

Legacy effects of altered flooding regimes on decomposition in a boreal floodplain

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Abstract

Background and aims Since long-term experiments are scarce, we have poor understanding of how changed flooding regimes affect processes such as litter decomposition.

Methods We simulated short- and long-term changed flooding regimes by transplanting turfs between low

(frequently flooded) and high (in-frequently flooded) elevations on the river bank in 2000 (old turfs) and 2014 (young turfs). We tested how incubation elevation, turf origin and turf age affected decomposition of standard litter (tea) and four types of local litter.

Results For tea, we found that the initial decomposition rate (k) and stabilization (S) of labile material during the second decomposition phase were highest at high incubation elevation. We found intermediate values for k and S in young transplanted turfs, but turf origin was not important in old turfs. Local litter mass loss was generally highest at high incubation elevations, and effects of turf origin and turf age were litter-specific.

Conclusion We conclude that incubation elevation, i.e., the current flooding regime, was the most important factor driving decomposition. Soil origin (flooding history) affected decomposition of tea only in young turfs. Therefore, we expect that changes in flooding regimes predominantly affect decomposition directly, while indirect legacy effects are weaker and litter- or site-specific.

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Keywords River management · Ecosystem function · TBI · Tea bag method · Floodplain · Boreal zone

Introduction

The flow regime of many rivers worldwide is significantly affected by management, damming and changes in climate (Erwin 2009; Nilsson et al. 2005) which decrease or increase the magnitude, duration, frequency

and timing of flood pulses (Hirabayashi et al. 2013; Nilsson et al. 2005). This has profound direct and indirect impacts on ecosystem processes and species composition instream, as well as in the bordering riparian ecosystems through changes in water availability, pH, sedimentation, dispersal, species re-assembly and shifts in trophic interaction (Keddy 2000; Nilsson et al. 1997; Ström et al. 2011). However, we have little understanding of long-term legacy effects of altered flooding regimes on riparian ecosystem functioning in the field, because long-term field experiments where ecosystem processes, like decomposition, are studied are scarce (Britson et al. 2016). Yet, decomposition is a fundamental factor for riparian and instream ecosystem functioning as it drives nutrient availability and cycling (Moore 1990; Moore et al. 2007; Swift et al. 1979; Webster and Benfield 1986). Understanding these effects is vital for modelling effects of future flooding regimes and climate on element dynamics and matter fluxes between riparian and instream ecosystems (Erwin 2009; IPCC 2013).

Altered flooding regimes may cause legacy effects on litter decomposition via several direct and indirect pathways. First, flooding may directly increase the level of soil moisture and alter abiotic conditions, thereby increasing the activity of decomposer organisms and speeding up decomposition (Hefting et al. 2005; Xiong and Nilsson 1997). However, extended flooding can cause oxygen deprivation which may hamper decomposition rates, though this may be alleviated by oxygen diffusion from roots (Keddy 2000). Second, flooding may alter the decomposer community composition directly, or indirectly via changes in other abiotic or biotic conditions (Hieber and Gessner 2002; Langhans and Tockner 2006). This will affect the functional capacity of these communities to degrade organic compounds. Third, changes in flooding regime may induce gradual changes in plant community composition and import and export of drift-line debris, thereby changing the quantity and quality of the litter that enters the soil food web and hence the rate of litter breakdown (Britson et al. 2016; Ström et al. 2011; Xiong and Nilsson 1997, 1999).

Short- and long-term legacy effects of changes in the flooding regime on decomposition of plant litter in the field can be determined with space-for-time or before-after impact designs (Britson et al. 2016; Hasselquist et al. 2015; Whittinghill et al. 2014). However, such comparisons are often confounded with changes in other environmental conditions, such as climate or soil type.

Therefore, we simulated changes in the flow regime experimentally by transplanting turfs between low (frequent flooding) and high elevation (infrequent flooding) and transplanting control turfs to their own elevation as a control. We repeated the experiment at two time points with a 14-year interval, to study both short- (young turfs) and long-term (old turfs) effects of altered flooding regimes on litter breakdown. In each turf we incubated standard litter (rooibos and green tea; Keuskamp et al. 2013), as well as four local litter types of which two are characteristic at low elevations and two at high elevations.

We hypothesized that decomposition will be affected by an interaction between current incubation elevation (high or low), turf origin (high or low) and time since transplantation, referred to as turf age (young or old), both for tea and local litter types. For litter decomposition based on tea, we assumed a two-phased exponential-decay model, with an initial fast phase and the weight loss curve leveling off in the second phase when recalcitrant material is stabilized (Keuskamp et al. 2013). First, we hypothesized that incubation elevation would have a strong impact on decomposition. We expected high initial decomposition rates (k) for the tea at low incubation elevation, because flooding will increase soil moisture, and possibly also temperature in the boreal system, which may enhance litter breakdown (Hefting et al. 2005; Langhans and Tockner 2006). In addition, for the tea we expected that less litter would be remaining at low compared to high elevation, leading to lower stabilization (S) rates of the labile fraction of the material. In line with this, for the local litters we expected higher total weight loss at low than at high incubation elevation. Our second hypothesis was that turf origin would have legacy effects on decomposition processes. As a result, for turfs that were transplanted between elevations, regardless of the direction of transplantation, we expected that tea and litter decomposition in recently transplanted, young turfs would be intermediate compared to control turfs at the original elevations, resulting in an interaction between incubation elevation and turf origin. However, for both the tea derived decomposition rates and local litter weight losses the effects of turf origin may disappear in the old turfs. This is because legacy effects of soil transplantation may disappear over time, due to gradual changes in plant and soil community composition driven by the new flooding regime that prevails at the incubation elevation. This would show as a three-way interaction between incubation elevation, turf origin and turf age affecting decomposition.

Methods

Site description

To test the short- and long-term effects of changed flooding regimes on ecosystem functioning we set up a soil turf transplantation experiment in a floodplain meadow in Strycksele, Northern Sweden (64°22'N, 19°22'E). The free flowing, 455 km long Vindel River has a mean annual discharge of ca 200 m³ s⁻¹ at its confluence with the Ume River, which is ca. 30 km from the Baltic Sea (Swedish Meteorological and Hydrological Institute, SMHI). The river flow is characterized by a clear spring flood from the end of May to mid-June, during which discharge can reach 1410 m³ s⁻¹ (in 2010). The floodplain meadow in Strycksele is characterized by a belt of *Calamagrostis* and *Carex* species at low elevation, shrubs and *Salix* bushes at intermediate levels, and species-rich grassland on the floodplain which gradually changes into a mixed birch and pine forest. In the period of the study, between 2000 and 2014, the higher elevation was flooded roughly every fourth year, for 4.25 ± 1.6 days in the years of flooding, while low elevation turfs were flooded yearly for on average 21.1 ± 2.7 days (SMHI; Supplementary material 1). In the same period, mean annual growing season (average air temperature above +5 °C) was 150 days, mean annual temperature was +2.1 °C (± 2.7 S.E.), and precipitation was 588.4 mm (± 31.8 S.E.) per year (SMHI).

Experimental setup

In 2000 and 2014, we excavated in total 64 soil turfs along the river bank in Strycksele, using eight replicated random blocks spread over a ca. 250 m long reach, which was 15 to 35 m wide. Each block consisted of eight turfs, four in the middle of the vegetation zone representative for low (tall graminoids) and four at high elevation (species rich grassland), with the high elevation turfs positioned more or less straight above the low elevation turfs. The turfs at high and low elevations differed on average 1.86 m (± 0.06 S.E.) in elevation. Within each block, two turfs (70 × 100 cm) at high and two at low elevations were excavated in June 2000 (referred to as “old turfs”). Shortly before spring flood in May 2014, we excavated four additional turfs (30 × 20 cm) in each block, two at high and two at low elevations (referred to as “young turfs”). Turfs

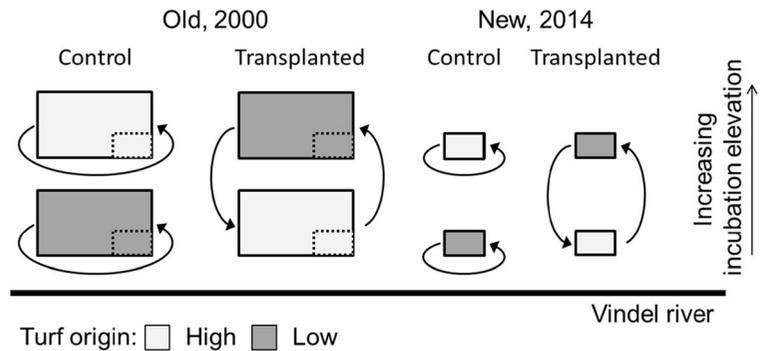
included whole plants and were excavated ca. 20–30 cm depth, which is deeper than the rooting zone in this site. In both years, half of the turfs on both high and low elevations were rotated 180° and carefully put back on the same location as a control for excavation disturbance (Fig. 1). The other turfs were carefully placed in cradles and transplanted to their new incubation elevation. Per block, each litter incubation elevation thus included two pairs of young and old turfs, originating from low and high elevations, respectively (Fig. 1). Turfs transplanted from high to low elevation simulated the effect of increased flooding regimes, while turfs transplanted from low to high elevation simulated the effects of decreased flooding. The turf size in 2000 was larger than in 2014 because the old turfs were also used for a long-term vegetation monitoring study by Ström et al. (2011). To be able to compare litter mass loss in young and old turfs we incubated our litter bags in a 20 × 30 cm area in a corner of the old turfs (Fig. 1). We conducted two decay experiments in each turf. First, we incubated tea bags as a standard litter substrate (Keuskamp et al. 2013) during which the turfs were flooded naturally. Second, we incubated local litter collected at the study site, immediately after flooding.

Tea Bag Index experiment

The Tea Bag Index (TBI) protocol of Keuskamp et al. (2013) uses Lipton green tea (EAN 87 22,700 05552 5) and rooibos tea (EAN 87 22,700 18,843 8) in woven, nylon mesh bags (0.28 mm mesh). We buried two weighted, air-dry tea bags of each type (green and rooibos) in each turf on the 23rd of May 2014. We determined the moisture content (drying 48 h at 60 °C) and loss of material by handling of five extra bags of each tea type. Tea bags were retrieved after three months, cleaned without water, dried (48 h at 60 °C) and weighed without label.

Using tea bags with a known material composition allows for calculation of initial decomposition rate and stabilization of the labile fraction during the second phase of decomposition (Keuskamp et al. 2013). In this way, a short term incubation provides insight in longer term decomposition. That is, the TBI method assumes a two-phased decomposition model for the labile fraction and no decay of the recalcitrant fraction. Initially, decomposition rate is fast while the mass loss levels off in the second phase when only recalcitrant and stabilized labile material is left. Green tea decomposes fast and

Fig. 1 Schematic overview of the eight different treatments that differed in incubation elevation and turf origin (shading) and turf age (started in 2000 or 2014). Direction of transplantation is indicated with arrows. Subplots where the litterbags were buried in the long-term turfs are indicated with dashed squares



after three months, green tea will be in the second phase of decomposition. Rooibos tea decomposes much slower and after three months it is still in the first phase of decomposition. Thereby, the mass loss of rooibos tea can be used to quantify initial decomposition rate (k). Mass loss of green tea can be used to determine which fraction of the labile components is decomposed during the incubation and which fraction is stabilized (S) (see Keuskamp et al. (2013) and Supplementary material 2 for a more detailed explanation).

Local litter incubations

At each incubation elevation in our study site we collected two abundant local litter types: *Betula pubescens* and a mixture of *Agrostis stolonifera* and *Deschampsia cespitosa* from high elevation and *Calamagrostis canescens* and *Carex acuta* from low elevation. Litter was collected as standing dead material after snow melt at the end of May 2014, air-dried and enclosed in 3×8 cm nylon bags (1.5 mm mesh), with one gram of litter per bag (4 litters \times 8 turfs \times 8 replicates = 256 bags). One bag of each litter type was buried vertically in the 8 cm of the top soil of each turf on the 27th of June. Bags were retrieved after 3 months, gently rinsed with water, dried (48 h at 60 °C) and weighed. We determined the moisture content (drying 48 h at 60 °C) and loss of material by handling on six extra bags of each litter type.

Environmental conditions

To characterize local environmental conditions we inserted temperature loggers (DS1921G; Thermochron; Maxim Integrated Products; San Jose; California; USA) in waterproof silicone enclosures in each turf. Mean soil temperature was calculated per turf for the incubation

periods of tea and the local litter separately. We determined flood duration by visual inspection of the temperature readings, as the number of days that lacked diurnal fluctuations (Helfield et al. 2007). To determine soil abiotic properties we collected 16 composite soil samples from the top 5 cm of the soil (one at each incubation elevation of each treatment block). In May 2014, soil pH was determined after shaking 5 g of soil with 50 ml demineralized water. In August we collected an additional soil sample (as before) and determined soil moisture by drying (72 h at 103 °C) a subsample of 30 g. We determine soil C and N content (% of dry weight) by combustion on ground samples, using a FLASH 2000 Organic Elemental Analyzer (Interscience; Breda; the Netherlands).

To characterize litter quality of the tea and the local litter types we have determined litter C, N and P content. C and N concentration (% of dry weight) were determined by combustion of grinded material, using a FLASH 2000 Organic Elemental Analyzer (as before). P-content (% of dry weight) was determined through acid digestion (with 2% persulphate; 30 min at 121 °C) after incinerating the samples for 30 min at 500 °C. The digested samples were analyzed using a QuAatro segmented flow analyzer (Seal analytical Inc.; Beun de Ronde; Abcoude). We analyzed five samples for each litter type. As microbial community composition is much less important as a driver compared to environmental and litter quality drivers, we did not measure microbial community composition directly (Makkonen et al. 2012; Veen et al. 2015).

Statistics

We used six general linear mixed effects models (LMM) including incubation elevation (high or low), turf origin (high or low), and turf age (young or old turfs) as fixed

factors, replicate block as a random factor and respectively, the decomposition rate (k), stabilization (S) and litter mass loss of the four local litter types (*B. pubescens*, *Agrostis/Deschampsia* mixture, *C. canescens* and *C. acuta*) as dependent factors. Analyses were performed using the nlme package (Pinheiro et al. 2016) in R 3.2.0 (R Core R Core Team 2016). Except for stabilization (S), dependent variables were y^{-1} transformed to improve homogeneity of variances and homoscedasticity. When we found an interaction, we tested the differences with Tukey post hoc tests in the Multcomp package (Hothorn et al. 2008), while regarding the different treatment combinations as separate groups. Differences in environmental conditions at high and low elevations were tested using pairwise t-tests on block means, and the differences in litter quality with a one-way ANOVA in R.

Results

Environmental conditions and litter quality

Shortly after the start of the incubation of the tea, the lowest turfs were flooded with an average duration of 25.7 days (Table 1). The soil temperature was roughly one degree lower at low incubation elevation (Table 1) and at low incubation elevation, old turfs that originated from high elevation had a somewhat lower temperature compared to the other turfs at low elevation (Supplementary material 3). Soil moisture content was higher at low incubation elevation than high elevation. Soil pH ranged from 5.3 to 6 and tended to be higher at low incubation elevation (Table 1). The sandy to silty soils were rather nutrient poor and C and N concentrations did not differ between elevations (Table 1).

Litter types differed significantly from each other. Green tea was the most nutrient rich, for both N and P, and had the lowest C:N ratio, while values of rooibos were comparable to those of the local litters. Within the local litters, *B. pubescens* had the lowest C:N ratio, and *C. canescens* the highest (Table 2).

Tea Bag Index experiment

Decomposition rates of the labile fraction (k) (Supplementary material 2), were lower at low than at high incubation elevation (LMM, $F_{1, 48} = 75.21$, $P < 0.001$; Fig. 2a) and in turfs from low origin (LMM, $F_{1, 48} = 11.39$, $P = 0.001$). In addition, the interaction

between turf origin and turf age (LMM, $F_{1, 48} = 7.72$, $P = 0.008$), and between incubation elevation and turf age (LMM, $F_{1, 48} = 4.70$, $P = 0.035$) affected k . These interactions indicate that k values converged between treatments in old turfs, but that in young turfs k values were determined by turf origin and incubation elevation, resulting in intermediate values in turfs that were transplanted to another elevation compared to rotated control turfs (Fig. 2a).

Stabilization (S) of the labile fraction of green tea (Supplementary material 2), was higher at high incubation elevation (LMM, $F_{1, 49} = 512.85$, $P < 0.001$; Fig. 2b) and lower in young turfs compared to old turfs (LMM, $F_{1, 49} = 19.31$, $P < 0.001$). Further, we found a significant three-way interaction (LMM, $F_{1, 49} = 7.98$, $P = 0.007$), indicating that at high incubation elevation, S was lower in young turfs that originated from low elevation compared to control turfs originating from high elevation and to old turfs (Fig. 2b, left side), while at low elevation, S was not affected by turf origin and turf age (Fig. 2b, right side).

Local litter incubations

Mass loss of all local litter types was higher at low incubation elevation than high incubation elevation (*B. pubescens*, LMM, $F_{1, 49} = 19.50$, $P < 0.001$; *Agrostis/Deschampsia*, LMM, $F_{1, 49} = 8.43$, $P = 0.006$; *C. canescens*, LMM, $F_{1, 48} = 5.50$, $P = 0.003$; *C. acuta*, LMM, $F_{1, 49} = 5.83$, $P = 0.020$; Fig. 3). Mass loss tended to be higher in young turfs (Fig. 3), but this was only significant for the *Agrostis/Deschampsia* litter (LMM, $F_{1, 49} = 7.39$, $P = 0.009$; Fig. 3b) and nearly significant in *C. acuta* (LMM, $F_{1, 49} = 3.79$, $P = 0.057$; Fig. 3c). In *C. canescens* we found a higher mass loss in turfs with high origin (LMM, $F_{1, 48} = 5.50$, $P = 0.023$; Fig. 3d) and an interaction between turf age and turf origin (LMM, $F_{1, 48} = 4.66$, $P = 0.036$). This indicated intermediate values in young turfs, and a significant difference between high and low turf origins in old turfs (Figure 3d).

Discussion

We found that incubation elevation was a strong driver of decomposition, both for tea and natural litter. We found that the Tea Bag Index decomposition rate (k) and stabilization (S) were intermediate in turfs recently transplanted between incubation elevations, while turf

Table 1 Site characteristics at high and low elevation (\pm S.E.)

Variable	n	High	S.E.	Low	S.E.	<i>P</i> value
Flooding frequency 2000-2014 (#)	1	7	–	14		
Flooding duration 2000-2014 (days yr ⁻¹)	15	5.6	0.59	36.5	4.2	
Flooding duration 2014 (days)	32	0	–	25.7	0.24	
Soil temperature during tea incubation (°C)	32	12.7	0.20	13.7	0.19	<0.001
Soil temperature during litter incubation (°C)	32	13.5	0.13	13.9	0.18	0.026
Soil moisture (% weight, Aug.)	8	24.47	1.15	36.34	1.54	<0.001
Soil pH	8	5.48	0.07	5.71	0.07	0.066
Soil total N (%)	8	0.29	0.04	0.31	0.04	0.597
Soil total C (%)	8	4.11	0.50	4.77	0.57	0.388

Bold values indicate significant differences between high and low elevation

P values of the variables determined on all turfs (32 samples) were tested with a LMM (see Supplementary material 3 for all test results). Variables determined per replicate block (16 samples) were tested with a paired t-test with the pairs being the two elevation of one replicate block

origin did not affect decomposition in the old turfs, and values converged to that of not-transplanted control turfs. For the weight loss of local litters, a variety of responses and interactions between turf origin, turf age and incubation elevation indicate that long-term legacy effects of flooding regime can occur in some cases, but depend on litter type.

Effects of incubation elevation

In line with our hypothesis and existing literature we found that stabilization of the labile fraction (*S*) was highest at high elevation and decomposition of local litter was stimulated at low incubation elevation (Graziani and Day 2015; Hefting et al. 2005; Xiong and Nilsson 1997). In contrast with our hypothesis, however, we found the

lowest TBI decomposition rate (*k*) at low incubation elevation. The combination of a low *k* and *S* at low incubation elevation seems counterintuitive, as the first predicts small, and the second large mass loss. However, this may be explained by the flooding event during tea incubation. Flooding can reduce oxygen availability for some time, which may decrease microbial activity (Wagner et al. 2015) and hence *k*. At the same time, the flooding may have increased the amount of nutrients available for microbial communities, for example through flood deposits and by inducing plant death. This may result in the extended breakdown of more recalcitrant material and thus a lower *S* (Johnston 1991; Wagner et al. 2015; Wright et al. 2017).

For the mass loss of the local litter, differences between incubation elevations must be associated with

Table 2 Leaf elemental concentrations

Species	N (%)		C (%)		C:N ratio		P (%)	
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
<i>Betula pubescens</i>	1.30b	0.03	47.7ab	0.25	36.8b	0.81	0.15b	0.01
<i>Agrostis/Deschampsia</i>	0.87cd	0.07	40.4d	0.60	48.1ab	4.35	0.12bc	0.02
<i>Carex acuta</i>	0.96cd	0.06	43.2c	0.15	45.9ab	2.71	0.06c	0.01
<i>Calamagrostis canescens</i>	0.72d	0.06	41.6d	0.46	59.9a	5.52	0.06c	0.01
Green tea	3.99a	0.11	46.5b	0.24	11.7c	0.29	0.34a	0.02
Rooibos tea	1.09bc	0.05	48.1a	0.14	44.4b	2.22	0.07c	0.02

Mean percentage nitrogen (N), carbon (C) and phosphorous (P) and their standard error of mean (S.E.) of the 4 incubated litter types and tea. Letters behind the means indicate significant differences between local litter types, based on a One-way ANOVA and a Tukey post-hoc test

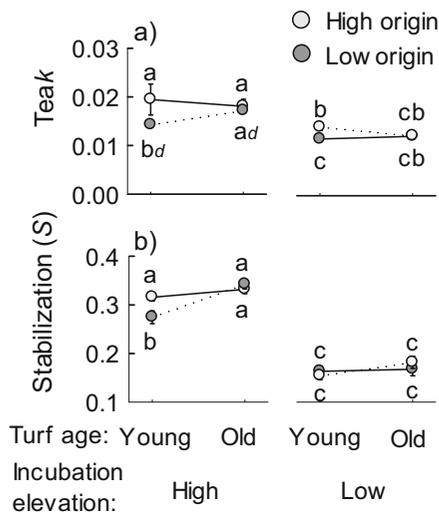


Fig. 2 Decomposition rate of the labile fraction of rooibos (a) and Stabilization of the labile fraction of green tea (S) at both incubation elevations, in young and old turfs subjected to short-term and long-term regime shifts, respectively. Error bars are SE. Letters indicate significant differences, and the subscript d indicates a difference with $P = 0.086$

legacy effects of flooding (e.g., deposited sediment, soil moisture, vegetation die-back), because the litter bags themselves were not exposed to a flooding event. Soil moisture and soil temperature were higher at low incubation elevation, and this can enhance decomposer activity and hence litter breakdown there (Berg et al. 1993; Graziani and Day 2015). In line with our tea bag experiment, and despite differences in setup, the local litter incubations show that the incubation elevation strongly affects plant litter breakdown, indicating that changes in flooding regimes will have an immediate impact on decomposition processes. This is in line with the direct, but prolonged changes in soil community composition during and after flooding, as observed by Wagner et al. (2015).

Legacy effects of turf origin

Our second hypothesis that turf origin resulted in legacy effects on decomposition processes was supported because, tea bag derived parameters k and S were intermediate in young turfs that were transplanted between elevations. Therefore, decomposition processes were affected by history of previous flooding regimes. Such legacy effects may result from impacts of flooding regimes on sedimentation, plant and soil community composition and functioning that respond slowly or fast to

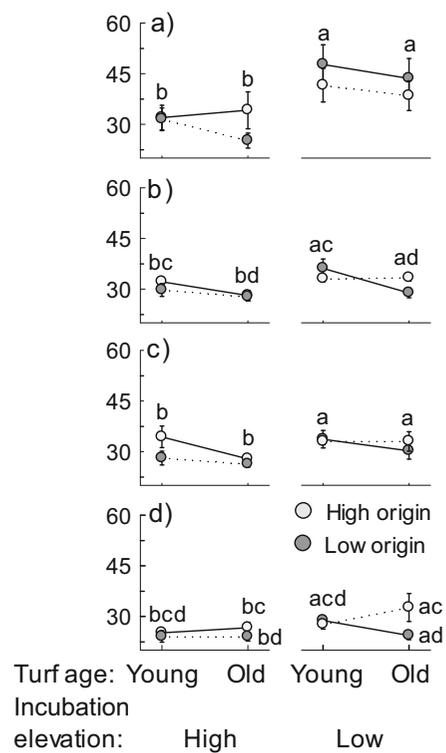


Fig. 3 Mass losses of the four different litter types; **a** *Betula pubescens*, **b** *Agrostis/Deschampsia* **c** *Carex acuta* **d** *Calamagrostis canescens* incubated at different elevations, in turfs with different experimental ages (young and old) and origin (from high or low elevation). Dashed lines indicate turfs that were transplanted between incubation elevations, and solid lines indicate controls, that originate from the incubation elevation. Error bars are SE. Letters above bars indicate significant differences for the grouped points below it, but in *C. canescens* the interaction between origin and experimental duration necessitated using letters for individual points

changed flooding regimes (Keddy 2000; Mace et al. 2016; Ström et al. 2011; Wagner et al. 2015). For instance, it took a few years for the vegetation of turfs transplanted to low elevation to converge, and this process was slower in turfs transplanted to high elevation (Ström et al. 2011). Our finding that legacy effects of flooding regimes history only affected decomposition in young turfs, indicates that the impact of the current flooding regimes quickly overrules the influence of historical conditions (Ström et al. 2011). We currently do not know how long such legacy effects may last, but our study and Wagner et al. (2015) suggest at least one growing season.

In contrast to our findings for the Tea Bag Index, the impact of turf origin on litter mass loss of local litter was much weaker, or sometimes even opposite. This

indicates that the effect of soil history can be litter-specific and is often overruled by the environmental conditions tied to incubation elevation, even in young turfs, i.e., shortly after the flooding regime changed. The weaker or opposite response of local litter to turf origin compared to tea may be explained by differences in setup. Local litter was not exposed to a flooding event, while the tea was. Yet, the period after the flood is a meaningful period for decomposition of local litter, as much of this litter is deposited during flooding as drift line material. The larger mesh size will also allow for a more realistic decomposer community to enter the litter. For *C. canescens* we found that turf origin affected litter mass loss only in old turfs, but not in young ones, indicating a long-term effect of historical flooding regimes on decomposition. This will, however, only bear relevance to the field situation if such a species (and thus its litter) persists long under the new flooding regime, which is the case for *C. canescens* (Ström et al. 2011).

For the local litters, we frequently observed that mass loss tended to be higher in young turfs (e.g., significantly in the *Agrostis/Deschampsia* mixture), implying that general disturbance effects of excavating the turfs affected decomposition. It is well known that soil disturbance can cause local and temporal changes in soil properties such as aeration, pH, nutrient availability and in microbial community composition and activity (Allison and Martiny 2008; Dorland et al. 2003; Wagner et al. 2015; Wardle et al. 2004), which all are known to affect litter decomposition (e.g., Hattenschwiler et al. 2005; Veen et al. 2015). In addition to previous studies however, our results now show that such disturbance effects can be modulated by litter type and flooding history.

Litter type effects

Differences in mass loss between the litter types aligned with their differences in C:N ratio, showing a negative relation (Cornwell et al. 2008). Previous work has shown that not only litter quality per se drives litter mass loss, but that specialization of the soil community may be a small but relevant driver (Veen et al. 2015). The idea is that litter decomposition is accelerated underneath the same plant species as where the litter originated from, a process referred to as ‘home field advantage’ (Ayres et al. 2009; Freschet et al. 2012; Gholz et al. 2000; Veen et al. 2015). In our study however, we found no support for this idea, as decomposition of local litters was not faster than expected at their home elevation

(ESM 3). Therefore, our results indicate that local soil decomposer communities did not favor the breakdown of local litter types from their original elevation, which is in line with a previous wetland litter transplant experiment (Fenoy et al. 2016). Species-specific relationships between litter and decomposers might be rare in riparian zones because flooding causes a high degree of litter mixing along lateral and longitudinal gradients (Xiong and Nilsson 1997) providing limiting scope for the development of specialized decomposer communities. Direct measurements on microbial community composition are however needed to test this hypothesis.

Implications for upscaling

Although decomposition is a key driver of carbon cycling in many ecosystems, it is not the only factor that determines carbon fluxes and pools in the riparian system, especially on larger temporal and spatial scales. Our findings of the tea and litter incubations imply that when flooding regimes change, decomposition will be directly affected by the new flooding conditions at a local scale (Wagner et al. 2015). However, on larger spatio-temporal scales, the few examples using a chronosequence approach suggest that indirect effects via changes in species composition and biomass production may play an important additional role for litter accumulation in temperate zones (Britson et al. 2016; Langhans et al. 2008; Moore et al. 2007; Vendrami et al. 2012; Wardle et al. 2004; Whittinghill et al. 2014). Such vegetation change may drive changes in litter quality, which is known as key a driver of litter decomposition rates (Britson et al. 2016; Cleveland et al. 2014; Cornwell et al. 2008; Makkonen et al. 2012; Trofymow et al. 2002). Since species composition only changes gradually (Ström et al. 2011; Wright et al. 2017) while the decomposition rates react directly to the new conditions, there may be a transitional unbalance between litter production and decomposition, temporally resulting in litter accumulation or a reduction of the litter layer. In our changing world, there is an increasing need to quantify carbon sinks and sources, and our study is among the first to shed light on the relevant temporal scales to address effects of changed flooding regimes.

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References

- Allison SD, Martiny JBH (2008) Resistance, resilience, and redundancy in microbial communities. *Proc Natl Acad Sci U S A* 105:11512–11519. <https://doi.org/10.1073/pnas.0801925105>
- Ayres E, Steltzer H, Simmons BL, Simpson RT, Steinweg JM, Wallenstein MD, Mellor N, Parton WJ, Moore JC, Wall DH (2009) Home-field advantage accelerates leaf litter decomposition in forests. *Soil Biol Biochem* 41:606–610. <https://doi.org/10.1016/j.soilbio.2008.12.022>
- Berg B, Berg MP, Bottner P, Box E, Breymeyer A, Deanta RC, Couteaux M, Escudero A, Gallardo A, Kratz W, Madeira M, Malkonen E, McLaugherty C, Meentemeyer V, Munoz F, Piussi P, Remacle J, Desanto AV (1993) Litter mass-loss rates in pine forests of Europe and eastern United States - some relationships with climate and litter quality. *Biogeochemistry* 20:127–159. <https://doi.org/10.1007/bf00000785>
- Britson A, Wardrop D, Drohan P (2016) Plant community composition as a driver of decomposition dynamics in riparian wetlands. *Wetl Ecol Manag* 24:335–346
- Cleveland CC, Reed SC, Keller AB, Nemergut DR, O'Neill SP, Ostertag R, Vitousek PM (2014) Litter quality versus soil microbial community controls over decomposition: a quantitative analysis. *Oecologia* 174:283–294. <https://doi.org/10.1007/s00442-013-2758-9>
- Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, Hobbie SE, Hoorens B, Kurokawa H, Perez-Harguindeguy N, Quested HM, Santiago LS, Wardle DA, Wright IJ, Aerts R, Allison SD, van Bodegom P, Brovkin V, Chatain A, Callaghan TV, Diaz S, Garnier E, Gurvich DE, Kazakou E, Klein JA, Read J, Reich PB, Soudzilovskaia NA, Vaieretti MV, Westoby M (2008) Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol Lett* 11:1065–1071. <https://doi.org/10.1111/j.1461-0248.2008.01219.x>
- Dorland E, Bobbink R, Messelink JH, Verhoeven JTA (2003) Soil ammonium accumulation after sod cutting hampers the restoration of degraded wet heathlands. *J Appl Ecol* 40:804–814. <https://doi.org/10.1046/j.1365-2664.2003.00845.x>
- Erwin KL (2009) Wetlands and global climate change: the role of wetland restoration in a changing world. *Wetl Ecol Manag* 17:71–84. <https://doi.org/10.1007/s11273-008-9119-1>
- Fenoy E, Casas JJ, Diaz-Lopez M, Rubio J, Guil-Guerrero JL, Moyano-Lopez FJ (2016) Temperature and substrate chemistry as major drivers of interregional variability of leaf microbial decomposition and cellulolytic activity in headwater streams. *FEMS Microbiol Ecol* 92. <https://doi.org/10.1093/femsec/fiw169>
- Freschet GT, Aerts R, Cornelissen JHC (2012) Multiple mechanisms for trait effects on litter decomposition: moving beyond home-field advantage with a new hypothesis. *J Ecol* 100:619–630. <https://doi.org/10.1111/j.1365-2745.2011.01943.x>
- Gholz HL, Wedin DA, Smitherman SM, Harmon ME, Parton WJ (2000) Long-term dynamics of pine and hardwood litter in contrasting environments: toward a global model of decomposition. *Glob Chang Biol* 6:751–765. <https://doi.org/10.1046/j.1365-2486.2000.00349.x>
- Graziani DJ, Day FP (2015) Thresholds of change in decomposition rate along a dune/swale transect on a Virginia Barrier Island. *J Coast Res* 31:148–154. <https://doi.org/10.2112/jcoastres-d-13-00102.1>
- Hasselquist EM, Nilsson C, Hjalten J, Jorgensen D, Lind L, Polvi LE (2015) Time for recovery of riparian plants in restored northern Swedish streams: a chronosequence study. *Ecol Appl* 25:1373–1389. <https://doi.org/10.1890/14-1102.1>
- Hattenschwiler S, Tiunov AV, Scheu S (2005) Biodiversity and litter decomposition in terrestrial ecosystems. *Ann Rev Ecol Evol Syst*
- Hefting MM, Clement JC, Bienkowski P, Dowrick D, Guenat C, Butturini A, Topa S, Pinay G, Verhoeven JTA (2005) The role of vegetation and litter in the nitrogen dynamics of riparian buffer zones in Europe. *Ecol Eng* 24:465–482. <https://doi.org/10.1016/j.ecoleng.2005.01.003>
- Helfield JM, Capon SJ, Nilsson C, Jansson R, Palm D (2007) Restoration of rivers used for timber floating: effects on riparian plant diversity. *Ecol Appl* 17:840–851
- Hieber M, Gessner MO (2002) Contribution of stream detritivores, fungi, and bacteria to leaf breakdown based on biomass estimates. *Ecology* 83:1026–1038. <https://doi.org/10.2307/3071911>
- Hirabayashi Y, Mahendran R, Koiraia S, Konoshima L, Yamazaki D, Watanabe S, Kim H, Kanae S (2013) Global flood risk under climate change. *Nat Clim Chang* 3:816–821. <https://doi.org/10.1038/nclimate1911>
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous Inference in General Parametric Models. *Biom J* 50:346–363
- IPCC (2013) Summary for policymakers. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) *Climate change 2013: the physical science basis*, Cambridge, United Kingdom and New York, USA
- Johnston CA (1991) Sediment and nutrient retention by freshwater wetlands—effects on surface-water quality. *Crit Rev Environ Control* 21:491–565

- Keddy PA (2000) *Wetland ecology; principles and conservation*. Cambridge University Press, Cambridge
- Keuskamp JA, Dingemans BJJ, Lehtinen T, Sameel JM, Hefling MM (2013) Tea Bag Index: a novel approach to collect uniform decomposition data across ecosystems. *Methods Ecol Evol* 4:1070–1075. <https://doi.org/10.1111/2041-210x.12097>
- Langhans SD, Tockner K (2006) The role of timing, duration, and frequency of inundation in controlling leaf litter decomposition in a river-floodplain ecosystem (Tagliamento, northeastern Italy). *Oecologia* 147:501–509. <https://doi.org/10.1007/s00442-005-0282-2>
- Langhans SD, Tiegs SD, Gessner MO, Tockner K (2008) Leaf-decomposition heterogeneity across a riverine floodplain mosaic. *Aquat Sci* 70:337–346. <https://doi.org/10.1007/s00027-008-8062-9>
- Mace OG, Steinauer K, Jousset A, Eisenhauer N, Scheu S (2016) Flood-induced changes in soil microbial functions as modified by plant diversity. *Plos One* 11. <https://doi.org/10.1371/journal.pone.0166349>
- Makkonen M, Berg MP, Handa IT, Haettenschwiler S, van Ruijven J, van Bodegom PM, Aerts R (2012) Highly consistent effects of plant litter identity and functional traits on decomposition across a latitudinal gradient. *Ecol Lett* 15: 1033–1041. <https://doi.org/10.1111/j.1461-0248.2012.01826.x>
- Moore PD (1990) *Soils and Ecology: Temperate wetlands*. In: Williams W (ed) *Wetlands: a threatened landscape*. Blackwell Publishers, Oxford
- Moore TR, Bubier JL, Bledzki L (2007) Litter decomposition in temperate peatland ecosystems: the effect of substrate and site. *Ecosystems* 10:949–963. <https://doi.org/10.1007/s10021-007-9064-5>
- Nilsson C, Jansson R, Zinko U (1997) Long-term responses of river-margin vegetation to water-level regulation. *Science* 276:798–800. <https://doi.org/10.1126/science.276.5313.798>
- Nilsson C, Reidy CA, Dynesius M, Revenga C (2005) Fragmentation and flow regulation of the world's large river systems. *Science* 308:405–408. <https://doi.org/10.1126/science.1107887>
- Pinheiro J, Bates D, DebRoy S, Sarkar D, Team. RC (2016) nlme: Linear and nonlinear mixed effects models. 3.1–128 edn
- R Core Team (2016) R: a language and environment for statistical computing. 3.2.5 edn. R Foundation for Statistical Computing, Vienna
- Ström L, Jansson R, Nilsson C, Johansson ME, Xiong SJ (2011) Hydrologic effects on riparian vegetation in a boreal river: an experiment testing climate change predictions. *Glob Chang Biol* 17:254–267. <https://doi.org/10.1111/j.1365-2486.2010.02230.x>
- Swift MJ, Heal OW, Anderson JM (1979) *Decomposition in terrestrial ecosystems*. University of California Press, Berkeley
- Trofymow JA, Moore TR, Titus B, Prescott C, Morrison I, Siltanen M, Smith S, Fyles J, Wein R, Camiré T, Duschene L, Kozak L, Kranabetter M, Visser S (2002) Rates of litter decomposition over 6 years in Canadian forests: influence of litter quality and climate. *Can J For Res* 32:789–804. <https://doi.org/10.1139/x01-117>
- Veen GF, Freschet GT, Ordóñez A, Wardle DA (2015) Litter quality and environmental controls of home-field advantage effects on litter decomposition. *Oikos* 124:187–195. <https://doi.org/10.1111/oik.01374>
- Vendrami JL, Jurinitz CF, Castanho CT, Lorenzo L, de Oliveira AA (2012) Litterfall and leaf decomposition in forest fragments under different successional phases on the Atlantic Plateau of the state of Sao Paulo, Brazil. *Biota Neotropica* 12:136–143
- Wagner D, Eisenhauer N, Cesarz S (2015) Plant species richness does not attenuate responses of soil microbial and nematode communities to a flood event. *Soil Biol Biochem* 89:135–149. <https://doi.org/10.1016/j.soilbio.2015.07.001>
- Wardle DA, Bardgett RD, Klironomos JN, Setälä H, van der Putten WH, Wall DH (2004) Ecological linkages between aboveground and belowground biota. *Science* 304:1629–1633. <https://doi.org/10.1126/science.1094875>
- Webster JR, Benfield EF (1986) Vascular plant breakdown in fresh-water ecosystems. *Annu Rev Ecol Syst* 17:567–594. <https://doi.org/10.1146/annurev.es.17.110186.003031>
- Whittinghill KA, Finlay JC, Hobbie SE (2014) Bioavailability of dissolved organic carbon across a hillslope chronosequence in the Kuparuk River region, Alaska. *Soil Biol Biochem* 79: 25–33. <https://doi.org/10.1016/j.soilbio.2014.08.020>
- Wright AJ, de Kroon H, Visser EJW, Buchmann T, Ebeling A, Eisenhauer N, Fischer C, Hildebrandt A, Ravenek J, Roscher C, Weigelt A, Weisser W, Voisenek L, Mommer L (2017) Plants are less negatively affected by flooding when growing in species-rich plant communities. *New Phytol* 213:944–955. <https://doi.org/10.1111/nph.14185>
- Xiong SJ, Nilsson C (1997) Dynamics of leaf litter accumulation and its effects on riparian vegetation: A review. *Bot Rev* 63: 240–264. <https://doi.org/10.1007/bf02857951>
- Xiong SJ, Nilsson C (1999) The effects of plant litter on vegetation: a meta-analysis. *J Ecol* 87:984–994. <https://doi.org/10.1046/j.1365-2745.1999.00414.x>