fractions of variation (Fig. 2), while 18% of the variation in ecosystem functioning was explained jointly between community composition and environment.

### VP2: partitioning the individual functional indicators

When analysing each functional indicator separately, no significant variation was explained for either bryophyte biomass accrual or FPOM dynamics. For the remaining five functional indicators, the total amount of variation explained was high, ranging from 47% (fungal biomass accrual in coarse mesh bags) to 83% (algae biomass accrual) (Table S4.1).

Unique fractions of variation were explained by the between-region spatial component for algal biomass accrual and litter decomposition, and by community composition for all processes (Table S4.1). Unique fractions of variation explained by the environment were only significant for litter decomposition (Table S4.1). Variation explained jointly by community composition and environment ranged from 25% (fungal biomass accrual in fine mesh bags) to 48%

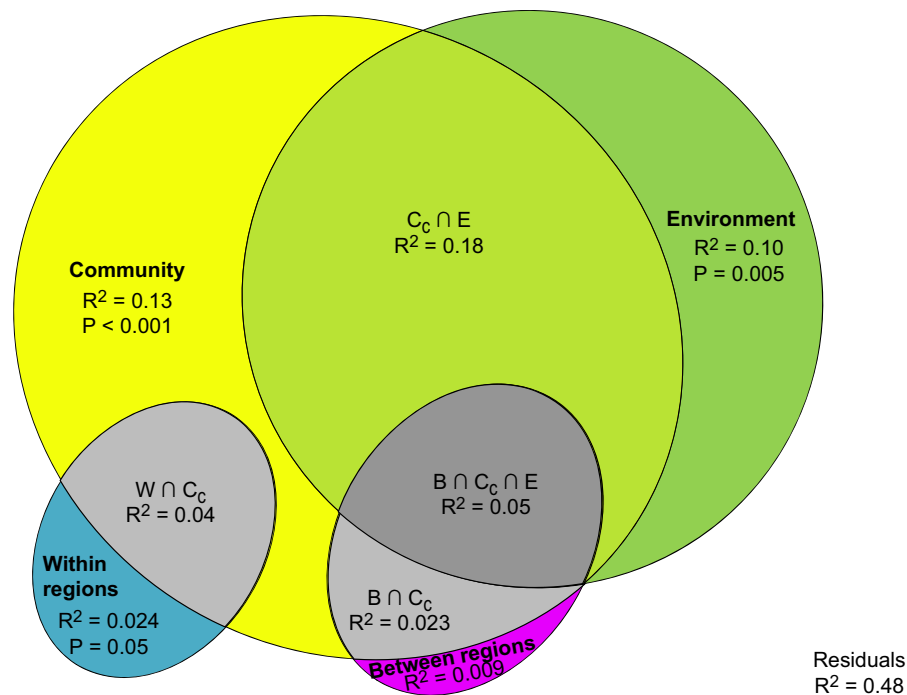
(litter decomposition in fine mesh bags). Variation explained jointly by the within-region component and community composition was as high as 17% for fungal biomass accrual in coarse mesh bags (Table S4.1). Finally, the shared fraction explained by the between-region spatial component, community composition and environment was high for algal biomass accrual (38%).

### VP3: importance of different organism groups for stream ecosystem functioning

When fitting the four community groups separately, the total variation in ecosystem functioning explained by the predictor matrices ranged from 44% (diatoms) to 54% (fish) (Table S4.2; Fig. 3a, c; all  $P < 0.001$ ). The unique fractions explained by the predictors were all significant when fitting diatom and fish abundances as community matrices (Table S4.2; Fig. 3c). The between-region spatial component was not significant when fitting macrophyte and invertebrate communities (Table S4.2; Fig. 3a). The within-region spatial component was significant or nearly so in all analyses. The between- and within-region spatial components have shared effects with community composition in the diatom analysis only (Table S4.2). The joint variations associated with the spatial scales (B or W) were always small (ranging from 0.9% to 5%, Table S4.2; Fig. 3a, c), regardless of which taxonomic group was fitted as the community matrix. However, the joint variation explained by the community matrices and the environment was always higher (ranging from 8% when fitting macrophytes to 18% when fitting invertebrates, Table S4.2; Fig. 3a, c), regardless of which taxonomic group was fitted as the community matrix.

### VP4: incorporating species traits

Traits of invertebrates and fish combined with spatial scales and environment explained 38% to 41%, respectively, of variation in ecosystem functioning (Fig. 3b, d). Unique fractions were associated not only with spatial scales and environment, but also with the composition of species traits for fish only (Fig. 3d). Variation explained jointly by the species traits and environment matrices was 15% when fitted with invertebrate traits (Fig. 3b). The other joint fractions explained were either marginal (ranging from 0.1 to 4%) or not testable (negative  $R^2$ ).



**Fig. 2** Venn diagram showing variation in ecosystem functioning in 36 streams explained by four sets of explanatory variables: between- (B; in magenta) and within- (W; in blue) region spatial components, community composition (C<sub>C</sub>; in yellow) and environment (E; in green) and their joint effects (the overlapping parts of the circles represented as ∩). The four community groups are fitted together. Sets of explanatory variables that do not significantly explain any important fraction of variation in ecosystem functioning ( $P > 0.05$  or adjusted

$R^2 \leq 0.05$ ) are coloured in grey tones. For each testable fraction, an adjusted  $R^2$  is given and  $P \leq 0.05$  are indicated in regular font while  $P < 0.1$  are in italics. The residual variation that was not explained by the variance partitioning analysis is reported in the right hand corner. The size of the circles is proportional to the effects of the set of explanatory variables, the bigger the circle the greater the importance of this set of explanatory variables in explaining variation in ecosystem functioning. (Color figure online)

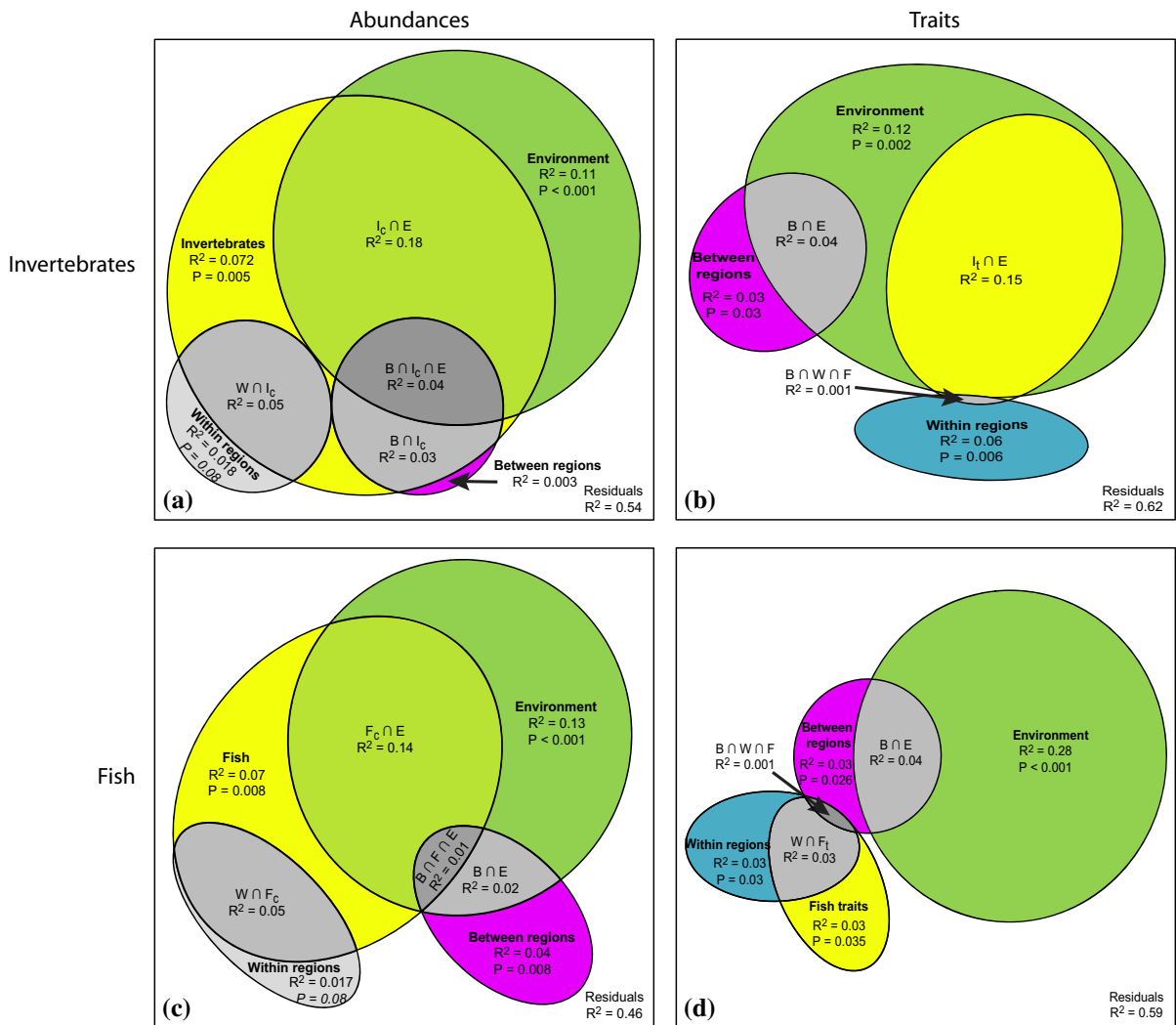
## Discussion

In line with our hypotheses, variation in our matrix of multiple functional indicators was explained not only by environmental variables and community composition, but also by the geographic position of our study reaches. This indicates significant spatial structuring in ecosystem functioning, beyond that attributable to the sorting of species and the processes they regulate along environmental gradients. Spatial structuring of ecosystem functioning was found at the between-region scale, suggesting local ecosystem functioning was structured by larger scale spatial variation likely to reflect differences in the phenotypes of functionally important species. Additionally, significant spatial structuring was often apparent within regions, potentially arising from the connectivity of species and materials among habitat patches and/or associated with self-organisation of particular key species. Overall, the proportion

of variation in ecosystem functioning explained by our environmental and community matrices did not exceed that explained purely by spatial structuring, and the joint variation among these factors was sometimes high (up to 48%). Finally, contrary to our expectations, the use of traits rather than taxonomic identities did not improve the amount of variation explained. Nevertheless, the use of traits did allow better discrimination of the role of space.

Environment and community composition explain greater amounts of variation in ecosystem functioning

Our variance partitioning based on matrices of environment, community composition, and spatial scales (both between- and within-regions) was able to explain a relatively high proportion (52%) of total variation in ecosystem functioning, compared with



**Fig. 3** Venn diagrams showing variation in ecosystem functioning in 36 streams explained by four sets of explanatory variables: between- (B; in magenta) and within- (W; in blue) region spatial components, environment (E; in green), and community composition (in yellow) of either invertebrates (I; **a, b**) or fish (F; **c, d**), and their joint effects (the overlapping parts of the circles represented as  $\cap$ ). Community composition was fitted as either species abundances ( $I_c$  or  $F_t$ ; **a, c**) or species traits ( $I_t$  or  $F_t$ ; **b, d**). Sets of explanatory variables that do not significantly explain any important fraction of variation in

ecosystem functioning ( $P > 0.05$  or adjusted  $R^2 \leq 0.05$ ) are coloured in grey tones. For each testable fraction, an adjusted  $R^2$  is given and  $P \leq 0.05$  are indicated in regular font while  $P < 0.1$  are in italics. The residual variation that was not explained by the variance partitioning analysis is reported in the right hand corner. The size of the circles is proportional to the effects of the set of explanatory variables, the bigger the circle the greater the importance of this set of explanatory variables in explaining variation in ecosystem functioning. (Color figure online)

most studies partitioning the influence of space and environment on community composition (Grönroos et al. 2013; Heino et al. 2015). Moreover, unique environmental effects were often significant, supporting the idea that stream ecosystems and their communities are generally under strong abiotic control (Reice 1994; Johnson et al. 2004), as found in variance

partitioning analyses of community composition (e.g. Pinel-Alloul et al. 1995; Göthe et al. 2013; Grönroos et al. 2013). However, the shared variation between the environmental and community matrices were sometimes as high as 48% in our study. This suggests that environmental effects on functioning are often mediated through effects on community composition

(Jonsson 2006; O'Connor and Donohue 2013; Törnroos et al. 2015), such that not only species and communities but also the processes they regulate frequently sort along environmental gradients. This indicates that intermediary impacts of environmental variation on ecosystem processes via biotic interactions, behaviour, and trait expression are at least as important as those reflecting direct abiotic control (McKie et al. 2009; Brose and Hillebrand 2016).

#### Spatial structuring of ecosystem functioning occur between- and within-regions

Our analyses were able to partition variation associated with spatial structuring at two scales, but we are not able to definitively isolate the underlying causal processes. Spatial structuring at the between-region scale occurred in analyses focussing on specific organism groups (e.g. diatoms, fish), and was the only unique fraction of spatial structuring detected in analyses of each individual functional indicator (VP2). This structuring is most likely to arise from variation in characteristics of the local stream environments and species phenotypes that were (i) not well-represented in our sampling scheme and/or (ii) strongly confounded with the larger between-region scale, and thus was captured by our spatial components rather than environmental or community matrices (e.g. different vegetation zones in a single region (Ahti et al. 1968)). The degree of variability in environmental variables is subject to large scale gradients (e.g. latitudinal gradients in diel light and temperature regimes, or in timing of inputs of resources such as leaf litter), and can differ strongly among regions as a result of shifting precipitation, vegetation, land cover and/or geology (Ahti et al. 1968; Hillebrand 2004; Sponseller et al. 2014). Our environmental data comprised a comprehensive set of variables routinely measured in studies of stream ecosystem functioning, but mostly quantified as mean values derived from a limited number of sampling events, and it is thus likely that we missed much of this variability. Large scale environmental variation also drives divergence in species phenotypes (McKie and Cranston 2005; Boyero et al. 2017). For example, our northern sites experience 2 h less of complete night time darkness in early September than the southernmost sites (Raab and Vedin 1995), a difference which might have implications for the phenotypes

and activity patterns of primary producers, consumers, and the processes they mediate. Notably, many of the traits that have been identified as most useful for characterising linkages between biodiversity and ecosystem functioning in ecological networks—such as growth rates, body size and resource use rates (Brose and Hillebrand 2016)—are also highly plastic, and particularly subject to regional variation in thermal regimes and composition of the resource base. Fortunately, many of these relationships are also highly predictable (Ashton et al. 2000; McKie and Cranston 2005; Boyero et al. 2017), highlighting the potential of developing more finely tuned and spatially explicit trait classification schemes that embed relationships between important spatial and environmental attributes (e.g. latitude, degree days, nutrient concentrations) and values for traits such as body size and growth rates.

The unique fraction of spatial structuring within-regions was only significant in analyses that partitioned variation in all functional indicators, such as the analysis including all organism groups (VP1), and those focussing on diatom communities (VP3) and fish and invertebrate species traits (VP4). These tests are imperfect assessments of the true importance of spatial structuring at a given scale, since they do not account for shared fractions of variation. Nevertheless, these results do indicate that spatial structuring is most likely to emerge at smaller, within-region scales when multiple ecosystem processes, potentially regulated by multiple flows of organisms, nutrients and energy within and across habitat boundaries, are considered simultaneously. This potentially reflects the role of meta-ecosystem processes, including mass-effects governing flows of organisms and materials (nutrients, carbon, etc.), which are more likely to have influenced spatial structuring within- than between-regions, owing to greater spatial proximity and potential connectedness of sites at this scale (Leibold et al. 2004; Cottenie 2005; Logue et al. 2011). It is less likely that spatial structure arising from self-organisation of keystone or foundational species underpins within-region spatial variation in our study, since our studied processes are not clearly dependent on such species, and environmental heterogeneity among our study reaches was likely too great to have favoured self-organisation arising from intraspecific interactions (e.g., Cornacchia et al. 2018; Widenfalk et al. 2018). It is also possible that spatial structuring within

regions might arise from variation in species phenotypes occurring over smaller spatial scales (Des Roches et al. 2018). Notably, within-region spatial structuring was never significant in analyses focusing on each functional indicator separately (VP2), which were instead generally characterised by a very large joint variation between community and environment. This suggests that species-sorting along environmental gradients is a more important driver of individual ecosystem processes (e.g. litter decomposition, biomass accrual of individual organism groups), dependent on a narrower range of organisms and specific nutrients.

All ecosystem processes are not structured by space, environment and community in the same way

Interestingly, in our analyses that partitioned variation in each of our functional indicators separately, we were only able to explain variation in leaf decomposition (58–63% of total variation explained), and the biomass accrual of algae and fungi (up to 83% of variation explained). These represent true ecosystem-level processes regulated by several organisms groups that largely operate at the same local scales over which we quantified community composition and most of our environmental variables. Despite the differences in our capacity to explain variation in all of our indicators separately, inclusion of all functional indicators in the combined ecosystem functioning matrix increased the total variation explained, and was necessary for detecting spatial structuring in functioning at the within-region scale, suggesting that all indicators together better characterised the ecosystem functioning and spatial connectivity of the whole ecosystem.

Influence of taxonomic groups and species traits on global ecosystem functioning

We observed differences in the importance of different components of the biota in our analyses fitting each of the taxonomic groups separately. Macrophyte community composition had the largest unique effect (12%) on overall ecosystem functioning, which might reflect knock-on effects of the multiple influences of macrophyte beds on local environments (e.g. reductions in flow and light, changed nutrient status, and

increased habitat surface area (van Donk et al. 1993; Jeppesen et al. 1998)), on other co-occurring taxonomic groups (Johnson and Hering 2010) and ultimately on ecosystem functioning. Diatoms, invertebrates and fish (7%) also had significant unique effects on functioning, which might reflect direct bottom-up (e.g. algae as resource subsidy for leaf-consuming detritivores) or top-down (e.g. trait-mediated effects of fish on consumer behaviour) control on processes within the food web (Raffaelli et al. 2002; Gessner et al. 2010; Kéfi et al. 2012).

Against our expectations, the total variation explained in our analyses did not increase when species were characterised by their traits rather than taxonomic identities for both invertebrates and fish, contradicting the idea that species traits rather than taxonomic identities better capture the key attributes of biota regulating ecosystem functioning (Lavorel and Garnier 2002; Enquist et al. 2015). However, most species trait databases, including those used here, suffer from two main shortcomings when used to predict ecosystem functioning. Firstly, trait allocations based on these databases may have limited capacity to capture the breadth of spatial–temporal variability in species phenotypes (i.e. intraspecific variation). For example, although our organism groups were all sampled at the same time of year, species were not necessarily at an identical developmental stage in all regions, as suggested by differences in biomass of some of our detritivore taxa (Appendix S2, Table S2.2). Such systematic differences in the body size of key consumers among regions are likely to be further associated with differences in their feeding behaviours (Layer et al. 2013; Frainer and McKie 2015). Secondly, information on true functional effect traits (e.g. resource acquisition rates) is often limited in large-scale databases (Truchy et al. 2015), which are instead biased towards traits regulating species responses to environmental variation (e.g., environmental tolerances) that are likely to predict functioning only indirectly. Nevertheless, the use of traits did have value in our analyses by reducing complexity in the data set, whereby information on many species is reduced to information on a lower number of traits, which might explain why the role of spatial structuring was more discriminated in our analyses of all ecosystem processes combined.

## Conclusion

Field studies are often able to explain a substantial portion of variation in ecosystem functioning based on information on abiotic and biotic parameters, quantified at local scales, alone (Dangles et al. 2004; Young and Collier 2009; Frainer et al. 2014; Frainer and McKie 2015). However the proportion of unexplained variation is often very high, especially at larger (e.g. whole catchment, regional or continental) scales (McKie and Malmqvist 2009; Woodward et al. 2012; Dirzo et al. 2014). Significantly, these are the scales where many vital ecosystem services arise (e.g. water purification and nutrient cycling services), derived from multiple ecosystem processes and organism groups that link across habitat boundaries within larger scale spatial networks (Truchy et al. 2015; Brose and Hillebrand 2016). Overall, our results reveal the extent to which this variation might be attributed to spatial structuring, and highlight the need for more research on the mechanisms underpinning such structuring to support improved management of ecosystem functioning and services. Indeed, the approaches needed to improve delivery of a set of ecosystem functions and services are likely to differ substantially according to how they are structured spatially. This might range from a focus on improving local-scale environmental conditions when species sorting is the dominant mechanism regulating variation in functioning, to a focus on improving conditions for the particular key stone or foundational species that drive significant organisation in ecosystem functioning (Pringle et al. 2010). However, in many cases it is likely that key linkages in flows of organisms and materials among habitat patches and between ecosystem types will be needed to achieve the greatest improvements in ecosystem functioning and service delivery.

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*Appendix to:*

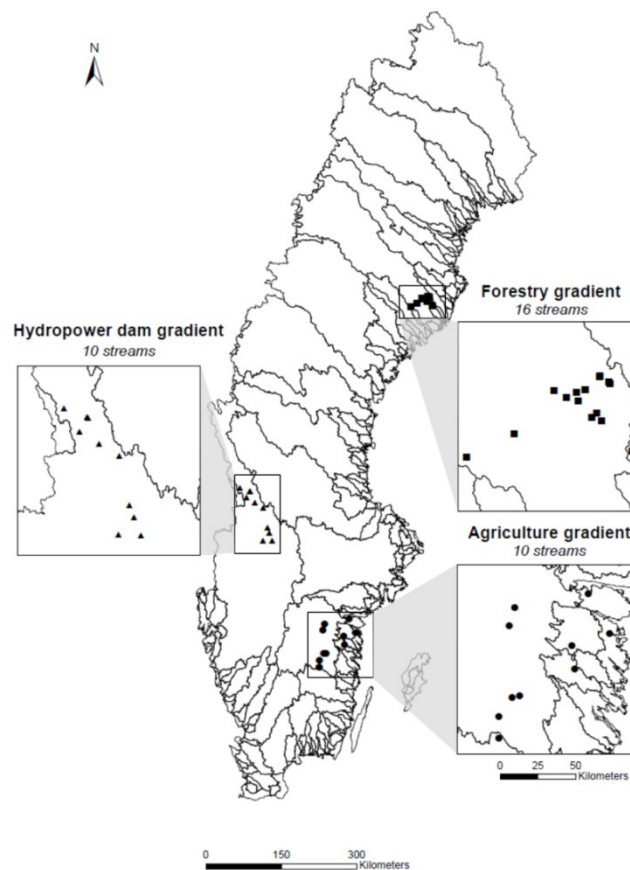
Truchy, A., Göthe, E., Angeler, D. G., Ecke, F., Sponseller, R. A., Bundschuh, M., Johnson, R. K. And McKie, B. G. 2019 Partitioning spatial, environmental and community drivers of ecosystem functioning.

## *Appendix S1*

### Study sites and their environmental parameters

#### *Study sites*

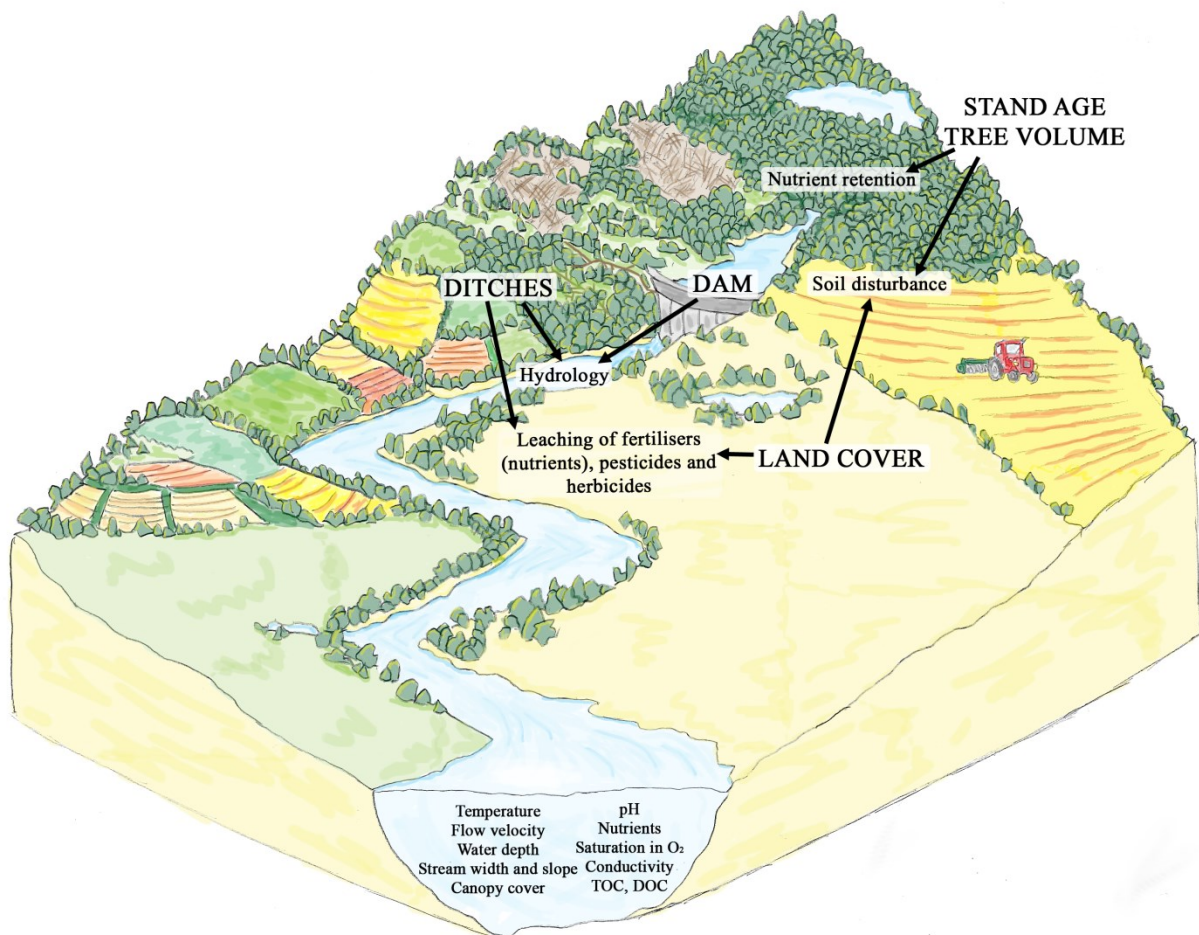
We quantified biodiversity, ecosystem functioning and environmental characteristics in 36 streams across three distinct regions in Sweden . In each region, we sampled reaches situated on 10-16 second or third order streams, which ranged from well-forested reference streams to streams heavily impacted by human activities (Table S1.1), to ensure inclusion of strong environmental gradients in our analyses. Sampling in the southern region centred on catchments in the agricultural plains of the province of Östergötland, which ultimately drain into the Baltic Sea to the East, and was conducted in August-December 2012 (Figure S1.1; Table S1.1). The central and northern regions were sampled in August-November 2013, in the Klarälven and Krycklan-Vindelälven river catchments respectively (Figure S1.1; Table S1.1).



**Figure S1.1** Location of the 36 streams across Sweden sampled in the provinces of Östergötland (filled circles), Värmland (filled triangles) and Västerbotten (filled squares) and representing three environmental gradients. The forestry gradient comprised 16 streams while the hydropower dam and agriculture gradients each consisted of 10 streams. The different environmental gradients were situated in regions where the pressure of interest was pre-dominated. Polygons represent the main Swedish catchments according to the Swedish Meteorological and Hydrological Institute (SMHI). In both regions of Värmland and Västerbotten, some sites were geographically so close to each other that their symbols overlap on the map.

### *Quantifying environmental variables*

Two types of environmental predictors were included in the study, namely (i) catchment-level and (ii) local stream variables (Figure S1.2). Both were quantified simultaneously with biological sampling.



**Figure S1.2** Measured catchment parameters (in upper case) and their large-scale (catchment) and local-scale (in-stream) outcomes (in lower case). Arrows represent the relationship between a catchment parameter and its implication at the large-scale. For instance, intensive agricultural practices increase the soil disturbance, the leaching of fertilisers, pesticides and herbicides through the network of ditches. Ditches affect the hydrology of the system by draining the water of the surroundings while dams modify the hydrology by retaining water in reservoirs and controlling floods for example. Lands covered with forest (greater tree volume and stand age) are characterised by a less

disturbed soil that is able to retain nutrients. Then, each of the measured catchment parameter influences directly or indirectly all the in-stream parameters.

### 1) *Catchment parameters*

Catchment land use information (comprising percent agricultural land and coniferous forest, spatial location of clear-cuts) were obtained using the Swedish Landcover Map (2004) along with the Swedish Forestry Agency's clear-cut records since 2001. Stand age and tree volume information were also retrieved from the SLU Forest Map (Department of Forest Resource Management, Swedish University of Agricultural Sciences). Ditches were hand-digitalised based on a Digital Elevation Model (DEM, 2m grid, Lantmäteriet, 2011) using the Hillshade tool (ArcGIS, ESRI ArcMap, 10.2) and setting the sun angle at 90° and an altitude of 20 m a.s.l.. The cumulative length of ditches in the catchment was then divided by the stream length in order to quantify the extent of ditching within a catchment. The deviation in discharge attributable to river regulation, the volume of water regulated and proportion of runoff stored in upstream magazines were all obtained from the Swedish HYPE (HYdrological Predictions for the Environment) model, available from the Swedish Meteorological and Hydrological Institute (SMHI, <http://vattenwebb.smhi.se/>). We further applied the Dundee Hydrological Regime Assessment Method (DHRAM, (Black *et al.* 2005)) onto discharge data for the year of sampling and one year prior to sampling (from SMHI), generating 19 parameters characterising the extent of alterations to the hydrological regimes of the waterbody (Table S1.1).

### 2) *Local stream variables*

Stream temperatures were recorded continuously during the study periods using button data loggers SL5x (Signatrol, Tewkesbury, UK). Flow velocity (MiniAir 20 with a Mini sensor 22m 5m.s<sup>-1</sup>, Schiltknecht, Gossau, Switzerland) and water depth were measured every sampling occasion. Stream width, slope and canopy cover (canopy analyser LI-CORE® LAI-2000, Lincoln, Nebraska, USA) were also recorded. Turbidity, pH, dissolved oxygen saturation (HDO) and conductivity were assessed *in situ* every third week using a MANTA multiparameter water quality probe (Eureka Environmental Engineering, Austin, Texas, USA). Water samples were taken twice (in August and in November) and analysed for alkalinity, nutrients (total nitrogen, ammonium, nitrites and nitrates, total phosphorus, and orthophosphate), at the Department of Aquatic Sciences and Assessment, SLU using SWEDAC accredited methods (Fölster *et al.* 2014). Total organic carbon concentration (TOC) and dissolved organic carbon concentration (DOC) were analysed with a Shimadzu TOC-VCPH carbon analyser. DOC was filtered through 0.45 µg cellulose acetate filters and the absorbance was measured at 254 nm (Perkin-Elmer Lambda 40) in a 5 cm cuvette.

**Table S1.1.** Characteristics of the studied streams. Streams were sampled in three distinct regions of Sweden, encompassing each a dominant anthropogenic pressure (agriculture, forestry management or hydropower). Physical (including slope, water depth, stream width, temperature and flow) and chemical (alkalinity, pH, conductivity, TOC, turbidity, nutrients and oxygen saturation, among others) characteristics, measured at the sampling location (local scale; in blue) or at the catchment scales (regional scale; in black) are reported<sup>1</sup>. The Dundee Hydrological Regime Assessment Method (DHRAM, (Black *et al.* 2005)) generated 19 parameters characterising the extent of alterations to the hydrological regimes (e.g. 1d min, 30d max or duration of low pulses; in italics).

	Stream name	Catchment	Location	Slope (°)	Water depth (cm)	Width (m)	Flow (m/s)	%Agriculture land	%Clearcuts	%Coniferous	Stand age (years)	Tree volume (m <sup>3</sup> fo/ha)	Ditching	V regulated (Mm <sup>3</sup> )
Agriculture	Silverån	Emån	57°43'N, 15°22'E	2,18	24,55	5,50	0,51	7,79	11,52	60,66	48,0627441	171,6624451	2,46	0,00
	Bulsjöån	Motala ström	57°51'N, 15°21'E	1,31	18,55	15,44	0,29	17,65	11,01	48,56	47,1713982	169,4484711	2,39	23,90
	Borkhultsån	Söderköpingsån	58°16'N, 16°11'E	0,87	37,15	5,35	0,28	16,48	11,21	41,60	47,1109276	155,824173	5,04	0,00
	Kisaån	Motala ström	57°58'N, 15°36'E	1,75	28,35	6,62	0,23	7,44	14,11	52,65	48,656086	175,0560913	2,73	0,00
	Pinnarpsbäcken	Motala ström	57°58'N, 15°30'E	2,62	15,83	8,82	0,35	12,39	13,35	52,21	38,765152	132,780304	2,91	0,00
	Storån nedre delar	Storån	58°08'N, 16°12'E	1,75	28,15	11,01	0,38	11,44	12,11	46,56	48,3952217	153,6428528	3,46	14,30
	Flemmabäcken	Motala ström	58°31'N, 15°33'E	3,49	13,05	3,86	0,10	20,86	8,95	46,97	40,2294426	125,6291122	4,02	0,00
	Börumsbäcken	Coastal	58°20'N, 16°37'E	3,06	15,90	3,76	0,34	11,93	12,29	60,04	52,5987396	130,1325378	2,59	0,00
	Kapellån	Motala ström	58°23'N, 15°29'E	2,18	22,10	9,20	0,46	41,04	9,65	31,84	40,4689407	144,9109497	2,65	0,00
	Vadsbäcken	Coastal	58°35'N, 16°23'E	0,87	16,40	3,30	0,18	70,50	3,91	17,51	47,4972725	130,1004639	3,40	0,00
River regulation	Hynnan	Göta älv	60°54'N, 12°28'E	1,75	21,44	9,12	0,42	0,03	20,88	34,03	60,7375412	83,4036331	1,00	0,00
	Väjån	Göta älv	59°59'N, 13°22'E	2,18	21,40	12,00	0,08	0,00	12,32	68,54	55,7713203	183,9199371	1,48	0,00
	Götån	Göta älv	60°12'N, 13°31'E	1,75	20,88	7,66	0,15	0,00	11,24	65,19	53,7552948	134,2993774	1,18	0,00
	Likan	Göta älv	60°40'N, 13°02'E	0,44	26,24	9,97	0,53	0,00	29,80	47,80	64,6940765	93,435112	0,97	0,00
	Acksjöälven	Göta älv	60°07'N, 13°35'E	1,31	23,76	5,86	0,20	0,00	11,67	65,34	54,0216942	166,3370819	1,84	3,60
	Lettan	Göta älv	60°45'N, 12°43'E	1,31	16,64	6,42	0,18	0,16	17,75	41,56	56,9729538	122,3674011	1,42	190,50
	Hagälven	Göta älv	59°59'N, 13°42'E	0,87	45,60	5,83	0,64	0,15	11,02	60,92	50,7843628	167,7662048	2,59	25,80
	Halgån	Göta älv	60°35'N, 13°21'E	0,44	18,76	13,35	0,24	0,00	15,15	31,15	62,733223	90,30056	1,14	16,70
	Täsan	Göta älv	60°51'N, 12°51'E	1,75	16,28	18,70	0,21	0,05	12,04	42,75	68,7648544	87,8171463	1,09	141,80
	Örän	Göta älv	60°52'N, 12°50'E	1,31	16,60	6,98	0,23	0,00	9,74	44,57	68,425354	97,2809753	0,99	28,00
Forestry management	Stortjärnbäcken	Umeälven	64°14'N, 19°47'E	1,75	25,64	0,82	0,25	0,00	4,36	77,28	87,0976715	172,7565002	2,42	0,00
	Fågelvinbäcken	Umeälven	64°10'N, 19°26'E	1,31	20,16	0,66	0,42	2,55	0,41	65,38	69,970459	121,9825439	0,70	0,00
	Stormyrbäcken	Umeälven	64°15'N, 19°47'E	1,75	26,68	1,08	0,31	0,00	2,34	69,09	74,4313202	134,7668152	2,13	0,00
	Kamplidenbäcken	Umeälven	64°17'N, 19°54'E	2,18	17,40	0,60	0,22	0,00	3,60	63,96	70,9387741	147,6938782	2,02	0,00
	Hjuksvallbäcken	Umeälven	64°06'N, 20°03'E	1,75	16,48	1,50	0,26	0,00	20,49	64,90	80,5819168	149,0672607	1,73	0,00
	Kläppmyrbäcken	Umeälven	64°17'N, 19°54'E	0,44	19,38	1,26	0,16	0,00	3,61	64,41	66,7414474	133,3684845	2,62	0,00
	Brattmyrlidenbäcken	Umeälven	64°16'N, 19°57'E	0,44	42,60	0,72	0,13	0,00	7,04	71,79	62	111,4444427	2,27	0,00
	Renbergsbäcken	Umeälven	64°15'N, 19°49'E	1,75	18,08	2,84	0,27	0,00	13,23	53,15	74,875	101,1875	1,86	0,00
	Svartbäcken	Umeälven	64°16'N, 19°57'E	0,44	27,28	1,90	0,39	0,00	10,61	71,89	63,711441	119,5259247	2,56	0,00
	Krycklan	Umeälven	64°15'N, 19°50'E	1,31	17,72	5,72	0,35	0,00	12,27	53,73	63,1277275	114,6869888	1,36	0,00
	Bergmyrbäcken	Umeälven	64°14'N, 19°43'E	2,18	31,92	1,47	0,39	0,00	5,89	59,33	58,3334961	106,7478943	2,66	0,00
	Bastumyrbäcken	Umeälven	64°11'N, 19°51'E	2,18	20,32	1,90	0,28	0,53	17,75	52,67	60,7334518	114,0999222	2,47	0,00
	Kvarnbäcken	Umeälven	64°07'N, 19°11'E	0,87	17,52	2,48	0,34	0,07	16,70	62,32	63,2695236	113,3261261	4,37	0,00
	Västra Nybyggsbäcken	Umeälven	64°11'N, 19°54'E	2,62	24,00	1,47	0,35	0,00	14,59	51,19	56,7056808	92,1049347	2,69	0,00
	Kluddbäcken	Umeälven	64°12'N, 19°53'E	2,62	20,96	1,91	0,44	0,53	9,55	30,74	56,5665817	105,8886032	2,82	0,00
Krickmyrbäcken	Umeälven	64°15'N, 19°40'E	1,75	15,56	1,13	0,32	0,00	51,27	50,95	36,6247215	54,3210297	3,70	0,00	

Table SI.1 continues

Stream name		V deviation (%)	Water stored (%)	1d min	1d max	3d min	3d max	7d min	7d max	30d min	30d max	90d min	90d max	date min	date max	nb hi pulses	nb lo pulses	duration hi pulses
Agriculture	Borkhultsån	0,00	0,00	0,34	1,6	0,34	1,58	0,34	1,57	0,36	1,44	0,41	1,11	263	194,5	2	2,5	45,75
	Börumsbäcken	0,00	0,00	0,01	2,74	0,01	2,4	0,01	1,62	0,01	0,78	0,04	0,44	300,5	208	10,5	5	9,01
	Bulsjöån	73,59	28,26	1,16	9,6	1,17	9,11	1,18	8,64	1,43	7,28	2,03	5,05	295	53,5	9,5	5,5	9,48
	Flemmabäcken	0,00	0,00	0,01	1,05	0,01	0,9	0,01	0,65	0,02	0,33	0,03	0,22	299	208	8,5	6,5	10,81
	Kapellån	0,00	0,00	0,34	1,6	0,34	1,58	0,34	1,57	0,36	1,44	0,41	1,11	263	194,5	2	2,5	45,75
	Kisaån	0,00	0,00	0,4	4,55	0,41	4,53	0,41	4,45	0,45	3,66	0,64	2,45	302	60,5	3	2	33,25
	Pinnarpsbäcken	0,00	0,00	0,05	2,54	0,05	1,95	0,06	1,54	0,07	1,04	0,13	0,61	298	130,5	11	6	8,45
	Silverån	0,00	0,00	0,13	2,93	0,13	2,88	0,14	2,72	0,17	1,91	0,4	1,03	209,5	143,5	6	3,5	15,5
	Storån nedre delar	76,87	72,77	0,98	4,45	0,99	4,42	1	4,37	1,09	4,08	1,37	3,14	302	215,5	3	2,5	37,63
	Vadsbäcken	0,00	0,00	0,02	5,86	0,02	4,65	0,02	2,84	0,02	1,22	0,06	0,75	302	207	11	5	8,49
River regulation	Bastumyrbäcken	0,00	0,00	0,04	2,04	0,04	1,9	0,04	1,8	0,05	1,41	0,12	0,64	58	133,5	11	6	8,12
	Bergmyrbäcken	0,00	0,00	0,01	0,47	0,01	0,45	0,01	0,41	0,01	0,28	0,01	0,13	58,5	135	9,5	6	9,24
	Brattmyrledenbäcken	0,00	0,00	0,02	1,96	0,02	1,81	0,02	1,73	0,03	1,12	0,05	0,52	58,5	137,5	7,5	4,5	11,69
	Fågelvinbäcken	0,00	0,00	0,08	1,79	0,08	1,77	0,09	1,7	0,11	1,29	0,14	0,69	170	135,5	2,5	5	14,3
	Hjuksvallbäcken	0,00	0,00	0,04	3,05	0,04	2,84	0,04	2,57	0,05	1,99	0,06	0,92	265,5	131	9	7	9,91
	Kamplidenbäcken	0,00	0,00	0,04	3,02	0,04	2,86	0,04	2,76	0,04	1,8	0,08	0,84	147	137,5	7	6	12,74
	Kluddbäcken	0,00	0,00	0,15	9,39	0,16	9,01	0,16	8,26	0,19	5,91	0,38	2,81	58,5	134	7	5	12,39
	Kläppmyrbäcken	0,00	0,00	0,04	3,02	0,04	2,86	0,04	2,76	0,04	1,8	0,08	0,84	147	137,5	7	6	12,74
	Krickmyrbäcken	0,00	0,00	0,04	1,88	0,04	1,81	0,04	1,67	0,05	1,22	0,09	0,59	58,5	134	7	4	12,44
	Krycklan	0,00	0,00	0,03	2,65	0,04	2,57	0,04	2,41	0,04	1,58	0,07	0,74	58,5	134,5	8	5	11,02
Forestry management	Kvarnbäcken	0,00	0,00	0,03	2,82	0,04	2,72	0,04	2,43	0,04	1,74	0,1	0,8	58,5	133,5	9,5	5	9,42
	Renbergsbäcken	0,00	0,00	0,03	2,65	0,04	2,57	0,04	2,41	0,04	1,58	0,07	0,74	58,5	134,5	8	5	11,02
	Stormyrbäcken	0,00	0,00	0,01	0,86	0,01	0,83	0,01	0,75	0,01	0,53	0,03	0,24	58,5	134,5	10,5	5,5	8,36
	Stortjärnbäcken	0,00	0,00	0	0,4	0,01	0,39	0,01	0,35	0,01	0,24	0,01	0,11	58,5	135	7	7,5	12,63
	Svartbäcken	0,00	0,00	0,02	1,96	0,02	1,81	0,02	1,73	0,03	1,12	0,05	0,52	58,5	137,5	7,5	4,5	11,69
	Västra Nybyggsbäcken	0,00	0,00	0,02	1,61	0,02	1,53	0,02	1,39	0,03	0,95	0,06	0,44	58,5	135	8	6,5	11,13
	Acksjöälven	58,50	41,60	0,05	1,63	0,05	1,58	0,05	1,4	0,06	0,88	0,12	0,62	227,5	209	5,5	1,5	15,46
	Götån	0,00	0,00	0,07	4,5	0,07	4,24	0,08	3,45	0,09	1,74	0,26	0,95	164,5	209	7	4	12,8
	Hagälven	125,40	116,10	0,11	3,42	0,11	3,31	0,12	3,06	0,12	2,02	0,29	1,38	224	208	7,5	2,5	11,53
	Halgån	93,80	70,20	0,14	2,72	0,15	2,62	0,17	2,28	0,29	1,4	0,38	1,21	183,5	303,5	7,5	1	10,47
Hynnån	0,00	0,00	0,13	7,87	0,13	6,99	0,13	6,36	0,16	3,7	0,6	2,1	162	213	14	3,5	6,38	
Lettan	205,60	218,25	0,3	6,5	0,3	6,1	0,31	5,6	0,42	4,44	0,78	3,39	216,5	341	7,5	4	11,92	
Likan	0,00	0,00	0,08	5,05	0,08	4,71	0,09	4,44	0,11	2,41	0,39	1,4	164,5	174,5	9	3,5	9,58	
Tåsan	291,20	111,38	0,58	13,35	0,59	12,65	0,61	10,49	1,15	8,4	2,11	6,77	194	302,5	8,5	2,5	11,94	
Väjån	0,00	0,00	0,04	4,11	0,04	3,85	0,04	3,13	0,06	1,63	0,22	0,83	164,5	208	10,5	4	8,61	
Örån	108,60	77,80	0,2	3,28	0,2	3,11	0,23	2,83	0,41	2,25	0,58	1,72	198	346	7,5	3,5	11,61	

Table SI.1 continues

	Stream name	duration lo pulses	rate increase	rate decrease	nb rises	Alkalinity	pH	Conductivity	TOC	TN	NO <sub>2</sub> +NO <sub>3</sub> <sup>-</sup>	NH <sub>4</sub> <sup>+</sup>	TP	PO <sub>4</sub> <sup>-</sup>	Turbidity	Temperature	HDO saturation	Pesticide use
Agriculture	Borkhultsån	35,67	0,02	-0,01	27	0,63	7,51	10,30	8,00	409,00	11,50	9,00	11,00	1,50	19,13	15,76	102,01	very low
	Börumsbäcken	17,96	0,13	-0,04	2,5	1,47	7,29	20,34	18,70	1805,50	945,50	71,00	146,50	108,00	447,87	12,21	88,93	low
	Bulsjöån	17,27	0,38	-0,11	9	0,44	7,11	9,43	10,90	574,00	80,00	52,50	10,00	3,00	5,34	14,04	93,31	very low
	Flemmabäcken	14,12	0,03	-0,01	1	0,76	7,47	15,63	37,10	1840,00	352,50	42,50	141,00	60,00	144,23	12,19	88,85	very low
	Kapellån	35,67	0,02	-0,01	27	2,54	7,48	30,70	16,20	2137,00	1383,50	71,00	166,50	122,00	258,72	13,51	76,72	low
	Kisaån	45,75	0,06	-0,03	23	0,66	7,38	10,95	9,75	432,00	5,00	10,00	9,50	3,00	3,54	15,60	91,50	very low
	Pinnarpsbäcken	15	0,12	-0,03	5	0,55	7,49	11,02	11,40	693,50	210,00	3,50	13,00	4,00	64,82	13,09	100,33	very low
	Silverån	25,79	0,09	-0,04	5	0,23	6,93	5,92	13,25	500,00	45,00	4,50	10,00	3,50	31,64	12,45	97,06	very low
	Storån nedre delar	42,5	0,1	-0,03	20	0,74	7,31	12,35	12,55	831,50	171,50	33,50	49,00	19,50	58,29	13,76	93,51	very low
	Vadsbäcken	18,13	0,32	-0,07	0,5	3,06	7,56	53,75	19,55	2225,50	1078,00	110,50	342,00	256,50	611,99	12,71	77,12	medium
River regulation	Bastumyrbäcken	15,38	0,13	-0,03	0	0,17	6,26	36,96	27,47	289,00	16,50	3,25	18,50	8,00	596,99	8,12	97,99	-
	Bergmyrbäcken	15,43	0,02	-0,01	3	0,13	6,17	28,36	23,67	267,00	2,75	3,75	11,50	4,50	6421,75	8,18	95,29	-
	Brattmyrledenbäcken	21,75	0,07	-0,02	1,5	0,10	6,15	28,27	21,58	269,50	5,00	3,25	16,00	7,00	19,52	7,44	89,27	-
	Fågelvinbäcken	18,6	0,02	-0,01	12,5	0,06	5,54	29,12	31,72	592,50	21,00	21,50	34,00	8,50	606,22	9,05	89,90	-
	Hjuksvallbäcken	12,43	0,15	-0,04	0,5	0,11	6,19	34,11	26,07	528,50	128,50	5,00	26,00	6,50	77,02	8,91	94,79	-
	Kamplidenbäcken	16,69	0,09	-0,03	1	0,12	5,85	33,17	31,07	471,00	9,50	11,50	31,00	13,00	162,06	7,28	89,43	-
	Kluddbäcken	18,42	0,36	-0,1	2,5	0,06	5,40	27,24	41,89	397,00	2,00	6,00	24,50	6,50	231,83	8,41	96,95	-
	Kläppmyrbäcken	16,69	0,09	-0,03	1	0,11	5,60	31,35	33,46	487,00	6,50	4,50	30,00	10,00	272,31	7,29	83,99	-
	Krickmyrbäcken	23,17	0,07	-0,02	2	0,06	5,94	28,38	28,54	530,50	5,00	8,50	31,00	8,00	118,11	8,38	94,88	-
	Krycklan	20,5	0,08	-0,03	1,5	0,14	6,55	30,22	13,39	269,00	7,00	3,75	9,50	2,50	8,85	9,40	94,13	-
Forestry management	Kvarnbäcken	19,83	0,15	-0,03	0,5	0,09	6,19	28,75	27,82	621,50	47,50	15,00	44,00	6,50	111,86	9,04	96,06	-
	Renbergsbäcken	20,5	0,08	-0,03	1,5	0,13	6,32	29,95	18,84	304,00	5,00	4,25	19,00	3,00	83,59	8,96	93,77	-
	Stormyrbäcken	18,73	0,04	-0,01	3	0,07	5,48	27,46	34,48	375,50	8,00	7,00	25,00	11,00	25,55	7,61	88,18	-
	Stortjärnbäcken	12,7	0,01	0	2	0,12	5,89	30,99	27,04	367,50	12,00	8,50	38,00	13,50	92,19	7,78	92,97	-
	Svartbäcken	21,75	0,07	-0,02	1,5	0,14	6,14	30,09	21,78	274,50	5,50	2,75	11,00	4,00	31,92	7,80	97,98	-
	Västra Nybyggsbäcken	13,9	0,07	-0,02	1	0,18	6,20	30,38	29,02	255,00	7,50	2,50	14,00	4,50	4,29	7,68	94,73	-
	Acksjöälven	52,25	0,04	-0,02	14	0,12	6,65	29,09	12,05	338,00	23,50	7,00	7,00	2,50	4,62	12,14	93,87	-
	Götån	19,23	0,15	-0,06	5	0,15	6,74	32,25	10,10	293,50	29,00	6,00	6,50	3,50	72,44	7,40	97,50	-
	Hagälven	32,92	0,14	-0,05	21,5	0,20	7,04	37,78	5,70	272,00	73,00	7,00	4,00	1,50	0,93	11,00	97,47	-
	Halgån	91,5	0,05	-0,03	29,5	0,10	6,77	22,04	7,90	234,50	12,00	6,00	5,50	1,50	0,24	10,66	94,03	-
Hynnan	23,55	0,44	-0,14	2,5	0,13	6,63	27,62	12,10	320,50	16,00	4,50	8,00	2,00	9,04	7,51	94,84	-	
Lettan	19,7	0,2	-0,09	67,5	0,13	6,48	26,66	7,40	293,00	62,00	11,00	9,00	3,00	10,45	7,11	96,45	-	
Likan	22,3	0,27	-0,09	3	0,23	6,94	28,81	9,40	243,50	0,50	2,25	7,00	3,00	18,05	7,72	97,00	-	
Tåsan	32,5	0,4	-0,24	109,5	0,21	6,58	32,92	4,75	174,00	17,50	7,50	7,00	2,50	6,60	7,58	22,34	-	
Väjån	17,58	0,23	-0,07	2	0,16	6,60	32,16	10,45	329,00	13,00	5,50	8,00	2,00	2,96	10,69	86,83	-	
Örån	29,33	0,12	-0,07	93	0,08	6,23	18,16	8,55	215,50	4,00	4,00	6,00	3,00	46,74	6,18	92,12	-	

<sup>1</sup> Tree volume: the volume of forest standing stock, including bark but excluding branches and roots; Ditching: meters of ditches in the catchment per meter of stream in the same catchment; V regulated: volume of water stored in the reservoir and available for regulation; V deviation: the average volume deviated between the current flow regime and the natural flow regime based on daily averages; Water stored: percentage of annual runoff that can be stored in the reservoir; TOC: total organic carbon; TN: total nitrogen; TP: total phosphorus; HDO saturation: saturation level of dissolved oxygen in the water

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*Appendix to:*

Truchy, A., Göthe, E., Angeler, D. G., Ecke, F., Sponseller, R. A., Bundschuh, M., Johnson, R. K. And McKie, B. G. 2019 Partitioning spatial, environmental and community drivers of ecosystem functioning.

## *Appendix S2*

### Sampling methods to quantify ecosystem functioning

#### *Quantifying ecosystem processes*

To quantify algal biomass accrual, four pairs of tiles (25 × 25cm, Seramiksan) were attached at the stream bottom (unglazed surface uppermost) and left from beginning to end of August (30 days in total) to allow sufficient time for algal colonisation and growth. In order to assess invertebrate grazing pressure, the edges of one tile of each pair were coated with a 5-mm wide layer of petroleum jelly while the other tile was left as a control (Lamberti & Resh 1983). We assessed algal biomass accrual using a BenthosTorch (bbe Moldaenke GmbH, Kiel-Kronshagen, Germany) which measures the fluorescence of chlorophyll *a* and converts it to an estimate of chlorophyll biomass (Kahlert & McKie 2014). The measured values were standardised to chlorophyll *a* mg.m<sup>-2</sup>.degree-day<sup>-1</sup> to factor out potential influences of temperature on algal biomass accrual.

To assess litter decomposition, 5.0 ± 0.1 g of air-dried arboreal *Betula* spp. leaves were enclosed in mesh bags, which were then deployed in the stream channels. The litter was collected from sites outside of our sampling regions, from trees near Uppsala and Umeå (59°48'42.1"N 17°39'47.1"E and 63°49'57.5"N 20°17'44.5"E, respectively). Half the bags were constructed from a coarse mesh (10 mm), allowing colonisation by both invertebrates and microbes. The remainder half was made with fine mesh (0.5 mm) which excludes invertebrates, and allowed for the quantification of microbial-mediated decomposition. Five replicates of each mesh type were attached to the stream bottom for 40 days. After retrieval, leaves were cleaned under tap water and six 12-mm diameter leaf discs were cut from six different leaves in order to assess for biomass accrual of aquatic fungi. The remaining leaves were oven-dried for 48 hours at 110°C and then ashed at 550°C for four hours to get ash free dry mass (AFDM). Leaf mass loss was corrected for leaching losses (determined with a 24h laboratory trial) and temperature, and the breakdown rate coefficient  $k_{dd}$  calculated for each litterbag using the negative exponential decay model (Benfield 1996).

Fungal biomass was estimated as ergosterol, a component of eumycotic cell walls (Gessner 2005). Briefly, using alkaline methanol, ergosterol was extracted from freeze-dried leaf material and subsequently purified by solid-phase extraction (Sep-Pak® Vac RC tC18 500 mg sorbent; Waters, Milford, USA). The ergosterol concentration was quantified by high-performance liquid chromatography (HPLC; 1200 Series, Agilent Technologies, Santa Clara, USA) at a wavelength of 282 nm. Ergosterol concentrations were finally converted to fungal biomass assuming an average mycelia concentration of 5.5 mg ergosterol.g<sup>-1</sup> fungal dry weight (Gessner & Chauvet 1993). The fungal biomass accruals were then standardised to µg.g<sup>-1</sup>.degree day<sup>-1</sup>, based on the assumption that no fungi colonisation happened prior to the immersion in stream water (Krauss, Sridhar & Bärlocher 2005).



Suspended FPOM was sampled by filling a 1 L water bottle at the water surface. Water bottles were frozen and later filtered through a 0.063 mm sieve to capture FPOM. To assess short-term particle deposition rates, 16 × 16 cm Astroturf mats (Wolters et al. 2004) were attached at the stream bottom to trap transported FPOM. After three days, the mats were retrieved and frozen. Mats were later thawed and cleaned in a tray and filtered through a 0.063 mm sieve. For both suspended and deposited FPOM, retained material was oven-dried for 24 h at 60°C, weighed to the nearest 0.01 mg and ashed at 550°C for 4 h in order to assess the fraction of inorganic particles in our FPOM samples. We then calculated the ratio between suspended and deposited of organic particles as a proxy for FPOM dynamics.

*Fontinalis dalecarlica* is a widespread bryophyte in Sweden and was selected to be a phytometer (Dietrich, Nilsson & Jansson 2013; Dietrich, Nilsson & Jansson 2015). Two reference sites, flowing through undisturbed forests and where *F. dalecarlica* was abundant, were selected from outside our sampled regions (forestry gradient: 63°53'2.0"N 20°18'19.8"E; hydropower and agriculture gradients: 59°40'20.7"N 15°56'2.8"E). The green tips of the bryophytes, representing the sprouts of the year, were cut and enclosed in fine mesh bag ( $6.0 \pm 0.1$ g). Five replicate bags were deployed in the 36 streams for  $83 \pm 1$  days in the agricultural region and for  $97 \pm 2$  days for the two remaining regions, considered as cooler. Back in the laboratory, samples were washed under tap water, weighed to the nearest 0.01g, oven-dried at 60°C for 48h and weighed again. Initial dry weights were back calculated using a linear regression made from extra samples. The biomass accrual of *F. dalecarlica* was then calculated as a dry weight difference corrected for temperature and exposure days.

#### *Functional traits*

Trait categories were extracted from Schmidt-Kloiber and Hering (2015) for fish and Tachet et al. (Tachet et al. 2010) for invertebrates. We focused on traits which are closest in their definition to true functional effect traits (Truchy et al. 2015) (Table S2.1), i.e. most likely to be correlated with the effects of organisms on ecosystem processes (Hooper et al. 2002; Lavorel & Garnier 2002; Naeem & Wright 2003).

Fish traits were binary coded representing a presence/absence of the trait (Schmidt-Kloiber & Hering 2015). Invertebrates traits were fuzzy coded from 0 (no affinity with to the category) to a maximum value of 3 or 5 (high affinity), allowing species to have more than one trait state simultaneously (Tachet et al. 2010). We then calculated trait scores weighted individually for each species.

We found that **dry biomass of our detritivore species was usually the highest in the northern region (forestry) and the lowest in the southern region (agriculture; Table S2.2)**, supporting the idea of a latitudinal variation in intraspecific body size (Ashton, Tracy & de Queiroz 2000). These results also highlight the limited capacity of large-scale trait database to capture spatiotemporal variability in species phenotypes.

**Table S2.1.** Trait categories extracted from Schmidt-Kloiber and Hering (2015) for fish and Tachet *et al.* (2010) for invertebrates. A brief description of the states of the traits is included along with their implication for the studied ecosystem processes. All traits were quantitative and the score taken by a given trait state ranges from 0 to 10.

Organism group	Trait categories	Trait states	Implication for ecosystem functioning
Fish	Resource consumption	Body length (1) L < 20 cm; (2) 20-39 cm; (3) L > 39 cm	Big individuals are more likely to perform better, having a greater impact on ecosystem processes.
		Diet (1) invertivorous; (2) piscivorous; (3) phytophagous; (4) omnivorous; (5) carnivorous; (6) other	Invertivorous and omnivorous are the fish that would affect most strongly the studied processes.
	Habitat use	Reproduction habitat (1) phytophilic; (2) lithophilic; (3) phyto-lithophilic; (4) psammophilic; (5) other	Reflects the potential for both trophic and non-trophic interactions in the different habitats.
		Feeding habitat (1) benthivorous; (2) water column	Benthivorous fish are more likely to affect processes occurring in the stream bed, where most of our ecosystem processes were quantified.
Macroinvertebrates	Resource consumption	Maximum size (1) L ≤ 0.25 cm; (2) 0.25-0.5 cm; (3) 0.5-1 cm; (4) 1-2 cm; (5) 2-4 cm; (6) 4-8 cm; (7) L > 8 cm	Big individuals are more likely to perform better their function e.g. breaking up leaf litter than smaller individuals.
		Feeding habits (1) absorber; (2) deposit-feeder; (3) shredder; (4) scraper; (5) filter-feeder; (6) piercer; (7) predator; (8) parasite	Describes both the feeding mode and the degree of dietary flexibility, influencing in return specific ecosystem functions
	Habitat use	Substrate preference (1) flags/boulders/cobbles/ pebbles; (2) gravel; (3) sand; (4) silt; (5) macrophyte; (6) twigs/roots; (7) organic detritus/litter; (8) mud	Reflects the relative abundances of species with preferences for the habitats in which our processes (or functional indicators) act – and if a process like decomposition occurs across multiple habitats, then a diversity of preferences is good.
		Current velocity preferendum (1) null; (2) slow; (3) medium; (4) fast	Relates to microhabitat preferences, which are likely to dictate conditions under which species operate the most efficiently.
	pH preferendum (1) pH ≤ 4; (2) 4-4.5; (3) 4.5-5; (4) 5-5.5; (5) 5.5-6; pH > 6		

**Table S2.2** Mean biomass ± SE of detritivore species according to the dominant anthropogenic pressure. Only species that were common between all the studied sites are shown.

	Forestry	Hydropower	Agriculture
<i>Amphinemura</i> spp.	3.6.10 <sup>-4</sup> ± 6.24.10 <sup>-5</sup>	2.5.10 <sup>-4</sup> ± 1.33.10 <sup>-5</sup>	1.8.10 <sup>-4</sup> ± 2.68.10 <sup>-5</sup>
<i>Leuctra</i> spp.	5.6.10 <sup>-4</sup> ± 2.70.10 <sup>-5</sup>	5.5.10 <sup>-4</sup> ± 2.74.10 <sup>-5</sup>	4.1.10 <sup>-4</sup> ± 2.65.10 <sup>-5</sup>
Limnephilidae	3.6.10 <sup>-3</sup> ± 8.20.10 <sup>-4</sup>	2.6.10 <sup>-3</sup> ± 7.00.10 <sup>-4</sup>	1.5.10 <sup>-3</sup> ± 5.50.10 <sup>-3</sup>
<i>Nemoura</i> spp.	2.2.10 <sup>-3</sup> ± 9.31.10 <sup>-5</sup>	3.2.10 <sup>-3</sup> ± 3.10.10 <sup>-4</sup>	4.2.10 <sup>-3</sup> ± 1.00.10 <sup>-3</sup>
<i>Protonemura meyeri</i>	8.3.10 <sup>-4</sup> ± 1.20.10 <sup>-4</sup>	5.4.10 <sup>-4</sup> ± 4.52.10 <sup>-5</sup>	7.7.10 <sup>-4</sup> ± 5.56.10 <sup>-5</sup>

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*Appendix to:*

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## *Appendix S3*

### Sampling methods of the organism groups

Primary producers (benthic diatoms and macrophytes) and consumers (benthic invertebrates and fish) were sampled in each stream reach.

Benthic diatoms were collected according to the European/Swedish standard method (SS-EN 14407; CEN 2004) by scraping biofilm from the upper surface of five cobbles, which were then pooled. The samples were stored in light-blocking bottles and preserved with Lugol's iodine solution before identification and counting.

Macrophytes were sampled following the Swedish EPA's protocol (Naturvårdsverket 2003). For each stream, depending on the stream width, six to 10 transects were chosen to sample in total 100 quadrats. Along each transect, 25 x 25 cm quadrats were placed side by side from one bank to the other. In each quadrat the presence of bryophytes and vascular plant species were recorded using an aquascope. Relative frequencies of species in the quadrats were then calculated.

The benthic invertebrate community was assessed following the European and Swedish standard methods (SS-EN 10870:2012; (Naturvårdsverket 2010)). In brief, five samples were taken using standardised kick sampling with a hand net (0.5-mm mesh size). Each sample was taken by disturbing the bottom substratum for 60s along a 1 m long stretch. Samples were preserved in 70% ethanol in the field and processed in the laboratory by sorting against a white background. Invertebrates were identified to the lowest taxonomic unit possible, generally to species level, and counted using dissecting and light microscopes.

Finally, the fish communities were electro-fished following the European standard method (SS-EN 14011: 2006). Briefly, sampling was performed once during September-October. At each site, a 20-50 m long representative stretch of reach was electro-fished (total sampled area depended on stream width, longer reaches were sampled in smaller streams) using a bank-based generator operated by a two-crew team using a single handheld anode. The number of successive removals at each site varied between one and three. Fish were identified to species and counted. Species densities (number of individuals.m<sup>-2</sup>) were estimated accounting for the probability of catch at each site.

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## Appendix S4

### Partitioning the individual functional factors

**Table S4.1.** Results from the variance partitioning of different ecosystem processes (VP-II) in 36 streams explained by four sets of explanatory variables: between- (B) and within- (W) region spatial components, community composition ( $C_c$ , all four community groups) and environment (E), and their joint effects (represented as  $\cap$ ). The global model corresponds to  $B + (W) + C_c + E$  depending whether W was selected by the forward selection procedure or not, potentially leading to empty cells. For each fraction, an adjusted  $R^2$  is given and when testable the associated p-value is indicated. P-values smaller than 0.05 are in bold and when  $0.05 < P < 0.10$ , figures are in italics.

	Algal biomass accrual		Litter decomposition (coarse bags)		Litter decomposition (fine bags)		Fungi biomass accrual (coarse bags)		Fungi biomass accrual (fine bags)	
	$R^2$	P	$R^2$	P	$R^2$	P	$R^2$	P	$R^2$	P
B	0.03	<b>0.03</b>	0.05	<b>0.046</b>	0.04	<b>0.04</b>	-0.02		-0.01	
W							-0.01			
$C_c$	0.12	<b>0.005</b>	0.15	<b>0.017</b>	0.06	<i>0.067</i>	0.36	<b>0.006</b>	0.32	<b>0.003</b>
E	-0.01		0.10	<b>0.038</b>	0.11	<b>0.023</b>	0.03		-0.04	
$W \cap B$							0.001			
$B \cap C_c$	-0.03		0.04		0.04		-0.009		0.09	
$W \cap C_c$							0.17			
$W \cap E$							-0.008			
$B \cap E$	0.01		-0.05		-0.05		0.02		0.0001	
$C_c \cap E$	0.34		0.29		0.48		-0.007		0.25	
$W \cap B \cap E$							0.0001			
$W \cap B \cap C_c$							0.001			
$B \cap C_c \cap E$	0.38		0.005		-0.05		-0.01		-0.10	
$W \cap C_c \cap E$							-0.06			
$W \cap B \cap C_c \cap E$							-0.004			
Global model	0.83	<b>&lt; 0.001</b>	0.58	<b>0.002</b>	0.63	<b>&lt; 0.001</b>	0.47	<b>0.007</b>	0.51	<b>0.031</b>
Residuals	<i>0.17</i>		<i>0.42</i>		<i>0.37</i>		<i>0.53</i>		<i>0.49</i>	

**Table S4.2.** Results from the variance partitioning of ecosystem functioning in 36 streams explained by four sets of explanatory variables: between regions (B), within regions (W), community composition ( $C_c$ ) and environment (E) and their joint effects (represented as  $\cap$ ). The community groups were fitted separately. For each fraction, an adjusted  $R^2$  is given and when testable the associated p-value is indicated. P-values smaller than 0.05 are in bold and when  $0.05 < P < 0.10$ , figures are in italics.

	Benthic diatoms		Macrophytes	
	$R^2$	P	$R^2$	P
W	0.02	<b>0.041</b>	0.01	
B	0.03	<b>0.042</b>	0.02	<i>0.075</i>
$C_c$	0.07	<b>0.010</b>	0.12	<b>0.001</b>
E	0.14	<b>&lt; 0.001</b>	0.19	<b>&lt; 0.001</b>
$W \cap B$	-0.009		-0.001	
$B \cap C_c$	0.009		0.02	
$W \cap C_c$	0.03		0.05	
$W \cap E$	-0.02		-0.03	
$B \cap E$	-0.03		0.02	
$C_c \cap E$	0.13		0.08	
$W \cap B \cap E$	0.01		-0.0002	
$W \cap B \cap C_c$	0.002		-0.006	
$B \cap C_c \cap E$	0.06		0.014	
$W \cap C_c \cap E$	-0.003		0.004	
$W \cap B \cap C_c \cap E$	-0.005		0.004	
Global model	0.45	<b>&lt; 0.001</b>	0.50	<b>&lt; 0.001</b>
<i>Residuals</i>	<i>0.56</i>		<i>0.50</i>	