

Shifts in the Diversity and Composition of Consumer Traits Constrain the Effects of Land Use on Stream Ecosystem Functioning

André Frainer^{*,†}, Brendan G. McKie^{†,1}

*Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

†Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

¹Corresponding author: e-mail address: brendan.mckie@slu.se

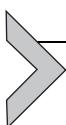
Contents

1. Introduction	170
2. Methods	172
2.1 Land-Use Gradient	172
2.2 Ecosystem Functioning	173
2.3 Detritivore Richness, Density and Metabolic Capacity	174
2.4 Functional Traits	174
2.5 Isotopes	175
2.6 Fungal Biomass	177
2.7 Data Analyses	177
3. Results	180
3.1 Land-Use Gradient	180
3.2 Leaf Decomposition	180
3.3 Detritivore Biotic Variables	181
3.4 Fungal Biomass	183
3.5 Structural Equation Model	183
3.6 Isotopes	185
4. Discussion	185
Acknowledgements	190
Appendix	190
References	196

Abstract

Species functional traits provide an important conceptual link between the effects of disturbances on community composition and diversity, and their ultimate outcomes for ecosystem functioning. Across 10 boreal streams covering a gradient of increasing intensity of land-use management, from forested to agricultural sites, we analysed

relationships between leaf decomposition, the feeding traits of detritivores and measures of anthropogenic disturbances in two seasons. The direct effect of increasing land-use intensity on decomposition was positive and was associated with increases in nutrient concentrations and current velocities. However, this relationship was countered by negative effects associated with a loss of detritivore functional diversity along the gradient during autumn and shifts in species trait composition during spring, limiting the net change in functioning associated with increasing land-use management overall. Our results highlight the key roles that trait identity and diversity can play in mediating the effects of human disturbance on ecosystem functioning.



1. INTRODUCTION

Species loss can affect ecosystem functioning at similar or even higher levels than other major environmental disturbances (Hooper et al., 2012; Lavorel and Garnier, 2002; Poff et al., 2006; Tilman et al., 2012). However, it is often challenging to disentangle the direct effects of species loss on ecosystem functioning from those of anthropogenic disturbances, which may themselves be driving diversity change, such as alterations in pH (McKie et al., 2009) or nutrient enrichment (Woodward et al., 2012). Species functional traits provide an important conceptual link between the effects of disturbances on community composition and diversity, and their ultimate outcomes for ecosystem functioning (Enquist et al., 2015; Lavorel and Garnier, 2002; Mouillot et al., 2013). However, relationships between functional traits, their responses to disturbances and outcomes for ecosystem functioning remain poorly assessed for most systems. A combined perspective on these linkages should improve prospects for developing a more mechanistic framework that couples disturbances, diversity and functioning in a changing world.

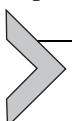
Disturbances affect the distribution and composition of functional traits in predictable sequences, with correlated clusters of traits, termed ‘response traits’, either favoured or suppressed (Lavorel and Garnier, 2002; McKie et al., 2009; Poff et al., 2006). In general, smaller, fast-growing, short-lived organisms with more generalist feeding traits are more likely to persist over the long term at highly disturbed sites, whereas larger, slow-growing, long-lived and more specialised organisms are often more vulnerable to local extinction (Statzner and Bêche, 2010; Woodward et al., 2012). Such shifts in species trait composition may further impact ecosystem functioning, particularly when traits crucial for key ecosystem processes (known as ‘effect

traits') are impacted (Lavorel and Garnier, 2002; Pakeman, 2011). However, it is unclear whether the traits typically characterised as response traits are necessarily identical with effect traits (Lavorel and Garnier, 2002; Pakeman, 2011). Indeed, while traits related to mobility or development time are often more closely related to disturbances, traits related to resource consumption and nutrient requirements may be more closely related to ecosystem functioning.

Further complications arise from the potential for disturbances to affect not only the identity of traits but also the dominance hierarchies and interaction strengths among the species bearing those traits (Thébaud and Loreau, 2005). Changes in both species richness and evenness can alter trait relative abundances, and hence the dominance of particular traits, with potentially strong impacts on ecosystem functioning (Hillebrand et al., 2008; McKie et al., 2008; Nilsson et al., 2008). Changes in both the richness and relative abundances of traits can further impact functioning by altering the intensity of antagonistic or facilitative species interactions, which may hinder or enhance key processes, respectively (Jonsson and Malmqvist, 2003; Jousset et al., 2011). Finally, species interactions can also change as a result of sublethal effects of abiotic stressors on the behaviour of particular species (Newcombe and Macdonald, 1991), further highlighting the need to disentangle the direct effects of disturbances on functioning from those arising from shifts in species trait composition and diversity.

In this study, we investigated the impacts of an increase in land-use intensity on the distribution and diversity of functional traits within a guild of stream-living detritivorous invertebrates, and how these shifts in turn affected a key ecosystem process, leaf litter decomposition. The land-use gradient consisted of 10 streams ranging from fully forested to streams flowing through long-established managed meadows, and was associated with changes in stream hydromorphology, nutrient concentrations and riparian vegetation. As relationships between detritivores and leaf litter decomposition may vary greatly across seasons (Frainer et al., 2014), we conducted our study in both autumn and spring. Leaf decomposition is an important ecological process, which can be used in environmental assessment (Gessner and Chauvet, 2002; Pascoal et al., 2003), with rates of leaf decomposition often differing between impacted and control sites (McKie and Malmqvist, 2009). However, classification of ecological status based on ecosystem process rates is not always straightforward (Bergfur et al., 2007; Pascoal et al., 2001), particularly as relationships between disturbance gradients and functional response are often not monotonic (McKie et al., 2006; Woodward et al., 2012).

We expected that decomposition overall would be stimulated by increases in nutrients along the land-use gradient, but that this effect might be countered by a reduction in leaf processing capacity among the detritivores, associated with shifts in trait identity and diversity. Specifically, we hypothesised that (1) increases in the intensity of agricultural land use will affect the identity and evenness of traits present, with a greater dominance of generalist consumers, while pristine streams will have more obligate leaf-consumers, and a more even distribution of functional traits; and (2) the greater dominance of more generalist consumers in the agricultural sites will lower leaf decomposition rates, reflecting their reduced specialisation and dependency on the litter resource.



2. METHODS

2.1 Land-Use Gradient

During autumn 2011 and spring 2012, we investigated multiple parameters associated with the ecosystem-level process of leaf decomposition in 10 streams, which represented a gradient of increasing intensity of land-use management in the catchment.

The major changes along the land-use gradient are detailed below, but included: (i) an increase in the amount of managed (ploughed, sowed and fertilised) meadow adjacent to the study streams (from none to extensive), (ii) a decline in the proportion of forest in the catchment; (iii) a shift in the composition of riparian vegetation (from predominantly coniferous to deciduous) and (iv) an increase in channel modification and other measures (agricultural ditches) to facilitate drainage.

The least managed streams flowed through mature forest (not subject to clear-cutting for >80 years), whereas the most managed streams flowed through agricultural meadows, subject to tillage and fertilisers, and with more modified channel forms and reduced riparian vegetation (Pettersson et al., 2004). Agricultural meadow sites date from at least the mid 1800s and are mostly used for production of hay, but crop farming and limited animal husbandry (mostly cattle) occur upstream in some catchments (Pettersson et al., 2004). All meadows are interspersed with blocks of forest, so that even the most agricultural sites have some forest in the catchment (Table A.1). All streams had predominantly rocky substrates (boulders, cobbles and some gravel), with some coarse sand (Table A.1) and were of comparable width. However, the more agricultural streams were generally more channelised (i.e. hydromorphologically modified to facilitate drainage and

transport), being more strongly straightened and deeper than the forested sites and with simpler and coarser stony substrates at the sampling points. All streams had some riparian vegetation, ranging up to 3 m width for the most agricultural streams, to extensive forest around the less impacted sites. The riparian vegetation of the agricultural sites was mostly composed of broadleaf trees, especially birch (*Betula* spp.), alder (*Alnus incana* (L.) Moench) and willow (*Salix* spp.), while birch and Norwegian spruce (*Picea abies* (L.) H. Karst) dominated the forested sites. Across the land-use gradient, dissolved concentrations of total nitrogen ranged from 0.23 to 1.12 mg/L, with nitrate [N–NO₃] ranging from 0.01 to 0.56 mg/L. Phosphorus concentrations were mostly below the detection limit (<4 mg/L) (see Table A.1 for mean values of each sampling site).

We measured water velocity and discharge halfway through the experimental period in each season, by taking water velocity measurements at 60% depth every 0.5 m across the stream channel. Discharge was calculated as:

$$Q = \sum (\nu_i * A_i), \quad (1)$$

where ν_i is the water velocity (m/s) at 60% depth at point i and A is the cross-sectional area (m²) of the channel corresponding to point i (Gordon et al., 2004). Stream substratum was estimated as percentage substratum cover of five categories: (1) silt and sand; (2) coarse sand; (3) sand-pebbles; (4) pebbles–boulders and (5) boulders (Giller and Malmqvist, 1998). Riparian vegetation width was also characterised based on estimates of the width of riparian tree cover, from 0 (no trees, only grass) to 5 (riparian tree vegetation extending at least 10 m to each side of the channel).

2.2 Ecosystem Functioning

We studied the decomposition of silver birch (*Betula pendula* Roth) leaves, which were collected freshly abscised from the ground and air-dried for 2 weeks at the start of autumn. An amount of 4 ± 0.05 g dried leaves was placed in litter bags of two different mesh sizes: 0.5 mm (fine mesh bags), which allows microbial colonisation of the leaves while excluding stream invertebrates, and 10 mm (coarse mesh bags), which allows both invertebrates and microbes to colonise the litter. Five litter bag pairs consisting of one coarse and fine mesh bag each were evenly spaced over 50 m of riffle habitat (fast flowing rocky habitat with flow broken by emergent stones) in each stream, and retrieved when leaves at the fastest decomposing site had reached approximately 50% dry mass remaining in the coarse mesh bags.

(6 weeks in autumn and 4 weeks in spring). After retrieval, the litter bags were immediately transported to the laboratory for processing, where the leaves were removed from the bags, rinsed under tap water, oven-dried at 60 °C for 48 h and weighed to nearest 0.01 g.

We calculated decomposition as a rate k , using the exponential equation (Petersen and Cummins, 1974):

$$-k = \frac{\ln(M_t) - \ln(M_0)}{dd}, \quad (2)$$

where M_t is the final mass, M_0 is the initial mass and dd is the sum of daily average water temperature in °C.

2.3 Detritivore Richness, Density and Metabolic Capacity

We sorted and identified to species level all leaf-eating detritivores found in the litter bags. After identification, individuals of each species from each sample were pooled and placed in separate pre-weighed aluminium pans, oven-dried for 48 h at 60 °C and weighed to 0.1 mg. We calculated the metabolic capacity (MC) of each species according to the formula:

$$MC = m_i^{0.75} * x_i, \quad (3)$$

where m is the average individual body mass of species i , x is the number of individuals of species I and the exponent 0.75 represents a general relationship between metabolism and body size across a wide range of vertebrate and invertebrate species (Brown et al., 2004). We also quantified detritivore density as the sum of all detritivore individuals found per litter bag.

2.4 Functional Traits

Our analyses focused on the leaf-eating detritivores colonising our litter bags, a functional guild often termed ‘shredders’ (Cummins and Klug, 1979). However, while all species in this guild consume leaves, they vary both in their feeding mode and in their degree of dependency on litter as a primary nutrient resource. The most obligate leaf-shredders, with diets represented by >70% leaf material (see Table A.2), are best exemplified by the caddisfly genus *Halesus* and the stonefly *Nemoura avicularis* Morton. Less obligate leaf-consumers include those that gain significant proportions of their diet either by scraping biofilm from leaf or rock surfaces (e.g. the stonefly *Amphinemura* spp.) (Lieske and Zwick, 2007) or by gathering deposited and/or drifting fine particles (such as *Taeniopteryx nebulosa* Linnaeus,

another stonefly), and these species are more likely to rasp, rather than actively chew, leaf surfaces. Many detritivores also include increasing proportions of prey items in their diets as they complete their larval development, particularly various caddisflies (Wissinger et al., 2004). However, none of our detritivore species fall exclusively into any one of these categories (Göthe et al., 2009; Layer et al., 2013), rather they vary in their association with these different types of feeding traits and behaviours. Accordingly, we used fuzzy coding when scoring species–trait associations, allowing membership of our species in more than one trait grouping simultaneously, with trait scores weighted individually for each species (Table A.2). All trait codings are based on the information compiled in the Freshwater Ecology database (Schmidt-Kloiber and Hering, 2011).

Using these traits to describe the species, we calculated two measures of functional diversity. Firstly, we assessed functional identity (F_{identity}) by using community-weighted mean trait values (Garnier et al., 2004) based on the mass ratio hypothesis (Grime, 1998), which captures the identity of the dominant traits within a community. F_{identity} was calculated using the R package *FD* (Laliberté and Shipley, 2011), which yields a matrix where traits are weighted by the abundance of all species sharing it. This matrix was resolved with principal component analysis (R package *vegan*; Oksanen et al., 2011) for each season individually to obtain the axis that explained most of the variation across sites. Secondly, we calculated the functional dispersion ($F_{\text{dispersion}}$) of each community using the R package *FD* (Laliberté and Shipley, 2011). $F_{\text{dispersion}}$ is a measure of functional trait distribution that accounts for the dissimilarity among traits (Laliberté and Legendre, 2010). To assess $F_{\text{dispersion}}$, a centroid was calculated from the trait-based distance matrices for each season, where species were weighted by their abundance. From this, the distances between the centroid and each species, which are weighted again by their abundances, were further calculated. The sum of these distances is $F_{\text{dispersion}}$.

2.5 Isotopes

Due to the potential for algal productivity to be stimulated in the agricultural sites by increased nutrient concentrations, we used isotope analyses to investigate the degree to which the potentially omnivorous stream benthic detritivores shifted in their resource assimilation along the disturbance gradient. We sampled invertebrate detritivores from each stream in each of the two seasons (during October and May) by kick-sampling riffles where the

litter bags had been previously deployed. From each stream, species were kept separately in clean tap water for 24 h in a climate-controlled room at 6 °C to allow emptying of digestive tracts before processing for isotope analyses. We also sampled resources potentially contributing to detritivore diets. Leaf litter and grass were collected directly from the ground adjacent to the streams (leaf litter and dead grass), while aquatic moss (*Fontinalis* sp.) was sampled from within the streams (water moss) in both autumn and spring. We used algal isotope data (K. Stenroth, unpublished data) sampled in each stream during summer to characterise the isotopic signal of auto-trophic periphyton. Algal samples consisted of biofilm and green algae that were scraped from boulders and separated before isotope analysis. We were unable to obtain sufficient periphyton for isotope analysis during October. Hence, these samples are regarded as representative of the algae consumers that had access to earlier in the season, prior to the autumn dieback, though we interpret the findings with some caution given the potential for the isotopic signature of algae to have shifted from summer to early autumn (Campbell and Fourqurean, 2009). All material was oven-dried at 60 °C for 24 h, weighed to 1 ± 0.5 mg and stored in small tin capsules. Samples were analysed by the Davis Isotope Facilities (Davis, USA) for ^{13}C and ^{15}N .

Isotope results are reported as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, which is defined as the contribution of heavy isotopes to the samples, relative to an international standard (in ‰), according to the formula

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000, \quad (4)$$

where $X = ^{13}\text{C}$ or ^{15}N and $R = ^{13}\text{C}/^{12}\text{C}$ or $^{15}\text{N}/^{14}\text{N}$ (Peterson and Fry, 1987). Positive values denote samples with higher amounts of the heavy isotopes (^{13}C or ^{15}N) than the standard, whereas negative values characterise samples with lower heavy isotopes than the standard. In stream ecosystems, higher concentration of ^{13}C (positive $\delta^{13}\text{C}$) typically refers to carbon originated from terrestrial sources, such as leaf litter or grasses, and depletion of ^{13}C (thus more negative $\delta^{13}\text{C}$) is typically related to carbon originating from aquatic autotrophic sources, such as algal biofilm or aquatic mosses (Leberfinger et al., 2010). $\delta^{15}\text{N}$ is indicative of the trophic level, with primary producers having the lowest $\delta^{15}\text{N}$ and predators having the highest $\delta^{15}\text{N}$ (Fry, 2006). Lipids introduce a bias to isotope signal due to a depletion in ^{13}C relative to proteins and carbohydrates (Post et al., 2007).

We corrected the isotope value of consumers characterised by dry mass C:N >3.5% (>5% lipid) following the equations provided by Post et al. (2007).

We conducted our statistical analyses of shifts in isotopic composition by pooling detritivore species into genera. This was necessary for two reasons: (1) all genera but not all species were found at all sites, and (2) we were not able to collect the 1 mg minimum dry weight for each species from each stream required for isotope analysis. While we acknowledge this approach might obscure species-specific differences in isotope signal, we expected larger differences between than within genera, and pooling at the genus level allowed the most extensive analysis of cross-site variability in isotopic composition.

2.6 Fungal Biomass

We quantified fungal ergosterol content as a measure of fungal biomass, an important predictor of decomposition rates (Gessner et al., 2007). Ergosterol was extracted from one of the two sets of five leaf discs cut from each fine mesh bag, with the other set used for mass estimations. Ground leaf discs were shaken on a vortex mixer for 30 min in 1000 µL EtOH 99.5% at 5 °C, followed by centrifugation at 5 °C and 14,000 RPM for 15 min (Dahlman et al., 2002). The liquid extract was then analysed on high-performance liquid chromatography (Mobile phase: 100% MetOH; flow: 1.5 mL; wavelength: 280 nm).

2.7 Data Analyses

The land-use gradient was analysed using a principal components analysis (PCA) based on the environmental data measured for each site in autumn using the package *vegan* (Oksanen et al., 2011) in the software R (R Core Team, 2014). Environmental variables were standardised to zero mean ± 1 SD prior to the PC analysis. When two variables were significantly correlated with a coefficient greater than 0.75 (Pearson's product moment correlation), the variable with most significant correlations across the entire environmental data set was removed from further analyses. The resultant variable set included water temperature, water velocity, total nitrogen (TN), pH, riparian width, stream depth and width and substrate type. The choice of TN as our measure of nutrient variation along the gradient is justified not only on statistical grounds but also because it most accurately reflects the total increase in nutrients associated with changed land

use, and the total pool of nutrients available for microbes to utilise. Total nitrogen export from our studied meadows can include a high organic N component (up to 30%, [Table A.1](#)), reflecting the use of organic fertilisers (manure) and the high proportion of forests in our catchments. Furthermore, aquatic hyphomycete fungi can utilise, and sometimes are dependent upon, specific forms of organic nitrogen for growth ([Bengtsson, 1982](#); [Thornton, 1963](#)).

The PC best describing the land-use gradient (principal component one (PC1)) was used as our measure of land use—the main predictor variable—in subsequent analyses. Two environmental characteristics, discharge and water nutrient concentrations, can differ greatly between autumn and spring, potentially modifying the land-use gradient between the two seasons. To assess the extent to which this natural variability may have affected our land-use gradient, we conducted a similar PCA with the spring data and compared it to the autumn land-use gradient using Pearson product-moment correlation test.

An initial assessment of the relationship between leaf decomposition and land use was obtained using mixed effect model analysis carried out with the R package *nlme* ([Pinheiro et al., 2012](#)), which included the land-use gradient, season and mesh size as fixed factors, and all two- and three-way interactions. Stream identity was fitted as a random block factor. Parameters characterising detritivore community structure (density, MC, F_{identity} , $F_{\text{dispersion}}$ and richness) and fungal biomass (ergosterol) were analysed using the same model. For each model, non-significant interaction terms were removed following stepwise backwards selection. After removing a non-significant interaction term, we compared the competing models using Akaike's Information Criteria (AIC) and selected those models with the lowest AIC. Fixed effect terms were never removed from the models. When only fixed effect terms remained in the analysis, our statistical output was obtained based on Type II ANOVA using the R package *car* ([Fox and Weisberg, 2011](#)). This statistical approach prevents the occurrence of equivocal statistical significance in the fixed effect terms, which can originate in an unbalanced design when there are no significant interaction terms ([Langsrud, 2003](#)). Error terms of each final model were estimated using Restricted Maximum Likelihood (REML).

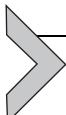
Replication for the F_{identity} and $F_{\text{dispersion}}$ analyses was lower, due to exclusion of litter bags with only one species present, for which these indices cannot be calculated. Density, richness, MC, $F_{\text{dispersion}}$ and ergosterol were log-transformed to normalise variance. Of the 200 litter bags retrieved, data

from five coarse mesh bags were excluded from the models (Ängerman stream in autumn ($n=1$), and Granån (3) and Österån (1) streams in spring), due to extremely low levels of final leaf mass remaining (14% dry mass in one mesh bag and <3% in the other four mesh bags, whereas all other litter bags contained above 40% remaining dry mass). The causes of these isolated cases of extremely high leaf mass loss are not known, but are evidently very localised (e.g. high local turbulence). Such extreme values are typically excluded (Frainer et al., 2015) as they undermine reliable calculation of decomposition rates and related parameters (e.g. detritivore density) using the litter-bag technique and cause the data to irretrievably violate assumptions of normality.

Relationships between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of consumer body tissues (as response variables) and land use were analysed using multiple linear regressions, which also included detritivore genus and seasons as dummy predictor variables. Consumer $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes may vary across regions simply due to variation in resource $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopes, which themselves are influenced by precipitation (Ma et al., 2012) and soil fertilisation (Choi et al., 2005), among other biogeochemical factors (Fry, 2006). Therefore, comparisons of consumer isotopes across regions must be analysed with caution. We addressed this issue by comparing variation in consumer isotopes along the land-use gradient in parallel with a similar comparison of variation in resource isotopes.

Isotope mixing models were generated to characterise relationships between detritivores and their resources using the R package *siar* (Parnell and Jackson, 2013). Such mixing models account for variation in both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the resource and consumer to estimate which sources of C and N are most associated with consumer isotopic signal.

To disentangle direct and indirect causal pathways that might explain variability in decomposition rates, we used structural equation modelling (SEM), which allows partitioning causal pathways in complex data (Grace et al., 2010). We tested for the effect of the exogenous variable land use on the detritivore density, MC, functional identity (F_{identity}) and functional dispersion ($F_{\text{dispersion}}$) and ergosterol, all fitted as endogenous variables (i.e. with potential to be both affected by land use, and to affect other endogenous and response variables), and outcomes for leaf decomposition rates using SEM with the R package *lavaan* (Rosseel, 2012). Due to the role of seasonality in affecting the litter decomposition (Frainer et al., 2014), we had the same model split by seasons, based on a multigroup approach (Rosseel, 2012). Variables were transformed as in the linear regressions described above.



3. RESULTS

3.1 Land-Use Gradient

PCA of the environmental variable set with the smallest degree of autocorrelation among them yielded two axes explaining 36% (axis 1) and 22% (axis 2) of the variation among sites (Fig. 1). Higher water temperature and pH were most associated with the least disturbed sites (Fig. 1, left side of the PC1), whereas coarser substrates and deeper channels, higher total nitrogen concentration and higher water velocity were most characteristic of agriculturally disturbed sites (Fig. 1, right side of the PC1). Autumn and spring PCAs were highly correlated ($r=0.86$, $p=0.001$).

3.2 Leaf Decomposition

Temperature-corrected leaf decomposition rates (detailed in Table A.3) were higher in coarse than fine mesh bags ($F_{1,178}=232.79$, $p<0.001$) and were affected by a two-way interaction between land use and season

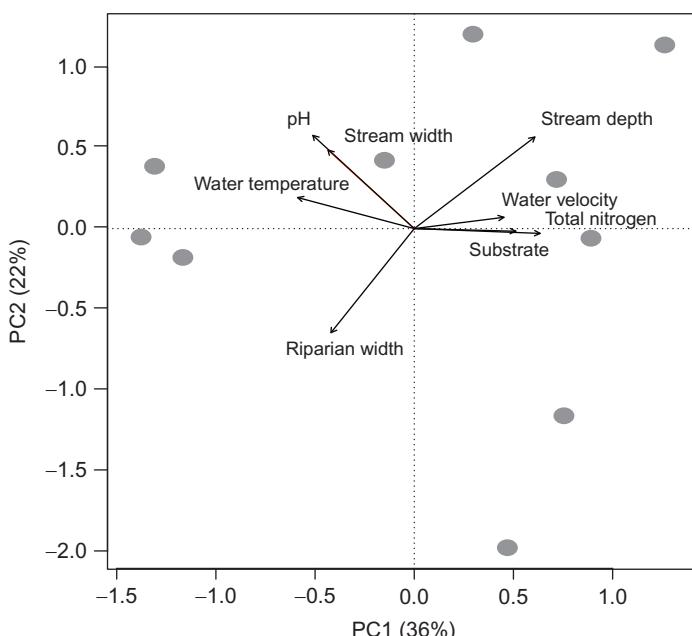


Figure 1 Principal component analysis of the environmental variables, with axis 1 used to represent the land-use gradient.

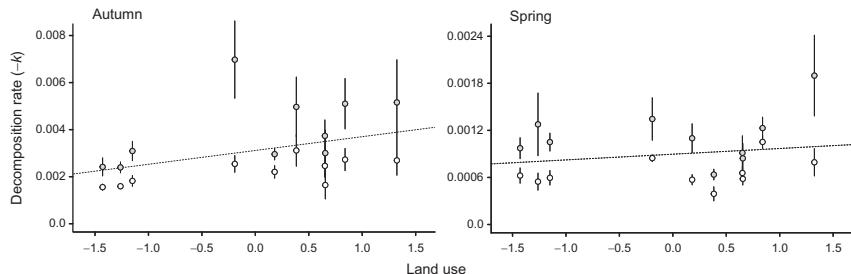


Figure 2 Relationship between land use and leaf decomposition in the fine (open circles) and coarse (grey circles) mesh bags, in both autumn (left panel) and spring (right panel). Each point plots the mean ± 1 SD for a single stream. Trend lines show the relationship between land use and leaf decomposition pooled across the two mesh sizes.

($F_{1,178} = 15.86$, $p < 0.001$). Decomposition rates of both mesh sizes increased moderately along the land-use gradient in autumn (Fig. 2) but were constant across the land-use gradient in spring (Fig. 2).

3.3 Detritivore Biotic Variables

Detritivore density ranged from 1 to 64 individuals per litter bag and was negatively related to the land-use gradient ($F_{1,84} = 7.32$, $p < 0.027$), decreasing as the agricultural impact increased (slope = $-0.67 \pm 0.25\text{SE}$). There was no difference in density between seasons ($F_{1,84} = 0.36$, $p = 0.45$). Detritivore metabolic capacity (MC) was higher in spring (mean $\pm \text{SE} = 0.064 \pm 0.01$) than in autumn (0.031 ± 0.005) ($F_{1,84} = 8.53$, $p = 0.004$), but was not related to the land-use gradient ($F_{1,84} = 4.63$, $p = 0.064$). Detritivore species richness per litter bag ranged from one to six species and was lowered in the more agricultural sites in autumn, but did not vary along the land-use gradient in spring (land use \times season interaction: $F_{1,83} = 5.2$, $p = 0.025$).

The principal component analysis of functional identity (F_{identity}) strongly differentiated traits associated with feeding and diet. Shredding traits, associated with the most obligate leaf-consumers, occurred on the positive side of PC1, whereas the negative side of PC1 was characterised by biofilm-scraper/grazer traits, associated with less obligate leaf consumer species (Fig. 3). These associations occurred in both autumn and spring, with PC1 overall explaining 89–90% of the variation. The second principal component (PC2) was predominantly associated with variation in predator and FPOM consumer traits, and explained $\sim 10\%$ of the variation in both seasons.

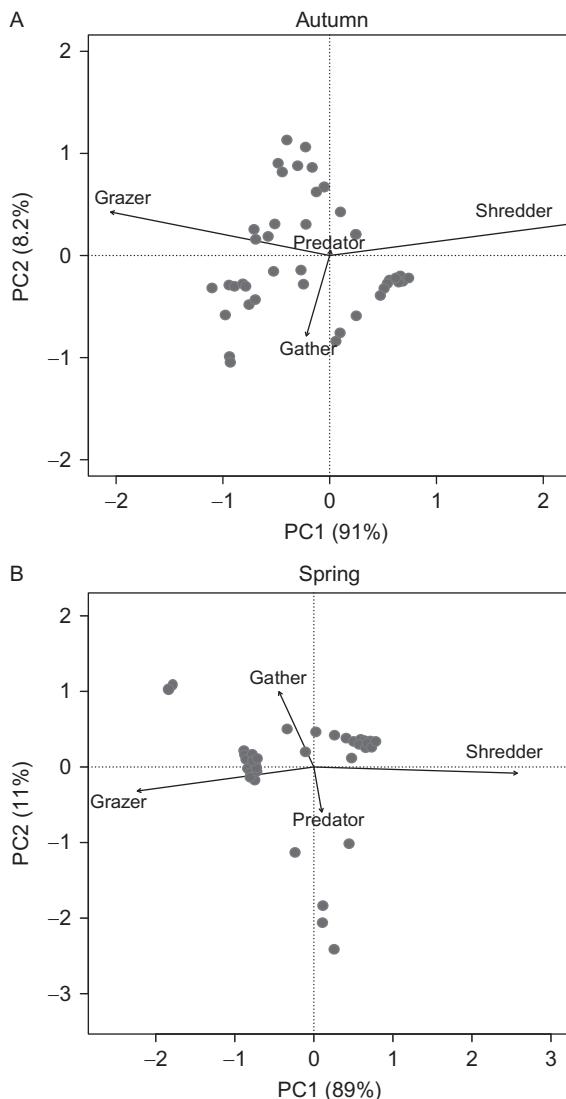


Figure 3 Principal component analysis of the functional traits according to their relative abundances (F_{identity}), calculated as the community-weighted mean trait values. Circles represent the sampling sites ($n=5$ per site, 10 sites in total) in (A) autumn and (B) spring.

F_{identity} did not differ between seasons ($F_{1,75}=0.03, p=0.60$). There was a trend for increasing F_{identity} along the land-use gradient ($\text{slope}=0.090 \pm 0.04\text{SE}$), which was near significance at the 5% level ($F_{1,74}=5.07, p=0.054$). This result indicates a higher abundance of

leaf-shredding traits in the more agricultural sites. Functional dispersion ($F_{\text{dispersion}}$) was affected by an interaction between land use and season ($F_{1,74}=12.74$, $p<0.001$), with higher trait dominance associated with the more agricultural sites in autumn, with the opposite relationship observed in spring. There was a weak, negative correlation between $F_{\text{dispersion}}$ and F_{identity} in autumn (Pearson's product moment = -0.34 , $p=0.023$), but there was no correlation between $F_{\text{dispersion}}$ and F_{identity} in spring ($p>0.65$).

3.4 Fungal Biomass

Fungal biomass, measured as ergosterol content, ranged between 161.66 and 2318.16 mg/L. Ergosterol did not differ between the two seasons ($F_{1,83}=1.41$, $p=0.24$), and it was not related to the land-use gradient ($F_{1,83}=0.13$, $p=0.73$).

3.5 Structural Equation Model

Chi-square, standardised root mean square residual (SRMSR) and root mean square error of approximation ([Table A.4](#)) statistics indicated good overall fit for both the autumn and spring structural equations models (SEMs).

Here, we present the significant ($p<0.05$) standardised correlation coefficients (r values); other results are detailed in [Table A.4](#).

In autumn ([Fig. 4A](#), [Table A.4](#)), the direct effect of the land-use gradient on leaf decomposition was positive ($r=0.50$). Land use was also positively related to F_{identity} ($r=0.62$), with abundances of shredding traits increasing along the gradient. $F_{\text{dispersion}}$ declined along the land-use gradient ($r=-0.38$), with the more agricultural assemblages characterised by a greater dominance of fewer, similar traits. Detritivore density and MC also decreased along the land-use gradient ($r=-0.45$ and -0.32 , respectively). $F_{\text{dispersion}}$ was positively related to leaf decomposition ($r=0.25$), indicating that higher functional evenness was related to higher decomposition rates. Detritivore density was negatively related to leaf decomposition ($r=-0.40$). Fungal biomass was not related to land use, but was positively related to leaf decomposition ($r=0.25$). Fungal biomass was also negatively related to F_{identity} ($r=0.23$), indicating that higher fungal biomass was related to higher abundance of biofilm feeders, rather than leaf eaters. Finally, density and MC were correlated ($r=0.75$).

In spring ([Fig. 4B](#), [Table A.4](#)), F_{identity} increased along the land-use gradient ($r=0.55$), indicating an increased dominance of more obligate

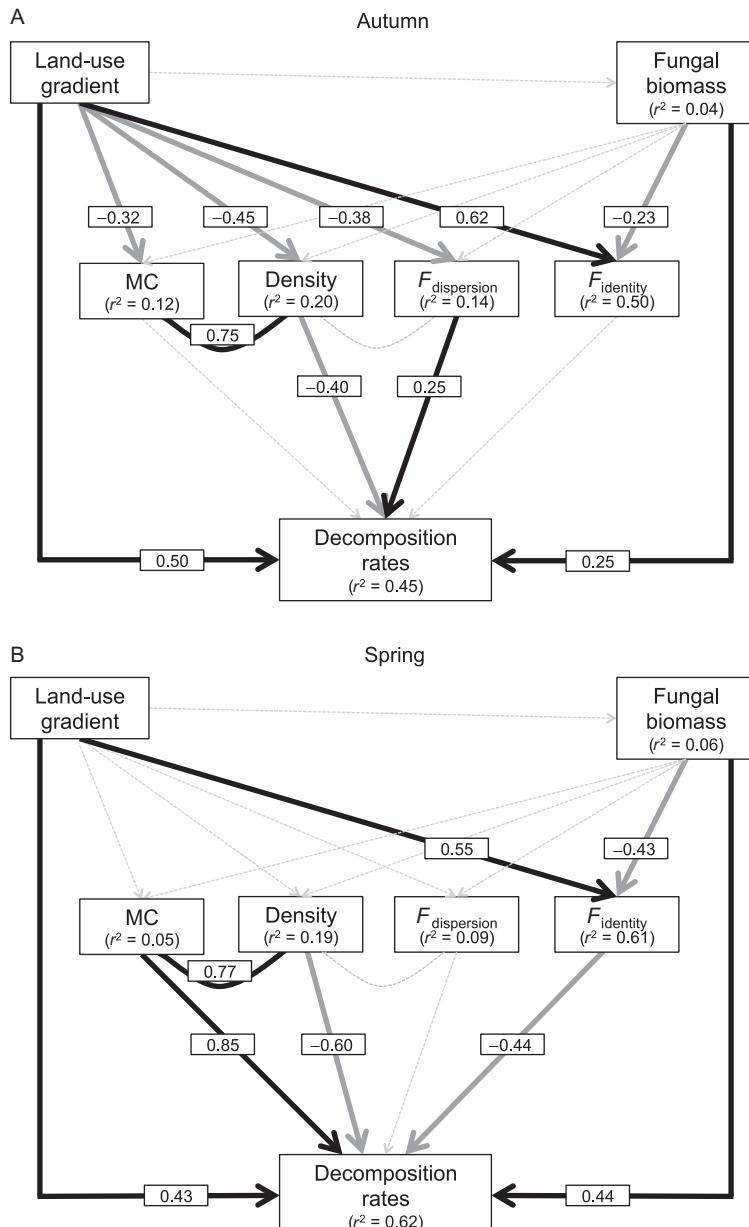


Figure 4 Structural equation modelling of leaf decomposition in (A) autumn and (B) spring. Black and grey lines indicate significant ($p < 0.05$) positive and negative relationships ($p < 0.05$), while dashed lines indicate non-significant relationships. Significant non-standardised coefficients are shown in boxes. r^2 values are shown for each response variable. Model chi-square = 12.12, d.f. = 8, $p = 0.146$.

leaf-shredder traits at the more agricultural sites. Neither detritivore metabolic capacity, density, $F_{\text{dispersion}}$ nor fungal biomass varied with land use, but leaf litter decomposition rates ($r=0.43$) increased along the gradient. Both MC and density affected leaf decomposition. However, while higher MC was positively related to leaf decomposition rates ($r=0.85$), detritivore density negatively affected leaf decomposition ($r=-0.60$). $F_{\text{dispersion}}$ had no relationship to leaf decomposition during spring, but increasing F_{identity} had a negative effect ($r=0.44$). Fungal biomass was not affected by the land-use gradient, but was positively related to decomposition ($r=0.44$). Similar to the autumn results, fungal biomass was negatively related to F_{identity} ($r=0.43$). Density was correlated with MC ($r=0.77$).

3.6 Isotopes

The mixing models indicate that all detritivore species feed on multiple resources, but allochthonous carbon constitutes a large portion of their diet, accounting for more than 40% of the isotopic signal across all genera. The detritivore genera analysed in our study differed in $\delta^{13}\text{C}$ ($F_{5,38}=7.22$, $p<0.001$), but there was no relationship between $\delta^{13}\text{C}$ and land use ($F_{1,38}=1.26$, $p=0.27$, Fig. 5A), and no differences in $\delta^{13}\text{C}$ between the two seasons ($F_{1,38}=1.10$, $p=0.30$). $\delta^{15}\text{N}$ also differed among the detritivore genera ($F_{5,38}=4.38$, $p=0.003$, Fig. 5B) and had a positive relationship with land use (slope = $3.09 \pm 2.40\text{SE}$, $F_{1,38}=25.51$, $p<0.001$), but did not differ between seasons ($F_{1,38}=0.16$, $p=0.69$). Carbon isotope values differed among resource types (C4 plants, algae and water moss) ($F_{5,58}=38.83$, $p<0.001$), but were not affected by the land-use gradient ($F_{1,58}=0.01$, $p=0.98$, Fig. 5C) and did not differ between seasons ($F_{1,58}=1.58$, $p=0.21$). $\delta^{15}\text{N}$ differed between the resource types ($F_{5,58}=10.99$, $p<0.001$) and had a positive relationship with land use (slope = $0.42 \pm 0.48\text{SE}$, $F_{1,58}=21.58$, $p<0.001$, Fig. 5D), but this relationship was more positive for moss than for C4 plants and algae (resource type \times season interaction: $F_{2,58}=4.49$, $p=0.015$).



4. DISCUSSION

Shifts in the diversity and composition of consumer functional traits explained a substantial proportion of variation in the key process of leaf decomposition along our gradient of increasing agricultural land-use intensity. Specifically, we found that an overall increase in decomposition

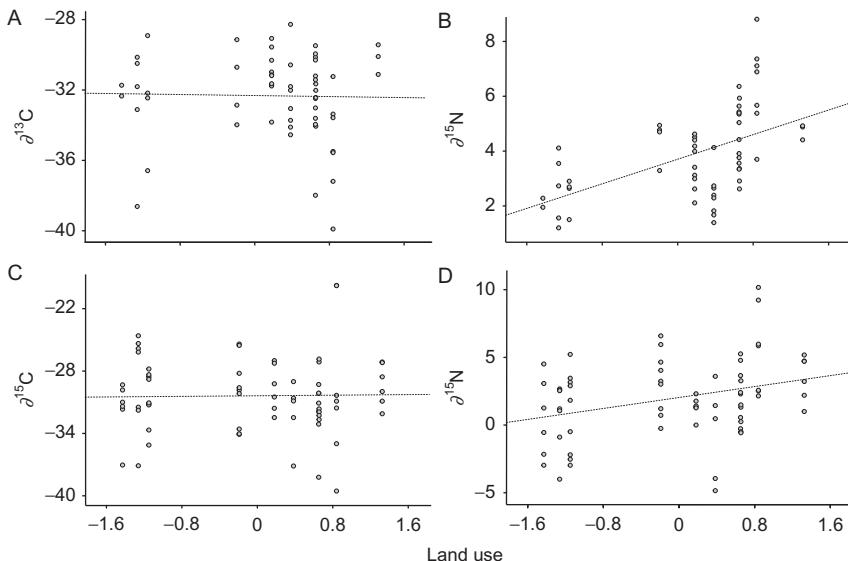


Figure 5 Relationships between land use and (A) $\delta^{13}\text{C}$ and (B) $\delta^{15}\text{N}$ isotope of invertebrate detritivores, and between land use and (C) $\delta^{13}\text{C}$ and (D) $\delta^{15}\text{N}$ isotope of resource types. Detritivore isotopes are pooled across genera. All isotopes are pooled across the two seasons, autumn and spring.

along the land-use gradient was largely offset by negative effects associated with losses of functional diversity and changes in the composition of functional traits within the detritivore consumer guild. These findings highlight the potential for shifts in species traits and functional diversity to mediate the effects of human disturbance on ecosystem functioning.

The direct effect of increasing land use intensity on leaf decomposition was positive in both the autumn and the spring, according to our SEMs. This is in line with the increase in nutrients along the gradient, which stimulate microbial activity and hence decomposition from the bottom up (Ferreira et al., 2006b; Gessner et al., 2007), and also possibly the simultaneous increase in water velocity, which can facilitate greater physical abrasion of leaf litter (Ferreira et al., 2006a; Spänhoff et al., 2007). However, our SEMs further reveal that these positive effects were partly offset by a loss of detritivore functional diversity along the gradient in the autumn, and were completely offset by a shift in functional trait composition in the spring. Consequently, linear regression analysis of the overall effect of land use on leaf mass loss found a net positive effect of land use on decomposition during the autumn only, with no similar relationship apparent during spring.

Thus, while shifts in the functional characteristics of our assemblages modified the effects of land use on functioning in both seasons, the relative importance of functional diversity and functional identity differed.

In autumn, our measure of functional diversity, functional dispersion ($F_{\text{dispersion}}$), was positively related to leaf decomposition overall, but declined along the land-use gradient. Disturbances in stream ecosystems often drive decreases in invertebrate richness and evenness, including of detritivores (Dolédec et al., 2011; McKie et al., 2006). This can result in dominance of consumer guilds by a few functional traits (Hillebrand et al., 2008) and altered ecosystem functioning (Frainer et al., 2014; McKie et al., 2008). In our study, higher $F_{\text{dispersion}}$ was associated with a more even distribution of dissimilar traits and was positively associated with leaf decomposition during the autumn, similar to findings from a previous study (Frainer et al., 2014). This is indicative of a positive effect of niche differentiation on functioning, whereby a consumer assemblage encompassing contrasting traits and patterns of resource use are able to process the resource more efficiently overall, though further research is required to more explicitly identify the underlying mechanisms (Cardinale, 2011).

Contrary to our expectations, an increase in the intensity of agricultural management did not favour a greater dominance of generalist feeding traits associated with less obligate leaf-consumers in the more disturbed streams (Statzner and Bêche, 2010). Rather, we saw the opposite effect in both autumn and spring. The most obligate leaf-shredding traits were more abundant in the more agricultural streams, whereas traits related to biofilm-grazing/scraping, which indicate the presence of detritivores that can consume substantial amounts of algae, microbes and particulate matter associated with biofilms (Lieske and Zwick, 2007), were more abundant in the forested and less disturbed streams. These findings indicate that dietary flexibility, which normally becomes more prominent in disturbed assemblages, was not strongly associated with other response traits typically conferring tolerance in our assemblages.

In spring, shifts in functional identity helped to offset the generally positive impact of land use on functioning. Unexpectedly, lower processing rates were associated with the shift in trait composition towards the more specialised leaf-eaters in the agricultural sites. The dominant taxa most associated with shredding traits in our agricultural streams were species of the stonefly genus *Nemoura* (e.g. *N. avicularis*), which emerge as winged adults throughout the spring, while the less obligate leaf feeders in the forested sites were dominated by another stonefly genus, *Amphinemura* (e.g. *A. sulcicollis* and *A. borealis*), which emerge later in the summer (Brinck, 1949). *Nemoura*

spp., in common with many aquatic insects, reduce or cease feeding and growth several days prior to emergence (Lancaster and Downes, 2013; Svensson, 1966), and thus it is likely these species were not feeding as actively on the litter as the later emerging *Amphinemura* species. Accordingly, life-history traits correlated with feeding traits of our detritivores are likely to explain why less obligate leaf feeders were associated with higher leaf processing rates during the spring.

Further factors with potential to limit the effectiveness of decomposition mediated by detritivores include the availability of alternative food sources and variation in the extent of microbial activity. Algal productivity often increases in agricultural streams (Von Schiller et al., 2008), constituting a potential alternative food resource of high quality, particularly for biofilm-feeding detritivores (Lieske and Zwick, 2007). In our study, both consumer and resource $\delta^{13}\text{C}$ isotope values were similar along the land-use gradient, indicating that there was no increase in assimilation of algal carbon along the gradient. This result most likely reflects the low rates of algal productivity attributable to limited light over the winter months preceding our sample date, though we cannot rule out that a shift in the isotope values of algae between the sample dates for periphyton and consumers might have influenced the results. Fungal biomass had a positive effect on decomposition rates in our SEMs, similar to relationships observed previously (reviewed in Gessner et al., 2007). However, there was no relationship between the land-use gradient and fungal biomass, indicating that any effects of elevated nutrients on fungal activity in the agricultural streams did not lead to a net increase in biomass accrual, at least over the time period of our study. Interestingly, the negative relationship between fungal biomass and detritivore functional identity (Fig. 4), associated with a shift from more to less-obligate litter feeding traits, indicates that less-obligate litter consumers were increasingly favoured as fungal biomass increased.

The negative effects of detritivore density on decomposition, apparent in both autumn and spring, are in line with previous observations and are likely to reflect effects of negative density-dependent interactions on per-capita consumption rates (Klemmer et al., 2012; McKie et al., 2008; Reiss et al., 2009). However, disentangling the outcomes of this effect for ecosystem functioning during autumn is complicated by the overall decline in density along the land-use gradient. This decline might partly be a consequence of faster decomposition in the agricultural sites, if the number of individuals who are able to persist in a litter patch declines at a faster rate than the resource. No similar concurrent changes in land-use, decomposition and

density occurred in the spring, suggesting other, season-specific, mechanisms might have been important. For example, it is possible that ambient stocks of broad leaf litter were greater in the agricultural streams during the autumn, in line with the higher abundance of broad-leaf trees in the riparian zone, reducing colonisation of our litterbags relative to the more coniferous-forested sites (see [McKie and Malmqvist, 2009](#)). During spring, litter standing stocks were very greatly reduced across all sites, possibly obscuring this difference. Regardless of the underlying mechanisms, the lower autumn densities in the agricultural sites might have influenced the overall positive association between land use and functioning, if negative density-dependent effects on leaf processing were alleviated, even if for only part of the study period. These results emphasise the potentially dynamic nature of the relationships between density and leaf mass loss over the whole decomposition process.

The positive effects of metabolic capacity (MC) on decomposition were also in line with previous observations ([McKie et al., 2008](#); [Perkins et al., 2010](#)). Higher MC is expected to positively affect leaf decomposition, as increased metabolic demands drive greater resource consumption ([Reiss et al., 2009](#); [Vaughn et al., 2007](#)). However, whereas density was important in both seasons, MC was important during spring only. This is opposite to findings from a previous study ([Frainer et al., 2014](#)) from the same region, which was, however, conducted solely in minimally disturbed forested streams, with differing communities from those of our agricultural streams. These findings further stress how the relative importance of key biotic drivers of functioning can vary in space and time, influenced by differences in environmental parameters and the taxonomic (and functional) composition of communities ([Dell et al., 2015](#)).

In our study, shifts in trait identity and diversity along the land-use gradient appear to have limited the stimulating effect of nutrients and current velocity on net decomposition rates, which might indicate that ecosystem functioning is little impaired in our systems and that management regimes can continue unchanged. However, the detrital food web also represents a key pathway for uptake of nutrients, mediated especially by microbes, and for its subsequent cycling in the production of both biomass and faecal pellets by consumers ([Wotton and Malmqvist, 2001](#)). These linkages are thus important in the capacity of a stream ecosystem to retain and utilise additional nutrients, and in an intact ecosystem, energy flows through the detrital food web should be stimulated as nutrient loadings increase ([Robinson and Gessner, 2000](#)). It is thus unclear whether the limitation in overall decomposition rates, associated in our study with changes in

the functional characteristics of the detritivore assemblages, is necessarily positive for wider ecosystem integrity or for longitudinal patterns of nutrient and energy cycling.

Our study detected important short-term consequences of changes in the diversity and composition of species traits for ecosystem functioning within two seasons, but it is possible that the observed changes are of significance over longer, multi-generational timescales also. Greater biodiversity has been linked with increased system stability and resilience, in part because more diverse assemblages are expected to encompass a greater redundancy of functional traits (Holling, 1973; Yachi and Loreau, 1999). This can assist in buffering the effects of community fluctuations on functioning and may confer a greater capacity to resist or recover from disturbances (Allen et al., 2005; Díaz and Cabido, 2001). Approaches such as those used in our study can assist in identifying which types of species, in terms of their functional attributes, are important in maintaining ecosystem functioning and stability (Cardinale, 2011), at least at small ecological scales (i.e. within single habitats or seasons). However, since resilience depends on the relative distributions of traits both within and across ecological scales (e.g. trophic levels, size classes, habitats and seasons), there is a need for research that is broader in scope to assess the true extent of functional redundancy in ecosystems (Angeler et al., 2014) and its potential to moderate the effects of human disturbances on ecosystem functioning (Allen et al., 2005). Nevertheless, shifts in functional trait indices, such as those observed here, can act as early-warning signals (*sensu* Mouillot et al., 2013) of building stress in an ecosystem, where declines in functional diversity may have longer-term implications for the capacity of an ecosystem to maintain ecosystem functioning if stressor loads increase in the future.

ACKNOWLEDGEMENTS

We are grateful to Emma Fältström, Melina Duarte and Petter Esberg for invaluable lab and field assistance. We also thank Margareta Zetherström and E. Fältström for the ergosterol analyses. Micael Jonsson contributed helpfully to the design of the study. This work was partially supported by a grant from the Kempe Foundation to A. Frainer and from the Swedish Research council (VR 621-2006-375) to Professor Björn Malmqvist.



Supplementary material on study site description, detritivore trait scores, decomposition rates, and structure equation modelling results.

Table A.1 Characteristics of the Study Streams

Stream	Discharge (cm ³ /s)	Width (m)	Depth (cm)	Water Velocity (cm/s)	Temperate (Mean (°C) ± SD)			Agricultural Area in the Sub- catchment (%)	Nitrogen Runoff from Agricultural Fields (%) ^c	Organic Nitrogen Runoff from Agricultural Fields (%) ^d	Total Nitrogen			PO ₄ (µg/L)	pH	
					Autumn	Spring	Riparian Vegetation ^a				N NH ₄ (mg/L)	N NO ₃ (mg/L)	Total Nitrogen (mg/L)			
Bjänsjö	41.3	3.7	19.1	0.54	2.5 ± 1.8	12.8 ± 1.4	4.00	2.00	6	53	26	0.10 ± 0.0	0.03 ± 0.02	0.42 ± 0.0	0.04 ± 0.0	6.93
Tavelån	39.4	5.2	27.7	0.45	2.4 ± 2.2	11.3 ± 1.2	5.00	4.00	11	85	29	0.10 ± 0.0	0.02 ± 0.01	0.24 ± 0.01	0.04 ± n.a.	7.19
Österåن	64.4	4.5	22.5	0.64	2.3 ± 1.5	12.2 ± 1.1	5.00	3.00	2	14	28	0.10 ± 0.0	0.05 ± 0.04	0.33 ± 0.04	0.04 ± 0.0	6.71
Ångerån	93.6	4.5	30.0	0.70	n.a.	10.8 ± 1.1	2.00	3.00	9	57	31	0.10 ± 0.0	0.08 ± 0.02	0.54 ± 0.06	0.04 ± 0.0	5.82
Flarkän	134.0	5.0	45.7	0.67	1.5 ± 1.4	9.5 ± 2.0	2.00	3.00	20	103	31	0.24 ± 0.20	0.17 ± 0.15	0.60 ± 0.30	0.04 ± 0.0	6.79
Pell-Febodväcken	18.8	1.9	20.7	0.62	1.5 ± 1.2	8.4 ± 1.8	5.00	4.00	8	59	26	0.10 ± 0.0	0.01 ± 0.0	0.35 ± 0.02	0.04 ± 0.01	5.12
Vebomarksån	123.7	4.0	32.0	0.57	1.6 ± 1.3	9.9 ± 1.7	5.00	4.00	5	34	31	0.36 ± 0.07	0.15 ± 0.10	0.77 ± 0.15	0.04 ± 0.0	4.81
Kålabodaån	118.9	4.0	38.0	0.76	1.5 ± 1.4	9.9 ± 2.0	2.00	4.00	33	155	32	0.10 ± 0.0	0.12 ± 0.07	0.45 ± 0.05	0.04 ± 0.0	5.94
Bostaån	177.7	3.0	35.0	1.33	2.2 ± 2.1	8.3 ± 1.2	4.00	4.00	24	125	27	0.10 ± 0.0	0.37 ± 0.28	0.84 ± 0.40	0.04 ± 0.0	6.46
Granån	123.5	3.0	64.3	0.71	1.9 ± 1.8	11.1 ± 1.4	1.00	5.00	13	72	31	0.10 ± 0.0	0.05 ± n.a.	0.46 ± n.a.	0.04 ± 0.0	6.19

^aRiparian vegetation was characterised based on estimates of the width of the riparian tree cover: 1 = no trees, only grass; 2 = grass and scattered trees; 3 = tree cover <3 m wide; 4 = tree cover from 5 to 10 m wide; 5 = tree cover extending at least 10 m from each side of the channel.

^bSubstrate type refers to the dominant stream substrate at each sampling site: 1 = silt and fine sand; 2 = mostly coarse sand; 3 = coarse sand and pebbles; 4 = pebbles and boulders; 5 = dominance of boulders.

^cModelled nitrogen runoff (kg/year) from agricultural fields relative to the background nitrogen runoff across the entire catchment, summed over all other potential sources, including: forest and logging activities, mires, sewage and lakes. Percentages above 100% denote higher N run-off from agricultural activities than from background concentrations. Data obtained from www.vattenwebb.smhi.se (accessed on 30 January 2015).

^dModelled organic nitrogen runoff (kg/year) from agricultural fields calculated as the background nitrogen concentration (assumed to be 100% organic nitrogen) relative to the total N runoff due to agricultural activities alone (assuming a contribution of 100% inorganic nitrogen from the agricultural activities). Data on total N concentration from agricultural meadows and background concentrations were obtained from www.vattenwebb.smhi.se (accessed on 30 January 2015)

Sites are ordered according to their positioning on the land-use gradient (PCA axis one). Values are the average found in autumn (±SD) and n.a. indicates missing data.

Table A.2 Functional Traits Used to Calculate Functional Dispersion and Identity

	Habitat Preferences		Feeding Potential					Emergence Period				Water Velocity				
	Fine Sediment	Coarse Sediment	Detritus	Vegetation	Edge	Grazer	Shredder	Gather	Predator	Winter	Spring	Summer	Autumn	Slow	Median	Fast
<i>Amphinemura</i> spp.	0.50	6.00	1.50	2.00	0.00	4.00	2.50	3.50	0.00	0.00	5.00	5.00	0.00	2.00	2.00	6.00
<i>Capnopsis</i>	3.00	0.00	4.00	3.00	0.00	2.00	4.00	4.00	0.00	1.00	7.00	2.00	0.00	0.00	10.00	0.00
<i>Leuctra</i> spp.	0.00	5.00	3.00	2.00	0.00	3.00	3.00	4.00	0.00	0.00	6.00	4.00	0.00	0.00	10.00	0.00
<i>Nemoura</i> spp.	2.00	2.00	2.00	3.00	1.00	0.00	7.00	3.00	0.00	0.00	5.00	5.00	0.00	2.00	2.00	6.00
<i>N. avicularis</i>	2.00	2.00	4.00	2.00	0.00	0.00	7.00	3.00	0.00	0.00	6.00	4.00	0.00	3.33	3.33	3.33
<i>Protonemura meyeri</i>	0.00	6.00	2.00	2.00	0.00	3.00	5.00	2.00	0.00	1.00	6.00	3.00	0.00	0.00	0.00	10.00
<i>Taeniopteryx nebulosa</i>	3.00	0.00	2.00	5.00	0.00	3.00	2.00	5.00	0.00	0.00	10.00	0.00	0.00	0.00	10.00	0.00
<i>Halesus</i> spp.	0.00	0.00	10.00	0.00	0.00	1.00	7.00	0.00	2.00	0.00	0.00	3.00	7.00	10.00	0.00	0.00
<i>Limnephilidae</i> spp.	0.00	4.50	5.50	0.00	0.00	1.75	6.25	0.00	2.00	0.00	2.00	6.00	2.00	5.00	5.00	0.00
<i>Potamophylax latipennis</i>	0.00	6.00	4.00	0.00	0.00	2.00	6.00	0.00	2.00	0.00	0.00	6.00	4.00	0.00	10.00	0.00
<i>P. rotundipennis</i>	0.00	6.00	4.00	0.00	0.00	2.00	6.00	0.00	2.00	0.00	3.00	6.00	1.00	5.00	5.00	0.00
<i>P. cingulatus</i>	0.00	6.00	4.00	0.00	0.00	2.00	6.00	0.00	2.00	0.00	0.00	8.00	2.00	0.00	10.00	0.00
<i>Aselus aquaticus</i>	2.00	2.00	2.00	2.00	2.00	3.00	3.00	4.00	0.00	0.00	0.00	0.00	0.00	3.33	3.33	3.33

Scores were obtained from the Freshwater Ecology database ([Schmidt-Kloiber and Hering, 2011](#), and references below).

Table A.3 Birch Leaf Litter Decomposition Rates (Mean, SD) of Coarse and Fine-Mesh Bags Across the Land-Use Gradient in Autumn and Spring

Season	Mesh Size	Land-Use Gradient	Decomposition Rate (degree/day)	SD
Autumn	Coarse	-1.42	0.0024	0.0004
		-1.26	0.0024	0.0002
		-1.15	0.0031	0.0004
		-0.19	0.0070	0.0016
		0.18	0.0030	0.0002
		0.38	0.0050	0.0013
		0.65	0.0037	0.0007
		0.65	0.0030	0.0010
		0.84	0.0051	0.0011
		1.32	0.0052	0.0018
Fine	Fine	-1.42	0.0016	0.0001
		-1.26	0.0016	0.0001
		-1.15	0.0018	0.0002
		-0.19	0.0025	0.0004
		0.18	0.0022	0.0003
		0.38	0.0031	0.0007
		0.65	0.0025	0.0005
		0.65	0.0016	0.0006
		0.84	0.0027	0.0005
		1.32	0.0027	0.0006
Spring	Coarse	-1.42	0.0010	0.0001
		-1.26	0.0013	0.0004
		-1.15	0.0011	0.0001
		-0.19	0.0013	0.0003
		0.18	0.0011	0.0002
		0.38	0.0006	0.0001

Continued

Table A.3 Birch Leaf Litter Decomposition Rates (Mean, SD) of Coarse and Fine-Mesh Bags Across the Land-Use Gradient in Autumn and Spring—cont'd

Season	Mesh Size	Land-Use Gradient	Decomposition Rate (degree/day)	SD
Autumn	Coarse	0.65	0.0009	0.0002
		0.65	0.0008	0.0002
		0.84	0.0012	0.0001
		1.32	0.0019	0.0005
	Fine	-1.42	0.0006	0.0001
		-1.26	0.0005	0.0001
		-1.15	0.0006	0.0001
		-0.19	0.0008	0.0000
		0.18	0.0006	0.0001
		0.38	0.0004	0.0001
		0.65	0.0007	0.0001
		0.65	0.0006	0.0001
		0.84	0.0011	0.0001
		1.32	0.0008	0.0002

Table A.4 Standardised Path Coefficients of the Structural Equation Model

	Response	Predictor	Estimate	SE	Z-value	P-value	Standardised Correlation
Autumn	Decomposition rate (degree/day)	Land use	0.28	0.05	5.45	<0.001	0.95
		MC	0.03	0.10	-0.28	0.778	-0.05
		CWM	-0.32	0.13	-2.46	0.014	-0.42
		<i>F</i> _{dispersion}	0.09	0.04	2.37	0.018	0.281
		Density	-0.15	0.14	-1.09	0.276	-0.197
		Ergosterol	0.06	0.024	2.47	0.013	0.272
CWM		Land use	0.29	0.04	8.19	<0.001	0.74
		Ergosterol	-0.06	0.03	-2.11	0.03	-0.19
<i>F</i> _{dispersion}		Land use	-0.37	0.12	-2.95	0.003	-0.41
		Ergosterol	-0.06	0.09	-0.68	0.49	-0.09
Density		Land use	-0.13	0.055	-2.425	0.015	-0.34
		Ergosterol	0.04	0.041	0.936	0.349	0.13

Table A.4 Standardised Path Coefficients of the Structural Equation Model—cont'd

Response	Predictor	Estimate	SE	Z-value	P-value	Standardised Correlation	
MC	Land use	-0.19	0.079	-2.444	0.015	-0.35	
	Ergosterol	0.03	0.06	0.43	0.667	0.062	
Ergosterol	Land use	-0.27	0.197	-1.373	0.17	-0.203	
Covariances							
Density – MC		0.02	0.01	4.13	< 0.001	0.77	
$F_{\text{dispersion}}$ – MC		0.01	0.01	2.29	0.022	0.23	
Spring	Decomposition rate (degree/day)	Land use	0.02	0.02	1.76	0.078	0.06
	MC	0.12	0.02	5.21	< 0.001	1.02	
	CWM	-0.07	0.03	-2.10	0.036	-0.33	
	$F_{\text{dispersion}}$	-0.02	0.01	-1.89	0.058	-0.24	
	Density	-0.19	0.04	-4.30	< 0.001	-0.81	
	Ergosterol	0.03	0.01	3.61	< 0.001	0.45	
CWM	Land use	0.24	0.04	5.47	< 0.001	0.58	
	Ergosterol	-0.10	0.03	-3.14	0.002	-0.33	
	$F_{\text{dispersion}}$	Land use	0.25	0.15	1.7	0.089	0.28
	Ergosterol	0.03	0.10	0.32	0.752	0.05	
Density	Land use	-0.05	0.06	-0.91	0.361	-0.15	
	Ergosterol	0.05	0.04	1.29	0.198	0.21	
MC	Land use	-0.10	0.12	-0.87	0.382	-0.14	
	Ergosterol	0.05	0.08	0.67	0.503	0.11	
Ergosterol	Land use	-0.56	0.20	-2.75	0.006	-0.39	
Covariances							
Density – MC		0.03	0.01	4.09	< 0.001	0.77	
$F_{\text{dispersion}}$ – Density		0.03	0.01	3.14	0.002	0.35	

Chi-square = 12.12, d.f. = 8, $p = 0.15$. SRMR = 0.066. Significant relationships are highlighted in bold.

Trait data-scores: detailed references

Eder, E., Hödl, W., Moog, O., Nesemann, H., Pöckl M., Wittmann, K., 1995. Crustacea (authors depending on taxagroup). In: Moog, O. (Ed.), Fauna Aquatica Austriaca, Lieferungen 1995, 2002. Wasserwirtschaftskataster, Bundesministerium für Land- und Forstwirtschaft, Umwelt und Wasserwirtschaft, Wien.

- Graf, W., Murphy, J., Dahl, J., Zamora-Muñoz, C., López-Rodríguez, M.J., Schmidt-Kloiber, A., 2006. Trichoptera Indicator Database. Euro-limpacs Project, Workpackage 7—Indicators of Ecosystem Health, Task 4, www.freshwaterecology.info, Version 5.0 (accessed on 27 September 2011).
- Graf, W., Murphy, J., Dahl, J., Zamora-Muñoz, C., López-Rodríguez, M.J., 2008. In: Schmidt-Kloiber, A., Hering, D (Eds.), Distribution and Ecological Preferences of European Freshwater Organisms. Trichoptera, vol. 1. Pensoft Publishers, Sofia-Moscow, 388 p.
- Graf, W., Lorenz, A.W., Tierno de Figueroa, J.M., Lücke, S., López-Rodríguez, M.J., Davies, C., 2009. In: Schmidt-Kloiber, A., Hering, D (Eds.), Distribution and Ecological Preferences of European Freshwater Organisms. Plecoptera, vol. 2. Pensoft Publishers, Sofia-Moscow, 262 p.
- Graf, W., Lorenz, A.W., Tierno de Figueroa, J.M., Lücke, S., López-Rodríguez, M.J., Murphy, J., Schmidt-Kloiber, A., 2007. Plecoptera Indicator Database. Euro-limpacs project, Workpackage 7—Indicators of Ecosystem Health, Task 4, www.freshwaterecology.info, Version 5.0 (accessed on 27 September 2011).
- Graf, W., Schmidt-Kloiber, A., 2011. Additions to and Update of the Trichoptera Indicator Database. www.freshwaterecology.info, Version 5.0 (accessed on 27 September 2011).
- Schmedtje, U., Colling, M., 1996. Ökologische Typisierung der aquatischen Makrofauna. Informationsberichte des Bayerischen Landesamtes für Wasserwirtschaft 4/96, 543 p.
- Schmidt-Kloiber, A., Hering D. (Eds.), 2011. www.freshwaterecology.info —The Taxa and Autecology Database for Freshwater Organisms, Version 4.0 (accessed on 27 September 2011).

REFERENCES

- Allen, C.R., Gunderson, L., Johnson, A.R., 2005. The use of discontinuities and functional groups to assess relative resilience in complex systems. *Ecosystems* 8, 958–966.
- Angeler, D.G., Allen, C.R., Birgé, H.E., Drakare, S., McKie, B.G., Johnson, R.K., 2014. Assessing and managing freshwater ecosystems vulnerable to environmental change. *Ambio* 43, 113–125.
- Bengtsson, G., 1982. Patterns of amino acid utilization by aquatic hyphomycetes. *Oecologia* 55, 355–363.
- Bergfur, J., Johnson, R.K., Sandin, L., Goedkoop, W., 2007. Assessing the ecological integrity of boreal streams: a comparison of functional and structural responses. *Fundam. Appl. Limnol.* 168, 113–125.
- Brinck, P., 1949. Studies on Swedish stoneflies (Plecoptera). *Opuscula Entomol.* (Suppl. XI), 250.

- Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M., West, G.B., 2004. Toward a metabolic theory of ecology. *Ecology* 85, 1771–1789.
- Campbell, J.E., Fourqurean, J.W., 2009. Interspecific variation in the elemental and stable isotope content of seagrasses in South Florida. *Mar. Ecol. Prog. Ser.* 387, 109–123.
- Cardinale, B.J., 2011. Biodiversity improves water quality through niche partitioning. *Nature* 472, 86–89.
- Choi, W.-J., Chang, S.X., Allen, H.L., Kelting, D.L., Ro, H.-M., 2005. Irrigation and fertilization effects on foliar and soil carbon and nitrogen isotope ratios in a loblolly pine stand. *For. Ecol. Manag.* 213, 90–101.
- Cummins, K.W., Klug, M.J., 1979. Feeding ecology of stream invertebrates. *Annu. Rev. Ecol. Syst.* 10, 147–172.
- Dahlman, L., Näsholm, T., Palmqvist, K., 2002. Growth, nitrogen uptake, and resource allocation in the two tripartite lichens *Nephroma arcticum* and *Peltigera aphthosa* during nitrogen stress. *New Phytol.* 153, 307–315.
- Dell, A.I., Zhao, L., Brose, U., Pearson, R.G., Alford, R.A., 2015. Population and community body size structure across a complex environmental gradient.
- Díaz, S., Cabido, M., 2001. Vive la différence: plant functional diversity matters to ecosystem processes. *Trends Ecol. Evol.* 16, 646–655.
- Dolédec, S., Phillips, N., Townsend, C., 2011. Invertebrate community responses to land use at a broad spatial scale: trait and taxonomic measures compared in New Zealand rivers. *Freshw. Biol.* 56, 1670–1688.
- Enquist, B.J., Norberg, J., Bonser, S.P., Violle, C., Webb, C.T., Henderson, A., Sloat, L.L., Savage, V.M., 2015. Scaling from traits to ecosystems: developing a general trait driver theory via integrating trait-based and metabolic scaling theories.
- Ferreira, V., Graça, M.A.S., de Lima, J.L.M.P., Gomes, R., 2006a. Role of physical fragmentation and invertebrate activity in the breakdown rate of leaves. *Arch. Hydrobiol.* 165, 493–513.
- Ferreira, V., Gulis, V., Graça, M.A.S., 2006b. Whole-stream nitrate addition affects litter decomposition and associated fungi but not invertebrates. *Oecologia* 149, 718–729.
- Fox, J., Weisberg, S., 2011. An R companion to applied regression, second ed. Sage, Thousand Oaks, CA. Available at: <http://socserv.socsci.mcmaster.ca/jfox/Books/Companion>.
- Frainer, A., McKie, B.G., Malmqvist, B., 2014. When does diversity matter? Species functional diversity and ecosystem functioning across habitats and seasons in a field experiment. *J. Anim. Ecol.* 83, 460–469.
- Frainer, A., Moretti, M.S., Xu, W., Gessner, M.O., 2015. No evidence for leaf trait dissimilarity effects on litter decomposition, fungal decomposers, and nutrient dynamics. *Ecology* 96, 550–561.
- Fry, B., 2006. Stable Isotope Ecology. Springer Verlag, New York.
- Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C., Toussaint, J.-P., 2004. Plant functional markers capture ecosystem properties during secondary succession. *Ecology* 85, 2630–2637.
- Gessner, M.O., Chauvet, E., 2002. A case for using litter breakdown to assess functional stream integrity. *Ecol. Appl.* 12, 498–510.
- Gessner, M.O., Gulis, V., Kuehn, K.A., Chauvet, E., Suberkropp, K., 2007. Fungal decomposers of plant litter in aquatic ecosystems. In: Kubicek, C.P., Druzhinina, I.S. (Eds.), Environmental and Microbial Relationships. Springer Verlag, Berlin; Heidelberg, Germany, pp. 301–324.
- Giller, P.S., Malmqvist, B., 1998. The Biology of Streams and Rivers. Oxford University Press, Oxford, UK.
- Gordon, N.D., McMahon, T.A., Finlayson, B.L., Gippel, C.J., Nathan, R.J., 2004. Stream Hydrology: An Introduction for Ecologists. John Wiley & Sons, Chichester, UK.

- Göthe, E., Lepori, F., Malmqvist, B., 2009. Forestry affects food webs in northern Swedish coastal streams. *Fundam. Appl. Limnol./Arch. Hydrobiol.* 175, 281–294.
- Grace, J.B., Anderson, T.M., Olff, H., Scheiner, S.M., 2010. On the specification of structural equation models for ecological systems. *Ecol. Monogr.* 80, 67–87.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910.
- Hillebrand, H., Bennett, D.M., Cadotte, M.W., 2008. Consequences of dominance: a review of evenness effects on local and regional ecosystem processes. *Ecology* 89, 1510–1520.
- Holling, C.S., 1973. Resilience and stability of ecological systems. *Annu. Rev. Ecol. Syst.* 4, 1–23.
- Hooper, D.U., Adair, E.C., Cardinale, B.J., Byrnes, J.E.K., Hungate, B.A., Matulich, K.L., Gonzalez, A., Duffy, J.E., Gamfeldt, L., O'Connor, M.I., 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. *Nature* 486, 105–108.
- Jonsson, M., Malmqvist, B., 2003. Mechanisms behind positive diversity effects on ecosystem functioning: testing the facilitation and interference hypotheses. *Oecologia* 134, 554–559.
- Jousset, A., Schmid, B., Scheu, S., Eisenhauer, N., 2011. Genotypic richness and dissimilarity opposingly affect ecosystem functioning. *Ecol. Lett.* 14, 537–545.
- Klemmer, A.J., Wissinger, S.A., Greig, H.S., Ostrofsky, M.L., 2012. Nonlinear effects of consumer density on multiple ecosystem processes. *J. Anim. Ecol.* 81, 770–780.
- Laliberté, E., Legendre, P., 2010. A distance-based framework for measuring functional diversity from multiple traits. *Ecology* 91, 299–305.
- Laliberté, E., Shipley, B., 2011. FD: measuring functional diversity from multiple traits, and other tools for functional ecology. R Package Version 10–11.
- Lancaster, J., Downes, B.J., 2013. *Aquatic Entomology*. Oxford University Press, Oxford, UK.
- Langsrød, Ø., 2003. ANOVA for unbalanced data: use Type II instead of Type III sums of squares. *Stat. Comput.* 13, 163–167.
- Lavorel, S., Garnier, E., 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Funct. Ecol.* 16, 545–556.
- Layer, K., Hildrew, A.G., Woodward, G., 2013. Grazing and detritivory in 20 stream food webs across a broad pH gradient. *Oecologia* 171, 459–471.
- Leberfinger, K., Bohman, I., Herrmann, J., 2010. The importance of terrestrial resource subsidies for shredders in open-canopy streams revealed by stable isotope analysis. *Freshw. Biol.* 56, 470–480.
- Lieske, R., Zwick, P., 2007. Food preference, growth and maturation of *Nemurella pictetii* (Plecoptera: Nemouridae). *Freshw. Biol.* 52, 1187–1197.
- Ma, J.-Y., Sun, W., Liu, X.-N., Chen, F.-H., 2012. Variation in the stable carbon and nitrogen isotope composition of plants and soil along a precipitation gradient in northern China. *PLoS One* 7, e51894.
- McKie, B.G., Malmqvist, B., 2009. Assessing ecosystem functioning in streams affected by forest management: increased leaf decomposition occurs without changes to the composition of benthic assemblages. *Freshw. Biol.* 54, 2086–2100.
- McKie, B.G., Petrin, Z., Malmqvist, B., 2006. Mitigation or disturbance? Effects of liming on macroinvertebrate assemblage structure and leaf-litter decomposition in the humic streams of northern Sweden. *J. Appl. Ecol.* 43, 780–791.
- McKie, B.G., Woodward, G., Hladyz, S., Nistorescu, M., Preda, E., Popescu, C., Giller, P.S., Malmqvist, B., 2008. Ecosystem functioning in stream assemblages from different regions: contrasting responses to variation in detritivore richness, evenness and density. *J. Anim. Ecol.* 77, 495–504.

- McKie, B.G., Schindler, M., Gessner, M.O., Malmqvist, B., 2009. Placing biodiversity and ecosystem functioning in context: environmental perturbations and the effects of species richness in a stream field experiment. *Oecologia* 160, 757–770.
- Mouillot, D., Graham, N.A.J., Villéger, S., Mason, N.W.H., Bellwood, D.R., 2013. A functional approach reveals community responses to disturbances. *Trends Ecol. Evol.* 28, 167–177.
- Newcombe, C.P., Macdonald, D.D., 1991. Effects of suspended sediments on aquatic ecosystems. *N. Am. J. Fish Manag.* 11, 72–82.
- Nilsson, E., Olsson, K., Persson, A., Nyström, P., Svensson, G., Nilsson, U., 2008. Effects of stream predator richness on the prey community and ecosystem attributes. *Oecologia* 157, 641–651.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2011. vegan: community ecology. R Package Version 2.0–2.
- Pakeman, R.J., 2011. Multivariate identification of plant functional response and effect traits in an agricultural landscape. *Ecology* 92, 1353–1365.
- Parnell, A., Jackson, A., 2013. siar: Stable isotope analysis in R. R Package Version 4.2. Available at: <http://CRAN.R-project.org/package=siar>.
- Pascoal, C., Cássio, F., Gomes, P., 2001. Leaf breakdown rates: a measure of water quality? *Int. Rev. Hydrobiol.* 86, 407–416.
- Pascoal, C., Pinho, M., Cássio, F., Gomes, P., 2003. Assessing structural and functional ecosystem condition using leaf breakdown: studies on a polluted river. *Freshw. Biol.* 48, 2033–2044.
- Perkins, D.M., McKie, B.G., Malmqvist, B., Gilmour, S.G., Reiss, J., Woodward, G., 2010. Environmental warming and biodiversity–ecosystem functioning in freshwater microcosms: partitioning the effects of species identity, richness and metabolism. *Adv. Ecol. Res.* 43, 177–209.
- Petersen, R.C., Cummins, K.W., 1974. Leaf processing in a woodland stream. *Freshw. Biol.* 4, 343–368.
- Peterson, B.J., Fry, B., 1987. Stable isotopes in ecosystem studies. *Annu. Rev. Ecol. Syst.* 18, 293–320.
- Pettersson, M., Lundberg, T., Staafjord, J., 2004. Ängs och betesmarker i Västerbottens län. Länsstyrelsen Västerbottens län meddelande.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Core Team, 2012. nlme: linear and nonlinear mixed effects models. R Package Version 31–104.
- Poff, N.L., Olden, J.D., Vieira, N.K.M., Finn, D.S., Simmons, M.P., Kondratieff, B.C., 2006. Functional trait niches of North American lotic insects: traits-based ecological applications in light of phylogenetic relationships. *J. N. Am. Benthol. Soc.* 25, 730–755.
- Post, D.M., Layman, C.A., Arrington, D.A., Takimoto, G., Quattrochi, J., Montaña, C.G., 2007. Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152, 179–189.
- R Core Team, 2014. R: A Language and Environment for Statistical Computing. Available at: <http://www.R-project.org/>.
- Reiss, J., Bridle, J.R., Montoya, J.M., Woodward, G., 2009. Emerging horizons in biodiversity and ecosystem functioning research. *Trends Ecol. Evol.* 24, 505–514.
- Robinson, C.T., Gessner, M.O., 2000. Nutrient addition accelerates leaf breakdown in an alpine springbrook. *Oecologia* 122, 258–263.
- Rosseel, Y., 2012. lavaan: an R package for structural equation modeling. *J. Stat. Softw.* 48, 1–36. Available at: <http://www.jstatsoft.org/v48/i02>.
- Schmidt-Kloiber, A., Hering, D., 2011. The Taxa and Autecology Database for Freshwater Organisms. Available at: <http://www.freshwaterecology.info> (accessed September 2011).

- Spähnoff, B., Augspurger, C., Küsel, K., 2007. Comparing field and laboratory breakdown rates of coarse particulate organic matter: sediment dynamics mask the impacts of dissolved nutrients on CPOM mass loss in streams. *Aquat. Sci.* 69, 495–502.
- Statzner, B., Béche, L.A., 2010. Can biological invertebrate traits resolve effects of multiple stressors on running water ecosystems? *Freshw. Biol.* 55, 80–119.
- Svensson, P.-O., 1966. Growth of nymphs of stream living stoneflies (Plecoptera) in northern Sweden. *Oikos* 17, 197–206.
- Thébaud, E., Loreau, M., 2005. Trophic interactions and the relationship between species diversity and ecosystem stability. *Am. Nat.* 166, E95–E114.
- Thornton, D.R., 1963. The physiology and nutrition of some aquatic hyphomycetes. *J. Gen. Microbiol.* 33, 23–31.
- Tilman, D., Reich, P.B., Isbell, F., 2012. Biodiversity impacts ecosystem productivity as much as resources, disturbance, or herbivory. *Proc. Natl. Acad. Sci. U. S. A.* 109, 10394–10397.
- Vaughn, C.C., Spooner, D.E., Galbraith, H.S., 2007. Context-dependent species identity effects within a functional group of filter-feeding bivalves. *Ecology* 88, 1654–1662.
- Von Schiller, D., Martí, E., Riera, J.L., Ribot, M., Marks, J.C., Sabater, F., 2008. Influence of land use on stream ecosystem function in a Mediterranean catchment. *Freshw. Biol.* 53, 2600–2612.
- Wissinger, S., Steinmetz, J., Alexander, J.S., Brown, W., 2004. Larval cannibalism, time constraints, and adult fitness in caddisflies that inhabit temporary wetlands. *Oecologia* 138, 39–47.
- Woodward, G., Gessner, M.O., Giller, P.S., Gulis, V., Hladyz, S., Lecerf, A., Malmqvist, B., McKie, B.G., Tiegs, S.D., Cariss, H., Dobson, M., Elosgé, A., Ferreira, V., Graça, M.A. S., Fleituch, T., Lacoursière, J.O., Nistorescu, M., Pozo, J., Risnoveanu, G., Schindler, M., Vadineanu, A., Vought, L.B.M., Chauvet, E., 2012. Continental-scale effects of nutrient pollution on stream ecosystem functioning. *Science* 336, 1438–1440.
- Wotton, R.S., Malmqvist, B., 2001. Feces in aquatic ecosystems. *Bioscience* 51, 537–544.
- Yachi, S., Loreau, M., 1999. Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proc. Natl. Acad. Sci. U. S. A.* 96, 1463–1468.