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Research article

Agricultural land use weakens the relationship between biodiversity and ecosystem functioning

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Leaf litter decomposition is a significant ecosystem process for streams' energy provisioning, while species-specific decomposition rates often form a continuum from slow to fast decomposing species allowing for resources' availability to stream consumers over a longer time period after leaf fall. Leaf litter mixtures in streams typically comprise leaf species varying in their traits, allowing for litter diversity effects on decomposition. At the same time, agricultural land use, habitat characteristics, water quality and invertebrate composition modulate leaf litter decomposition. To identify leaf litter diversity effects and disentangle the roles of agricultural intensity, habitat characteristics, water quality and invertebrate composition for leaf litter processing in streams, we quantified leaf litter decomposition of three leaf species covering a gradient from slow to fast decomposing species, tested either individually or as a three-species mixture. The study was conducted over 21 days across 18 streams with a gradient of agricultural intensity (percent agricultural land use) in their catchments. We found leaf litter diversity effects in terms of complementarity under low to intermediate agricultural intensity, given that slow decomposing leaf species decomposed almost twice as fast in the three-species mixture compared to the observations on individual leaf species. This leaf litter diversity effect decreased with increasing agricultural intensity, suggesting that agriculture weakens the biodiversity–ecosystem functioning relationship. However, pathways by which agriculture affected decomposition differed between single-species and mixed-species scenarios. For the single-species scenario, negative effects of agriculture appeared to be mediated through effects on the proportion of sensitive detritivore species and altered habitat characteristics. For the mixed-species scenario, altered water quality negatively affected the proportion of sensitive detritivore species, in turn reducing the diversity effect on functioning. Our results suggest that the weakened biodiversity–ecosystem functioning relationship under increasing agricultural intensity might be a significant factor threatening carbon cycling and food web integrity in streams.

Keywords: biodiversity–ecosystem functioning, complementarity, detritivore, detritus breakdown, leaf litter mixture, litter quality

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Introduction

Ecosystem processes that regulate the flux and transformation of energy and nutrients are paramount for the functioning of ecosystems (Gessner and Chauvet 2002). One ecosystem process of prime importance for the energy supply in heterotrophic stream food webs is the decomposition of terrestrially-derived leaf litter by microbial decomposers and invertebrate detritivores (Gessner and Chauvet 2002). Microbial decomposers contribute comparatively little to bulk leaf litter decomposition in temperate regions (Hieber and Gessner 2002). However, fungi especially play a key role in increasing litter nutrient content and degrading recalcitrant structural components, increasing the palatability and nutrient content of litter as a food source for invertebrate detritivores (Bärlocher 1985).

The rates at which leaf litter is microbially colonized and subsequently decomposed by detritivores strongly depend on the leaf species (Swan et al. 2009). The chemical composition of leaf litter is a crucial factor that controls process rates, since decomposers and detritivores prefer substrates with a high content of labile carbon (C) and nutrients (Graça 2001, Gessner et al. 2007). Leaf litter mixtures in streams typically comprise multiple leaf species varying in chemical composition, and consumers are able to optimize net energy and nutrient intake and resolve stoichiometric imbalances by feeding across multiple leaf species (Hladyz et al. 2009, Frainer et al. 2016). This 'complementary resource use' by detritivores (McKie et al. 2008) and decomposers such as fungi (Jabiol et al. 2013) can further enhance rates of C and nitrogen (N) cycling in leaf litter mixtures compared to single species (Gessner et al. 2010, Handa et al. 2014).

The generic term 'complementarity' is used to describe a broad class of mechanisms underpinning the influences of biodiversity on ecosystem functioning (Gessner et al. 2010), which occur when the interplay among species results in a non-additive change in ecosystem process rates. Complementary resource use by detritivores is one example whereby different species feeding on different components of the leaf litter resource might result in not only more efficient leaf litter decomposition, but also greater biomass production (Cardinale et al. 2006). Another mechanism is facilitation, whereby the activities of some organisms enhance activities of others (Gessner et al. 2010). An example is fungal-mediated N-transfer among leaf litter species of different chemical composition (Handa et al. 2014), which speeds conditioning and decomposition of less nitrogen rich species, and thus facilitates feeding by detritivores. In contrast to these mechanisms involving multiple species, the 'selection effect' occurs when biodiversity effects are mainly caused by a single species, which harbors traits that change its performance in multi-species assemblages (Tilman et al. 1997, Loreau and Hector 2001). For instance, leaf chemistry in terms of tannin and lignin content can lead to an increased (positive selection) or decreased (negative selection) feeding of detritivores on leaf species in multi-species assemblages compared to the monoculture (Hättenschwiler and Bretscher 2001, López-Rojo et al. 2021). The relative importance of complementarity and the selection effects for leaf litter decomposition documented in manipulative experiments, including those conducted in situ in some form of enclosure, have been idiosyncratic. While some studies resulted in positive (faster decomposition of slow decomposing litter species) effects of diversity on functioning, others reported constraining (slower decomposition of fast decomposing litter species) or null effects (Kominoski et al. 2010).

An additional challenge in predicting substrate diversity effects is understanding the influence of altered biotic and abiotic environmental factors, which might modify the biodiversity effects. For example, human impacts that shape assemblages of organisms and their resources may affect biodiversity effects on leaf litter decomposition through alteration of the occurrence and relative abundances of key species (Heffernan et al. 2014). In this context, agricultural land use is associated with changes in the structure of the riparian vegetation and in-stream habitat characteristics, and impacts on the water quality of streams (Allan 2004). As a consequence, agricultural land use has the potential to disrupt biodiversity effects on leaf litter decomposition by altering the leaf litter mixtures entering streams as well as the diversity and composition of detritivore communities, ultimately altering the process rates of leaf litter (Truchy et al. 2022).

In this study we aimed to identify leaf litter diversity effects and disentangle the roles of agricultural intensity, habitat characteristics, water quality and invertebrate metrics (e.g. Shannon index, metabolic capacity, and $\mathrm{SPEAR}_{\mathrm{pesticides}}$ as an index of the ratio of sensitive to tolerant species) for leaf litter processing in streams. We quantified microbially-mediated and detritivore-mediated leaf litter decomposition of three leaf species that cover a gradient from slow to fast decomposing species (pedunculate oak, black locust, and black alder), tested either individually or as a three-species mixture. The study was conducted for 21 days across 18 streams in southern Sweden, ranging from forested least-disturbed sites (low agricultural intensity in the streams' catchments) to sites heavily degraded by high agricultural activity, including those associated with the use of fertilizers and land-use changes in the riparian zone (e.g. loss of riparian vegetation and consequently increased sediment transport into the streams). The agricultural practices in the streams' catchments consisted of production of crops such as cereals, beets, brassicas, potatoes, and legumes (Raderschall et al. 2021) and a minor share of orchards and pasture (own observation, Fig. 1). In accordance with previous studies (Truchy et al. 2022), we expected increasing agricultural intensity to compromise leaf litter decomposition rates driven by alterations in habitat characteristics, water quality and invertebrate metrics. The hypothesized pathways by which leaf litter decomposition rates are affected were visualized and tested using structural equation models. Consistent with biodiversity–ecosystem functioning theory (Gessner et al. 2010), we hypothesized that the strongest complementarity effects will be observed in streams supporting the highest detritivore diversity, which are expected to be our sites exhibiting low agricultural intensity

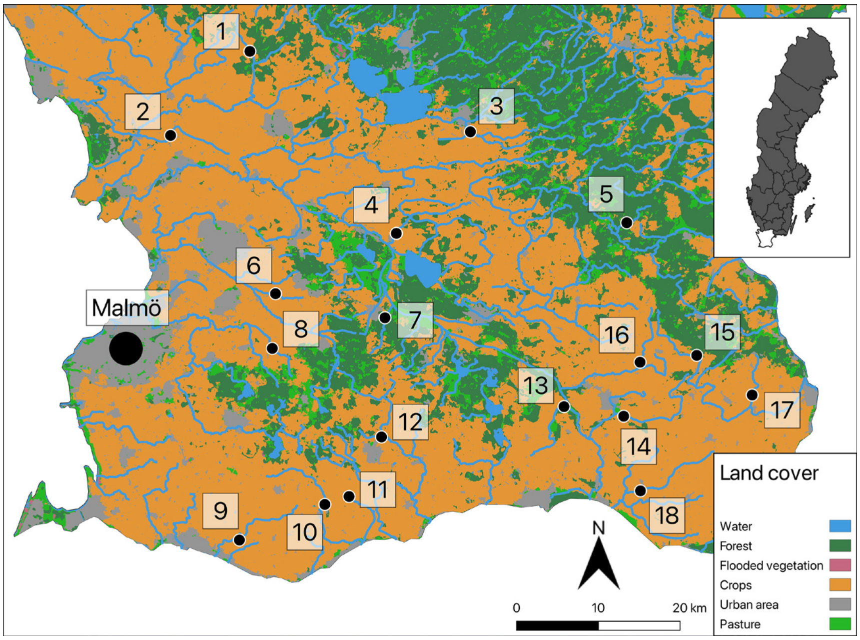

Figure 1. Location of the study area (Skåne County; white area) and the sampling sites (black dots) in southern Sweden. Colors depict land cover types based on ESRI land cover data (ESRI 2022). Both 'crops' and 'pasture' are considered as 'agricultural land' in the analyses.

in their catchments. Complementarity should increase the overall leaf litter decomposition rates in mixed-species leaf litterbags in general and the leaf litter decomposition rates of slow-decomposing leaf species in particular. Under increasing agricultural intensity, we hypothesized that biodiversity effects in general and complementarity in particular will weaken, in line with expected reductions in detritivore diversity, and also possible impacts of reduced habitat and water quality on the activity of organisms.

Material and methods

General study design

Environmental variables, stream-inhabiting macroinvertebrate communities, and a measure of ecosystem function (i.e. leaf-litter decomposition) were quantified across 18 low-order streams (Strahler stream order ≤ 3) situated in Skåne County, southern Sweden (Fig. 1, Supporting information), over a three-week period from 31 May to 21 June 2016. The sampling sites (i.e. stream reaches of ~25 m) were chosen to represent a gradient of agricultural intensity in the streams' catchments that is associated with an increasing pressure on in-stream species assemblages and functions they provide (Blann et al. 2009). Stream catchments were dominated by deciduous forests (including black alder and pedunculate oak trees in the riparian area), agriculture, or a combination of both (Fig. 1, Table 1). Agricultural intensity was quantified by first calculating the percentage contribution of each land-use category by delineating the topographic sub-catchments for each sampling site in QGIS (ver. 3.28.0-Firenze; QGIS 2021) using ESRI land cover data (ESRI 2022) and afterwards extracting the land-use data for the contributing sub-catchments. Sampling sites with additional major upstream anthropogenic pressures (such as wastewater treatment plants, industrial facilities, and large urban areas) that potentially confound the interpretation of results were avoided. The streambeds were composed predominantly of medium and fine substrates (~ 30 and 50%, respectively), with some boulders and cobbles present at most of the sites (Table 1). To quantify decomposition of the three tested leaf species and detect potential litter diversity effects, we immersed leaves in single-species and mixed-species leaf litterbags at the sampling sites for up to 21 days.

Environmental variables

We visually assessed the streambed substrate characteristics and plant cover within and along the streams at the time of study commencement for the respective stream reach of 25 m: the percentage contribution of coarse (boulder and cobble), medium (pebble and gravel), and fine sediments (sand and silt) as well as the coverage of the streambed by leaves and woods (ø < 10 cm), woods (ø > 10 cm) and submersed/immersed plants was estimated. In addition, the coverage by trees and shrubs along the riverbanks was estimated by eye. All variables except the sediment composition were measured using an ordinal scale that relied on the percentage proportion: $0\% = 0$, $1–20\% = 1$, $21–40\% = 2$, $41–60\% = 3$, $61–80\% = 4$, $81–100\% = 5$.

Conductivity, pH, dissolved oxygen concentration, flow velocity, stream width, and water depth were measured *in situ* at the study commencement and every seventh day thereafter (ProfiLine Multi 3320, Wissenschaftlich Technische Werkstätten GmbH; MiniAir20 with a Mini sensor 0.02–5 m s^{-1}, Schiltknecht, Gossau, Switzerland). All variables were

Table 1. Descriptive statistics of environmental variables at the study sites (means, standard errors, minimum, and maximum; n = 18). For more details see the Supporting information. [a]Measured using an ordinal scale (0–5). [b]Quantified for the entire stream catchment. [c]Mean from the left and right banks.

Variable	Unit	Mean	SE	Min	Max
Catchment size	ha	3171	608	914	11864
Width	m	2.3	0.2	1.4	4.8
Depth	m	0.19	0.02	0.07	0.34
Velocity	m s^{-1}	0.22	0.02	0.04	0.44
Temperature	°C	14.7	0.32	12.0	17.1
pH		7.73	0.05	7.36	8.01
Oxygen	mg l^{-1}	11.0	0.58	6.33	15.19
Conductivity	μS cm^{-1}	53.98	4.77	28	119
Alkalinity	meq l^{-1}	3.74	0.22	1.64	5.06
DIN	μg l^{-1}	2320.48	387.70	497	6020
PO_4^{3-}-P	μg l^{-1}	101.44	32.97	7	578
Coarse substrates (boulder and cobble)	%	20.0	3.9	0.0	50.0
Medium substrates (pebble and gravel)	%	31.1	4.6	5.0	70.0
Fine substrates (sand and silt)	%	48.3	6.2	10.0	90.0
In-stream leaves and wood (ø < 10 cm)[a]		0.9	0.08	0	1
In-stream wood (ø > 10 cm)[a]		0.3	0.1	0	1
Immersed plants[a]		1.2	0.3	0	4
Submerged plants[a]		1.0	0.1	0	1
Agricultural land use[b]	%	67.1	5.9	8.5	97.1
Forestry[b]	%	19.7	5.2	0.0	73.6
Tree cover along the bank[c]		1.9	0.4	0	4
Shrub cover along the bank[c]		3.1	0.3	0	5

measured at the same stream location, where we set up a transect for water depth measurements (measured every 30 cm along the transect), which were averaged for every sampling site before entering the analyses. Stream temperatures were measured hourly using button data loggers (SmartButton; ACR Systems). Temperature data were converted to daily means for calculation of leaf litter breakdown rates per degree day (below), and were also averaged across the entire study period for use in statistical models. Water samples for analyses of alkalinity, total nitrogen, ammonium, nitrite and nitrate, total phosphorus, and phosphate were taken once at the commencement of the study and commercially analyzed using SWEDAC accredited methods.

Although we measured pesticides in the water phase at all sites during the study period (Supporting information), low rain fall in the study region during June 2016 (~ 18 l m^{-2} over the entire month; long-term monthly average for June 1991–2020: ~ 61 l m^{-2}; Sveriges meteorologiska och hydrologiska institut) led to low dissolved concentrations being measured, given that the main entry route of pesticides into running waters is through rainfall-induced surface run-off (Schulz 2004). Therefore, the pesticide data had only a minor explanatory power for the outcome of the present study and were excluded from further analyses, but are provided in the Supporting information for the sake of transparency.

Macroinvertebrate sampling, trait information, and variable selection

We quantitatively sampled macroinvertebrate communities at the commencement of our field experiment, using a Surber Sampler (500 μm mesh-size; surface 1/8 m^2). At each sampling site we took five samples by physically agitating benthic habitats, such as mineral substrates, in-stream leaf litter, and submerged vegetation, upstream of the Surber net for 60 seconds. By this, we anticipated to capture the entire suite of macroinvertebrates present in the sampling sites, which should provide a comprehensive inventory of the local community potentially influencing the decomposition process over the entire study period. Samples were preserved in 70% ethanol in the field and afterwards sorted in the laboratory. All macroinvertebrates in a given sample were identified to the lowest practical taxonomic level – mostly to the species level (except taxa such as Chironomidae, Eloeophila, Oligochatea, Pisidium, Simuliidae and Tricladida, Supporting information) – and counted using light microscopy. Afterwards, mean species abundances per sampling site were calculated and extrapolated to abundance per square meter.

Macroinvertebrate trait information was retrieved from Tachet et al. (2010). In extracting traits, we focused on those that are closest in their definition to true functional effect traits, viz. 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). Following the classifications of Frainer et al. (2014) and Truchy et al. (2019), we selected traits that 1) directly influence the assessed functional measures (e.g. feeding habits and maximum body size) and 2) reflect habitat use that regulate when and where different species are likely to be most active in their influences on functioning (Supporting information). Given the assessed measure of ecosystem function (i.e. leaf litter decomposition), we included only species that exhibited a value of > 0 for the trait expression ‘shredder’ in their feeding habit in further analyses.

In addition, we calculated the metabolic capacities of the macroinvertebrate communities following Brown et al. (2004) using the mean per capita body mass of sampled macroinvertebrate species, which was quantified by weighing up to 50 oven-dried (60°C for 24 h) specimen of each species to the nearest 0.01 mg. Finally, we used the SPEcies At Risk (SPEAR) calculator ‘Indicate’ (Helmholtz Centre for Environmental Research (UFZ), Leipzig, Germany) to calculate a standard risk indicator for pesticides (SPEAR$_{pesticides}$) that is computed based on trait data on 1) physiological sensitivity to insecticides and other pesticides with insecticidal mode of action, 2) generation time, 3) presence of aquatic stages, and 4) ability to migrate and recolonize. These traits are typically associated with greater tolerance to environmental disturbances to characterize variation (Liess and von der Ohe 2005). Accordingly, the $\text{SPEAR}_{\text{pesticides}}$ index captures information not only about potential legacy pesticide effects but also other effects caused by reduced water quality on the proportion of sensitive relative to tolerant taxa in macroinvertebrate communities (Schuwirth et al. 2015).

Using these data, we calculated community weighted means (CWM) for each trait following Lavorel et al. (2008) as well as a series of invertebrate metrics (density, species richness, Shannon index, functional dispersion, functional richness, functional evenness). We assessed collinearity among the variables (metabolic capacity, $\text{SPEAR}_{\text{pesticides}}$, CWMs, invertebrate metrics) using the Pearson correlation coefficient (PCC). When two or more strongly correlating variables were indicated ($\text{PCC} > 0.8$), we only kept the variable that was least correlated with the remaining variables. This procedure led to the inclusion of metabolic capacity, $\text{SPEAR}_{\text{pesticides}}$, CWMs for organic detritus as preferred habitat and shredding as feeding habit, density, Shannon index, and functional dispersion in the final analyses.

Leaf litter decomposition

We quantified the decomposition of terrestrially-derived leaf litter as a measure of stream ecosystem functioning. Leaves of two common European broad-leaved tree species, black alder *Alnus glutinosa* and pedunculate oak *Quercus robur*, as well as one invasive tree species, black locust *Robinia pseudoacacia*, were picked from trees shortly before abscission during autumn 2015 (Supporting information). The leaf material was afterwards stored at −20°C until further processing. Freezing may have slightly affected the litter decomposition process, but such effects are generally minor (Bärlocher 1992) as shown by the alder decomposition rates measured here that match with the range of the decomposition rates reported for the temperate zone ($k_{\text{dd; detritivore}} = 0.015\text{–}0.060$; $k_{\text{dd; microbial}} = 0.004\text{–}0.020$) in a global decomposition study (Boyero et al. 2016). Our selection of these leaf species, which contrasted key decomposition-related traits (C-, N-, P-content, N:P-, C:N-, C:P-ratio, lignin and cellulose content, and toughness, Supporting information) was motivated by 1) potential leaf litter diversity effects on functioning (facilitation or constraint) because of known differences in decomposition rates of the two N-fixing species alder (fast decomposition) and black locust (intermediate decomposition) as well as the N-poor species oak (slow decomposition; Abelho 2001) and 2) the attempt to capture the importance of macroinvertebrate traits over a wider range of substrate variability.

Leaf litter decomposition rates were quantified using coarse mesh (ø = 10.0 mm, allowing access for both detritivores and microbial decomposers) and fine mesh (ø = 0.5 mm, preventing detritivore access) leaf litterbags packed with oven-dried (48 h at 60°C) leaf material. Single-species leaf litterbags contained 2.00 (± 0.01 SE; n = 432) g leaf material of the respective leaf species, whereas mixed-species leaf litterbags contained 0.66 (± 0.01 SE; n = 144) g leaf material of each of the three tested leaf species leading to a total mass of 2.00 g. We immersed four leaf litterbags of each mesh type (coarse and fine), litter species (black alder, pedunculate oak, and black locust) and species combination (single- and mixed-species) at each sampling site, resulting in a total of 32 litterbags deployed in each of the assessed streams. The study sites were visited every seven days to inspect the stage of leaf litter decomposition and we retrieved the leaf litterbags from the field latest 21 days after deployment. We rinsed the remaining leaf material under running water to remove sediment particles and macroinvertebrates and sorted leaf material retrieved from mixed-species litterbags according to leaf litter species before further processing. The remaining leaf material was oven-dried at 60°C for 48 h, weighed to the nearest 0.01 mg, and ashed at 550°C for 4 h to quantify the ash free dry mass. Leaf litter decomposition was corrected using leaching factors that were determined in a 48 h lab experiment and represent the proportion mass remaining after leaching (black alder: 0.76; pedunculate oak: 0.81; black locust: 0.81). The detritivore-mediated share of leaf litter decomposition was calculated as the difference between the overall decomposition in coarse mesh bags and the microbially-mediated decomposition in fine mesh bags. Finally, the temperature-standardized leaf litter decomposition coefficients ($k_{\text{dd; microbial}}$ and $k_{\text{dd; detritivore}}$) were calculated for each leaf litterbag or species therein (in case of mixed-species leaf litterbags) using a negative exponential decay model (Benfield 2007).

Statistical analyses

Generalized linear models

In order to assess the individual and joint effects of 'leaf species identity' and 'leaf litter mixing' on the leaf litter decomposition rates ($k_{\text{dd; microbial}}$ and $k_{\text{dd; detritivore}}$), we fitted two-factorial generalized linear models (GLM) with an assumed Gaussian distribution of the response variable and a log link function. The GLMs' goodness-of-fit was inspected using the R package 'DHARMa' (Hartig 2022).

Diversity effects on leaf litter decomposition rates

To quantify the magnitude of the net biodiversity effect, the dominance effect and complementarity on leaf litter decomposition rates, we used the additive partition approach by Loreau and Hector (2001). This approach compares the observed functioning in mixed-species leaf litterbags with expected functioning based on leaf litter decomposition rates in single-species leaf litterbags (for a detailed description of the underlying calculations see Loreau and Hector (2001)). To facilitate the comparison with previous studies, we restore the nomenclature of Loreau and Hector (2001) and call the dominance effect the 'selection effect' in the following, because it quantifies the net biodiversity effect fraction attributable to processes analogous to natural selection (Fox 2005).

Afterwards, we used the R package 'drm' (www.r-project.org, Ritz et al. 2015) to fit several dose-response models (including lognormal, log-logistic, Weibull, Cedergreen-Ritz-Streibig and Michaelis-Menten models) to the data to assess the effects of the increasing agricultural intensity in the streams' catchments on the net biodiversity effect, complementarity, and the selection effect. The models fitting the data best were selected based on visual judgement and Akaike's information criterion (all models and their respective parameters are reported in the Supporting information).

Structural equation modeling

We used structural equation modeling (SEM), representing an analytical procedure for partitioning complex relationships in multivariate data sets (Shipley 2016), to disentangle linkages between habitat characteristics (depth, width, flow, percentage cover of fine substrate, medium substrate, and coarse substrate, submersed plants, percentage cover of leaves and woods [$ø < 10$ cm], and woods [$ø > 10$ cm]) as well as water quality parameters (alkalinity, pH, dissolved inorganic nitrogen [$NO_2^- + NO_3^- + NH_4^+$], phosphate, and oxygen, Table 1) and invertebrate metrics as drivers for leaf litter decomposition using the R package 'piecewiseSEM' (Lefcheck 2016).

Before building the models, we reduced the dimensionality of water quality parameters and habitat characteristics by applying two principal component analyses (PCAs) on standardized variables using the R package 'FactoMineR' (Lê et al. 2008). Before conducting the PCAs, we assessed collinearity among the variables using the Pearson correlation coefficient (PCC). When two or more strongly correlating variables were indicated ($PCC > 0.8$), we only kept the variable that was least correlated with the remaining variables. Based on the eigenvalues, the first two principal components (PCs) were extracted to describe the water quality parameters and the habitat characteristics in the SEMs.

We proposed a conceptual model of hypothesized relationships between predictor variables (agricultural intensity represented as %agricultural land use in the catchment, habitat characteristics, water quality parameters, invertebrate metrics, and leaf species identity) and the response variable ($k_{\text{dd; detritivore}}$) within a path diagram (Fig. 2). Our proposed model structure was based on knowledge of the leaf litter decomposition process, allowing a causal interpretation of the model outputs (Shipley 2016). However, the proposed model is only valid for the type of relations introduced and does not exclude potential other types of relations omitted here.

The overall influences of '%agricultural land use' (representing agricultural intensity) and 'leaf species identity' on leaf litter decomposition rates were modeled as exogenous effects, while for the former both direct (variation attributable to non-measured environmental variables) and indirect (variation attributable to changes in habitat characteristics and water quality parameters) relationships were considered (Fig. 2). To free up degrees of freedom and improve the model fit, any path with a coefficient < 0.1 was removed from the model when statistically non-significant. The models' goodness-of-fit was assessed with Fisher's test of direct separation and Bayesian information criterion scores. All statistical analyses were performed using the open-source statistical software R (www.r-project.org).

Results

Effects of leaf species identity and diversity on leaf litter decomposition in streams under increasing agricultural intensity

Leaf species identity significantly influenced detritivore-mediated leaf litter decomposition ($p < 0.001$ for the factor 'leaf species identity' in GLM) and this effect was observed independent of single-species or mixed-species leaf litterbags

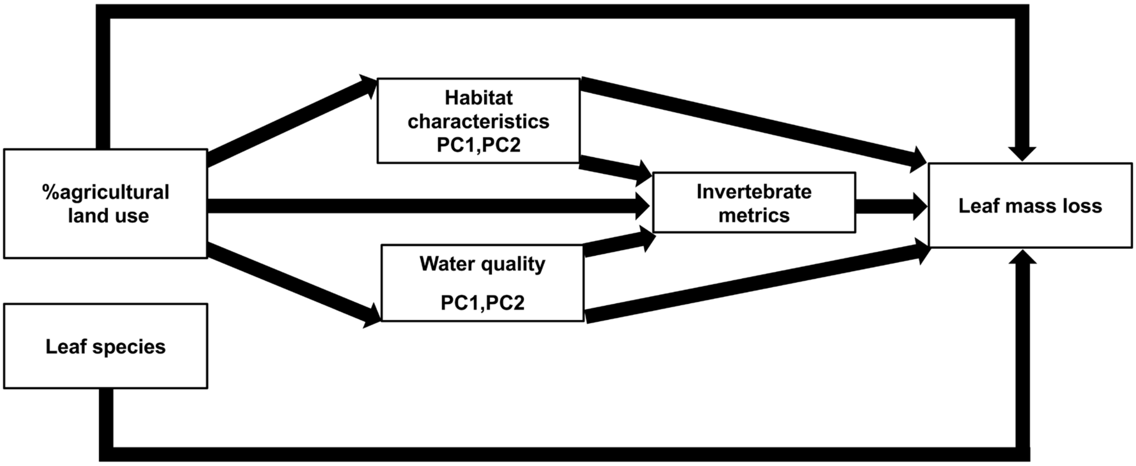

Figure 2. Conceptual structural equation model depicting pathways by which the percentage share of agricultural land use in the streams' catchments, leaf species identity, habitat characteristics, water quality parameters, and invertebrate metrics influence leaf litter decomposition rates based on previous studies. '%agricultural land use' was modelled to have both direct and indirect effects (mediated by habitat characteristics, water quality parameters, and invertebrate metrics) on leaf litter decomposition rates. Habitat characteristics and water quality parameters are represented by the first two principal components from the respective principal component analyses.

(p = 0.388 for the interaction 'leaf species identity × mixture'). Detritivores decomposed alder ($k_{\mathrm{dd;\ detritivore}} = 0.025 \pm 0.005$; mean ± SE) approx. 8-fold and 3.5-fold faster than oak ($k_{\mathrm{dd;\ detritivore}} = 0.003 \pm 0.001$) and black locust ($k_{\mathrm{dd;\ detritivore}} = 0.007 \pm 0.002$), respectively, in single-species litterbags (Fig. 3). In mixed-species leaf litterbags, the same pattern was observed, however, detritivores decomposed alder ($k_{\mathrm{dd;\ detritivore}} = 0.020 \pm 0.04$) only 4-fold and 2-fold faster than oak ($k_{\mathrm{dd;\ detritivore}} = 0.005 \pm 0.001$) and black locust ($k_{\mathrm{dd;\ detritivore}} = 0.011 \pm 0.001$), respectively (Fig. 3). The pattern of substantially faster alder decomposition by detritivores – compared to oak and black locust – was especially observed under low to intermediate agricultural intensity in the upstream catchment (≤30%), while the differences in decomposition among species became smaller with an increase in its intensity (Fig. 3). The observation of an ~ 2-fold faster detritivore-mediated decomposition of oak and black locust in mixed-species leaf litterbags, especially at low to intermediate agricultural intensity (≤ 30%), is coherent with our results on biodiversity effects, which showed a positive net biodiversity effect – driven by complementarity. The influence of the selection effect, on the other hand, was negligible (Fig. 4). Furthermore, both the net biodiversity effect and complementarity showed a monotonic, inverse S-shaped decrease along the gradient of agricultural intensity (Fig. 4).

For microbially-mediated leaf litter decomposition, leaf species identity and litter mixing showed significant influences ($p \leq 0.003$) on the decomposition rates, while both factors interacted (p = 0.048). Microorganisms decomposed alder ($k_{\mathrm{dd;\ microbial}} = 0.0022 \pm 0.0001$) approx. 1.5-fold and 1.3-fold faster than oak ($k_{\mathrm{dd;\ microbial}} = 0.0015 \pm 0.0005$) and black locust ($k_{\mathrm{dd;\ microbial}} = 0.0017 \pm 0.0001$), respectively, in single-species litter bags (Fig. 3). In mixed-species leaf litterbags, the same pattern was observed, however, microorganisms decomposed alder ($k_{\mathrm{dd;\ microbial}} = 0.0030 \pm 0.0003$) 3-fold and 2-fold faster than oak ($k_{\mathrm{dd;\ microbial}} = 0.0010 \pm 0.0001$) and black locust ($k_{\mathrm{dd;\ microbial}} = 0.0016 \pm 0.0001$), respectively (Fig. 3).

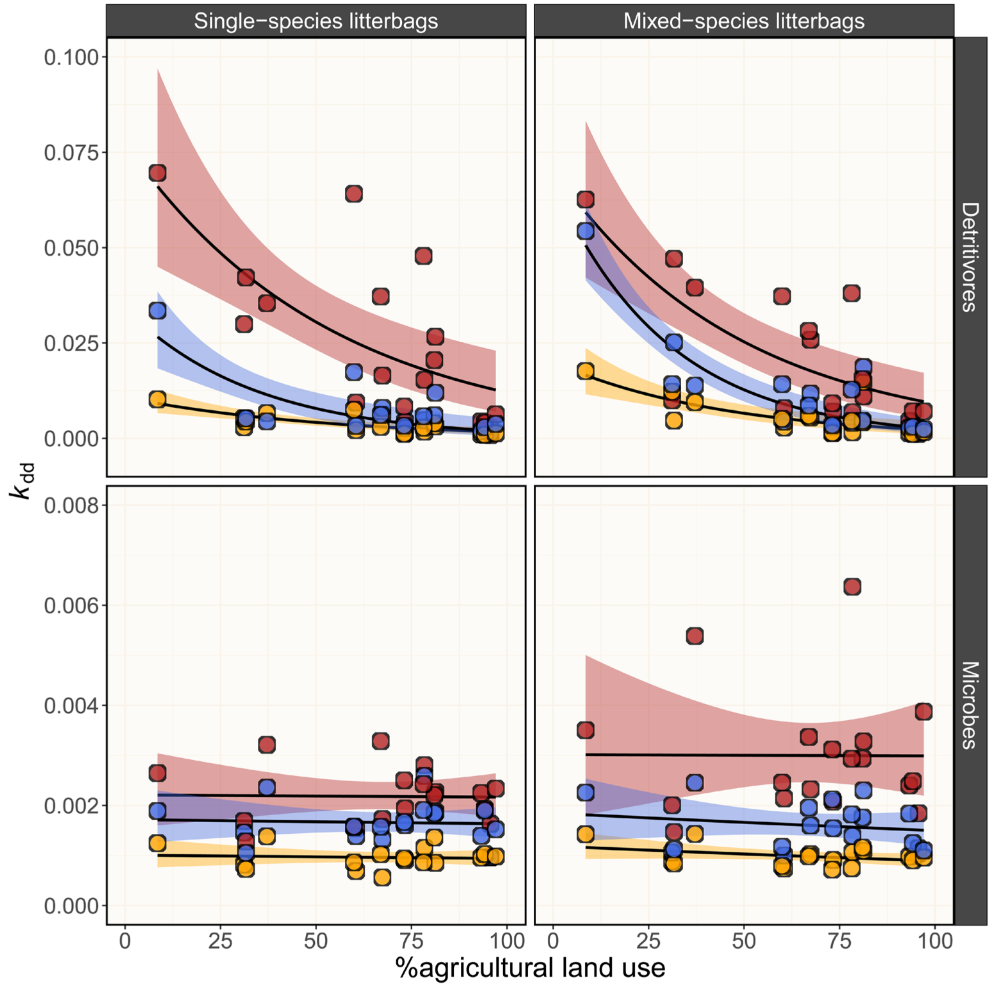

Figure 3. Detritivore-mediated (upper row) and microbially-mediated (lower row) leaf litter decomposition rates (k_{dd}) for alder (red), oak (yellow), and black locust (blue) along the gradient of agricultural land use in the streams' catchments for single-species (left column) and mixed-species (right column) leaf litterbags. Black lines depict generalized linear models applied to the leaf litter decomposition rates of individual leaf species together with the associated 95% confidence bands in the respective color.

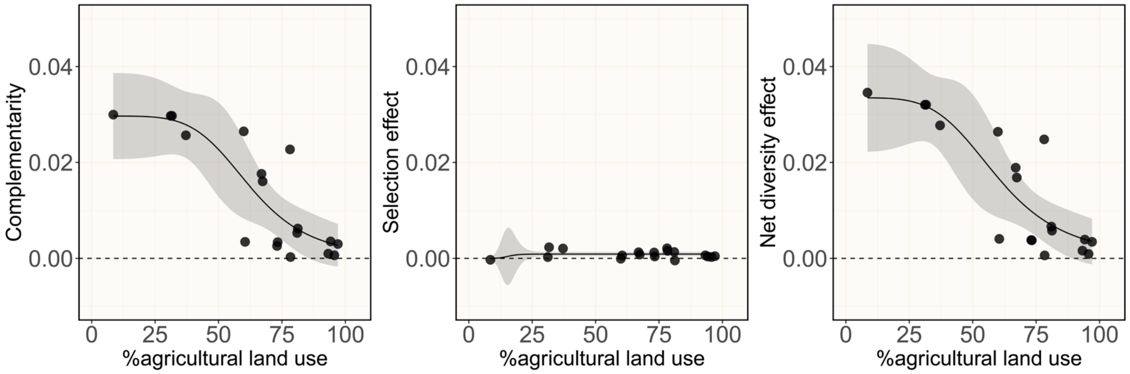

Figure 4. Dose-response models (solid lines; shaded areas depict the 95% confidence interval bands) and individual measurements (filled circles) for complementarity, the selection effect, and the net diversity effect along the gradient of agricultural land use in the streams' catchments, based on detritivore-mediated leaf litter decomposition rates.

Habitat characteristics and water quality parameters

The PCA on the habitat characteristics revealed that the first two PCs captured 49% of the total variation (PC1: 30%; PC2: 19%). PC1 was mainly (individual |loadings| ≥ 0.40) associated with increasing depth, fine sediment, and submersed plants, as well as decreasing flow, share of in-stream leaves and woods (ø < 10 cm), and in-stream woody debris (ø >10 cm). Depth, flow and velocity increased along PC2 (Table 2). The PCA on the water quality parameters revealed that the first two PCs explained 69% of the total variation (PC1: 39%; PC2: 30%). PC1 was associated with higher alkalinity, DIN, and phosphate. Oxygen and pH increased along PC2 (Table 2).

Direct and indirect effects of increasing agricultural intensity on leaf litter decomposition in streams

For single-species leaf litterbags, there were significant direct (path coefficient = −0.29) and indirect effects of agricultural intensity on leaf litter decomposition rates in the SEM (Fig. 5a). We found that negative indirect effects of agricultural intensity appeared to be mediated through effects on the proportion of sensitive invertebrate species ($\text{SPEAR}_{\text{pesticides}}$, Supporting information) and habitat characteristics: agricultural intensity had a negative effect on $\text{SPEAR}_{\text{pesticides}}$ ($R^2 = 0.32$; path coefficient = −0.57), while $\text{SPEAR}_{\text{pesticides}}$ itself positively affected leaf litter decomposition rates (path coefficient = 0.23, Fig. 5a). On the other hand, agricultural intensity positively affected PC1 of the habitat characteristics ($R^2 = 0.35$; path coefficient = 0.42), meaning that depth, the share of fine substrate, and the growth of submerged plants increased, while the water flow, and the share of in-stream leaves and woods (ø < 10 cm) as well as in-stream woody debris (ø > 10 cm) decreased along the agricultural intensity gradient. PC1 of the habitat characteristics finally negatively affected leaf litter decomposition rates (path coefficient = −0.19, Fig. 5a). The significant influence of leaf species identity on leaf litter decomposition rates became also apparent in the SEM. There was no evidence for a significant influence of any other predictor, including further invertebrate metrics or the water quality parameters (Fig. 5a).

For the mixed-species leaf litterbags, SEM showed evidence of significant direct (path coefficient = −0.49) and indirect effects of agricultural intensity on leaf litter decomposition rates (Fig. 5b). Negative indirect effects of agricultural intensity in the SEM were mediated through effects on the proportion of sensitive invertebrate species ($\text{SPEAR}_{\text{pesticides}}$, Supporting information) and water quality parameters: agricultural intensity had a negative effect on $\text{SPEAR}_{\text{pesticides}}$ ($R^2 = 0.32$; path coefficient = −0.66), while $\text{SPEAR}_{\text{pesticides}}$ positively affected leaf litter decomposition rates (path coefficient = 0.26, Fig. 5b). On the other hand, agricultural intensity positively affected PC1 of the water quality parameters ($R^2 = 0.34$; path coefficient = 0.35), meaning that alkalinity, DIN and PO_4^{3-}-P increased, while the pH and oxygen decreased along the agricultural intensity gradient. PC1 of the water quality parameters negatively affected

Table 2. Results extracted from the principal component analyses on habitat characteristics and water quality parameters; only two principle components (PC1 and PC2) were extracted for each principle component analysis based on eigenvalues. Percent of variation explained by the variables and |loadings| ≥ 0.40 (in bold) are shown.

	% variance PC1	% variance PC2	Loadings PC1	Loadings PC2
Habitat characteristics				
Depth	**14.4**	**30.5**	**0.55**	**0.63**
Width	1.6	**28.1**	0.18	**0.61**
Flow	**21.0**	**18.56**	**−0.67**	**0.49**
Fine sediment	**15.7**	6.9	**0.58**	−0.30
Submersed plants	**20.9**	3.6	**0.66**	0.22
Leaves and woods	**10.9**	3.2	**−0.48**	−0.20
Woods	**15.6**	9.3	**−0.57**	0.35
Water quality parameters				
Alkalinity	**28.3**	4.6	**0.74**	0.26
pH	7.0	**43.2**	0.37	**0.81**
DIN	**35.7**	3.9	**0.83**	−0.24
PO_4^{3-}-P	**28.7**	**14.3**	**0.75**	**−0.46**
Oxygen	0.3	**33.9**	0.08	**0.71**

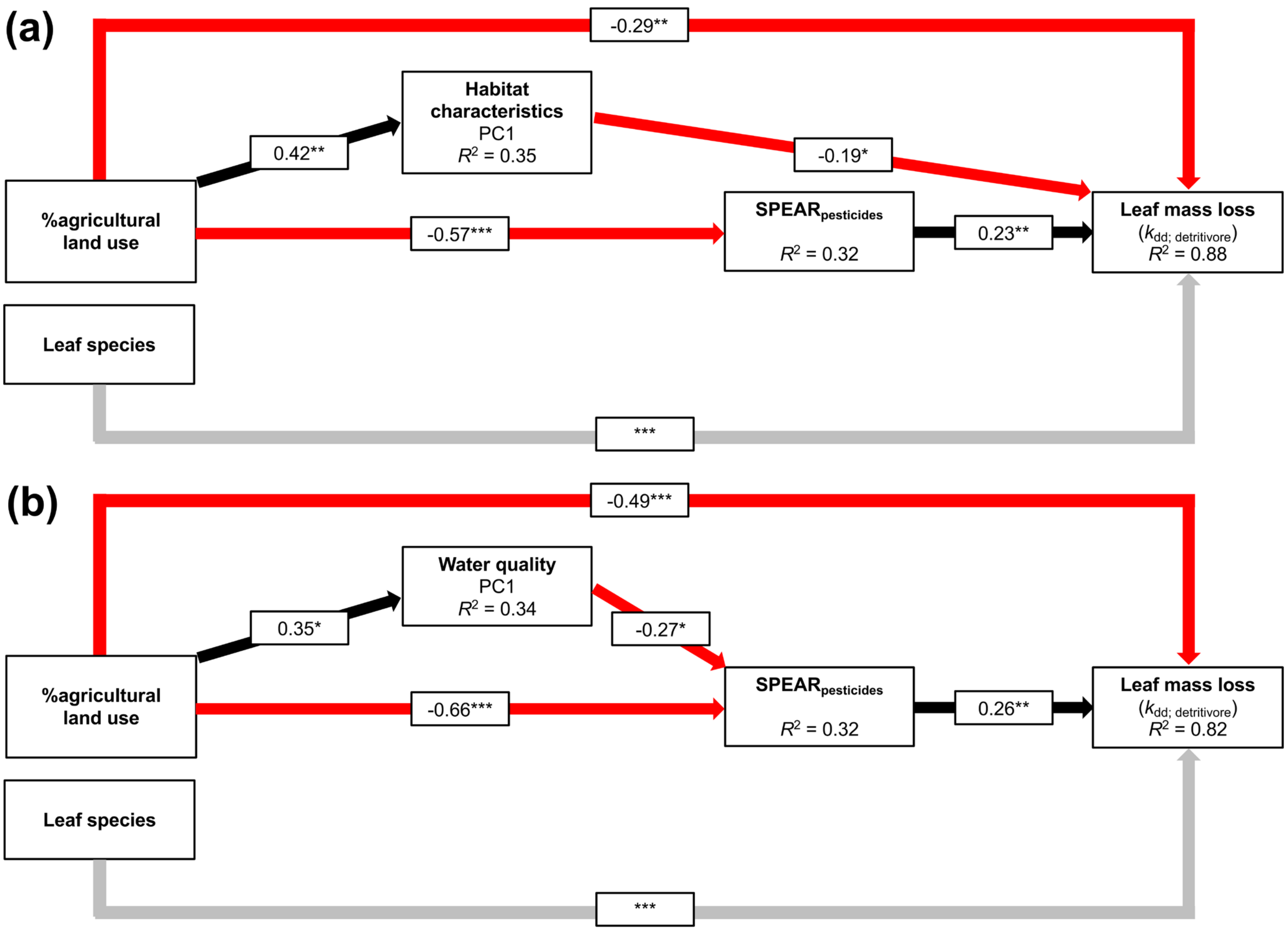

Figure 5. Piecewise structural equation models showing the pathways by which the percentage share of agricultural land use in the streams' catchments, leaf species identity, the SPEAR$_{pesticides}$ index, water quality parameters and habitat characteristics influence detritivore-mediated leaf litter decomposition rates in (a) single-species and (b) mixed-species leaf litterbags. Solid black and solid red arrows indicate significant positive and negative influences, respectively. Standardized path coefficients are shown. Note that leaf species identity entered the analyses as a factorial parameter, for which no path coefficients are produced (grey arrow). Marginal R^2 values indicate explained variance. Single-species litterbags: Fisher's $C=0.367$, $p=0.999$, 6 df, BIC = 52.224; mixed-species litterbags: Fisher's $C=3.505$, $p=0.743$, 6 df, BIC = 55.362. $^*p < 0.05$; $^{**}p < 0.01$; $^{***}p < 0.001$.

the SPEAR$_{pesticides}$ index (path coefficient = −0.27, Fig. 5b). The significant influence of leaf species identity on leaf litter decomposition rates became also apparent in the SEM. There was no evidence for a significant influence of any other predictor, including further invertebrate metrics or habitat quality parameters (Fig. 5b).

Discussion

Effects of leaf species identity and diversity on leaf litter decomposition in streams under increasing agricultural intensity

We observed strong preferential feeding responses of detritivores among the leaf species, with alder strongly favored irrespective of whether leaves were offered in single-species or mixed-species leaf litterbags as indicated by the fast detritivore-mediated leaf litter decomposition rates. Such preferential feeding is in line with previous studies (Hladyz et al. 2009). Preferential feeding patterns are likely explained by the nutrient content and recalcitrance of the individual leaf species that shape the attractiveness of the substrate for microbial decomposers and macroinvertebrate detritivores (Cornwell et al. 2008, Frainer et al. 2016). Both groups of heterotrophic organisms tend to prefer resources rich in labile compounds and nutrients as well as a low recalcitrance (Graça 2001, Gessner et al. 2007) to maximize their net energy intake and overcome imbalances in C:N:P ratios of leaf litter and their own tissue (Martinson et al. 2008, Hladyz et al. 2009).

Consequently, we found that the N-fixing and lignin-poor leaf species alder was preferably eaten by detritivores, followed by the N-fixing but lignin-richer black locust and the N-poor and highly lignin-rich oak, indicating that black locust and oak leaves are less attractive food sources (cf. Swan et al. 2008, Frainer and McKie 2015). On the other hand, indirect effects via leaf-associated microbial decomposers are conceivable. Fungal decomposers are known to shape the palatability and nutritious value of leaf litter (Bärlocher 1985, Hladyz et al. 2009). Since also fungal decomposers prefer nutrient-rich and low recalcitrant leaf litter (Gessner and Chauvet 1994), alder should have allowed fungi to grow better and be more productive, as leaf-bound nutrients and energy are more easily available. Oak and black locust, on the other hand, are N-poorer and are more recalcitrant and such leaf litter should have been colonized and processed less efficiently, retaining a high recalcitrance and low palatability, ultimately slowing down detritivore-mediated leaf litter decomposition (Gonçalves et al. unpubl., Gonçalves et al. 2023). Although we did not measure leaf-associated fungal biomass, the microbially-mediated decomposition patterns observed for the three leaf species at least indicate that microorganisms increased decomposition of alder vs oak and black locust leaf litter, irrespective if observed for single-species or mixed-species leaf litterbags. Rates of detritivore-mediated leaf litter decomposition decreased for all three leaf species as agricultural intensity increased. Similar results have been found in some studies (Piscart et al. 2009, Rasmussen et al. 2012). Most notably, Woodward et al. (2012), who quantified detritivore-mediated leaf litter decomposition rates across a broad nutrient gradient (DIN: 14–21641 $\mu g\ l^{-1}$; soluble reactive P: < 1 to 926 $\mu g\ l^{-1}$), also observed declining detritivore mediated leaf decomposition over nutrient concentrations > ~ 1000 μg DIN l^{-1}, similar to the concentration range at our sites (Table 1). These negative relationships between increasing agricultural impact and detritivore-mediated decomposition are likely to reflect a combination of a loss of sensitive, highly efficient detritivores in the more degraded environmental conditions (Frainer and McKie 2015) and potential direct effects of pesticides or high concentrations of, for instance, ammonium on detritivore activity and feeding rates (Woodward et al. 2012).

In contrast with detritivore-mediated decomposition, microbially-mediated leaf litter decomposition remained comparatively stable along the gradient of agricultural intensity in both single-species and mixed-species leaf litterbags, a pattern also observed in previous studies (Pascoal et al. 2005, Englert et al. 2015, but see Gulis and Suberkropp 2003 for elevated microbial decomposition in nutrient-enriched environments). This may be explained by redundancy in the microbial communities, by which the accomplished function remains stable because increased biomasses of tolerant species compensate for the loss of sensitive species (Naeem and Li 1997).

Mixing the leaf species can be seen as a very small-scale manipulation, where three resources are brought into greater proximity. This gives scope for biodiversity effects, as each leaf species exhibits their own structural and chemical characteristics, which in turn affect the formation and activity of microbial communities, detritivore preferences, and ultimately functional dynamics. The observed increase in the detritivore-mediated leaf litter decomposition rates of oak and black locust in mixed-species leaf litterbags under low to intermediate agricultural intensity reflects the importance of complementarity. Identifying the exact mechanism in a field study is challenging, but previous research points to several possibilities. Studies showed compounds being transported through rhizomorphs of fungal networks from a source site towards the growing front (Cairney 1992). Fungal translocation of N from N-rich leaf litter (alder) could have supported the microbial colonization of N-poorer leaf litter (Handa et al. 2014). These microbial processes might have increased nutrient content in oak and black locust, making them a more attractive food resource for detritivores. Litter mixing might also enhance complementarity by favoring greater niche differentiation of detritivores among leaf species (and among individual leaves at different decay stages), increasing species-specific feeding efficacies.

A further potential mechanism explaining the positive effects of litter mixing on decomposition relates to variation in litter stoichiometry. Alder leaves were almost always a preferred food source over oak and black locust leaves in mixed-species leaf litterbags. In most of the cases only midribs of alder leaves were obtained from coarse-mesh leaf litterbags while large leaf fragments of oak and black locust remained (Supporting information). Such feeding patterns can be explained from an energetic and stochiometric perspective, as consumers try optimizing their growth and reproduction through feeding on high-quality food sources. Meeting their nutrient demands seems especially challenging for detritivores, as the stoichiometric composition of their food sources can differ considerably from their body (Cross et al. 2003). The fact that stoichiometric imbalances between detritivores and leaf litter were found to be lowest for alder (Hladyz et al. 2009) may therefore explain the strong preferential feeding on alder leaf litter in mixed-species leaf litterbags. Consequently, feeding on leaves of lower nutritional value later in the study might have benefitted from the 'nutrient subsidy' provided by alder earlier in the experiment, such that some key nutrient requirements were already met and allowed more efficient feeding on the less nutritious species after alder depleted.

Irrespective of the underlying mechanism, complementarity could explain the approximately 2-fold increased detritivore-mediated leaf litter decomposition of oak and black locust in mixed-species leaf litterbags compared to their single-species counterparts under low to intermediate agricultural pressure. Leaf litter diversity effects on detritivore-driven decomposition were, however, modified along the agricultural intensity gradient, observed as monotonic decreases in the net biodiversity effect and complementarity as the share of agriculture in the upstream catchment increased. Bottom–up effects mediated through less developed networks of fungal hyphae extending among leaf species under increasing agricultural intensity may have shortened the transport of N across leaves and by this reduced their nutritious value. On the other hand, top–down effects, either as lethal or sublethal (reduced feeding efficacy or drift) effects of agriculture likely compromised complementarity among detritivores, for instance through variation in the degree of dominance (both numerical and functional dominance) and the identity of key species (McKie et al. 2008).

Direct and indirect effects of agricultural intensity on leaf litter decomposition in streams

The observed negative influence of increasing agricultural intensity in streams' catchments on detritivore-mediated leaf litter decomposition rates match with earlier studies (Piscart et al. 2009, Rasmussen et al. 2012). However, pathways by which agricultural intensity affected the assessed ecosystem function rates differed to some degree between single-species and mixed-species leaf litterbags. In both litterbag types, agricultural intensity showed a direct negative effect on the proportion of sensitive invertebrate species ($SPEAR_{pesticides}$), in turn affecting the detritivore-mediated leaf litter decomposition rates. These patterns have been reported previously (Schäfer et al. 2012) and indicate that stress associated with agricultural land use either alters the functional capacity of species with only minor alteration of the community (Kefford et al. 2012) or leads to the loss of keystone species (Paine 1969), affecting functioning. As a consequence, agricultural land use effects on the functional capacity and abundance of sensitive species seem to translate to similar indirect effects on detritivore-mediated leaf litter decomposition, given the positive relationship between the latter two measures.

The positive correlation between agricultural intensity and the first principal component of the habitat characteristics observed for single-species leaf litterbags is in line with previous studies that reported high sediment inputs, loss of riparian vegetation, and altered hydrology due to agricultural practices that caused excessive sedimentation and loss of in-stream habitat complexity (as reviewed by Lester and Boulton 2008). The subsequent negative impact on detritivore-mediated leaf litter decomposition in single-species leaf litterbags are possibly explained by sedimentation on the leaf litter surface that reduces the surface area of the leaves available for microbial colonization and detritivore feeding. Consequently, leaf litter with less abundant fungal communities and a lower available surface area for feeding should represent less attractive food and by this mechanism reduce leaf litter decomposition rates (cf. Truchy et al. 2022).

In contrast, the direct positive effect of agricultural intensity on the water quality parameters in the SEM for mixed-species leaf litterbags reflects the influx of DIN and PO_4^{3-}-P in agricultural streams due to the run-off of fertilizers (Moss 2008), a pattern that matches well with earlier studies (Truchy et al. 2022). Our finding that water quality parameters in terms of elevated DIN, PO_4^{3-}-P, and alkalinity were negatively associated with $SPEAR_{pesticides}$ may be driven by a response of that indicator to water quality, and/or past or current pesticide pollution (Schuwirth et al. 2015).

Finally, the direct (unexplained) effect of agricultural intensity on leaf litter decomposition rates revealed by the SEMs for single-species and mixed-species leaf litterbags seems to point at effects of habitat characteristics or environmental parameters not measured in the present study. These habitat characteristics and environmental parameters could be associated with river regulation (deviation in discharge, channelization, removal of dead wood and vegetation, ditching) and forest management (habitat clearing, standing age, tree volume; for more details see Truchy et al. 2022), which affect detritivore-mediated leaf litter decomposition either directly or indirectly through altered detritivore communities.

Conclusions

The results of the present study indicate that agricultural land use weakens the relationship between biodiversity and ecosystem functioning by detritivores through adverse effects on mechanisms that govern complementarity in mixed leaf litter assemblages. This disconnection of the biodiversity-ecosystem functioning relationship was found at an intermediate agricultural intensity in the streams' catchments and was seemingly independent of the leaf litter species. Because agricultural intensity is projected to increase in the future (Tilman et al. 2011), the effects observed here could have far reaching consequences for the C dynamics and food webs in streams that potentially propagate across ecosystem boundaries (Schulz et al. 2015). Nevertheless, further scrutiny of field studies on a larger scale in areas with different climate regimes, leaf litter input in terms of different leaf species, and altered flow regimes (e.g. intermittency) is needed to verify the generalization and transferability of our results across biogeographical regions.

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Author contributions

Alexander Feckler: Conceptualization (equal); Data curation (lead); Formal analysis (equal); Investigation (equal); Methodology (equal); Visualization (lead); Writing – original draft (equal); Writing – review and editing (equal). **Jacob Schnurr**: Investigation (equal); Writing – review and editing (equal). **Gabriela Kalčíková**: Investigation (equal); Writing – review and editing (equal). **Amélie Truchy**: Formal analysis (equal); Writing – review and editing (equal). **Brendan G. McKie**: Conceptualization (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Ralf B. Schäfer**: Conceptualization (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Ralf Schulz**: Conceptualization (equal); Methodology (equal); Writing – review and editing (equal). **Mirco Bundschuh**: Conceptualization (equal); Funding acquisition (lead); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

Data are available from GitHub (https://github.com/afllandau/https-10.1111-oik.09936). Data, associated metadata, and calculation tools are also available from the corresponding author upon reasonable request (alexander.feckler@rptu.de).

Supporting information

The Supporting information associated with this article is available with the online version.

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