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Assessing the Complex Effects of the Invasive Amphipod *Dikerogammarus villosus* on Leaf Litter Breakdown in Rivers

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ABSTRACT

1. Allochthonous organic matter is an essential resource of aquatic food webs, and freshwater amphipods, particularly species of the genus *Gammarus*, play a significant role in leaf litter decomposition. However, this important ecological function may be affected by the invasion of alien amphipods such as *Dikerogammarus villosus*, which has been reported to show lower leaf litter decay rates than native gammarids. The aim of this study was to determine whether the invasion of *D. villosus* would disrupt the ecological function of leaf litter breakdown under field conditions by comparing leaf litter decay rates at invaded and uninvaded river sites.
2. The experiment was conducted at six locations, four in Croatia and two in Germany, with one site upstream and one site downstream of an invasion front at each location. At each site, we placed preconditioned willow leaves in the river and sampled them three times to estimate leaf litter breakdown rates and invertebrate colonisation.
3. We hypothesized that leaf litter breakdown rates would be higher at the sites without *D. villosus* (upstream of the invasion front) compared to the invaded sites. Contrary to this hypothesis, the results indicated contrasting and obviously context dependent outcomes. This indicates a change but no general disruption of leaf litter processing by the invasion of the omnivorous *D. villosus*, even when it displaces native shredders.
4. The outcome of the experiments most probably depended on the biomass of native shredders in the leaf bags. At three locations with low biomass of native shredders in the upstream leaf bags, the downstream sites with *D. villosus* presence showed higher breakdown rates than the upstream sites. At the three locations with high biomass of native shredders, the downstream sites with *D. villosus* had lower breakdown rates than the upstream sites.
5. These findings underscore the complex interactions between invasive and native species in freshwater ecosystems and their potential impact on ecosystem services.

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1 | Introduction

Invasive species represent one of the greatest threats to freshwater biodiversity (Dudgeon et al. 2006; Strayer 2010; Havel et al. 2015) and are expected to affect ecosystem functioning (Ehrenfeld 2010; Pyšek et al. 2020). The number of invasive species in European rivers is constantly increasing (Nunes et al. 2015) due to human activities such as intentional introductions, canal construction, tourism, ship traffic and hydromorphological alterations (Leuven et al. 2009; Havel et al. 2015). Invasive macroinvertebrates often dominate in abundance and/or taxa richness, causing drastic changes in native macroinvertebrate assemblages in European rivers (van den Brink et al. 1990; Haas et al. 2002; Jazdzewski et al. 2004; Ćuk et al. 2019). While the effects on native biodiversity and community composition have been observed and described often, the consequences of invasion for ecosystem functioning have been studied far less (Sousa et al. 2011).

Stream macroinvertebrates can affect ecosystem functioning by changing the rate of detritus processing, because macroinvertebrate shredders are crucial for the breakdown of leaf litter and the recycling of nutrients (Wallace et al. 1982; Jonsson and Sponseller 2021). Allochthonous riparian leaf litter is an essential energy resource in aquatic food webs (Tank et al. 2010) and macroinvertebrate shredders play a key role in the production of small organic particles which can be used by other invertebrate functional groups (Wallace and Webster 1996; Tonin et al. 2018; Vannote et al. 1980). The efficiency and temporal stability of the community leaf litter decay rate can impact higher trophic levels (Kelly and Dick 2005).

One group of crustaceans, the superorder Peracarida (orders Amphipoda, Isopoda, Mysida), contains particularly successful invaders in European inland waters (Holdich and Pöckl 2007) and at the same time represent one of the most abundant shredders in many stream ecosystems (Piscart et al. 2009). Therefore, especially the invasion and a subsequent species turnover in Peracarida has the potential to change ecosystem functions, specifically leaf litter processing. One of the most successful Ponto-Caspian invaders of European aquatic ecosystems is the amphipod *Dikerogammarus villosus* (Sowinskyi, 1894) (Rewicz et al. 2014), which has not only been reported to change benthic invertebrate community composition, especially reducing native amphipod species (Bollache et al. 2004; Grabowski et al. 2007; Borza et al. 2015; Žganec et al. 2018; Boets et al. 2010) but which is also suspected to change ecosystem functions (Van Riel et al. 2006; Bollache et al. 2008; MacNeil et al. 2011). Most studies observed *D. villosus* to have lower rates of leaf litter processing compared to native amphipods, at least in laboratory settings (Boeker and Geist 2015; Jourdan et al. 2016; Kenna et al. 2017; Fincham et al. 2023; Pile et al. 2023). If that finding holds true for stream ecosystems in general, the invasion of *D. villosus* and the replacement of native amphipods would drastically reduce functional redundancy within the shredder guild and simultaneously reduce community grazing rate, which could have significant effects for stream food webs. However, some laboratory and mesocosm experiments have shown high leaf litter shredding efficiency of *D. villosus*, very similar to that of *Gammarus roeselii* Gervais, 1835 and *Gammarus. pulex* (Linnaeus 1758) (Gergs and Rothhaupt 2008; Bundschuh et al. 2013; Truhlar et al. 2014; Richter et al. 2018). There are also in situ field studies, showing that decomposition rates of the invasive species *D. villosus* are high (Worischka et al. 2018), and similar to the native species *G. fossarum* Koch, 1836 and *G. roeselii* (Little and Altermatt 2019). In fact it seems that the leaf decay rate and the specific differences in leaf decay rate between *D. villosus* and native amphipods depends on environmental factors such as temperature (Kenna et al. 2017) or the experimental arena containing hiding places or different numbers of conspecifics as well as the method of estimating consumption rates with or without continuous feeding (Richter et al. 2018).

Due to the differences in the results of the various laboratory studies and suspected high context dependency, it is still unclear whether *D. villosus* can provide the same ecosystem function in real stream ecosystem as native shredder communities. Therefore, the aim of this study was to investigate the effects of the invasive amphipod *D. villosus* on in situ leaf litter decomposition rates in different environmental contexts. Because native amphipod species have often shown higher leaf decay rates than *D. villosus* and seem to be replaced by *D. villosus*, we hypothesized that leaf litter breakdown rates would be higher at sites without invasive *D. villosus*. To test this hypothesis, we used six locations, with one site each where *D. villosus* was an abundant component of the macroinvertebrate assemblage and another site directly upstream of the *D. villosus* invasion front, where only native amphipods (*G. fossarum*, *G. pulex*, and *G. roeselii*) were dominant shredders in the macroinvertebrate assemblage. Two locations were located in tributaries of the Rhine River in Germany, and four in the Drava River (a tributary of the Danube River).

2 | Material and Methods

2.1 | Study Area

The six study locations were situated along the Blies and Lahn rivers (tributaries of the Rhine River) in Germany (two locations) and at four locations along the Drava River (a tributary to the Danube River) in Croatia (D1, D2, D3 and D4; Figure 1). At each location, two sampling sites were chosen: one upstream of *D. villosus* invasion front, where only native amphipods were found, and a nearby downstream site where *D. villosus* occurred alone (Blies and Lahn rivers), or co-occurred with native amphipods (Drava River, Table 1). These six locations exhibited variations in abiotic factors. The German Blies River is a silicate-rich low mountain stream with a streambed of fine to coarse material (German stream type 9.0) (UBA 2016). The German Lahn River is a large low mountain stream (German stream type 9.2) (UBA 2016), but it has been significantly modified due to impoundments (HMUKLV 2015). Four locations in Croatia are located along the upstream course of the Drava River, near the Čakovec and Dubrava reservoirs. All four sites are located along sections of the Drava River that belong to the category of "Very large lowland rivers–lower course of the Mura River and middle course of the Sava and Drava Rivers" (HR-R_5B) according to the Croatian national river typology. The site Drava 1 is located on the lower course of a derivation channel between the Varaždin and Čakovec reservoir. It is an artificial channel of the Varaždin Hydroelectric Power Plant (HPP), that is, artificial water body

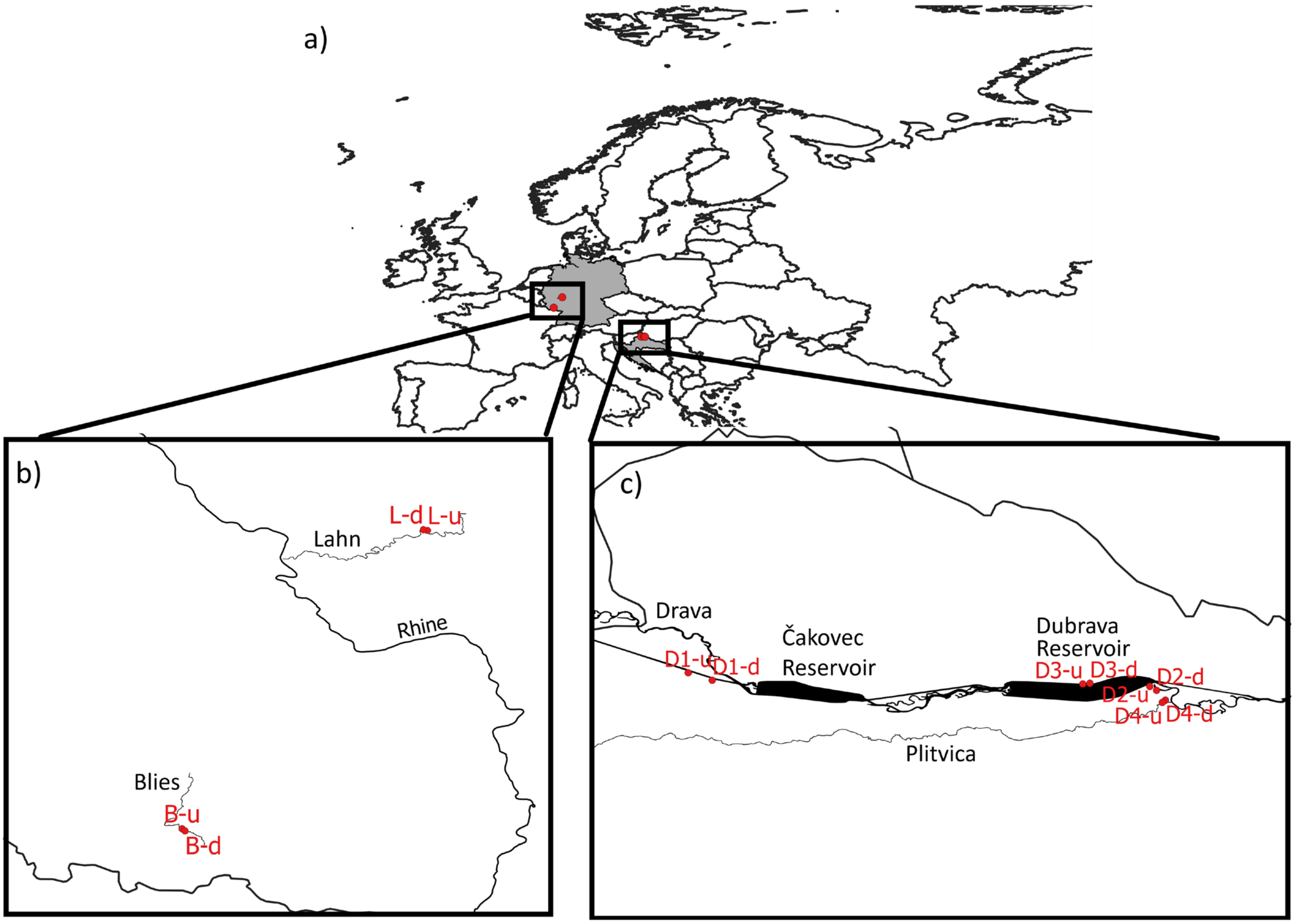

FIGURE 1 | (a) Location of the 12 study sites in Germany and Croatia, (b) four study sites in Germany on the Rhine tributaries Lahn (L-u, L-d) and Blies (B-u, B-d), (c) eight sites in Croatia: At derivation channel upstream of the Čakovec reservoir (D1-u, D1-d), at the old course of the Drava River (D2-u, D2-d), at the right drainage channel of the Dubrava reservoir (D3-u, D3-d) and at the mouth of the Plitvica River (D4-u, D4-d) into the old course of the Drava River. The site names with site abbreviations can be found in Table 1.

(AWB), with daily water level fluctuations, that is, hydropeaking (Tadić and Brleković 2019). The Drava 2 site, is located on the old course of the Drava River, downstream of the Dubrava Reservoir, with a natural gravel riverbed, receiving water from the right-side drainage channel of the upstream reservoir. The Drava 3 site is situated on the left artificial drainage channel of the Dubrava Reservoir, with relatively stable water temperature and water level. All Drava reservoirs in Croatia have two drainage channels on each side, which drain upwelling groundwater due to the large volume of the reservoirs and gravel sediments, and have relatively stable environmental conditions. The Drava 4 site is located at the mouth of the Plitvica River into the old course of the Drava River.

2.2 | Leaf Litter Decomposition Experiments

Two different types of leaf bags were used for the experiment, following the approach described by Bedford (2004). The fine leaf bags (mesh size 200 µm) were used to estimate microbial decomposition (no invertebrate shredding, Bedford 2004). The coarse leaf bags consisted of two materials, with the coarse fence material (size 8.5 × 8.5 cm, mesh size 7.5 mm) at the front to allow access for macroinvertebrates and the fine fence material (mesh size 500 µm) at the other end to reduce loss by mechanical destruction (Bedford 2004). Both bag types were similar in size (approximately 14 × 11 cm) with a fill area of 12 × 8.5 cm (Figure 2). Willow leaves (*Salix* sp.), collected near Dresden, Germany, and in Zagreb, Croatia, were air dried, weighed (2.5 g), and placed in the leaf bags without breaking the leaves. Willow leaves were used for the experiment because they are the most common at the sites where the experiment was conducted and therefore represent the most important source of allochthonous organic matter. Each bag was numbered and sealed with a plastic clip. The prepared leaf bags were conditioned in aerated stream water at room temperature for 10 days to develop a microbial community that would likely increase attractiveness to shredders in the river (e.g., Lange et al. 2005; Agatz and Brown 2014).

After conditioning, leaf bags were exposed in the Blies and Lahn rivers in August 2019, in the Drava River at two locations (Drava 1 and Drava 2) in October 2019, and at two additional locations (Drava 3 and Drava 4) in October 2021. In 2019, 11 leaf bags of each type (fine and coarse) were placed at each site of the four locations (8 sites), while 15 leaf bags of each type were used in 2021. The fine and coarse leaf bags were alternately attached to one of three ropes with approximately 30 cm spacing between the adjacent bags (Figure 2), and all three ropes were installed at

TABLE 1 | Basic information on the 12 sites at the six locations in Germany (Blies and Lahn) and Croatia (four Drava locations) where a leaf litter breakdown experiment was conducted in 2019 (Blies, Lahn, Drava 1, and Drava 2) and 2021 (Drava 3 and Drava 4).

Location	Site	Site code	Coordinates		River type	Site distance	Taxa number of shredders	Altitude
Blies	Upstream	B-u	49.33736	7.23817	9.0	1.2 km	4	235 m
	Downstream	B-d	49.32944	7.24875			4	234 m
Lahn	Upstream	L-u	50.41494	8.12464	9.2	1.2 km	2	113 m
	Downstream	L-d	50.41764	8.10983			2	112 m
Drava 1	Upstream	D1-u	46.33225	16.31747	AWB	2.4 km	4	169 m
	Downstream	D1-d	46.32564	16.33856			3	169 m
Drava 2	Upstream	D2-u	46.31681	16.72953	HR-R_4A	0.8 km	4	138 m
	Downstream	D2-d	46.32028	16.72353			4	137 m
Drava 3	Upstream	D3-u	46.32239	16.66462	AWB	0.7 km	4	144 m
	Downstream	D3-d	46.32300	16.67087			5	142 m
Drava 4	Upstream	D4-u	46.30619	16.73456	HR-R_5B	0.4 km	5	143 m
	Downstream	D4-d	46.30812	16.73725			6	136 m

FIGURE 2 | Arrangement of fine (white) and coarse (black) leaf bags on ropes at sampling site D1 in October 2019 (left) and at site D3 in October 2021 (centre). The far right photo shows fine (top) and coarse (bottom) bags. There were three ropes with leaf bags at each sampling site, one rope for each sampling point.

each sampling site, one for each sampling period. The ropes with the leaf bags were attached to the streambed, rocks, or trees with steel pins so that the leaf bags always remained in the water. Directly after conditioning, five leaf bags were sampled to determine the leaf loss during conditioning. The leaf bags on each location were sampled at three consecutive occasions. Sampling frequency was based on the expected breakdown rate of leaf litter at each site. The Lahn and Blies rivers were sampled 5, 12, and 19 days after exposure. At the Drava 2 site, samples were collected 5, 8, and 10 days after exposure. At the Drava 1 site, samples were collected 5, 10, and 13 days after exposure. At the Drava sites 3 and 4, in 2021, leaf bags were sampled 3, 7, and 11 days after exposure. At least three leaf bags of each type were collected at each site per sampling occasion. Coarse leaf bags were collected with a box and net to prevent macroinvertebrates from escaping through the coarse mesh. The fine bags were washed in the stream while still sealed to prevent collection of externally attached individuals. Immediately after removal from the water, the bags were stored individually in separate containers with 96% ethanol and processed within 24 h. To test the effect of 96% ethanol on leaf litter, we conducted an experiment with 1 g of willow leaves. The leaves were first soaked in water and then immersed in 96% ethanol for 24 h. After drying, the average mass of the leaves soaked in water only was 0.81 g, while the average mass of the leaves soaked in 96% ethanol was 0.76 g. This resulted in an average mass loss of 6.2% more than that observed with water alone. At the beginning of the experiment and during each sampling, five physicochemical variables were measured at each site: Water temperature (°C), pH, electrical conductivity (µS cm^{-1}), dissolved oxygen concentration (mg O_2 L^{-1}), and oxygen saturation (%) using WTW probes.

In the laboratory, litter from each individual leaf bag was rinsed with tap water to remove algae and sediment, while a sieve (mesh size 200 µm) prevented loss of organisms and leaf material > 200 µm. Macroinvertebrates were separated from leaves using a stereomicroscope to ensure all macroinvertebrates were collected. Leaf litter samples were placed in separate foil trays, covered with perforated aluminium foil, dried at 60°C for 16 h, and weighed.

Macroinvertebrates were sampled at all sites where the experiment took place. At four locations (Drava 1, Drava 2, Blies and Lahn) baskets made of chicken wire were (50 × 20 × 20 cm) filled with coarse gravel (grain size 4–8 cm, approximately 8 L per basket) and placed in the riverbed. At the 8 sites, three baskets each were exposed for 4 weeks before the start of the experiment. After this period, the baskets were retrieved, and the gravel was washed in containers to collect the macroinvertebrates, which were then preserved with 96% ethanol. At two other locations, Drava 3 and Drava 4, as well as Drava 2, five replicate samples (25 × 25 cm) were collected using a hand net (500 µm) on stony substrate. To compare benthic densities between baskets and net samples a theoretical area was calculated for the baskets. Since the baskets could be colonised from all sides but the bottom side, the sum of all accessible sides was used as theoretical sampling area (0.38 m^2 per basket). All invertebrates separated from the leaves in the leaf bags and from the sediment in the baskets or benthic samples were preserved in 75% ethanol. Subsequently, all individuals were identified to the family level, and families containing species belonging to the shredder functional feeding group were identified to the lowest possible taxonomic level. Amphipods belonging to the genera *Gammarus* and *Dikerogammarus* were determined to the species level. After identification, the total length of all specimens found in the coarse leaf bags was measured for further analysis.

2.3 | Data Analysis

Decomposition of the leaf litter proceeds exponentially over time (Bärlocher 2005). Therefore, the breakdown rates of the leaf litter were calculated using a linear regression model for log-transformed dry mass of willow leaves. Differences in calculated breakdown rates between coarse and fine leaf litter bags and between the two sites (upstream and downstream) were tested for each location using an ANCOVA after fitting a linear regression model to the data, to compare slopes between upstream and downstream sites for each leaf litter bag type at each location, which was performed using the lsmeans package (Lenth 2016) or lm function in base R version 4.3.2 (R Core Team 2023). Differences in the leaf mass loss between upstream and downstream sites and between fine and coarse leaf litter bags were tested by pairwise t-tests using the statistical software package Statistica 7.1 (Systat Software Inc. Richmond, CA, USA). Furthermore, ratio of breakdown coefficients at upstream, reference (kr) and downstream, impacted (ki) site and ratio between coefficients in coarse (kc) and fine (kf) bags were also calculated as in Gessner and Chauvet (2002).

To compare the macroinvertebrate assemblages at the different locations, the abundance of all shredders, the abundance of amphipods, and the abundance of non-amphipod shredders was calculated as a sum for all coarse leaf bags, as well as for baskets and benthic samples at each site. The functional feeding group was assigned to each taxon using Fauna Aquatica Austriaca (Moog 2002). Shredders other than peracarids had either a low affinity to feeding type “shredder” (less than 3 according to Moog 2002) or a very low abundance and were therefore not included in the analysis. After measuring the total length (Lt) of the peracarids, length-to-mass ratios were used to calculate the body dry mass (DM) of each amphipod species (*G. fossarum*, Burgherr and Meyer 1997; *G. roeselii*, *G. pulex* and *Asellus aquaticus*, Baumgärtner and Rothhaupt 2003; *D. villosus*, Hellmann et al. 2015). For *Synurella ambulans*, this relationship was determined using our samples ($DM = 0.0098 * Lt^{2.7974}$; $r^2 = 0.90$, $n = 205$). Differences in amphipod community composition in coarse leaf bags (based on biomass) and sampling (based on density) between sampling sites and locations were tested using PERMANOVA in Primer version 6.1.13 (Clarke and Gorley 2006). Physicochemical variables were compared between sites using principal component analysis (PCA) in Primer version 6.1.13.

3 | Results

The total density of macroinvertebrates at the selected sites ranged between 923 ind. m^{-2} at D4-d and 12,515 ind. m^{-2} at B-u (Figure 3). Average proportion of shredders in the macroinvertebrate community at all sites was 45.07% (range: 3.7%–85.2%). The shredder community at all locations consisted mainly of Peracarida, with a small number of caddisflies (Leptoceridae sp., *Anabolia nervosa* and *Limnephilus* sp.). Native Peracarida shredder species present at the four Croatian locations were *G. fossarum*, *G. roeselii*, *S. ambulans* and isopod *A. aquaticus*, while at the two German locations were *G. pulex* and *G. roeselii*. At all locations, the only invasive amphipod was *D. villosus* (Figures 3 and 4). Peracarida made up at least 99% of shredders, except at site D4-d where they accounted for 75% of all shredders. The invasive *D. villosus* was mostly absent from upstream sites, but was present in low density at location Drava 2 (20 ind. m^{-2}, 0.3% of macroinvertebrates). Community composition based on density differed significantly between upstream and downstream sites (PERMANOVA, pseudo-F = 9.63, $p < 0.01$), but did not show differences between the six locations (PERMANOVA, pseudo-F = 1.70, $p > 0.05$). The most abundant native peracarid species at the upstream sites were *G. fossarum* in Croatia, and *G. pulex* in Germany. Downstream sites in Germany, had only *D. villosus* present, while in native species *G. fossarum* and *G. roeselii* coexisted with *D. villosus*, albeit at lower density compared to the upstream sites (Figure 3).

The breakdown rates of the leaf litter in the coarse bags are not consistent between upstream and downstream sites across the different study locations. Analysed across all six locations, the loss of the leaf mass in coarse leaf bags showed no statistically significant difference between upstream and downstream sites (pairwise t-test, df = 5, $t = -0.932$, $p = 0.394$). However, at three locations (Drava 1, Blies and Lahn) breakdown rates in coarse leaf bags were significantly higher at the downstream

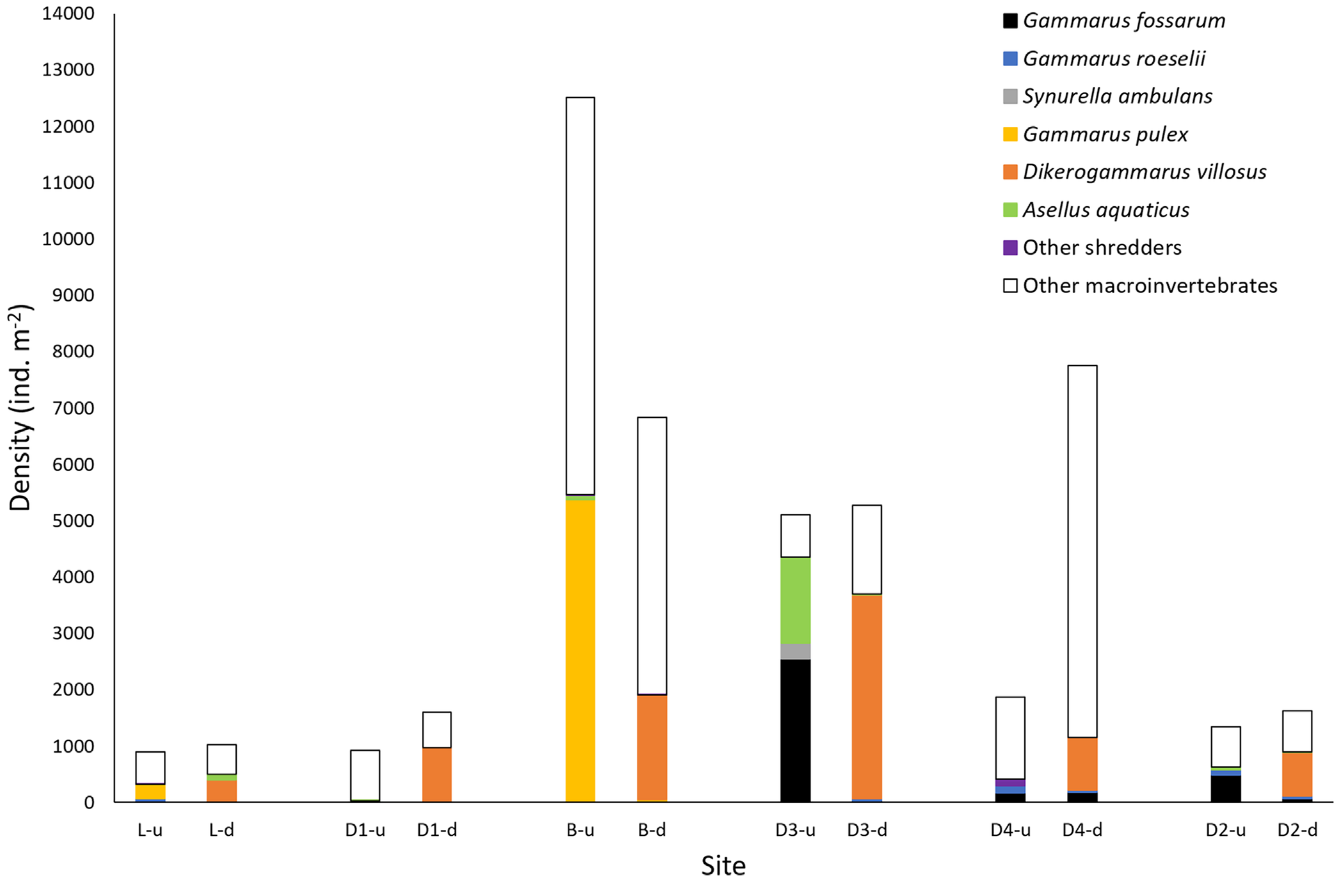

FIGURE 3 | Densities of all six shredding species of Peracarida (five native: *G. fossarum*, *G. roeselii*, *G. pulex*, *S. ambulans*, *A. aquaticus* and one invasive: *D. villosus*) found at all six locations (12 sites). Other shredders due to their low number were pooled into a group called other shredders and all other taxa were pooled in group called other macroinvertebrates. Locations: B—Blies, L—Lahn and D—Drava; letters u—upstream and d—downstream denote the sites for each location.

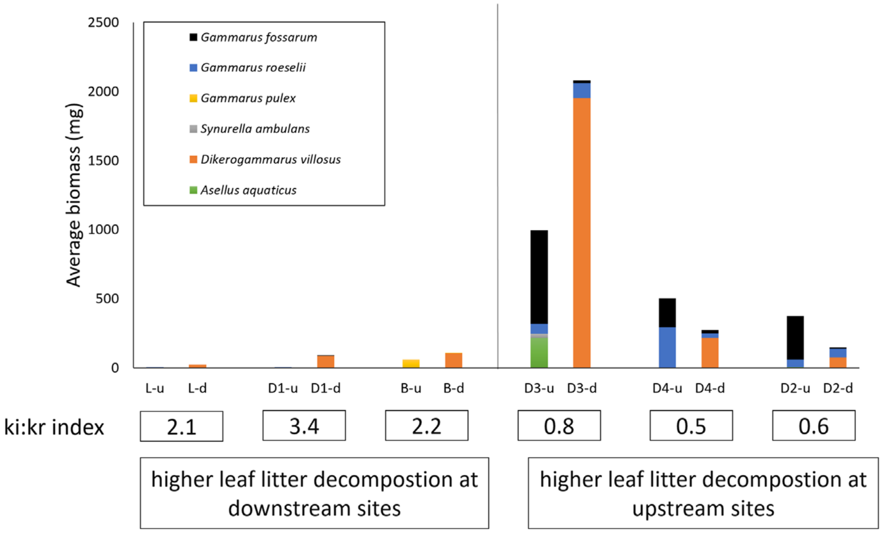

FIGURE 4 | Average biomass of six species of shredders (five native species: *G. fossarum*, *G. roeselii*, *S. ambulans*, *G. pulex*, and *A. aquaticus*; one invasive species: *D. villosus*) in coarse leaf bags for all 12 sites. Locations with higher breakdown rates at downstream sites are shown on the left, while locations with lower breakdown rates at the downstream sites are shown on the right. The ki:Kr index (ratio of breakdown coefficients) of upstream (kr, reference) and downstream (ki, impacted) sites is shown below each location (B—Blies, L—Lahn and D—Drava; letters u—upstream and d—downstream denote the sites for each location).

site (Figure 5; Table S1) where the invasive species *D. villosus* was present (ANCOVA, $F_{1,16}=9.98$–16.92, $p<0.01$; Figure S1). At the other three locations (Drava 2, Drava 3 and Drava 4), the breakdown rates in coarse bags were significantly lower at the downstream sites (ANCOVA, $F_{1,16}=5.08$–14.27, $p<0.01$; Figure S1) where the invasive species *D. villosus* was present (Figure 5; Table S1). We assume that the differences between those two groups of sites is caused by the relative proportion of native shredders to *D. villosus*. At the three locations with higher breakdown rates at the downstream sites (Drava 1, Blies and Lahn), the biomass of native amphipods (*G. roeselii* and/or *G. pulex*) in the leaf bags at the upstream sites was very low or even zero (Figure 4). However, the benthic samples showed a high density of *G. pulex* at the upstream sites of Blies and Lahn (B-u, L-u). Nevertheless, these high benthic densities did not translate to high densities or biomass in the leaf bags. In contrast, at the three locations with lower breakdown rates at the downstream sites (Drava 2, Drava 3 and Drava 4), the biomass of the native species *G. roeselii* and especially *G. fossarum* in the leaf bags of the upstream sites was much higher than at the other three locations (Drava 1, Blies and Lahn) and much higher than at the respective downstream sites (Figure 4). However, similar to the other three sites, the benthic density did not clearly correspond with the shredder biomass colonising the leaf bags. While the shredder densities in the benthic samples were higher at the downstream site in Drava 2 and Drava 4, the biomass in the leaf bags was lower and the opposite was observed at Drava 3. An indication of the effect of *D. villosus* presence on leaf litter decay is the lack of correlation between the intensity of the decay (calculated as kc:kf) and total shredder biomass at the downstream sites with *D. villosus* (Spearman correlation, $r_s=-0.09$, $p=0.919$, $n=6$), while a clear correlation was observed at the upstream sites without *D. villosus* (Spearmann correlation, $r_s=0.946$, $p=0.017$, $n=6$) (Figure 6).

The community composition in the leaf bags was similar to that observed in the benthic samples. *D. villosus* was found in the leaf bags at two upstream sites (Drava 1 and Drava 2) but with just one specimen per site. Relative abundance of shredders was 53.3% (10,027) of the 18,805 macroinvertebrates found in coarse leaf bags at all 12 sites (six locations). Amphipods dominated the shredder community also in the leaf bags (8545 individuals), and

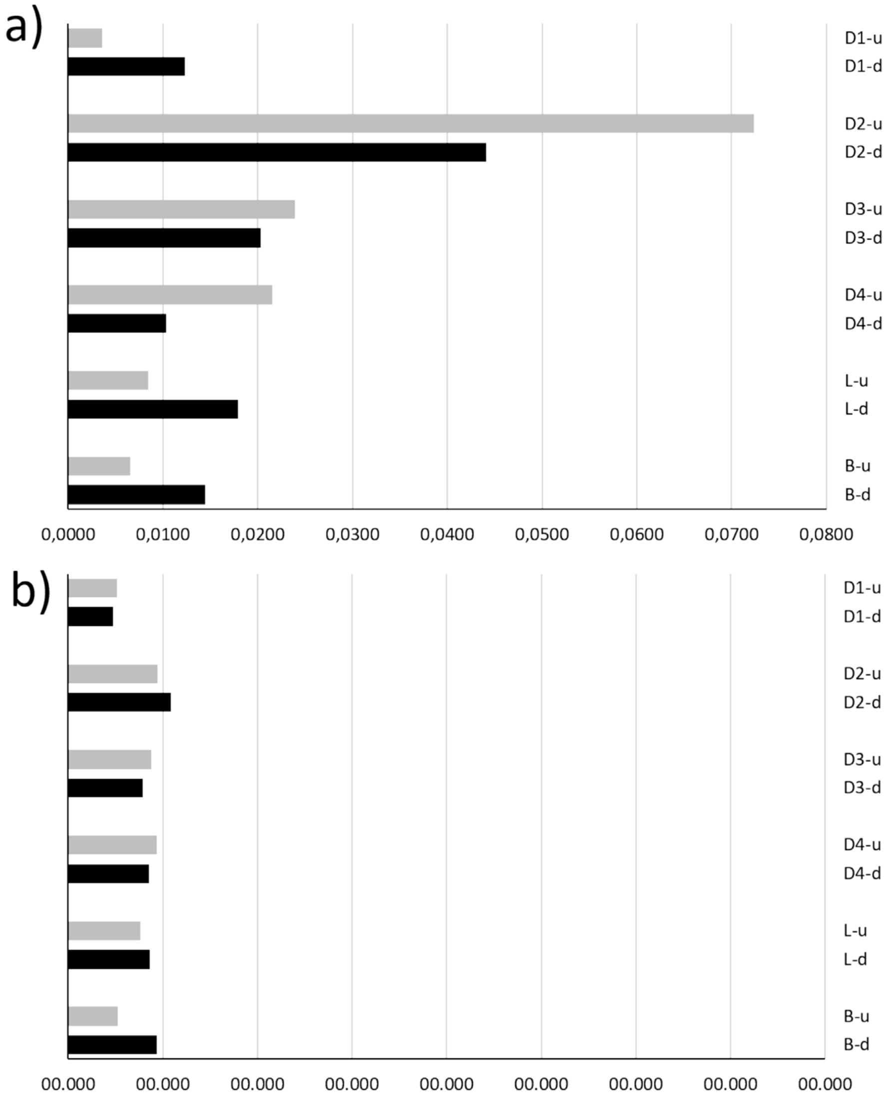

FIGURE 5 | Leaf litter breakdown rates (k) calculated from the linear regression of log transformed leaf mass versus time for coarse leaf bags (a) and fine leaf bags (b). Grey colour is for upstream sites and black for downstream sites.

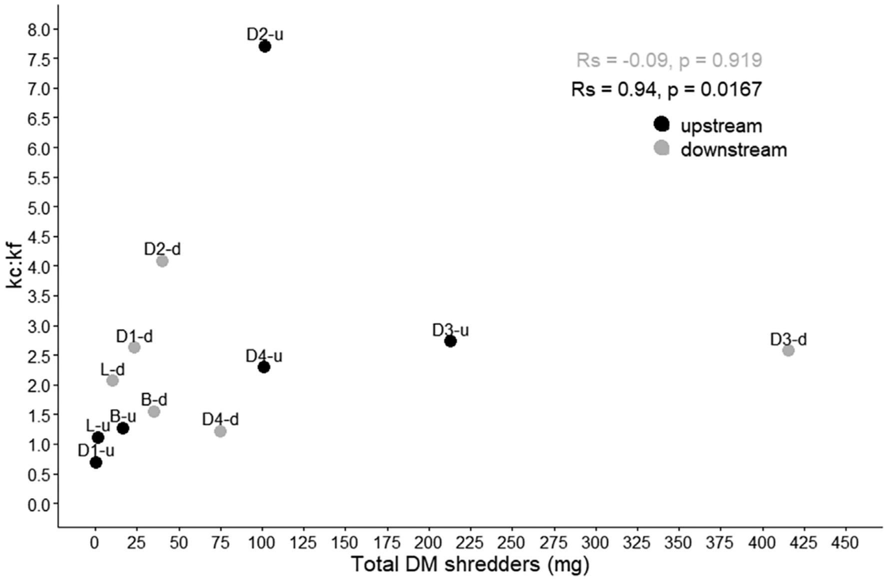

FIGURE 6 | Scatter plot showing the Spearman correlations between the intensity of decay (calculated as kc:Kf) and total shredder biomass at the downstream site. Upstream sites are shown in grey, and downstream sites are shown in black.

TABLE 2 | Physicochemical variables at each location for five measured variables (temperature, dissolved O_2, O_2 saturation, conductivity and pH). For each parameter, average values were shown for each location, min: minimum values, max: maximum values and the number of measurements.

		Drava 1	**Drava 2**	**Drava 3**	**Drava 4**	**Lahn**	**Blies**
Temperature, °C	Average	14.4	15.2	14.7	13.8	20.8	21.6
	Min	13.3	14.8	14.2	10.8	20.1	20.3
	Max	14.9	15.7	15.1	15.6	21.6	23.8
Dissolved O_2, mg L^{-1}	Average	9.9	6.1	5.2	8.8	7.3	7.8
	Min	9.6	4.8	4.5	7.9	6.8	6.32
	Max	10.3	6.8	5.6	9.7	8.0	9.1
O_2 Saturation, %	Average	98.4	61.9	52.4	85.7	82.6	91.7
	Min	93.0	48.3	44.2	76.1	78.5	71.7
	Max	100.7	70.5	55.9	94.2	88.5	109.8
Conductivity, μS cm^{-1}	Average	285	308	324	639	488	876
	Min	272	305	322	522	444	687
	Max	299	311	326	704	535	1274
pH	Average	8.2	7.9	7.5	7.6	7.8	8.0
	Min	8.1	7.8	6.1	6.1	7.7	7.7
	Max	8.2	8.0	8.0	8.2	8.0	8.3
	Number of measurements	4	4	4	4	3	3

G. fossarum (3132) and *D. villosus* (2814) had the highest abundance. At the downstream sites in Germany (Blies and Lahn), *D. villosus* was the only amphipod shredder, while in Croatia, native species co-occurred with *D. villosus* at the downstream sites. In Croatia, the average sizes of measured *D. villosus* individuals in coarse leaf bags were 8.2 mm (D2-d), 9.4 mm (D3-d), and 6.7 mm (D4-d), with a maximum length of 19.4 mm. At sites in Germany, the average lengths of *D. villosus* were 4.4 mm (L-d) and 4.5 mm (B-d), which are comparable to those of *G. pulex* (4.5 mm at L-u and 4.0 mm at B-u). The native species in Croatia, *G. fossarum*, had a maximum average length of 6.0 mm at site D3-u, and *G. roeselii* reached a maximum average length of 8.6 mm at site D4-u, both of which were smaller than *D. villosus*. The average lengths, along with minimum and maximum values for all Peracarida species at each site, are provided in Table S2. The shredder community composition in the coarse leaf bags based on biomass differed significantly between upstream and downstream sites (PERMANOVA, pseudo-F = 7.28, $p < 0.01$), as well as between the six locations (PERMANOVA, pseudo-F = 2.10, $p < 0.05$).

Besides systematic differences in the composition of shredder community, the different effects of *D. villosus* might have been caused by different environmental factors. In fact, the six locations of the leaf litter experiment significantly differed based on four basic physicochemical factors (PERMANOVA, pseudo-F = 22.861, $p = 0.001$; Table 2). However, we did not observe a grouping of the sites which might explain the higher leaf litter decay rates at the downstream sites on the locations Drava 1, Blies and Lahn. Although the two sites in Germany (Blies, Lahn) differed from the other sites by having higher temperature and conductivity, Drava 1 was very similar to Drava 4, as shown by a principal component analysis (PCA; Figure 7). The Drava 2 and Drava 3 locations were very similar to each other but separated from the other locations due to lower oxygen concentrations, caused by underground water received from the Dubrava reservoir.

4 | Discussion

The decay of the allochthonous riparian leaf litter in freshwater ecosystems is a crucial ecological process, providing nutrients and energy to aquatic food webs. The displacement of native species through the arrival and establishment of populations of invasive species can result in significant changes in benthic community structure (Dick and Platvoet 2000; Boets et al. 2010; Piscart et al. 2010; Rewicz et al. 2014). If the invasive species have lower leaf processing rates as observed in laboratory studies (e.g., *D. villosus*, Boeker and Geist 2015; Kenna et al. 2017) this species turn-over would lead to a reduction of leaf litter processing. A reduction of this central ecological function can be expected to reduce the energy flow towards higher trophic levels and negatively impact food web structure and secondary production in detritus-based stream ecosystems. To elucidate the potential impact of invasive species on the ecosystem function leaf litter processing, we analysed whether *D. villosus* as one of the most successful invertebrate invaders in European streams and rivers and an omnivore with very flexible feeding behaviour (Hellmann et al. 2015, 2017; Koester et al. 2018) generally reduces leaf litter decay by displacing native shredders.

Our field experiments suggested that the presence of *D. villosus* did change but not generally reduce the breakdown of leaf litter under natural conditions in situ. Similar observations have been reported for decapods, another important group of shredders in stream, where *Pacifastacus leniusculus* changed benthic community composition but increased detritus processing (Moore et al. 2012; Carvalho et al. 2016, 2022). This indicates that although the invasion of omnivore crustaceans might change community composition (Orlova et al. 2006; Hänfling et al. 2011; Klose and Cooper 2013; this study) and the invader seem not the have the exact same feeding behaviour as native amphipods, they affect but not necessarily disrupt detritus processing under realistic conditions. In fact, we observed in 3 out of 6 cases that the leaf litter decay was higher at the downstream sites (200%–340%) with *D. villosus* compared to the sites upstream of the invasion front. We conclude from this observation that stream ecosystems might possess a certain functional stability, specifically maintaining a similar level of leaf litter decay, even after a drastic change in species composition. However, functional stability cannot be assessed by simply analysing one ecosystem function at one point in time. In fact a long-term study indicates that several biological invasions in combination with climate change reduced functional richness and possibly ecosystem stability in the River Elbe (Worischka et al. 2023).

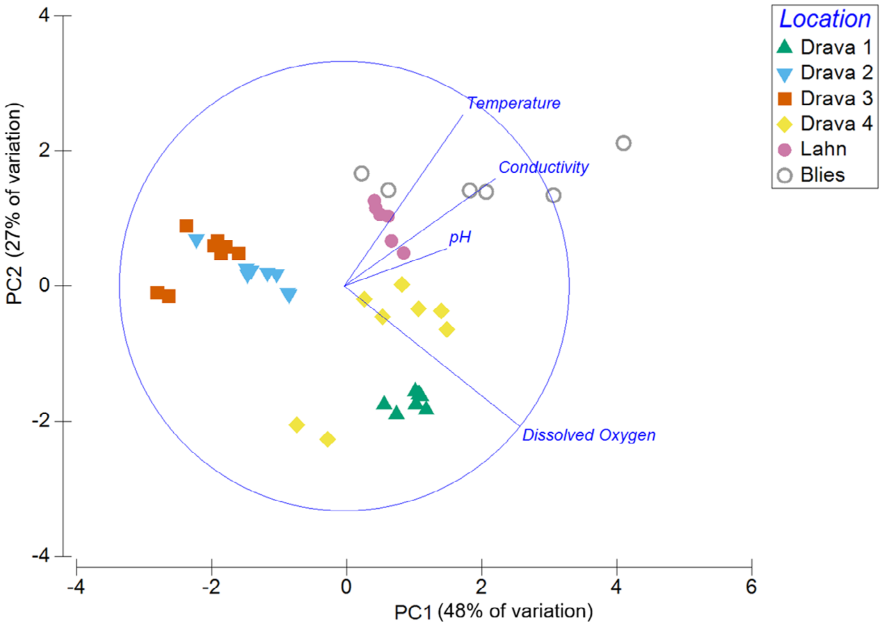

FIGURE 7 | Principal component analysis (PCA) of all 12 sites at the six locations with four basic physicochemical variables (temperature—°C, conductivity—μS cm^{-1}, pH and dissolved Oxygen—mg L^{-1}). The first two axes explain 75% of total variation (PC1—48% of variation and PC2—27% of variation).

The second main conclusion is that the effects of *D. villosus* on the breakdown of leaf litter in European rivers are highly context dependent. Although such a context dependency can arise from confounding factors or even statistical artefacts (Catford et al. 2022), we suppose that it can be traced to a real interaction of the *D. villosus* with native shredders and different effects of temperature on the various species. If the experimental results gained in this study reflect a general mechanism, the displacement of the native amphipods *G. roeselii* and *G. fossarum* by *D. villosus* would decrease leaf litter breakdown in European rivers. An invasion into communities where native amphipods had low densities or are dominated by *G. pulex*, on the other hand, might increase the breakdown rate of leaf litter.

At locations with a low biomass of native shredders in the leaf bags upstream of the invasion front, the breakdown of leaf litter was faster at downstream sites where the invasive species *D. villosus* was the dominant shredder (200%–340%). Only at the locations with high density of native shredders in the leaf bags upstream of the invasion front, breakdown of leaf litter was slower at the downstream sites with *D. villosus* (50%–80%), indicating negative effects of *D. villosus* invasion on leaf litter breakdown. However, lower biomasses of natives in the leaf bags are not always caused by a low number of native amphipods in the benthos, as can be seen in Blies and Lahn, where high densities of *G. pulex* were observed in the benthic samples but not in the leaf bags. Thus, we conclude that the inconsistency of our results seems to be caused by the context dependency of the very flexible feeding behaviour of *D. villosus* as well as the native amphipods. *G. pulex* is known to be capable of predation and can swich its trophic position from mostly shredder to nearly pure predator (Hellmann et al. 2013). Similarly, the resource use of *D. villosus* is highly flexible (Hellmann et al. 2015, 2017; Koester et al. 2016) and includes the potential for high leaf litter decay rates (Gergs and Rothhaupt 2008; Richter et al. 2018; Worischka et al. 2018). *D. villosus*'s feeding behaviour seems to depend on environmental factors such as the complexity of the environment (Richter et al. 2018) or temperature (Kenna et al. 2017; Fincham et al. 2023; Pile et al. 2023). In addition, two out of three experiments resulting in a higher leaf litter decay rate downstream of the invasion front were performed in August when water temperatures averaged between 20°C and 21°C. Previous experiments have shown that high temperatures benefit *D. villosus* more than native species regarding leaf litter processing (Fincham et al. 2023; Kenna et al. 2017; Truhlar et al. 2014). Although this might be one reason for the higher leaf litter decomposition rates at the downstream sites, the fact remains that almost no shredders were found in the bags upstream of the invasion front indicating that for some reason *G. pulex* did not use the provided resource. Even if invasive species have a lower per capita rate of shredding than native species, they can process more leaf litter because of their higher densities than native species (Pile et al. 2023). However, we also observed very high *D. villosus* densities in the leaf litter bags of one Drava location (D3), where leaf litter decomposition rates were higher upstream of the invasion front. Consequently, *D. villosus* biomass alone does not seem to explain the higher leaf decay rates at three locations. This view is also supported by the lack of correlation of the decay rate with *D. villosus* biomass in the downstream leaf bags.

Previous studies have observed that the breakdown of leaf litter is slower when *D. villosus* and native species co-occur compared to purely native communities. This is often attributed to native species being more cautious, hiding more, and feeding less due to the risk of predation by *D. villosus* (Truhlar et al. 2014; Little and Altermatt 2018). We suppose that this mechanism might have contributed to the differences of leaf litter decay rate at the three locations with lower rates downstream of the invasion front even when the mean peracarid biomass was higher downstream than upstream. However, our experiments do not allow an analysis of the mechanism of the observed reduction in leaf litter decay rate in mixed communities because we could not separate leaf litter breakdown between *D. villosus* and native species.

When comparing leaf litter breakdown rates between the upstream and downstream sites on Drava 3, we found no significant differences when all three sampling points were considered. However, with only the first two points in time, the leaf litter breakdown rate was significantly faster at the upstream site where only native species were present. The most likely reason for the similar breakdown rates of leaf litter at the end of the experiment is that the leaf bags we sampled at the upstream site at the end of the experiment were dominated by the amphipod *S. ambulans* and the isopod *A. aquaticus*. These two species are considered to have lower leaf decay rates than to the native amphipods *G. fossarum* and *G. roeselii* (Nesemann et al. 2002), so the breakdown rate of leaf litter in these leaf bags was lower. Replacing those less effective shredders, such as the two previously mentioned species, *D. villosus* could replace their functional role in decomposing organic matter. In order to obtain a definitive answer to the question of whether *D. villosus* can take over the functional role of the native shredder species, further similar experiments on the decomposition of leaf litter in situ, at a larger number of sites with different conditions (physicochemical variables, predation, pollution) have to be made. Also, further field studies of the larger scale variability of the functional role of *D. villosus* are needed, since this invasive species feeding behaviour is very opportunistic and depends on the environmental circumstances.

Leaf breakdown rates in fine leaf bags, in which only microbial decomposition occurred, were faster at the sites in Germany than in Croatia. However, the highest decomposition rate in fine bags was observed at the Drava 2 site. These results were unexpected because the experiment in Germany took place in August, when the water temperature was considerably higher (the average temperatures were between 20°C and 21°C) than in Croatia, where the experiment took place in October, when the water temperature was between 14°C and 15°C. The results of several mesocosm experiments (Chauvet and Suberkropp 1998; Dang et al. 2009) and field experiments (Boyero et al. 2016) have shown that temperature is a critical factor for microbial decomposition of leaf litter, and that sites with higher temperatures have higher microbial decomposition. Our results are similar to those of Bruder et al. (2014), where microbial decomposition was also similar at different temperatures. Although temperature may play a leading role in microbial decomposition, it is possible that other environmental conditions such as nutrient content (Enríquez et al. 1993), dissolved nutrients (Suberkropp 1995) and water current velocity (Bastias et al. 2020) also have an influence.

As expected, the leaf litter breakdown rates were higher in the coarse leaf bags than in fine bags supporting the general view that invertebrate shredders play a key role in leaf breakdown (Jonsson and Sponseller 2021). The difference between breakdown rates in fine and coarse leaf bags was small in the case of low invertebrate shredder biomasses (e.g., site D1-u) but larger at sites where shredder abundance and biomass were high (D2, D3, D4, B). Our results of lower leaf litter breakdown rates in fine leaf bags than in coarse leaf bags as well as the correlation of break down rates with shredder biomass are consistent with previous studies stating that leaf breakdown rates can be up to 15 times higher at sites where macroinvertebrate shredders are abundant, but also that the differences are much smaller or absent at sites where this is not the case (Steward 1992; Bohman and Tranvik 2001; Ferreira et al. 2015). The approach using fine and coarse leaf bags is often criticised because of the possible physical loss of leaf litter from coarse bags, but it was shown that the physical loss of leaves in coarse leaf bags is not significant and that leaf breakdown is faster in coarse leaf bags, which is consistent with the idea that shredders have a large effect on leaf litter breakdown (Bruder et al. 2014).

Author Contributions

Conceptualisation: C.W., S.W., K.Ž., D.V. Developing methods: C.W., S.W., K.Ž. Data analysis: T.K., C.W., K.Ž. Data interpretation: T.K., K.Ž. Conducting the research: T.K., S.B. Preparation figures and tables: T.K. Writing: T.K., S.B., C.W., S.W., K.Ž., D.V.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All data that are not presented in the manuscript could be available upon request.

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Supporting Information

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