Consequences of riparian forest invasions by alien plants for litter decomposition in small streams and ponds

Daša Jaďuďová,^{1*} Vladimíra Dekan Carreira,^{1,2} Marcela Sedlačková Přidalová,¹ Emília Židišinová,¹ Milan Novikmec,¹ Marek Svitok^{1,3,4}

¹Faculty of Ecology and Environmental Sciences, Technical University in Zvolen, Slovakia; ²cE3c - Centre for Ecology, Evolution and Environmental Change; CHANGE – Global Change and Sustainability Institute, Faculty of Sciences, University of Lisbon, Portugal; ³Faculty of Forestry and Wood Sciences, University of Life Sciences Prague, Praha - Suchdol, Czech Republic; ⁴Institute of Botany, Plant Science and Biodiversity Center, Slovak Academy of Sciences, Bratislava, Slovakia

ABSTRACT

Riparian forests play a crucial role in aquatic ecosystems by regulating light, temperature, channel stability and nutrient cycling. However, these forests are highly vulnerable to invasion by alien plant species, which can alter leaf litter inputs and decomposition dynamics, thereby impacting freshwater ecosystem functions. This study explores the decomposition rates of native black alder (*Alnus glutinosa*) and two riparian invaders, Japanese knotweed (*Fallopia japonica*) and Canada goldenrod (*Solidago canadensis*), in both headwater streams and pond mesocosms in Central Europe. We conducted experiments with 169 litter bags to assess decomposition rates and test the home-field advantage hypothesis. The hypothesis assumes that native litter decomposes faster due to the evolutionary adaptation of local decomposer communities. We found that invasive *S. canadensis* decomposed significantly faster than native *A. glutinosa* in both lotic and lentic environments. On the other hand, invasive *F. japonica* decomposed at a comparable rate (streams) or at a slower rate (ponds) than the native species. These findings contradict the home-field advantage hypothesis, suggesting that decomposition rates are primarily driven by litter nutrient content rather than geographic origin. The rapid breakdown of *S. canadensis* is likely driven by the low C:P ratio of its litter. The rapid decomposition of this litter may lead to short-term nutrient boosts that are quickly lost due to microbial activity, whereas the slow decomposition of *F. japonica* may limit immediate nutrient availability but extend their acces-

*Corresponding author: dasa.jadudova@gmail.com

Key words: *Alnus glutinosa*; *Solidago canadensis*; *Fallopia japonica*; litter decomposition; headwater streams; ponds.

Citation: Jaďuďová D, Dekan Carreira V, Sedlačková Přidalová M, et al. Consequences of riparian forest invasions by alien plants for litter decomposition in small streams and ponds. *J Limnol 2025;84:2223*.

Edited by: Diego Fontaneto, CNR-IRSA Water Research Institute, Verbania-Pallanza, Italy.

Contributions: all the authors made a substantive intellectual contribution, read and approved the final version of the manuscript and agreed to be accountable for all aspects of the work. Conflict of interest: The authors declare no competing interests, and all authors confirm accuracy.

Received: 27 March 2025. Accepted: 23 May 2025.

Publisher's note: all claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article or claim that may be made by its manufacturer is not guaranteed or endorsed by the publisher.

[®]Copyright: the Author(s), 2025 Licensee PAGEPress, Italy J. Limnol., 2025; 84:2223 DOI: 10.4081/jlimnol.2025.2223

This work is licensed under a Creative Commons Attribution-NonCommercial 4.0 International License (CC BY-NC 4.0). sibility over longer periods. Overall, the invasion of riparian zones by species with litter traits distinct from those of native species can disrupt ecosystem processes, leading to cascading effects on aquatic food webs and nutrient cycling. Understanding the effects of riparian forest invasions on organic matter processing is essential for managing biodiversity and maintaining ecosystem integrity in freshwater environments.

INTRODUCTION

The riparian forests are essential for aquatic ecosystems as they affect the light and temperature conditions of the water (Baxter et al., 2005), channel stability (Naiman and Décamps, 1997) and nutrient supply (Harner et al., 2009). The decomposition of leaf litter from riparian vegetation is a fundamental ecological process in freshwater ecosystems, particularly in small headwater streams (Vannote et al., 1980), supporting energy transfer from plant litter to higher trophic levels (Cummins et al., 1989; Gessner et al., 1999; Graça, 2001). Although less studied in standing waters, allochthonous organic matter may play an important role in lake ecosystem metabolism, particularly by fueling microbial processes (Jansson et al., 2007; Brett et al., 2017). For example, allochthonous organic material can substantially influence energy transfer and community structure in unproductive lakes by promoting microbial dominance in energy mobilization pathways. This can lead to decreased primary production, lower energy mobilization efficiency and shifts in community composition, potentially altering trophic interactions (Jansson et al., 2007). Since wetland size inversely correlates with the amount of litter inputs per unit area (Stoler and Relyea, 2020; Dekanová et al., 2023), the metabolism of small lakes and ponds may be considerably influenced by allochthonous organic matter inputs.





Riparian forests are highly susceptible to invasions by alien plants due to the high content of nutrients and moisture in soils, light availability, frequent occurrence of disturbances as well as easy dispersal of seeds and plant fragments along the streams (Daehler, 2003; Richardson et al., 2007; Boyero et al., 2012; Kominoski et al., 2013; Svitková et al., 2024). Invasive alien plants often dominate the riparian zones they invade due to their high competitive ability (Coleman and Levine, 2007; Pfeifer-Meister et al., 2008), potentially resulting in the complete replacement of native species (Naiman and Décamps, 1997; Ringold et al., 2008). Changes in native riparian vegetation and the associated shifts in plant functional traits can extend across ecosystem boundaries and impact food webs, organic matter processing and nutrient cycling in aquatic ecosystems (Kominoski et al., 2013; García et al., 2014). These effects on food webs occur through changes in the quantity and quality of basal resources, which alter colonization patterns and affect the density and composition of communities, ultimately leading to changes in the rate of organic matter decomposition. For instance, the shedding of low-quality leaf litter by some invasive plants can reduce the abundance of aquatic decomposers, potentially lowering decomposition rates (Davies and Boulton, 2009; Kominoski et al., 2013), as well as the growth and taxonomic richness of these organisms (Boyero et al., 2012), which may negatively affect aquatic ecosystem functioning (Richardson et al., 2007). On the other hand, the highly attractive leaves of some invasive species may cause a rapid depletion of resources, leading to a subsequent lack of supply (McNeish et al., 2012; Dekanová et al., 2021).

The differences in attractivity of native and alien leaf litter to decomposers are often explained by the home-field advantage hypothesis, which assumes that decomposers prefer to colonize substrates they frequently encounter and, therefore, the origin of the plant litter is the driving force behind the decomposition rate (Ayres et al., 2009). Thus, we may expect that native vegetation is the most suitable source for local decomposers adapted to the nutrient content of the native leaf litter, meaning that the native leaf litter should decompose faster than other leaf litter types (Gholz et al., 2000). The home-field advantage hypothesis was confirmed by some studies that observed slower decomposition of alien species litter compared to native species (García et al., 2012, 2014; Serra et al., 2013). However, there are also contradictory results, since several studies have shown that the leaf litter decomposition rate either did not differ between native and alien plant species (Reinhart and VandeVoort, 2006; Lecerf et al., 2007; Bottollier-Curtet et al., 2015; Kennedy and El-Sabaawi, 2017) or was even faster in alien species (McNeish et al., 2012; Kuglerová et al., 2017; Dekanová et al., 2021).

Another explanation for differences in decomposition rates between native and invasive litter may be interspecific variability in nutrient content (Tibbets and Molles, 2005; Cornwell *et al.*, 2008), meaning that the attractiveness of leaf litter to microbial decomposers is driven by its elemental quality, with decomposers favoring litter rich in labile compounds and readily available nutrients (Graca, 2001; Gessner *et al.*, 2007; Hladyz *et al.*, 2009; Bottollier-Curter *et al.*, 2015). Carbon, nitrogen and phosphorus content, along with their elemental ratios, are considered key predictors of leaf litter decomposition rates (Frost *et al.*, 2006; Bottollier-Curter *et al.*, 2015). Because decomposers face stoichiometric constraints when processing nutrientpoor litter, the mismatch between their nutritional requirements and the elemental composition of the resources represents a stoichiometric limitation that ultimately drives decomposition rates (Danger *et al.*, 2021).

Our preliminary research revealed that the rapid decomposition of invasive litter in a pond environment was dominated by microbial processes (Dekanová *et al.*, 2021). Here, we extended the experiment to replicated headwater streams and pond mesocosms to test whether the observed differences in microbial decomposition between invasive and native litter are consistent across freshwater ecosystems. Regarding differences between aquatic habitats, slower microbial decomposition in ponds than in streams can be reasonably expected due to variations in water flow, nutrient and oxygen concentrations, all of which influence microbial communities (Langhans *et al.*, 2008; da Silva *et al.*, 2019; Hill *et al.*, 2022). However, interspecific differences in decomposition rates are expected to remain consistent across habitat types.

To evaluate the hypotheses, we conducted litter bag experiments in 10 headwater streams and 32 pond mesocosms and compared the rate of leaf litter decomposition of the native species black alder (Alnus glutinosa (L.) Gaertn.), a typical riparian and floodplain forest species in Central Europe (Hrivnák et al., 2020; Hrivnák et al., 2024), with that of two alien invasive species: Japanese knotweed (Fallopia japonica (Houtt.) Ronse Decraene) and Canada goldenrod (Solidago canadensis L.). These invasive species pose serious threats to both natural ecosystems through biodiversity loss and habitat alteration, as well as significant economic burdens related to property damage and management costs (Shaw and Seiger, 2002; Fennel et al., 2018). The ecological and economic consequences of S. canadensis invasions are less studied but the species is known to reduce local biodiversity by displacing native plant species (Dong et al., 2015), altering soil properties and homogenizing habitats, leading to degraded soil quality and ecosystem functions (Bielecka et al., 2020; Zhu et al., 2022). Both F. japonica and S. canadensis are widely distributed along riparian zones in Central Europe, with a strong ability to form dense, monospecific stands (Fig. 1 e-g) that disrupt native plant communities (Slezák et al., 2020; Zelnik et al., 2020; Simon et al., 2023; Skokanová et al., 2024). However, their influence on the biodiversity and ecosystem functioning of adjacent freshwater systems remains less understood.

METHODS

Experimental sites

We conducted the litter bag experiments in 32 pond mesocosms and 10 headwater streams in the central part of Slovakia (Fig. 1a) during the autumn and winter of 2020 (pond mesocosms) and 2021 (streams), respectively.

The pond mesocosms consisted of 110-L polyethylene barrels with a depth of 1 m. The mesocosms were filled with 100 L of stream water (pH = 8.4 ± 0.1 , conductivity = $165\pm3.5 \ \mu\text{S cm}^{-1}$, dissolved oxygen = $2.4\pm3.5 \ \text{mg L}^{-1}$) on 25 August 2020 and set outdoors at the Technical University in Zvolen, Slovakia (Fig. 1d). On 3 September, we added 1.5 L of homogenized pond substrate and 0.8 L of pond water, obtained from the nearby pond Červená studňa (*Tab. S1*), to inoculate the mesocosms. Specimens of *Potamogeton natans* from the same pond were planted in each mesocosm (27±4 g of plant wet weight per mesocosm).

The studied streams were low-order $(2^{nd}-3^{rd})$, shallow (mean depth \pm SD: 0.2 \pm 0.06 m), slightly alkaline (pH: 7.7 \pm 0.2), well-oxygenated (11.4 \pm 0.6 mg O₂ L⁻¹) and with low conductivity (104 \pm 30 μ S/cm⁻¹) and showed no direct anthropogenic impact (Fig. 1 b,c; *Tab. S1*). Streams were shaded by riparian canopies (cover: 72 \pm 15%) dominated by black alder, with co-occurring willows, and no invasive species were observed in the studied reaches.

Leaf litter decomposition experiments

The litter bag experiments were conducted to compare microbial leaf litter decomposition rates of the invasive plant species *Fallopia japonica* and *Solidago canadensis* with the native species *Alnus glutinosa*. Leaves were collected from plants before abscission in autumn and air-dried in the laboratory (~ 25°C) until a constant weight was achieved (~ 7 days). The carbon, nitrogen and phosphorus content of the leaf litter for each species was measured (EA-TCD, AES-ICP) prior to the experiment (*Tab. S2*).

To assess decomposition attributable to microbial activity, we prepared single-species litter bags using nylon mesh with a 0.5 mm mesh size, which permits colonization by microbial decomposers while effectively excluding macroinvertebrates (Bärlocher, 2020). We weighed 6.1 ± 0.23 g of dried leaves from a single species for each litter bag in streams and 3.9 ± 0.25 g for each litter bag in pond mesocosms. More litter was used in streams to compensate for potentially higher losses. A total of 70 litter bags were exposed in streams, and 99 litter bags were exposed in pond mesocosms.



Fig. 1. Location of the 10 studied streams (black dots) and 32 mesocosms (white dot) in Slovakia (a), where the litter bag experiments were conducted. The insets show two of the studied headwater streams (b,c), the mesocosm facility at the Technical University in Zvolen (d) and examples of stream and pond riparian zones invaded by Japanese knotweed (*Fallopia japonica* (Houtt.) Ronse Decraene) (e) and Canada goldenrod (*Solidago canadensis* L.) (f,g). Note the placement of litter bags attached to a metal chain in one of the streams (b).

Three single-species litter bags (one per species) were placed equidistantly along the perimeter at the bottom of each mesocosm on 11 September 2020, arranged in a triangular layout to maximize separation and minimize potential interspecific interactions. Three additional bags were deployed to mesocosms on the same day and collected 24 h later to estimate the correction factor for handling losses and leaching. Each mesocosm was supplied with a temperature data logger (Minilog II-T; Vemco, Bedford, Nova Scotia, Canada) recording the water temperature every hour throughout the experiment. The remaining 96 bags were retrieved after eight weeks.

In streams, the litter bags were attached to metal chains anchored into the streambed sediment with iron bars on 15 November 2021. Each chain was equipped with a Minilog II-T data logger, which recorded water temperature hourly throughout the experiment. To account for handling losses and leaching, one bag was collected from each stream 24 hours after deployment (Benfield *et al.*, 2017; Zukswert and Prescott, 2017). These bags were used to adjust the initial weights of the leaf litter for mass losses unrelated to biological decomposition. The remaining 60 bags were retrieved after four weeks, with six bags per stream - two replicate bags for each of the three leaf species.

All litter bags were stored in plastic zip-locks immediately after collection, frozen in the field and transported to the laboratory. The bags were stored in a freezer at -18°C till laboratory processing. Before processing, the bags were defrosted at laboratory temperature for a few hours. The remaining leaves were gently rinsed using tap water to remove fine sediment. The leaves were oven-dried in marked paper bags at 45°C for 24 h. Immediately after drying, the litter was placed in a desiccator until reaching laboratory temperature. Subsequently, the litter was weighed on analytical balances to the nearest 0.01 mg.

Data analysis

To quantify the decomposition rates of invasive and native species, we used the exponential decay model to estimate the rate coefficients (Petersen and Cummins, 1974). The coefficients were calculated based on the proportion of mass remaining relative to the initial dry mass, ensuring that decomposition rates are standardized regardless of differences in initial litter amounts. The coefficients were quantified as mass loss per degree-day (k_{dd}), with degree-days determined by the cumulative sum of daily mean water temperatures, accounting for potential confounding effects of temperature differences among sites. We

also report the coefficients calculated as mass loss per day (k_d) to facilitate comparisons among studies.

Linear mixed-effects models (LMMs) (Pinheiro and Bates, 2000) were used to evaluate differences in decomposition rates among different species using the lme4 package (Bates et al., 2015). The models included the fixed effect of litter species, while the identity of streams and mesocosms was treated as a random intercept to account for repeated measurements at the same sites. We screened residuals of the LMMs in diagnostic plots using the DHARMa package (Hartig, 2022). In the LMM for streams, the rate coefficients were logarithmically transformed to meet distributional assumptions. The statistical significance of the fixed effects was assessed using F tests with Kenward-Roger approximation for denominator degrees of freedom, implemented via the ImerTest package (Kuznetsova et al., 2017). When a significant effect was revealed, we performed post hoc tests with Tukey-adjusted probabilities to compare the estimated marginal means, using the emmeans package (Lenth, 2016). Marginal (R_m^2) and conditional (R_c^2) pseudo-determination coefficients were calculated for each model to quantify the proportion of total variance explained by interspecific differences in decomposition rates and the total variance explained, respectively (Nakagawa et al., 2017), using the performance package (Lüdecke et al., 2021).

The analyses were performed in R (R Core Team, 2022), and the plots were created using the ggplot2 package (Wickham, 2016).

RESULTS

The observed decomposition rates varied widely and ranged from $-k_{dd} < 0.0001$ degree-days⁻¹ for *F. japonica* (lentic environment) to 0.014 degree-days⁻¹ for *S. canadensis* (lotic environment) (Tab. 1). In general, decomposition rates were higher in the headwater streams [average (SD) $-k_{dd} = 0.005$ (0.002) degree-days⁻¹] than in pond mesocosms [0.002 (0.001) degree-days⁻¹]. The mixed-effect models revealed significant differences in decomposition rates among the studied species in headwater streams ($F_{(2, 46.3)} = 26.8$, p < 0.0001, $R_m^2 = 0.27$, $R_c^2 = 0.73$) and pond mesocosms ($F_{(2, 62.0)} = 142.7$, p < 0.0001, $R_m^2 = 0.66$, $R_c^2 = 0.78$). *S. canadensis* decomposed significantly faster than native *A. glutinosa* in both streams (*post-hoc* test: $t_{(46.3)} = -6.7$, p < 0.0001) and ponds ($t_{(62)} = -12.1$, p < 0.0001). The rate of decomposition for *S. canadensis* was 1.5±0.8 (SD) times higher

Tab. 1. Summary characteristics of leaf litter decomposition rates of native (*A. glutinosa*) and invasive (*F. japonica*, *S. canadensis*) plant species in headwater streams and pond mesocosms expressed per degree-day (k_{dd}) and day (k_d) .

Environment /	-k _{dd} (degree-days ⁻¹)				$-\mathbf{k}_{d}$ (days ⁻¹)			
litter species	mean	SD	min	max	mean	SD	min	max
Headwater streams								
A. glutinosa	0.00460	0.00174	0.00321	0.01089	0.00993	0.00242	0.00634	0.01532
F. japonica	0.00467	0.00112	0.00309	0.00669	0.01038	0.00233	0.00664	0.01814
S. canadensis	0.00695	0.00272	0.00264	0.01432	0.01425	0.00322	0.00715	0.02108
Pond mesocosms								
A. glutinosa	0.00140	0.00035	0.00072	0.00208	0.00893	0.00214	0.00467	0.01349
F. japonica	0.00095	0.00048	< 0.00001	0.00239	0.00616	0.00321	< 0.00001	0.01593
S. canadensis	0.00271	0.00072	0.00087	0.00380	0.01722	0.00426	0.00563	0.02466

than that of native species in streams and 1.9 ± 0.7 times higher in pond mesocosms (Fig. 2). In contrast, the decomposition rate of invasive *F. japonica* litter did not differ significantly from that of native species in streams (t_(46.0) = 0.66, *p*=0.787) but was significantly slower than that of native species within ponds (t_(62.0) = 4.2, *p*=0.0003).

DISCUSSION

Our study demonstrates that invasive species do not exhibit uniform litter decomposition patterns across different environments, with S. canadensis displaying a pronounced tendency for faster decomposition than native A. glutinosa, whereas F. japon*ica* decomposes at a comparable or slower rate than native species depending on the habitat. These findings contradict the home-field advantage hypothesis, assuming that the origin of a plant species should be a driving force of the decomposition process (Ayres et al., 2009). This hypothesis was supported by several studies that reported slower decomposition of alien species litter compared to native species (Abelho and Graça, 1996; Bailey et al., 2001; García et al., 2012, 2014; Serra et al., 2013; Ferreira et al., 2015). However, the general validity of the home-field advantage hypothesis has been questioned by multiple studies (Braatne et al., 2007; Lecerf et al., 2007; Kuglerová et al., 2017; Fogelman et al., 2018; Dekanová et al., 2021; Yang et al., 2021). Based on our results, invasive species leaf litter appears to be rapidly utilized by decomposers, even if they are not adapted to this type of resource.

Rather than being determined by geographic origin, differences in decomposition rates between leaf species may be explained by interspecific variability in the physical characteristics of leaf litter and its nutrient content (Tibbets and Molles, 2005; Leishman *et al.*, 2007; Cornwell *et al.*, 2008). Thin and soft leaves with a higher specific leaf area (SLA) can be more easily processed by decomposers than tougher leaves with a lower SLA (Cornelissen *et al.*, 1999; Cornwell *et al.*, 2008). Regarding the species involved in our study, the SLA of the fastest-decomposing *S. canadensis* leaves was expectedly higher than that reported for the tougher leaves of the native *A. glutinosa* (*Tab. S2*). However, *F. japonica*, despite having thinner leaves, exhibited a significantly slower decomposition rate, suggesting that leaf physical structure alone does not fully explain interspecific differences in litter decomposition.

Beyond the physical characteristics of litter, carbon, nitrogen and phosphorus content, along with their elemental ratios, are often identified as crucial predictors of leaf litter decomposition rates (Frost et al., 2006; Bottollier-Curtet et al., 2015). Decomposers processing nutrient-depleted substrates tend to prefer litter with a higher content of labile compounds and readily available nutrients (Graça, 2001; Gessner et al., 2007). The mismatch between decomposer requirements and the elements available in their resources constitutes a stoichiometric constraint that ultimately controls litter decomposition rates (Danger et al., 2021). Therefore, elemental ratios, especially the C:N and C:P, can greatly influence the attractiveness of leaf litter (Mooshammer et al., 2012; Yang et al., 2021). The faster decomposition of S. canadensis is likely driven by its favourably low C:P ratio, while the slower rates in F. japonica and, to a lesser extent, A. glutinosa are likely due to their higher C:P ratios and the associated phosphorus limitation (Tab. S2). Although the decomposition of both A. glutinosa and F. japonica is presum-



Fig. 2. Differences in leaf litter decomposition rates of the native species (*Alnus glutinosa*) and invasive species (*Fallopia japonica*, *Solidago canadensis*) in headwater streams (a) and pond mesocosms (b). Observed values (small dots) are shown alongside estimated population means (large dots) and 95% confidence intervals (error bars). Statistically significant differences between litter types, revealed by pairwise post-hoc tests (p<0.05), are indicated by different italicized lowercase letters.

ably P-limited, the lower C:N ratio in *A. glutinosa* may help boost its decomposition relative to *F. japonica*. Bottollier-Curtet *et al.* (2011) also considered nutrient content, rather than geographic origin, as the primary driver of decomposition, evaluating the decomposition rates of five native and five invasive species. The fastest decomposing was the leaf litter of *Impatiens glandulifera*, which, like *S. canadensis* in our study, contained the highest amount of phosphorus among studied plant species.

The rapid decomposition of S. canadensis in a lentic environment was recently reported in other studies (Dekanová et al., 2021; Anda et al., 2023). Our study confirmed high decomposition rates in standing waters and revealed even faster decomposition of this species in running waters. When calculated on a per-day basis, the rates of S. canadensis leaf litter decomposition observed in the studied streams ($-k_d = 0.007 - 0.021 \text{ day}^{-1}$) and pond mesocosms (0.006-0.025 day⁻¹) are roughly comparable to those observed by Dekanová et al. (2021) in an artificial pond (0.011 day⁻¹) and by Anda et al. (2023) in wetlands (0.018-0.028 day-1). Although the decomposition rates reported for F. japonica are not directly comparable due to the use of different mesh sizes of litter bags, the relatively slow decomposition of this species observed in our research corresponds with the findings of some other studies conducted in ponds (Bottollier-Curtet et al., 2011) and headwater streams (Dangles et al., 2002; Braatne et al., 2007; Lecerf et al., 2007).

We observed that microbial leaf litter decomposition proceeds 2.6 to 5 times faster in forest streams than in pond mesocosms. This is consistent with the findings of Langhans et al. (2008) and Hill et al. (2022), who found significantly faster microbial decomposition in streams compared to ponds. The contrasting decomposition rates between lentic and lotic waters are likely caused by different physico-chemical and biological conditions in these environments. In contrast to well-oxygenated streams (11.4 mg O₂ L⁻¹, on average), low oxygen content in pond mesocosms (2.4 mg O₂ L⁻¹) may hinder the decomposition process. For example, Pattee and Chergui (1994) reported that decomposition in an oxbow lake nearly ceases after an initial phase of litter weight loss, a pattern they also confirmed under hypoxic conditions in the laboratory. Low oxygen concentrations can severely impair key decomposers - aquatic fungal communities - which typically dominate microbial decomposition (Hieber and Gessner, 2002; Pascoal et al., 2021). Low oxygen conditions reduce diversity, decrease biomass and inhibit sporulation of fungal communities (Medeiros et al., 2009). Consequently, fungal biomass on litter exposed to lentic environments is often lower than in lotic water bodies (Baldy et al., 2002; Langhans et al., 2008; da Silva et al., 2019). Moreover, higher concentrations of nutrients and potentially toxic leachates in standing waters can significantly impact microbial communities and the processes they mediate (Canhoto et al., 2013; Foulquier et al., 2014; Arroita et al., 2018), ultimately leading to slower litter decomposition in ponds.

The replacement of native riparian vegetation with monocultures of rapidly decomposing invasive plants, such as *S. canadensis*, may initially introduce a pulse of high-quality allochthonous litter into aquatic ecosystems. However, litter that is rapidly decomposed by microbes is less available to aquatic invertebrates and a large amount of carbon from these resources may be lost to microbial respiration (Siders *et al.*, 2018). Consequently, although initially abundant, this resource may become unavailable to aquatic detritivores before it can be effectively assimilated. In contrast, the slow microbial decomposition of invasive leaf litter such as F. japonica in ponds can limit nutrient release and delay the microbial conditioning process, which is critical for enhancing litter palatability through the breakdown of complex organic compounds and the accumulation of microbial biomass (Bärlocher and Kendrick, 1975; Graça et al., 2001; Danger et al., 2021). However, such recalcitrant leaves might serve as longer stored potential resources over multi-month intervals and stabilize fluctuations in the rates of leaf litter integration into aquatic food webs (Cereghetti et al., 2025). Overall, the formation of monospecific stands of invasive riparian plants with markedly different leaf litter traits than native species can impair the functioning of adjacent aquatic ecosystems. These shifts in litter decomposition dynamics underscore the potential for invasive species to disrupt ecosystem processes, with cascading consequences for aquatic food webs and nutrient cycling.

CONCLUSIONS

Our experiments revealed pronounced differences in decomposition rates among the three riparian species. The dominance of phosphorus-rich litter of *S. canadensis* could shift food webs toward a highly pulsed, microbially-driven regime, whereas stands of *F. japonica* might create slow-release nutrient stores and qualitatively different habitats. Both outcomes represent departures from the dynamics under native alder-dominated riparian vegetation, with unknown consequences for primary producers, invertebrates, fishes, amphibians and ecosystem processes.

While our experiments captured initial decomposition dynamics, field studies of invaded sites might help to assess how long-term dominance by *S. canadensis* or *F. japonica* shapes local aquatic communities and ecosystem functions. Moreover, it remains unclear how mixtures of invasive and native leaves decompose together. Since riparian zones often have mixedspecies leaf litter, future experiments should test whether the presence of *A. glutinosa* or other native leaves might slow down or alter the breakdown of *S. canadensis* litter or vice versa. Addressing these gaps will improve our understanding of how invasive riparian plants reshape freshwater ecosystem dynamics and will inform management strategies aimed at preserving native biodiversity and ecosystem functions.

ACKNOWLEDGEMENTS

The study was supported by the Slovak Research and Development Agency (APVV-16-0236 and APVV-19-0134) and by the Operational Programme Integrated Infrastructure funded by the European Regional Development Fund (ITMS 313011T721). We are grateful to K. Skokanová for providing the photo for Fig. 1e.

REFERENCES

Abelho M, Graça MAS, 1996. Effects of eucalyptus afforestation on leaf litter dynamics and macroinvertebrate community structure of streams in Central Portugal. Hydrobiologia 324:195-204.

- Anda A, Simon S, Simon-Gáspár B, 2023. Impacts of wintertime meteorological variables on decomposition of *Phragmites australis* and *Solidago canadensis* in the Balaton System. Theor. Appl. Climatol. 151:1963-1979.
- Arroita M, Flores L, Larrañaga A, Chauvet E, Elosegi A, 2018. Hydrological contingency: drying history affects aquatic microbial decomposition. Aquat. Sci. 80:31.
- 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.
- Bailey JK, Schweitzer JA, Whitham TG, 2001. Salt cedar negatively affects biodiversity of aquatic macroinvertebrates. Wetlands. 21:442-447. h
- Bates D, Maechler M, Bolker B, Walker S, 2015. Fitting linear mixed-effects models using lme4. J. Stat. Softw. 67:1-48.
- Baxter CV, Fausch KD, Saunders WC, 2005. Tangled webs: reciprocal flows of invertebrate prey link streams and riparian zones. Freshwater Biol. 50:20-220.
- Bärlocher F, Kendrick B, 1975. Leaf-conditioning by microorganisms. Oecologia 20:359-362.
- Bärlocher F, 2020. Leaf mass loss estimated by the litter bag technique, p. 43-51. In: F. Bärlocher, M. Gessner and M. Graça (eds.), Methods to study litter decomposition: a practical guide. Springer.
- Benfield EF, Fritz KM, Tiegs SD, 2017. Leaf-litter breakdown, p. 71-82. In: G.A. Lamberti and F.R. Hauer (eds.), Methods in stream ecology. Academic Press.
- Bielecka A, Borkowska L, Królak E, 2020. Environmental changes caused by the clonal invasive plant *Solidago canadensis*. Ann. Bot. Fenn. 57:33-48.
- Bottollier-Curtet M, Charcosset JY, Planty-Tabacchi AM, Tabacchi E, 2011. Degradation of native and exotic riparian plant leaf litter in a floodplain pond. Freshwater Biol. 56:1798-1810.
- Bottollier-Curtet M, Charcosset JY, Planty-Tabacchi AM, Tabacchi E, 2015. Chemical composition rather than plant geographic origin drives the breakdown of riparian plant litter with changes in associated invertebrate diversity. Plant Soil. 390:265-278.
- Boyero L, Barmuta LA, Ratnarajah L, Schmidt K, Pearson RG, 2012. Effects of exotic riparian vegetation on leaf breakdown by shredders: a tropical temperate comparison. Freshw. Sci. 31:296-303.
- Braatne JH, Sullivan SMP, Chamberlain E, 2007. Leaf decomposition and stream macroinvertebrate colonisation of Japanese knotweed, an invasive plant species. Int. Rev. Hydrobiol. 92:656-665.
- Brett MT, Bunn SE, Chandra S, Galloway AWE, Guo F, Kainz MJ, et al., 2017. How important are terrestrial organic carbon inputs for secondary production in freshwater ecosystems? Freshwater Biol. 62:833-853.
- Canhoto C, Calapez R, Gonçalves AL, Moreira-Santos M, 2013. Effects of Eucalyptus leachates and oxygen on leaf-litter processing by fungi and stream invertebrates. Freshw. Sci. 32:411-424.
- Cereghetti E, Bossart R, Bruder A, Krähenbühl A, Wolf F, Altermatt F, 2025. The year of a leaf: Tracking the fate of leaf litter and its nutrients during aquatic decomposition and

consumption. Ecology. 106:e4520. https://doi.org/10.1002/ ecy.4520

- Coleman H, Levine J, 2007. Mechanisms underlying the impacts of exotic annual grasses in a coastal California meadow. Biol. Invasion. 9:65-71.
- Cornelissen JH, Pérez-Harguindeguy N, Díaz S, Grime JP, Marzano B, Cabido M, et al., 1999. Leaf structure and defence control litter decomposition rate across species and life forms in regional floras on two continents. New Phytol. 143:191-200.
- Cornwell WK, Cornelissen JHC, Amatangelo K, Dorrepaal E, Eviner VT, Godoy O, et al., 2008. Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. Ecol. Lett. 11:1065-1071.
- Cummins KW, Wilzbach MA, Gates DM, Perry JB, Taliaferro WB, 1989. Shredders and riparian vegetation: leaf litter that falls into streams influences communities of stream invertebrates. BioScience. 39:24-30. https://doi.org/10.2307/ 1310804
- da Silva GVR, Castañeda-Ruiz RF, Malosso E, 2019. Comparison of aquatic hyphomycetes communities between lotic and lentic environments in the Atlantic rain forest of Pernambuco, Northeast Brazil. Fungal Biol. 123:660-668.
- Daehler CC, 2003. Performance comparisons of co-occurring native and alien invasive plants: implications for conservation and restoration. Annu. Rev. Ecol. Evol. S. 34:183-211.
- Danger M, Arce-Funck J, Beck M, Crenier C, Felten V, Wang Z, Maunoury-Danger F, 2021. Stoichiometry of plant litter decomposition in stream ecosystems, p. 23-49. In: C.M. Swan, L. Boyero and C. Canhoto (eds.), The ecology of plant litter decomposition in stream ecosystems. Springer Nature.
- Dangles O, Jonsson M, Malmqvist B, 2002. The importance of detritivore species diversity for maintaining stream ecosystem functioning following the invasion of a riparian plant. Biol. Invasions. 4:441-446.
- Davies JN, Boulton AJ, 2009. Great house, poor food: effects of exotic leaf litter on shredder densities and caddisfly growth in 6 subtropical Australian streams. J. N. Am. Benthol. Soc. 28:491-503.
- Dekanová V, Svitková I, Novikmec M, Svitok M, 2021. Litter breakdown of invasive alien plant species in a pond environment: Rapid decomposition of Solidago canadensis may alter resource dynamics. Limnologica 90:125911.
- Dekanová V, Novikmec M, Svitková I, Svitok M, 2023. Functional diversity of shredders, not species richness, drives the decomposition rate of leaf litter in ponds. Front. Ecol. Evol. 11:1286672.
- Dong LJ, Yu HW, He WM, 2015. What determines positive, neutral and negative impacts of Solidago canadensis invasion on native plant species richness? Sci. Rep. 5:16804.
- Fennel M, Wade M, Bacon KL, 2018. Japanese knotweed (*Fallopia japonica*):an analysis of capacity to cause structural damage (compared to other plants) and typical rhizome extension. PeerJ. 6:e5246.
- Ferreira V, Larrañaga A, Gulis V, Basaguren A, Elosegi A, Graça MAS, Pozo J, 2015. The effects of eucalypt plantations on plant litter decomposition and macroinvertebrate communities in Iberian streams. Forest. Ecol. Manag. 335:129-138.
- Fogelman KJ, Bilger MD, Holt JR, Matlaga DP, 2018. Decomposition and benthic macroinvertebrate communities

of exotic Japanese knotweed (*Fallopia japonica*) and American sycamore (*Platanus occidentalus*) detritus within the Susquehanna River. J. Freshwater Ecol. 33: 299-310.

- Foulquier A, Dehedin A, Piscart C, Montuelle B, Marmonier P, 2014. Habitat heterogeneity influences the response of microbial communities to severe low-flow periods in alluvial wetlands. Freshwater Biol. 59:463-476.
- Frost PC, Benstead JP, Cross WF, Hillebrand H, Larson, JH, Xenopoulos MA, Yoshida T, 2006. Threshold elemental ratios of carbon and phosphorus in aquatic consumers. Ecol. Lett. 9:774-779.
- García L, Richardson JS, Pardo I, 2012. Leaf quality influences invertebrate colonization and drift in a temperate rainforest stream. Can. J. Fish. Aquat. Sci. 69:1663-1673.
- García L, Pardo I, Richardson JS, 2014. A cross-continental comparison of stream invertebrate community assembly to assess convergence in forested headwater streams. Aquat. Sci. 76:29-40.
- Gessner MO, Chauvet E, Dobson M, 1999. A perspective on leaf litter breakdown in streams. Oikos. 85:377-384.
- Gessner MO, Gulis V, Kuehn KA, Chauvet E, Suberkropp K, 2007. Fungal decomposers of plant litter in aquatic ecosystems, p. 301-324. In: C.P. Kubicek and I.S. Druzhinina (eds.), The mycota, environmental and microbial relationships. Springer. ht
- 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. Change Biol. 6:751-765.
- Graça MAS, 2001. The role of invertebrate on leaf litter decomposition in streams a review. Int. Rev. Hydrobiol. 86:383-393.
- Graça MAS, Cressa C, Gessner MO, Feio MJ, Callies KA, Barrios C, 2001. Food quality, feeding preferences, survival and growth of shredders from temperate and tropical streams. Freshwater Biol. 46:947-957.
- Harner MJ, Crenshae CL, Abelho M, Sursova M, Shah JJF, Sinsabaugh RL, 2009. Decomposition of leaf litter from a native tree and an actinorhizal invasive across riparian habitats. Ecol. Appl. 19:1135-1146.
- Hartig F, 2022. DHARMa: Residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.4.6
- Hieber M, Gessner MO, 2002. Contribution of stream detrivores, fungi, and bacteria to leaf breakdown based on biomass estimates. Ecology. 83:1026-1038.
- Hill MJ, Thornhill I, Tiegs SD, Castro-Castellon A, Hernández-Avilés JS, Daw A, et al., 2022. Organic-matter decomposition in urban stream and pond habitats. Ecol. Indic. 142:109232.
- Hrivnák R, Svitok M, Kochjarová J, Jarolímek I, Machava J, Senko D, Slezák M, 2020. Drivers of plant species composition in alder-dominated forests with contrasting connectivity. Wetl. Ecol. Manag. 28:137-150.
- Hrivnák R, Svitok M, Hegedüšová Vantarová K, Jarolímek I, Kochjarová J, Májeková J, Slezák M, 2024. Environmental thresholds for plant species richness of black alder (*Alnus glutinosa*) forests in Central Europe. Wetl. Ecol. Manag. 32:591-604.
- Jansson M, Persson L, De Roos AM, Jones RI, Tranvik LJ, 2007.

Terrestrial carbon and intraspecific size-variation shape lake ecosystems. Trends Ecol. Evol. 22:316-322.

- Kennedy KT, El-Sabaawi RW, 2017. A global meta-analysis of exotic versus native leaf decay in stream ecosystems. Freshwater Biol. 62:977-989.
- Kominoski JS, Follstad Shah JJ, Canhoto C, Fischer DG, Giling DP, González E, et al., 2013. Forecasting functional implications of global changes in riparian plant communities. Front. Ecol. Environ. 11:423-432.
- Kuglerová L, García L, Pardo I, Mottiar Y, Richardson JS, 2017. Does leaf litter from invasive plants contribute the same support of a stream ecosystem function as native vegetation. Ecosphere 8:e01779.
- Kuznetsova A, Brockhoff PB, Christensen RHB, 2017. ImerTest package: Tests in linear mixed effects models. J. Stat. Softw. 82:1-26.
- Langhans SD, Tiegs SD, Gessner MO, Tockner K, 2008. Leafdecomposition heterogeneity across a riverine floodplain mosaic. Aquat. Sci. 70:337-346.
- Lecerf A, Patfield D, Boiche A, Riipinen MP, Chauvet E, Dobson M, 2007. Stream ecosystems respond to riparian invasion by Japanese knotweed (*Fallopia japonica*). Can. J. Fish. Aquat. Sci. 64:1273-1283.
- Leishman MR, Haslehurst T, Ares A, Baruch Z, 2007. Leaf trait relationships of native and invasive plants: community- and global-scale comparisons. New Phytol. 176:635-643.
- Lenth RV, 2016. Least-squares means: the R package lsmeans. J. Stat. Softw. 69:1-33.
- Lenth RV, 2022. emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.7.4-1.
- Lüdecke D, Ben-Shachar MS, Patil I, Waggoner P, Makowski D, 2021. performance: An R Package for Assessment, Comparison and Testing of Statistical Models. J. Open Source Softw. 6:3139.
- McNeish RE, Benbow ME, McEwan RW, 2012. Riparian forest invasion by a terrestrial shrub (*Lonicera maackii*) impacts aquatic biota and organic matter processing in headwater streams. Biol. Invasions. 14:1881-1893.
- Medeiros AO, Pascoal C, Graça MAS, 2009. Diversity and activity of aquatic fungi under low oxygen conditions. Freshwater Biol. 54:142-149.
- Mooshammer M, Wanek W, Schnecker J, Wild B, Leitner S, Hofhansi F, et al., 2012. Stoichiometric controls of nitrogen and phosphorus cycling in decomposing beech leaf litter. Ecology. 93:770-782.
- Naiman RJ, Décamps H, 1997. The ecology of interfaces:riparian zones. Annu. Rev. Ecol. Evol. S. 28:621-658.
- Nakagawa S, Johnson PC, Schielzeth H, 2017. The coefficient of determination R 2 and intra-class correlation coefficient from generalized linear mixed-effects models revisited and expanded. J. R. Soc. Interface. 14:20170213.
- Pascoal C, Fernandes I, Seena S, Danger M, Ferreira V, Cássio F, 2021. Linking microbial decomposer diversity to plant litter decomposition and associated processes in streams, p. 163-192. In: C.M. Swan, L. Boyero and C. Canhoto (eds.), The ecology of plant litter decomposition in stream ecosystems. Springer.
- Pattee E, Chergui H, 1994. On the incomplete breakdown of submerged leaves. Int. Ver. The. 25:1545-1548.

- Petersen RC, Cummins KW, 1974. Leaf processing in a woodland stream. Freshwater Biol. 4:343-368.
- Pfeifer-Meister L, Cole E, Roy B, Bridgham S, 2008. Abiotic constraints on the competitive ability of exotic and native grasses in a Pacific Northwest prairie. Oecologia 155:357-366.
- Pinheiro JC, Bates DM, 2000. Mixed-effects models in S and S-PLUS. Springer, Cham: 544 pp.
- R Core Team, 2022. R: A language and environment for statistical computing. Vienna, R Foundation for Statistical Computing.
- Reinhart KO, VandeVoort R, 2006. Effect of native and exotic leaf litter on macroinvertebrate communities and decomposition in a western Montana stream. Divers. Distrib. 12:776-781.
- Richardson DM, Holmes PM, Esler KJ, Galatowitsch SM, Stromberg JC, Kirkman SP, Pyšek P, Hobbs RJ, 2007. Riparian vegetation: degradation, alien plant invasions, and restoration prospects. Divers. Distrib. 13:126-139.
- Ringold PL, Magee TK, Peck DV, 2008. Twelve invasive plant taxa in US western riparian ecosystems. J. N. Am. Benthol. Soc. 27:949-966.
- Serra MN, Albariño R, Villanueva VD, 2013. Invasive *Salix fragilis* alters benthic invertebrate communities and litter decomposition in northern Patagonian streams. Hydrobiologia 701:173-188.
- Shaw RH, Seiger LA, 2002. Japanese knotweed, p. 159-166. In: R.G. van Driesche, S. Lyon, B. Blossey and M.S. Hoddle, R. Reardon (eds.), Biological control of invasive plants in the Eastern United States. USDA ForestService.
- Siders AC, Compson ZG, Hungate BA, Dijkstra P, Koch GW, Wymore AS, et al., 2018. Litter identity affects assimilation of carbon and nitrogen by a shredding caddisfly. Ecosphere 9:e02340.
- Simon S, Simon-Gáspár B, Anda A, 2023. Carbon dioxide emission and its impacting factor from goldenrod (*Solidago canadensis*) and bulrush (*Typha angustifolia*) decomposition during the winter period. Ecohydrol. Hydrobiol. 23:177-185.

- Skokanová K, Španiel S, Šingliarová B, Mereda P, Hodálová I, Svitok M, 2024. Contrasting invasion patterns of two closely related *Solidago* alien species. J. Biogeogr. 51:1679-1692.
- Slezák M, Farkašovská Š, Hrivnák R, 2020. Non-native plant species in alder-dominated forests in Slovakia:what does the regional-and the local-scale approach bring? Folia Oecol. 47:100-108.
- Stoler AB, Relyea RA, 2020. Reviewing the role of plant litter inputs to forested wetland ecosystems:leafing through the literature. Ecol. Monogr. 90:e01400.
- Svitková I, Svitok M, Čejka T, Širka P, Galvánek D, Gömöry D, et al., 2024. Contrasting diversity patterns of native and alien species across multiple taxa in Central European river corridors. Ecol. Indic. 169:112859.
- Tibbets TM, Molles MC, 2005. C:N:P stoichiometry of dominant riparian trees and arthropods along the Middle Rio Grande. Freshwater Biol. 50:1882-1894.
- Vannote RL, Minshall GW, Cummins KW, Sedell JR, Cushing CE, 1980. The river continuum concept. Can. J. Fish. Aquat. Sci. 37:130-137.
- Wickham, H., 2016. ggplot2: Elegant graphics for data analysis. Springer, Cham: 260 pp.
- Yang R, Dong J, Li C, Wang L, Quan Q, Liu J, 2021. The decomposition process and nutrient release of invasive plant litter regulated by nutrient enrichment and water level change. PLoS One 16:e0250880.
- Zelnik I, Mavrič Klenovšek V, Gaberščik A, 2020. Complex undisturbed riparian zones are resistant to colonisation by invasive alien plant species. Water (Basel) 12:345.
- Zhu X, Li W, Shao H, Tang S, 2022. Selected aspects of invasive Solidago canadensis with an emphasis on its allelopathic abilities: a review. Chem. Biodivers. 19:e202200728.
- Zukswert JM, Prescott CE, 2017. Relationships among leaf functional traits, litter traits, and mass loss during early phases of leaf litter decomposition in 12 woody plant species. Oecologia 185:305-316.

Online supplementary material:

Tab. S1. Characteristics of the studied streams and a pond used as a source for the mesocosm experiment.

Tab. S2. Characteristics of native (A. glutinosa) and invasive (F. japonica, S. canadensis) leaf litter species used in the experiments.