

The legacy of forest disturbance on stream ecosystem functioning

André Frainer^{1,2,3}  | Brendan G. McKie⁴ 

¹Department of Ecology and Environmental Science, Umeå University, Umeå, Sweden

²Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, Tromsø, Norway

³Norwegian Institute for Nature Research (NINA), Fram Centre, Tromsø, Norway

⁴Department of Aquatic Sciences and Assessment, Swedish University of Agricultural Sciences, Uppsala, Sweden

Correspondence

André Frainer

Email: andre.frainer@nina.no

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Abstract

1. Forest clearance is a pervasive disturbance worldwide, but many of its impacts are regarded as transient, diminishing in intensity as forest recovers. However, forests can take decades to centuries to recover after severe disturbances, and temporal lags in recovery of ecosystem properties for different forest habitats are mostly unknown. This includes forest streams, where most studies of the impacts of forest clearance are restricted to the first years of recovery, typically finding that temporary increases in light and nutrient run-off diminish as forest recovers. Implications of longer term changes remain little investigated.
2. In a space-for-time substitution experiment, we assessed changes in organic matter processing and in the functional and taxonomic composition of litter-consuming detritivores along a riparian forest age gradient ranging from 1 to 120 years since last timber harvesting.
3. Variation in organic matter processing and detritivore functional diversity along the forest succession gradient were both expressed as second-order polynomial relationships (peaking at ~50 years along the forest age gradient). Decomposition rates were lowest in both the more recently clear-cut and older riparian forest streams.
4. Variation of litter decomposition rates among litter bags within streams, measured by the coefficient of variation, was lowest in recent clear-cuts and increased linearly along the succession gradient. This result indicates higher within-stream heterogeneity in decomposition rates in older forest streams.
5. *Synthesis and applications.* We found that the decomposition of leaf litter, a component of carbon cycling in forests, was higher in streams flowing through intermediately aged forest, and that several key attributes of the organisms regulating litter decomposition also varied systematically with forest age. These findings highlight the longer term consequences of forest succession following forest clear-cutting for stream habitats. Our findings further illustrate complications arising from the use of forested sites as references for newly cleared sites without properly accounting for forest age, given conclusions regarding biotic responses will depend on the age of the reference forests. Finally, our results emphasise the

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potential of intensive forest management centred on vast, one-time clear-cutting events to drive long-term homogenisation not only in forest age structure but also in the functioning of associated forest stream habitats..

KEYWORDS

clear-cutting, detritivores, disturbance legacy, forest succession, forestry, functional diversity, litter decomposition, space-for-time substitution

1 | INTRODUCTION

Fire, cyclones, volcanoes, forestry and other natural and anthropogenic perturbations can significantly reduce forest cover (Bixby et al., 2015; Chang et al., 2019; Klug et al., 2012; Richardson & Béraud, 2014; Swanson et al., 2011), leading to long-lasting effects in both aquatic and terrestrial ecosystems (Harding et al., 1998; Moreno-Mateos et al., 2017; Santos et al., 2020). In forest streams, the sudden opening of the canopy following such disturbance affects physical, chemical and biological conditions, and is often associated with a shift in the dominant resource base of food webs from allochthonous organic matter to autochthonous algal production (Akselsson et al., 2007; Larsen et al., 2009; McKie & Malmqvist, 2009; Moore & Richardson, 2012; Sweeney et al., 2004). Many of these changes are ameliorated or reversed as forest regrows. However, forest recovery can take decades to centuries after severe disturbances (Finegan, 1996), and is characterised by successional phases dominated by distinct plant species that can affect ecosystems differently. Presently, our understanding of how forest disturbances affect stream ecosystems is mostly limited to the first few months and years after disturbance.

The short-term effects of forest disturbances on stream ecosystems have been extensively studied in the context of forest management for timber production (McKie & Malmqvist, 2009; Webster & Waide, 1982; Yeung et al., 2017). However, despite decades of research, there is little consensus regarding the general effects of clear-cutting on stream ecosystems (Richardson & Béraud, 2014). Most studies have used variations of a control-impact design, where impacted streams are in forest plots ranging from 1 to 26 years since the last clear-cutting event (Ely & Wallace, 2010; Haefner & Wallace, 1981; Stone & Wallace, 1998; Yeung et al., 2017), whereas the mean age of trees in control forest plots may range from a few decades to several centuries (Warren et al., 2013; Yeung et al., 2017). Thus, the lack of consensus on clear-cutting effects might be explained by differences in the forest age of impacted and reference sites among studies, given the contrast between clear-cuts and forest plots may often be confounded by the successional stage of forest in each category. This attests to our limited understanding of how forest succession, from the initial disturbance through an extended recovery phase towards old growth forests, might alter biodiversity and functioning of stream ecosystems.

Forest management for timber production is a dominant land use across the world's vast boreal region. Following clear-cutting, the

first years of succession are typically dominated by shade-intolerant fast-growing grasses and small shrubs, which are subsequently over-shadowed by larger deciduous trees (Engelmark & Hytteborn, 1999; Finegan, 1996), with conifers becoming dominant at later successional stages (Josefsson et al., 2009). These changes in forest composition may cause a continuous and nonlinear shift in leaf quality, with transitions from refractory grass to labile deciduous leaves and later refractory, lignin-rich conifer needles. The relative availability of palatable compared with refractory litter inputs can affect the functional composition of consumers that rely on plant litter as a dietary component (including the ratio of more specialist and generalist detritivores) and rates of organic matter processing (Ferreira et al., 2016; Jonsson et al., 2017; Kominoski et al., 2011). This has potential to drive substantial heterogeneity in stream ecosystem functioning at a landscape scale, mirroring the mosaic of forest patches at different stages of recovery from the last clear-cut, that typically arises from forest management. Boreal forests have strongly marked seasons that might also modulate responses of stream biota to alterations to litter inputs (Frainer & McKie, 2015; Frainer et al., 2014). For example, increased streambed insolation associated with a more open canopy might benefit aquatic diversity during autumn, when sunlight begins to fade, but might decrease the diversity of litter-associated fauna in spring due to potential stimulation and dominance of algae and algal grazers (Roberts et al., 2007; Warren et al., 2013). This effect is likely to be most marked in clear-cuts, but might also be evident in old-growth forest sites where a more open canopy favours higher light exposure at the streambed (Warren et al., 2013).

In a space-for-time substitution experiment, we assessed how clear-cutting and subsequent riparian forest regrowth and succession affected the processing of leaf litter and the associated invertebrate detritivore community over a forest age gradient ranging from 1 to 120 years, in both autumn and spring. This experimental design has the potential to identify temporal trends in the responses to clear-cutting that may have been obscured in previous control-impact analyses. We hypothesised that (1) invertebrate communities associated with leaf litter would show a shift in functional composition, from dominance by more generalist detritivores that can also feed on algae during the first decades after clear-cutting, to more specialised leaf eaters during later phases of forest succession. As managed boreal forests in Sweden mostly have conifers at the later successional stages, due to a combination of natural forest succession and strategic thinning of deciduous trees (Skogsstyrelsen, 2012), we further hypothesised that (2)

the presence of obligate leaf eaters would decrease as deciduous litter inputs decline at more advanced stages of forest succession. Finally, (3) leaf litter decomposition rates would also show a non-monotonic relationship with riparian forest age, with rates increasing during the first decades of forest succession, but steadily decreasing once conifers became dominant.

2 | MATERIALS AND METHODS

2.1 | Study sites

We conducted a field study in 10 streams running through managed boreal forests in northern Sweden (19°07'E–20°21'E, 63°52'N–64°15'N; Figure 1; Figure S1). Streams differed in the time since their surrounding vegetation (minimum 0–10 m from the stream edge) was last clear-cut, ranging from recently clear-cut sites (<3 years), with stream banks largely unvegetated apart from grass, to 120-year-old riparian forest sites (Table 1). Information on forest age was obtained from dendrochronological inventories and internal databases from SLU Vindeln - Svartbergets Research Field Station. Visual inspection at the sampling sites and of satellite images (Google Earth Pro ©) confirmed that streams had ~200 m of similar riparian vegetation structure ranging upstream the sampling location. Although current forest management guidelines in Sweden recommend leaving a forest buffer strip along streams, clear-cutting regularly extends to the stream bank, especially on first- and second-order streams (Hylander et al., 2002). After logging, clear-cut patches follow the typical recovery trajectory for boreal forests. Human alterations to this successional development include the planting of conifer seedlings 1–2 years after clear-cutting and the removal of deciduous trees at later successional stages (thinning) to improve timber production (Skogsstyrelsen, 2012).

Streams that had been clear-cut ~20 years before this experiment contained scattered small spruce *Picea abies* and downy birch *Betula pubescens* trees (2–3 m high), with herbaceous vegetation dominant in the most recent clear-cuts (Figure 1). Forested sites older than 40 years were characterised by an open understory populated by low-growing shrub *Vaccinium* spp., moss and liverwort species (McKie & Malmqvist, 2009) and forest cover (>10 m high

trees) consisting of birch *Betula* spp., grey alder *Alnus incana*, willow *Salix* spp., with the conifers Scots Pine *Pinus sylvestris* and Norway Spruce *P. abies* also present. The oldest forests (>90 years old) had a similar understory, but were mostly dominated by Scots Pine, with a lower presence of deciduous trees (Figure 1).

Due to potential confounding effects related to differences in catchment size, spatial location and physical and chemical characteristics among streams, we sampled streams in a paired design, whereby the five streams flowing through relatively young (either clear-cut or undergoing early-mid successional-stage recovery) forest were each paired with a stream flowing through older forest (Table 1). Streams were paired firstly based on their spatial location, but were also carefully matched in key hydromorphological aspects including channel width, substrate and water velocity. Water samples (500 ml) were collected from each stream in both autumn and spring at the beginning and midway through each sampling period, and frozen for later analysis of nitrate (NO₃), ammonium (NH₄), total nitrogen, phosphate (PO₄) and total phosphorus (Tecator 5012, Foss Tecator) concentrations. Water velocity was quantified on the same dates using an electromagnetic flowmeter (Model 801), and we also measured pH (Mettler T90 Titrator, Mettler Instrumente AG) once at the start of each sampling period. Water temperature was recorded every 2 hr using Smartbutton (ACR systems) data loggers, deployed in concert with our litter decomposition assay.

2.2 | Litter decomposition

We assessed variation in ecosystem functioning along the riparian forest age gradient by quantifying leaf litter decomposition both in autumn and spring. In September 2010, we collected freshly abscised birch *B. pendula* leaf litter from the ground in one single location near Umeå University campus and let it air-dry for 2 weeks. Four grams of air-dried leaf litter were enclosed in fine- and coarse-mesh bags (mesh opening = 0.5 and 10 mm respectively), which allow quantification of leaf decomposition attributable primarily to microbial organisms and microbes and invertebrate detritivores together, respectively (Gessner & Chauvet, 2002).

Five replicate litterbags were placed in one riffle in each stream, with each coarse-mesh bag paired with a fine-mesh bag. Litterbag



FIGURE 1 Three streams along the riparian forest age gradient assessed in this study. From left to right, streams are ordered by their age since clearcutting: 2, 20 and 80 years

TABLE 1 Physical and chemical characteristics of the 10 streams assessed in autumn and spring. Water temperature refers to the sum of daily means during the study period

Season	Stream	Stream pair	Riparian age ^a	Water temp ^b	Stream width ^c	Stream depth ^d	Water velocity ^e	Water discharge ^f	NH ₄ ^g	NO ₃ ^h	TN ⁱ	TP ^j	pH
Autumn	Kvarnbäcken	▲	1	61.1	2	15.7	0.83	16.94	<0.1	0.02	0.45	<0.04	6.0
	Brannbäcken	■	2	87.6	1	21.7	0.41	8.50	<0.1	<0.01	0.32	<0.04	6.3
	Stromsjöleden	▼	3	67.2	0.7	4.7	0.04	0.25	0.15	0.12	0.75	0.06	5.1
	Karrbäcken	●	16	116.5	1.4	20.2	0.34	12.88	<0.1	<0.01	0.45	<0.04	4.7
	Kluddbäcken	◆	26	65.6	1	21.7	0.54	11.35	<0.1	<0.01	0.42	<0.04	5.7
	Kallbäcken	▼	45	63.0	0.8	3.7	0.19	0.60	0.13	0.24	0.80	<0.04	5.7
	Gardsjöbäcken	■	120	100.8	5	39.6	0.61	95.04	<0.1	0.019	0.36	<0.04	7.2
	Krycklan	▲	90	48.3	5	28.4	0.43	55.08	<0.1	<0.01	0.27	<0.04	6.7
	Bastumyrbäcken	◆	109	61.9	1	21	0.27	7.11	<0.1	<0.01	0.28	<0.04	6.7
	Kullabäcken	●	120	112.7	2	16.4	0.25	14.14	<0.1	0.19	0.64	<0.04	7.2
Spring	Kvarnbäcken	▲	1	232.2	2.5	16	0.42	10.89	<0.1	<0.01	0.44	<0.04	5.5
	Brannbäcken	■	2	291.9	1	12	0.20	1.83	<0.1	<0.01	0.18	<0.04	6.2
	Stromsjöleden	▼	3	207.7	0.4	9	0.26	0.59	0.58	0.22	1.56	<0.04	4.9
	Karrbäcken	●	16	185.4	1	11	0.10	1.15	<0.1	<0.01	0.31	<0.04	4.8
	Kluddbäcken	◆	26	165.3	1.5	6.7	0.53	4.05	<0.1	<0.01	0.27	<0.04	5.3
	Klallbäcken	▼	45	148.0	0.5	7	0.34	1.30	<0.1	<0.01	0.62	<0.04	5.5
	Gardsjöbäcken	■	120	181.9	7	22.1	0.42	69.18	<0.1	<0.01	0.28	<0.04	7.2
	Krycklan	▲	90	263.1	3	25.5	0.24	11.83	<0.1	<0.01	0.20	<0.04	6.6
	Bastumyrbäcken	◆	109	136.2	1.5	10	0.29	4.10	<0.1	0.02	0.24	<0.04	6.4
	Kullabäcken	●	120	231.7	2	14	0.21	5.39	<0.1	0.11	0.51	<0.04	7.0

^aYear; ^bSum of daily average temperature over the study period, in °C; ^cm; ^dcm; ^ecm/s; ^fcm³/s; ^gmg/L.

pairs were attached every 50 cm along a metal chain, and the two end points of the chain were anchored to the stream bottom using iron bars. After 44 (autumn) and 28 (spring) days, litterbags were retrieved from the streams and transported to the laboratory. These different exposure times allowed the assessment of seasonal differences in the effects of forest succession at similar overall point in the decomposition process (~50% mass loss), avoiding potential confounding effects related to litter processing stage and invertebrate colonisation. Leaves were cleaned under tap water, oven-dried for 48 hr and weighed to the nearest 0.01 g. Litterbags from one forested site (Gärdsjöbäcken) were lost in autumn due to extreme levels of ice formation. Decomposition rates were estimated assuming a negative exponential response, following the equation (Petersen & Cummins, 1974):

$$M_t = M_0 \cdot e^{-kt},$$

where M_t is final and M_0 is initial litter dry mass, k is the decomposition rate and t is either time or is the sum of mean daily temperatures for temperature-corrected decomposition rates.

2.3 | Fungal biomass

We quantified fungal biomass as the concentration of fungal ergosterol in the leaf litter. After litterbag retrieval, five leaf discs were cut from random leaves within each fine-mesh litter bag. Leaf discs were ground, placed in Eppendorf vials containing 1 ml ethanol 99.5% and shaken on a vortex mixer for 30 min at 5°C. Samples were centrifuged for 15 min at 14,000 RPM and at 5°C (Dahlman et al., 2002). The liquid extract was then analysed using high-performance liquid chromatography, at 100% MeOH mobile phase, 1.5 ml flow and 280 nm wavelength, to quantify ergosterol content in the sample.

2.4 | Invertebrate detritivores

Litter-consuming invertebrate detritivores colonising our litterbags were identified to species and counted. We estimated detritivore density as the number of individuals per litterbag. After identification, individuals were placed in small aluminium pans, oven-dried at 60°C for 24 hr and weighed to the nearest 0.1 mg. Average body mass was estimated as the ratio between detritivore biomass and density for each litterbag. Metabolic capacity (MC) indicates higher resource consumption for smaller individuals (Brown et al., 2004), and was estimated by scaling detritivore biomass at the litterbag level to 0.75.

Invertebrate shredder species, while feeding on leaf litter as their primary resource, vary in how much they feed on other resources, such as algae, fine particles or even small invertebrates (Klemmer et al., 2012; Schmidt-Kloiber & Hering, 2011; Wissinger et al., 2004). To capture this variation, we used functional trait information from

a freely available database (Schmidt-Kloiber & Hering, 2011). We extracted trait data on feeding type, whereby the more obligate litter consuming shredder species are distinguished from those with algal grazer, FPOM or predator feeding traits, patterns of habitat use (including substrate composition, e.g. coarse or fine substrates, and water current, e.g. preferences for high or low water velocity sites) and emergence period as adults, which distinguishes phenological strategies among the aquatic detritivore species and hence captures information about their life stage during our autumn and spring surveys. Species traits were fuzzy coded (Greenacre, 2013), allowing membership of each species across several trait groups simultaneously.

We assessed invertebrate functional diversity using two complementary metrics (Ricotta & Moretti, 2011). First, we assessed the distribution of functional traits in the community using Rao's Q measure of functional dispersion (Laliberté & Legendre, 2010), which calculates the dominance structure of dissimilar traits. Second, we assessed the identity of the most abundant functional traits in each litterbag via the community-weighted mean trait value (CWM, Grime, 1998) approach. For this, we multiplied a species-by-functional-traits matrix with a matrix of species abundance or species MC to estimate community composition effects due to species density ($CWM_{Abundance}$) or due to metabolic demands (CWM_{MC}) respectively. The resulting CWM matrices can then be analysed using principal component (PC) analyses. The site scores from the PC axis capturing most variation in CWM (first axis) were then used to characterise the identity of the dominant traits across all stream reaches in autumn and spring. Rao's Q and CWM were calculated using the R package `FD` (Laliberté & Shipley, 2011).

2.5 | Data analysis

Water chemistry and hydromorphological data were averaged for each stream and season and analysed using PC analyses with the package `VEGAN` (Oksanen et al., 2019) in R (R Core Team, 2020). Variables were centred and standardised to unit SD. The PC representing most variation in the data (PC1) was further tested against the riparian age gradient and season using mixed effect modelling (MEM) with the R package `NLME` (Pinheiro et al., 2012) and the package `PERFORMANCE` (Lüdecke et al., 2020) to assess marginal and conditional r^2 values (Nakagawa & Schielzeth, 2013). These analyses included the two-way interaction between season and riparian forest age. Stream pairs were fitted as random factors. Because we lacked replication across multiple years, the season factor is here regarded as testing for differences between the two study periods, and not as indicating causality that can be ascribed a general effect of season overall.

Variation in the response variables related to invertebrate detritivores (detritivore density, metabolic capacity, body size, functional dispersion and $CWM_{Abundance}$ PC1 and CWM_{MC} PC1) across the riparian forest age gradient were analysed using a similar MEM as described

above. Detritivore density, metabolic capacity, body size and functional dispersion, along with the coefficient of variation of litter decomposition, were ln-transformed to meet parametric assumptions. First- and second-order polynomial terms related to riparian age were added to the predictors to account for nonlinear trends in the relationship between the response variable (litter decomposition rate, detritivore density, MC, body size, $F_{\text{Dispersion}}$ and CWM) and forest age. Decomposition rates *per day* and *per degree day* were independently analysed using the MEM described above. These analyses included season, forest age and mesh size as fixed factors, and all their two- and three-way interactions, and stream pairs as random factors. For comparison with the binary categorical approach routinely applied in forest clear-cut studies (see meta-analysis by Richardson & Béraud, 2014 and references therein), we pooled sites into two categories according to the following definition: (a) recent clear-cuts with herbaceous vegetations or very young forests with only short, young and scattered birch trees present, and (b) conifer-dominated or dense canopies next to the stream banks. For simplicity, hereafter group 1 is referred to as 'clear-cut' and group 2 is referred to as 'forest'. In our case, applying these classifications allocates clear-cuts and forests ≤ 26 years old to the clear-cut category, and sites with forest age ranging from 45 to 120 years old to the forest control group. We analysed litter decomposition rates between clear-cut and forested streams using similar MEM as above, but substituting the age gradient with the categorical treatment as specified above.

3 | RESULTS

3.1 | Water chemical and physical variables

Our study streams were characterised by low concentrations of nutrients, with NH_4 , NO_3 and total P often below detection

limit. Streams ranged from acidic to circumneutral (pH: min = 4.7, max = 7.2) and had similar water velocity (mean = 0.35, $SD = 0.18$ m/s; Table 1). In our principal component analysis of stream environmental data, the first PC (PC1) explained 42% of the variation in the data and was positively related to total N, NO_3 and NH_4 , and negatively related to pH, discharge and water velocity (Figure S2a). We found a first-order negative association between riparian forest age and PC1, indicating that most recent clear-cut sites had higher concentration of total N, NH_4 and NO_3 , whereas older sites were characterised by lower nutrient concentrations and higher water discharge and pH ($F_{1,18} = 4.28$, $p = 0.038$; Table 1; Figure S2b). We did not find any clear evidence that the PC1 values differed between season ($p = 0.39$) nor that the association between PC1 and riparian forest age differed between seasons (season \times age interaction: $p = 0.91$).

3.2 | Leaf decomposition rates

Leaf litter decomposition rate was best described by a second-order polynomial regression. The relationship between riparian forest age and k degree day $^{-1}$ was more strongly peaked in autumn (second-order age \times season interaction: $F_{1,168} = 3.35$, $p = 0.019$), and more pronounced in coarse than fine mesh bags (second-order age \times mesh interaction: $F_{1,168} = 15.79$, $p < 0.001$; Figure 2a,b; Table S1). Decomposition rates calculated *per day* were similarly best described by a second-order polynomial regression but had an overall lower model fit (Figure S3; Table S1).

Our MEM based on forestry categories indicated a clear statistical difference between treatments ($F_{1,171} = 7.11$, $p = 0.008$), with forested sites having higher decomposition rates than clear-cut sites, but no difference between nor interaction with mesh size or season (mean k per degree day $\pm SD$ pooled across mesh sizes and

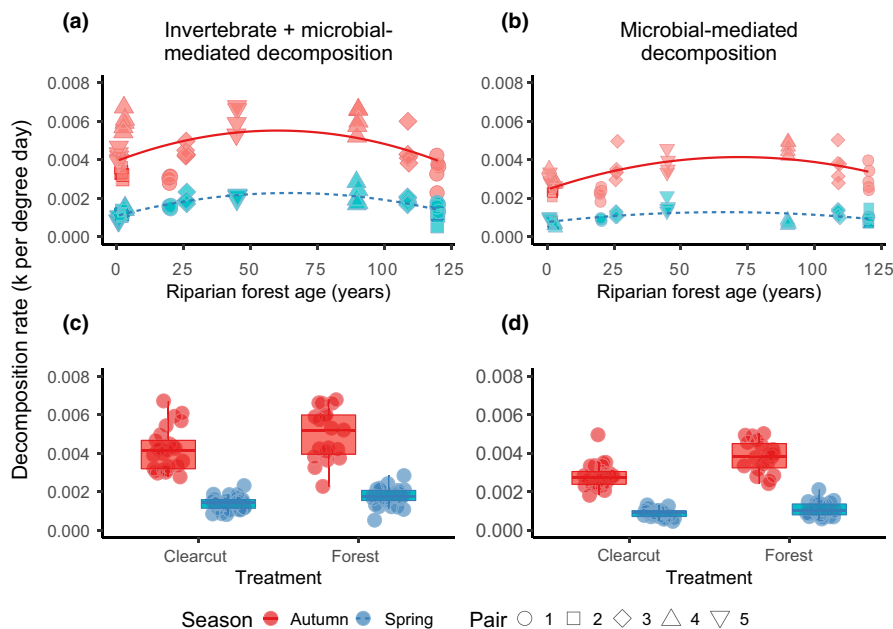


FIGURE 2 Birch litter decomposition rates *per degree day* along the riparian forest age gradient (a, b) and by forest type category (c, d) in two mesh sizes: coarse (left panels) and fine (right panels)-mesh bags. Shapes in panels a and b correspond to stream pairs (Table 1) and lines indicate best polynomial fit

seasons: forest = 0.0027 ± 0.0018 , clear-cut = 0.0023 ± 0.0015 ; Figure 2c,d).

The coefficient of variation (CV) of litter decomposition rates (which is the same for both *per day* and *per degree day* corrected rates) was higher in fine-mesh bags ($F_{1,35} = 4.24, p = 0.046$) and increased linearly with riparian forest age ($F_{1,35} = 12.71, p = 0.001$). We did not detect differences in the CV of litter decomposition rates between seasons ($p = 0.59$; Figure 3; Table S1).

3.3 | Invertebrate detritivores

Detritivore density (range: 0–91 ind/litterbag) was higher in recent clear-cuts and decreased nonlinearly with riparian forest age (second-order age: $F_{1,79} = 30.8, p < 0.001$; Figure 4a; Table S1).

Detritivore biomass (range: 0–61.4 mg dry mass) was higher in spring than autumn (season: $F_{1,78} = 33.25, p < 0.001$) and higher in both recent clear-cut and older forests (second-order polynomial: $F_{1,78} = 6.55, p = 0.002$; Figure 4b; Table S1).

Detritivore metabolic capacity (range: 0–0.28) decreased nonlinearly with increasing riparian forest age, and this relationship was attenuated in autumn, compared to spring (second-order polynomial \times season interaction: $F_{1,76} = 7.49, p = 0.001$; Figure 4c; Table S1).

Detritivore body size (range: 0.03–38.5 mg dm/ind) was related to riparian forest age as a negative unimodal relationship during spring, but not in autumn (second-order polynomial \times season interaction: $F_{1,76} = 14.37, p < 0.001$; Figure 4d; Table S1). We found no evidence that species richness (range: 0–4 spp) differed between seasons or that it was affected by the riparian forest age gradient (all $p > 0.40$; Figure 4e; Table S1).

FIGURE 3 Coefficient of variation (CV) of leaf decomposition rates along the riparian forest age gradient from two mesh sizes: (a) coarse and (b) fine-mesh bags. Shapes correspond to stream pairs (Table 1) and lines indicate best polynomial fit

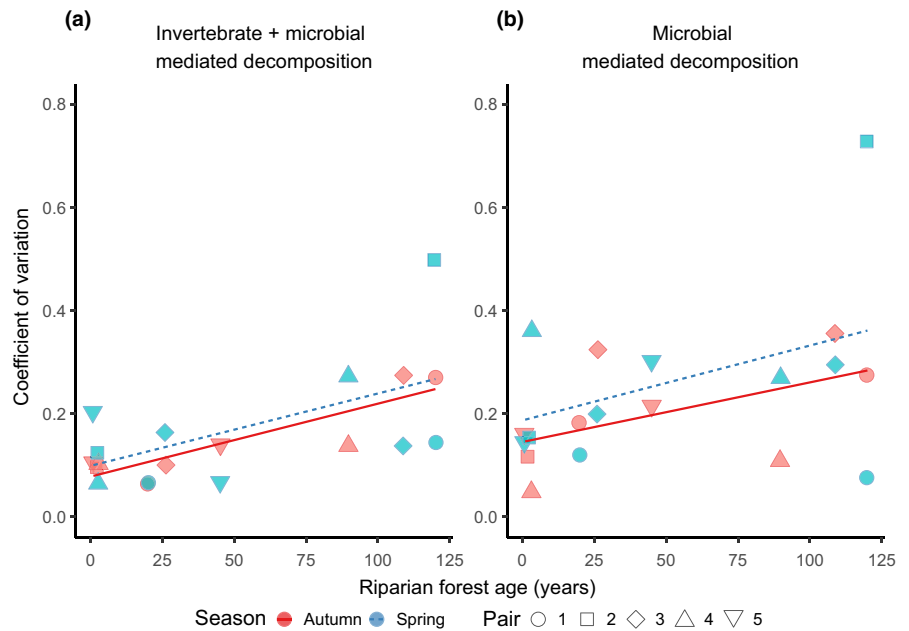
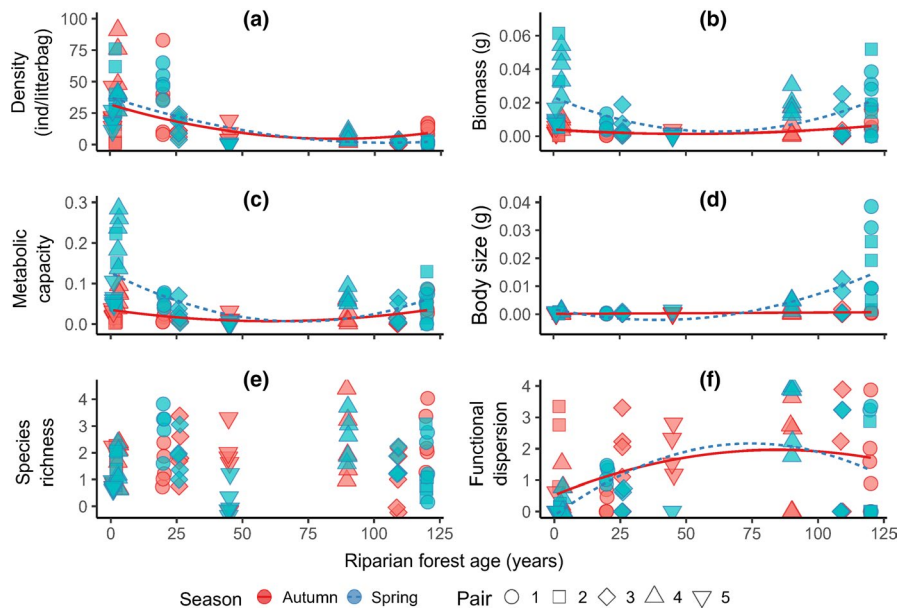


FIGURE 4 (a) Density, (b) biomass, (c) metabolic capacity, (d) body size, (e) species richness and (f) functional dispersion of invertebrate detritivores colonising birch litterbags in riffles along the riparian forest age gradient. Shapes correspond to stream pairs (Table 1) and lines indicate best polynomial fit



3.4 | Functional diversity and composition

Functional dispersion had a unimodal relationship with forest age (second-order polynomial: $F_{1,79} = 12.9, p < 0.001$), but we did not find a clear evidence for difference between seasons ($p = 0.24$; Figure 4f; Table S1).

Our principal component analysis of the abundance-weighted and metabolic-capacity-weighted mean trait values ($CWM_{Abundance}$ and CWM_{MC} respectively) was characterised by higher variation along the first PC axis (60 and 59%), with a smaller proportion of variation explained by the second axis (17% and 25%; Figure 5a,c). Both $CWM_{Abundance}$ and CWM_{MC} were linearly related to forest age in spring, but not in autumn (both season \times age interaction: $F_{1,76} > 6.5, p < 0.014$; Figure 5b,d; Table S1). In spring, traits related

to fast flow or indifferent flow velocity, leaf shredding and particle gathering and spring emergence period were more common in detritivore communities from more recent clear-cut sites. Detritivore communities at older forested sites were characterised by traits related to median water velocity and algal grazing, and autumn and summer emergence periods (Figure 5b).

3.5 | Fungal biomass

Fungal biomass measured as ergosterol concentration increased linearly with riparian forest age ($F_{1,87} = 6.18, p = 0.01$), but the evidence for difference between seasons was not statistically clear ($F_{1,87} = 3.27, p = 0.074$; Figure S4; Table S1).

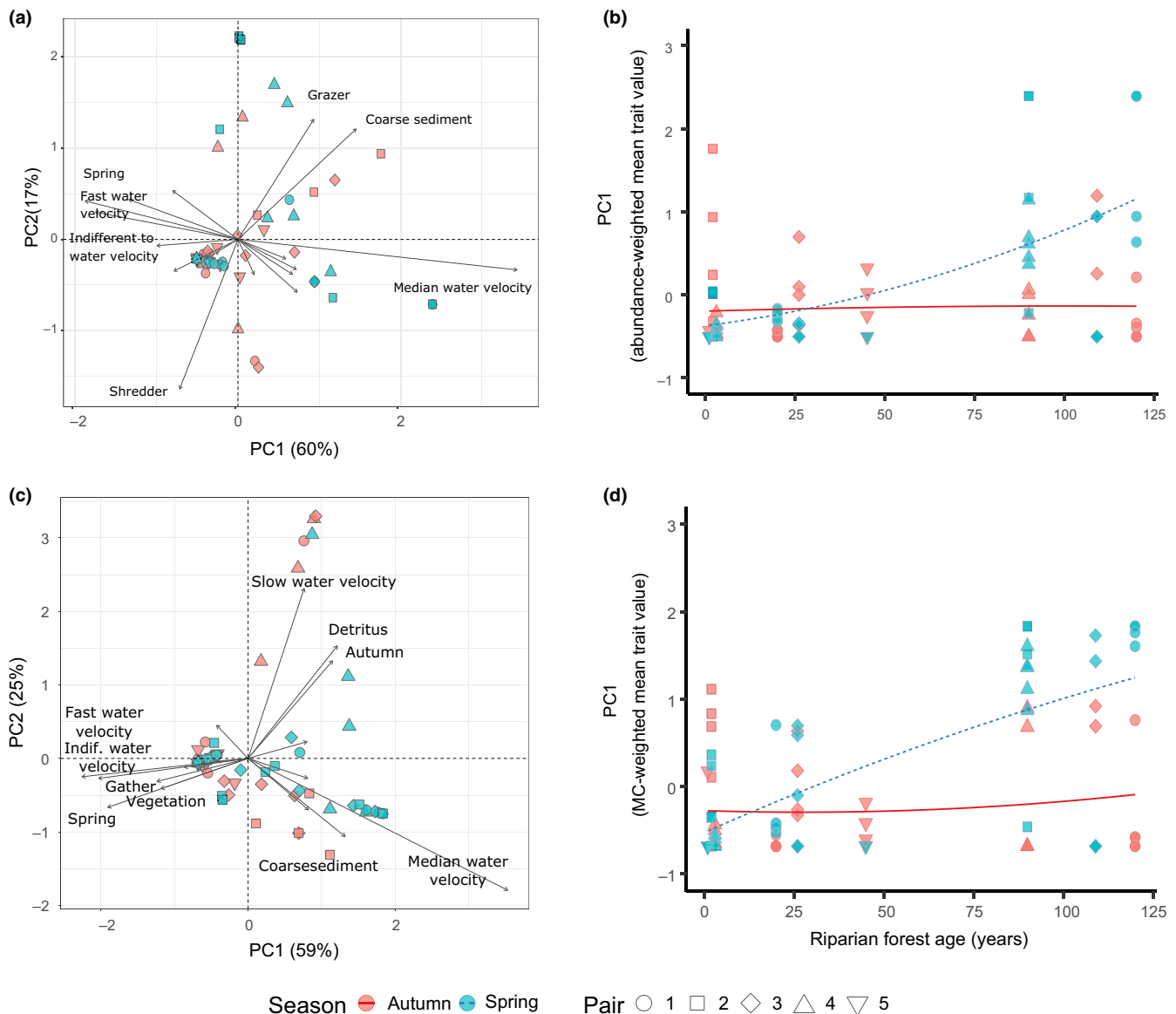


FIGURE 5 (a) Principal component analysis (PCA) of the abundance-weighted mean trait values, (b) relationship between PC1 of the abundance-weighted trait values and the riparian forest age gradient, (c) PCA of the metabolic capacity (MC)-weighted mean trait values and (d) relationship between PC1 of the MC-weighted trait values and the riparian forest age gradient. For clarity, only traits with scores > 1 are shown in the PCAs. Shapes correspond to stream pairs (Table 1) and lines indicate best polynomial fit

4 | DISCUSSION

Our space-for-time assessment of stream ecosystem functioning along a forest succession gradient allowed us to uncover important and previously undescribed legacy effects of forest age on key ecosystem processes in streams. The results indicate that as clear-cut sites recover from logging, leaf litter decomposition increases steadily until a point in the succession gradient (about 50 years in our study) where decomposition rates start to slow down again. Although leaf decomposition rates are similarly low at both ends of the gradient, the mechanisms driving those low processing rates differ. The hump-shaped relationship observed here is explained by an interplay between variation in the body size, density and functional traits of detritivore communities along the forest age gradient.

4.1 | Litter decomposition along the forest age gradient

The hump-shaped relationship between litter decomposition rate and riparian forest age was most apparent when decomposition rates, from both coarse and fine-mesh bags, were controlled for thermal differences among the streams. This result indicates that in streams situated in the middle of the successional gradient (i.e. ~50 years since clear-cutting in our study), invertebrates and microbes were more efficient at decomposing leaf litter relative to the available thermal energy (McKie & Malmqvist, 2009). The range of decomposition rates observed along the forest age gradient is comparable to the range observed in previous studies conducted in the region (Frainer et al., 2014, 2018). Low decomposition rates are indicative of microbial-dominated decomposition, with a minimal contribution from benthic invertebrate consumers (Boyero et al., 2011), and hence a low energy turn-over rate with a lower incorporation of resources exported from the surrounding terrestrial ecosystems into animal biomass. Higher decomposition rates are often associated with high energy turn-over rate mediated either by a range of functionally diverse benthic invertebrate species which complement one another in how they process different litter components, or by a few particularly efficient detritivore species that dominate the system (Frainer et al., 2018; McKie et al., 2008). High decomposition rates are also often associated with high-quality (higher nutrient to carbon ratio) litter input, particularly litter from deciduous trees (Lidman et al., 2017), which were most abundant in the riparian zone of the mid-successional streams in our study. The composition of both microbial and invertebrate communities present in those mid-successional streams is likely to have been shaped by the higher litter quality naturally available there, which might also have influenced decomposition rates of our litter assay. Although litter decomposition rates were overall higher in autumn than in spring, the hump-shaped relationship between litter decomposition and the successional gradient is evident in both seasons.

We found higher variability in litter decomposition rates at the local patch scale within streams, quantified as the coefficient of variability (CV) among litterbags, as forest age increased. This supports

the idea that streams with forested riparian zones have more heterogeneous habitats, resulting in a more patchy distribution of aquatic invertebrates (Malmqvist, 2002). This in turn is likely to result in a more heterogeneous effect of aquatic invertebrates on litter decomposition at local scales (Tiegs et al., 2009), which might be further reinforced by the tendency of individual species to strongly aggregate in specific litter patches (Presa Abos et al., 2006). Although overall decomposition rates in the older riparian forests were as slow as those in the newest clear-cuts, the higher CV in older forest streams possibly indicates greater variation in invertebrate communities and/or habitat features at local scales.

In contrast with the older forested sites, the most recent clear-cuts have both low within-stream variability (low CV) and generally low decomposition rates, indicating low responsiveness of both invertebrate detritivores and microbes to the availability of litter in our mesh bags in those streams. This lack of responsiveness is notable, given the litter used in our assay, *B. pendula* represents a relatively high quality litter resource in boreal northern Sweden, relative to the other common tree species in the region (i.e. conifers). In the middle of the riparian forest age gradient, mean decomposition rates were greatest, whilst the CV was closer to average, suggesting a more uniformly efficient use of leaf litter across the benthic communities in these streams.

4.2 | Biotic and abiotic variables and litter decomposition rates

Stream water chemistry is often affected by clear-cutting (Akselsson et al., 2007; McKie & Malmqvist, 2009). Tree-felling typically decreases the pool of some base cations in the soil and in its run-off (Akselsson et al., 2007; Ledesma et al., 2013), which in turn leads to lower pH. Clear-cutting also increases DOC, nitrate and phosphate (Löfgren et al., 2009) export to the watershed. In oligotrophic systems, such as ours, a small increase in nutrients typically stimulates higher litter decomposition rates (Woodward et al., 2012) because of positive effects on the activity of microbes colonising the leaf litter (McKie & Malmqvist, 2009; Woodward et al., 2012). Nonetheless, only three of our 10 streams had total nitrogen concentrations in the range 0.6–0.8 mg/L, two of which were in the older forest sites, and all 10 streams had minimum concentrations of total phosphorus and ammonium. Thus, it is likely that water nutrient concentrations had no or near negligible effects on the processing of dead organic matter in our streams. The lower pH found in some of our recent clear-cut sites has been associated with lower microbial-mediated decomposition rates in other studies (Dangles et al., 2004; McKie et al., 2006).

Organisms with a higher metabolic capacity (MC) have a larger energy demand relative to their biomass (Brown et al., 2004), and so we expected the sites containing detritivore assemblages with higher metabolic capacity to show the most rapid decomposition rates. Surprisingly, however, this was not evident in our data. In the recent clear-cuts, decomposition rates were low despite a high MC, associated with a high density of small-sized detritivores. Dominance of

small individuals is a commonly observed outcome of disturbances in streams (Statzner & Beche, 2010). Towards the middle of the gradient, where decomposition rates were highest, detritivore densities and individual body sizes were both low, yielding overall low MC values. Detritivore densities remained low in the old forest streams, but body sizes were much larger, which resulted in an increased MC.

The apparent discrepancy between MC and functioning is best explained by changes in functional diversity and functional characteristics of the invertebrate detritivores present in each site. Although all detritivores analysed in this study are expected to feed on leaf litter to some extent, they may also feed on other food sources depending on resource availability, and invertebrate ontogeny and size. The more obligate leaf-eating detritivores, which were found at the recent clear-cuts, were among the smallest-sized species found in our study, which is likely to have limited their influence on litter decomposition. The occurrence of non-obligate leaf-eaters increased along the forest age gradient, which helps explain why the oldest forest sites also had low overall invertebrate-mediated decomposition rates. Functional dispersion, which is an important predictor of leaf decomposition rates (Frainer & McKie, 2015; Frainer et al., 2014), was highest throughout the forest sites. More functionally dispersed detritivore communities are more likely to complement one another in the efficient use of different components of the litter resource, favouring higher decomposition rates relative to sites dominated by fewer functional traits (Frainer et al., 2014). Possibly, sites at the middle of our forest age gradient represented a set of optimum conditions, whereby higher functional dispersion and abundances of obligate leaf-eaters supported higher leaf decomposition rates. Optimal conditions for more efficient leaf decomposition were not met at either extreme of the gradient, reflected by the presence of small leaf consumers in recent clear-cuts, and the presence of large but less-obligate leaf consumers in older forest sites.

4.3 | Implications of forest age to control-impact studies and cross-study comparisons

Ecosystems from different biomes are likely to show different recovery trajectories over time, in line with differences in forest succession, and local climatic and seasonal characteristics. One consequence of this is that control-impact designs might not provide a good basis for cross-study comparisons of how forest succession affects stream ecosystems, especially in cases where the forest control groups have different ages across the various studies. Terrestrial vegetation characteristics are likely to be most similar across biomes in the first years following clear-cutting, typically dominated by shade-intolerant fast-growing grasses and small shrubs. In temperate regions, these vegetation types are later overshadowed by larger deciduous trees (Engelmark & Hytteborn, 1999; Finegan, 1996). Secondary succession forests in the neotropics may be dominated by long-lived pioneer trees (Finegan, 1996), whereas in boreal regions, conifers with lignin-rich leaves are normally abundant at later successional stages (Josefsson et al., 2009). More research is required to determine if the hump-shaped relationship observed here also applies to other biomes

and vegetation types, and ideally with a larger number of stream sites along a forest successional gradient than was possible in our region (where the regional history of clear-cutting and especially lack of very old forest sites constrained which portions of the forest age gradient we were able to cover). Nevertheless, our results clearly demonstrate how variation in forest age among reference sites might complicate comparisons between forested and clear-cut sites, if forest succession is not properly taken into account, given the forest sites are subject to temporal dynamics that can affect key ecosystem indicators commonly used in bioassessments and monitoring.

5 | CONCLUSIONS

The 120-year-old forest stands assessed here cannot be considered old relative to primal boreal forest (Linder & Östlund, 1998), and stream ecosystems flowing in older boreal forests (>200 years) may have different functional characteristics due to higher canopy openness and increased light availability (Warren et al., 2013). Nonetheless, our space-for-time design sheds light on previous investigations that have not detected forestry effects on freshwater communities or ecosystem functioning, with important implications for outcomes of different forest management strategies on the functioning of stream catchments. Lower intensity management strategies, emphasising smaller sized clear-cuts, tree thinning and protection of riparian buffers that results in a patchwork of forest in different successional stages is likely to generate a similar patchwork for organic matter processing. In contrast, more intensive forest management resulting in vast, large-scale clear-cuts has potential to drive a long-term homogenisation of stream ecosystem function at the landscape scale.

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AUTHORS' CONTRIBUTIONS

A.F. and B.G.M. designed the study; A.F. conducted field and lab activities and analysed the data; A.F. wrote the first draft of the manuscript with subsequent substantial contribution from B.G.M.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.cnp5hqc4h> (Frainer & McKie, 2021).

ORCID

André Frainer  <https://orcid.org/0000-0002-3703-7152>

Brendan G. McKie  <https://orcid.org/0000-0002-1796-9497>

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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