

The Best of Both Worlds? Hybridization Potentiates Exotic Bohemian Knotweed's (*Reynoutria* × *bohemica*) Impacts on Native Plant and Faunal Communities †

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Abstract: The Asian knotweed species complex gathers some of the world's most successful plant invaders including the Japanese knotweed (*Reynoutria japonica*), the giant knotweed (*R. sachalinensis*) and the hybrid of these two species, the Bohemian knotweed (*R. × bohemica*). Hybrid species often present higher competitive abilities compared to their parent species. While several studies have focused on the effects of knotweed invasion on plant communities, few have simultaneously considered (i) effects of the three taxa on native plant communities and (ii) effects on litter and soil faunal components. In this study, we compared the differential effects of three Asian knotweeds on vegetation and soil macroinvertebrates communities across seven sites on a regional scale in North Western France. All three knotweed species displayed similar negative effects on local plant species richness, while promoting the taxonomic richness of litter-dwelling macroinvertebrates. Below-ground macroinvertebrate taxonomic richness appeared strongly reduced by the presence of the hybrid *R. × bohemica*, significantly more so than those of sites colonized by *R. japonica* or *R. sachalinensis*. These changes of belowground communities were correlated to associated changes of composition and richness within plant communities. This study provides new insight into the consequences of ecosystem invasion by these species, especially revealing the even further strength of impacts of the hybrid Bohemian knotweed on local vegetation and belowground macroinvertebrates than those of other Asian knotweeds, which points to the need for monitoring the spatial spread of *R. × bohemica* and describing further its effects on ecosystem properties.

Keywords: *Fallopia*; Japanese knotweed; invasive species; litter fauna; soil fauna; macroinvertebrates

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1. Introduction

Today, the Japanese knotweed *Reynoutria japonica* (Houtt.) and the giant knotweed *R. sachalinensis* (F. Schmidt) are considered as invasives in Europe and North America, and are cited among the “world's worst invasive species” [1,2]. Introduced into Europe during the 1840s [3] and into North America during the 1870s [4], they rapidly spread geographically and are now recognized as noxious invaders, strongly modifying and reducing species richness of native plant communities [5–9], communities of litter-dwelling arthropods [7,10–13], and occasionally altering soil physicochemical properties [5,14–16].

Invasive plants are likely to disrupt the complex relationships between above- and belowground components of terrestrial ecosystems [17,18]. Amongst them, soil inverte-

brate communities play a key role in numerous ecological processes such as organic matter decomposition and nutrient-cycling [19], and their stability and diversity are positively connected to their associated plant communities [20,21]. Several examples of negative impacts of invasive plants on belowground fauna have been reported [22,23], but the intensity of these interactions seems to depend on the invasive species and the invaded communities [24,25]. Furthermore, recent meta-analyses also suggest the importance of both habitat structure and trophic level as drivers of invertebrate response to invasive plants [26–28].

Reynoutria japonica owes its invasive achievement to rapid growth [29], efficient regeneration from perennial rhizomes [30,31], large ecological valence [32] and an increased production of allelopathic metabolites in its non-native range [33]. Even though the spread of this invasive species can be limited by exclusively vegetative reproduction, its clonal dispersal has been involuntarily assisted by human activities [15,34]. Less invasive and scarcer than *R. japonica*, its sister species *R. sachalinensis* presents a poorer regeneration rate [35,36] and a lower investment into chemical defences, making it an easier target for herbivores [37]. Nonetheless, once implanted, *R. sachalinensis* forms large stands outgrowing *R. japonica* in height and stem density [8,38].

Resulting from the hybridization of the two aforementioned species, the hybrid Bohemian knotweed *R. × bohemica* (Chrték & Chrtková) was only described in 1983, yet it occurred in Europe since at least 1873 [39]. Morphologically, individuals of this hybrid knotweed present traits intermediate to its parent species [40], hampering identification. In fact, its spread has likely been underestimated in both Europe [41–43] and North-America [44–46]. Ecologically, *R. × bohemica* has proven to be a more successful invader than its parent species, through accelerated growth and regeneration [35,47], increased competitiveness [36,48], and increased production of allelopathic substances [6]. Finally, the ability of *R. × bohemica* to produce viable seeds [49] gives this hybrid an additional asset compared to its parents, to become the “ideal weed” [50], by facilitating the dispersal of offspring. Ellstrand and Schierenbeck [51] argue that invasiveness is an adaptive trait, subjected to evolution; invasiveness is therefore likely to be facilitated by hybridization, through genetic recombination, allowing for increased genetic variation. This is the case for the hybrid *R. × bohemica*, presenting $2n = 44, 66$ or 88 chromosomes, whereas *R. japonica* and *R. sachalinensis* are of diploid numbers $2n = 88$ and 44 respectively in invaded areas [29].

Although the negative impacts of invasive Asian knotweeds on native plant diversity are extensively documented (e.g., see review by Lavoie [52]), their effects on macrofaunal soil organisms are scarcely studied. Significant loss of native plant diversity related to invasion by Asian knotweed can lead to a loss of both species richness and abundance of native herbivorous invertebrates [7,12], and to a loss of native predator invertebrates through cascading effect [10,11]. Furthermore, perennial knotweed stands are responsible for substantial litter accumulation [38,53,54], consequently simplifying the structure of the litter-habitat [14]. This in turn reduces the diversity of plant organic matter resources in trophic chains. These two aspects (microhabitat and trophic resources) may possibly lead to cascading impacts on macrodetritivores as suggested by the plant functional diversity hypothesis linking above- and belowground organisms [55]. Asian knotweeds are therefore prone to indirectly alter higher trophic levels of soil fauna. The reduction of food sources may be further amplified by the knotweeds’ production of allelopathic metabolites (i.e., novel weapons hypothesis; [56]), inhibiting native seed germination [6,57], and eventually reaching belowground faunal communities through trophic cascades [58].

Yet, according to Lavoie [52] and to our awareness, belowground macroinvertebrates are absent from the body of literature on invasive Asian knotweeds effects. This study is an attempt to fill that existing knowledge gap. Given the complexity of the relationships between vegetation and soil fauna, we hypothesized that knotweed invasions alter the invaded plant communities, as well as the litter and soil-fauna communities depending

on the resources provided by the vegetation. We would also expect the hybrid *R. × bohemica* to display the strongest impact on the invaded plant and animal communities, since it has been proven to be the most competitive of the three Asian knotweed species. These hypotheses were tested on a regional scale on seven Asian knotweed-invaded sites in north western France, with the purpose of characterizing invaded and non-invaded (control) plant, litter- and soil-fauna communities.

2. Material & Methods

2.1. Study Sites and Sampling

Sampling and data collection were conducted on seven grassland sites in north western France (Normandy, temperate climate; see Table 1). The sites were selected for the occurrence of perennial (at least 7 years of age), non-managed knotweed stands leaving a close uninvaded area in the same landscape unit which we used as control. All selected knotweed stands presented a cover of at least 90%. On each site, occurring knotweed species were identified morphologically, following Bailey et al. [59] and Barney et al. [29].

Within each of the seven sites, five invaded and five uninvaded sampling plots were defined, with a spacing of at least five meters between the plots. For each plot, vegetation was surveyed in July 2018 and macrofauna between October and November 2018. Vegetation surveys were conducted using an one-square-meter quadrat, expressing the abundance of each species following the Braun-Blanquet scale [60]. In three invaded and three uninvaded plots, the invertebrate macrofauna (>0.5 mm) was hand-sorted during a fifteen-minute observation period inside a 25 cm × 25 cm quadrat in the organic layer (litter OL, OF and OH) as well as in the superficial twenty centimetres of soil. Animals were then sorted out from each layer, either above- or belowground, under a stereomicroscope and identified at the taxonomical rank of order.

To assess soil physicochemical properties on each plot, three soil cores were sampled at two soil depths (0–10 cm and 10–20 cm) and pH in water, total carbon content and total nitrogen content were measured for each soil sample. Lastly, we measured the depth of the litter layer on each plot (**Error! Reference source not found.**).

Table 1. Summary of the physico-chemical properties of the seven sampling sites. All values are accompanied by the associated standard deviation.

Invasive_Species	Site	Spatial Coordinates	Soil Type	pH	Organic_C Content (%)	Total_N Content (%)	Native Litter Amount (cm)	Invaded Litter Amount (cm)
<i>Reynoutria × bohemica</i>	Belbeuf	49.3908692N, 1.12413817E	Loam	7.90 ± 0.13	4.26 ± 1.95	0.278 ± 0.125	0.4 ± 0.4	9.8 ± 2.1
<i>R. × bohemica</i>	Gouville	48.8417835N, 1.00837984E	Silt loam	6.03 ± 0.33	2.64 ± 0.63	0.254 ± 0.058	2.9 ± 1.2	5.6 ± 1.5
<i>R. × bohemica</i>	Oissel	49.3564571N, 1.12406613E	Sandy loam	6.27 ± 0.59	1.42 ± 0.37	0.124 ± 0.030	0	14.9 ± 3.5
<i>R. japonica</i>	Sylvains-les-Moulins	48.8839602N, 1.08344571E	Silt loam	6.76 ± 0.17	5.46 ± 0.70	0.551 ± 0.070	5.6 ± 2.2	3.4 ± 0.8
<i>R. japonica</i>	Vimoutiers	48.9396947N, 0.18810666E	Sandy loam	7.46 ± 0.57	2.71 ± 0.48	0.260 ± 0.039	1.4 ± 0.9	3.1 ± 1.0
<i>R. sachalinensis</i>	Harfleur	49.514873N, 0.191627E	Loam	7.82 ± 0.14	3.52 ± 1.52	0.264 ± 0.066	4.6 ± 2.2	7.7 ± 2.7
<i>R. sachalinensis</i>	Quillebeuf	49.473142N, 0.524756E	Silt loam	8.00 ± 0.06	3.56 ± 1.00	0.324 ± 0.082	0.8 ± 0.8	0.7 ± 0.5

2.2. Data Analysis

Plant specific richness and above- and belowground macrofaunal taxonomic richness were assessed for the communities of invaded and uninvaded areas of each site (total and mean values across the sampled plots within each site). For each site and community,

richness differences between invaded and uninvaded areas were quantified with a relative richness ratio (thereafter abbreviated to RRR) following:

$$Relative\ Richness\ Ratio = \frac{Richness_{Invaded} - Richness_{Uninvaded}}{Richness_{Uninvaded}} \tag{1}$$

To compare communities between sites, matrices of pairwise Bray-Curtis dissimilarities [61] were computed for vegetation, aboveground and belowground macrofauna. Since raw abundance data (Table 2) of the macroinvertebrate inventories was very heterogeneous across our study sites (with often very few individuals per plot) we will focus on the results produced by the relative richness ratio and the dissimilarity between invaded and uninvaded areas.

Since normality of distribution wasn't verified for all computed RRR and dissimilarity values (Shapiro-Wilk test, $\alpha = 0.05$), the Kruskal-Wallis test ($\alpha = 0.05$) with Fisher's least significant post-hoc test were used to test for richness differences and community dissimilarities induced by the three knotweed species. Correlation between the dissimilarities of vegetation and macrofauna was tested using Pearson's correlation test ($\alpha = 0.05$). All statistical analyses and graphical output were achieved using R-4.0.2 [62], RStudio 1.2.5033 [63], and the libraries ade4 [64], agricolae [65], tidyverse [66] and vegan [67].

Table 2. Sampling results of the seven study sites. Richness values are presented as species richness for vegetation, and taxonomic richness at the rank of order for macroinvertebrates; they correspond to the total richness encountered across all plots of a site. The abundances of the macroinvertebrates are presented as mean values of the plots plus the computed standard deviation. Abbreviations: Rb = *Reynoutria × bohémica*; Rj = *Reynoutria japonica*; Rs = *Reynoutria sachalinensis*.

Site		Vegetation	Aboveground Macroinvertebrates		Belowground Macroinvertebrates	
		Richness	Richness	Abundance	Richness	Abundance
Belbeuf	Uninvaded	23	6	2.00 ± 1.00	6	2.33 ± 0.58
	Invaded (Rb)	8	7	26.00 ± 14.10	2	2.00 ± 1.73
Gouville	Uninvaded	12	3	0.67 ± 1.15	11	8.00 ± 2.00
	Invaded (Rb)	7	12	15.70 ± 14.60	11	12.00 ± 9.54
Oissel	Uninvaded	31	7	2.67 ± 1.15	9	14.00 ± 1.00
	Invaded (Rb)	1	9	13.30 ± 6.81	4	4.33 ± 2.89
Sylvains-lès-Moulins	Uninvaded	11	4	0.67 ± 1.15	7	3.33 ± 1.53
	Invaded (Rj)	7	9	2.67 ± 2.89	4	6.00 ± 6.08
Vimoutiers	Uninvaded	24	3	0.33 ± 0.58	6	1.67 ± 1.53
	Invaded (Rj)	19	6	0.33 ± 0.58	4	2.00 ± 0.00
Harfleur	Uninvaded	24	10	37.3 ± 49.9	11	24.30 ± 12.70
	Invaded (Rs)	5	6	8.67 ± 3.06	6	6.33 ± 2.31
Quillebeuf	Uninvaded	15	8	2.00 ± 1.73	9	5.67 ± 3.79
	Invaded (Rs)	11	5	0.00 ± 0.00	7	4.67 ± 1.53

3. Results

3.1. Impact of Knotweed Invasion on Taxonomic Richness of Native Communities

Across the seven study sites, the species richness of native, uninvaded vegetation varied from 11 to 31 species per site while native plant communities in invaded areas always displayed a reduced richness, ranging from 1 to 19 plant species, knotweed included. The RRR revealed an overall relative loss of $40.3 \pm 31.4\%$ of native species in knotweed-invaded areas (Figure 1). All three *Reynoutria* species caused significant relative loss of native species (M.-W. test; $n = 5, p < 0.05$), and notably this negative impact was significantly stronger (K.-W. test; $n = 5, p = 0.0005$) in areas invaded by *R. × bohémica* ($-64.5 \pm 28.8\%$) than in areas invaded by *R. japonica* ($-23.7 \pm 23.6\%$) or *R. sachalinensis* ($-20.5 \pm 13.3\%$).

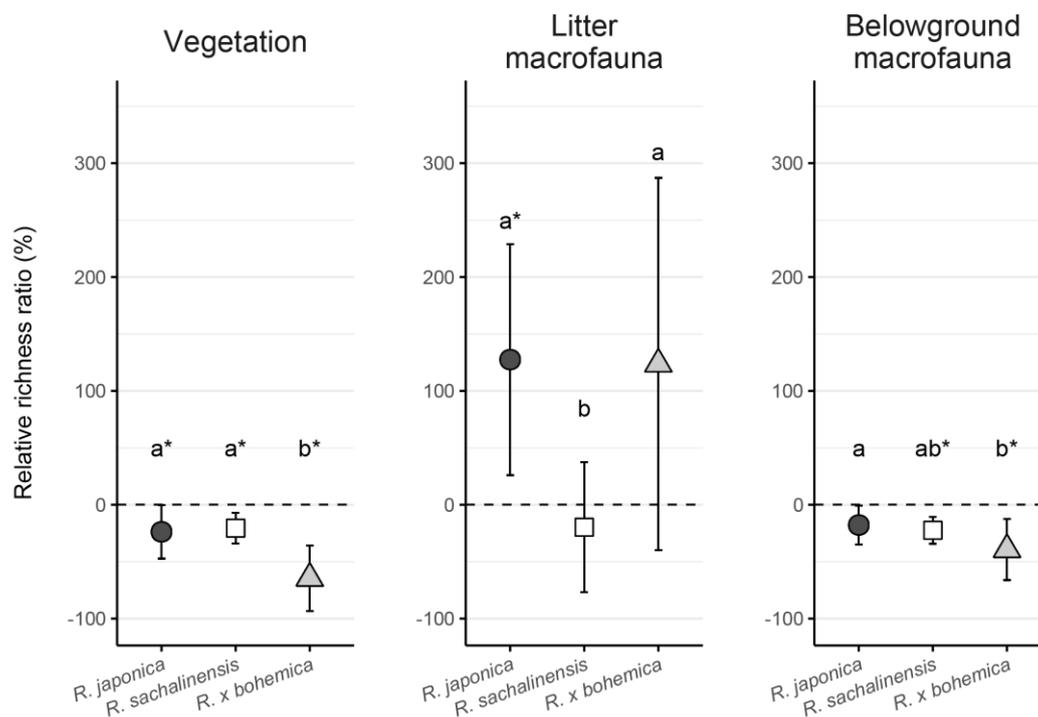


Figure 1. Relative taxonomic richness ratio (%) according to invader species. RRR that differ statistically from zero (M.-W. test, $\alpha = 0.05$) are marked with an asterisk. Within each of the three compartments, differences between the knotweed species are labelled with the group-letters from a Kruskal-Wallis test ($\alpha = 0.05$).

Native taxonomic richness of litter-dwelling macroinvertebrates varied from 3 to 10 taxa per uninvaded site. Knotweed invasion resulted in an overall gain of taxa of litter-dwelling macroinvertebrates, albeit a heterogeneous one. Invaded sites presented a total of 5 to 12 taxa of litter-dwelling macroinvertebrates per site, resulting in a mean increase of $83.8 \pm 136.0\%$ of taxonomic richness (corresponding to a mean increase of 1.1 taxa, with a minimum of -1 and a maximum of +4.3 taxa) compared to uninvaded areas, yet this richness increase was statistically different from zero only on sites invaded by *R. japonica* (M.-W. test; $n = 6, p = 0.036$). While sites invaded by *R. japonica* and *R. x bohemica* displayed an overall increase of litter-dwelling macroinvertebrate richness ($128.0 \pm 101.0\%$ and $124.0 \pm 164.0\%$, respectively), *R. sachalinensis*-invaded sites presented a decrease thereof ($-19.7 \pm 57.0\%$), thus statistically differentiating the effect of the latter species from the two former ones' (K.-W. test; $n = 6, p = 0.025$).

Contrastingly, for belowground macroinvertebrates in uninvaded areas taxonomic richness varied between 6 and 11 taxa per site, with a similar trend across *Reynoutria* species to the one observed for native plant richness (Figure 1). Indeed, sites invaded by any of the three invasive *Reynoutria* species displayed an average loss of belowground macroinvertebrate richness of $-28.3 \pm 22.2\%$ (corresponding to a mean value of -1 taxon, with a minimum of -3.8 and a maximum of +3.7 taxa). Both invasions by *R. x bohemica* and *R. sachalinensis* led to a significant relative loss of species (M.-W. test; $n = 9, p = 0.013$ and $n = 6, p = 0.036$, respectively). Furthermore, the negative impact of *R. x bohemica* ($-39.3 \pm 26.9\%$) was stronger (albeit not significantly: K.-W. test; $n = 6, p = 0.08$) than the loss associated with *R. japonica* ($-17.8 \pm 17.1\%$), and the presence of *R. sachalinensis* induced an intermediate reduction of richness ($-22.4 \pm 11.8\%$).

3.2. Impact of Knotweed Invasion on Composition of Native Communities

Bray-Curtis dissimilarity indices between uninvaded and knotweed-invaded areas showed that native plant communities were heavily impacted by knotweed invasion, with an average dissimilarity index of 0.88 ± 0.09 (Figure 2). The strongest impact on native

community composition was revealed in communities invaded by *R. × bohemica* (0.92 ± 0.08), where it was significantly higher (K.-W. test; $n = 8$, $p = 0.025$) than in presence of *R. japonica* (0.82 ± 0.07). *Reynoutria sachalinensis*-invaded communities displayed an intermediate impact (0.89 ± 0.10), not significantly different from the other two *Reynoutria* species.

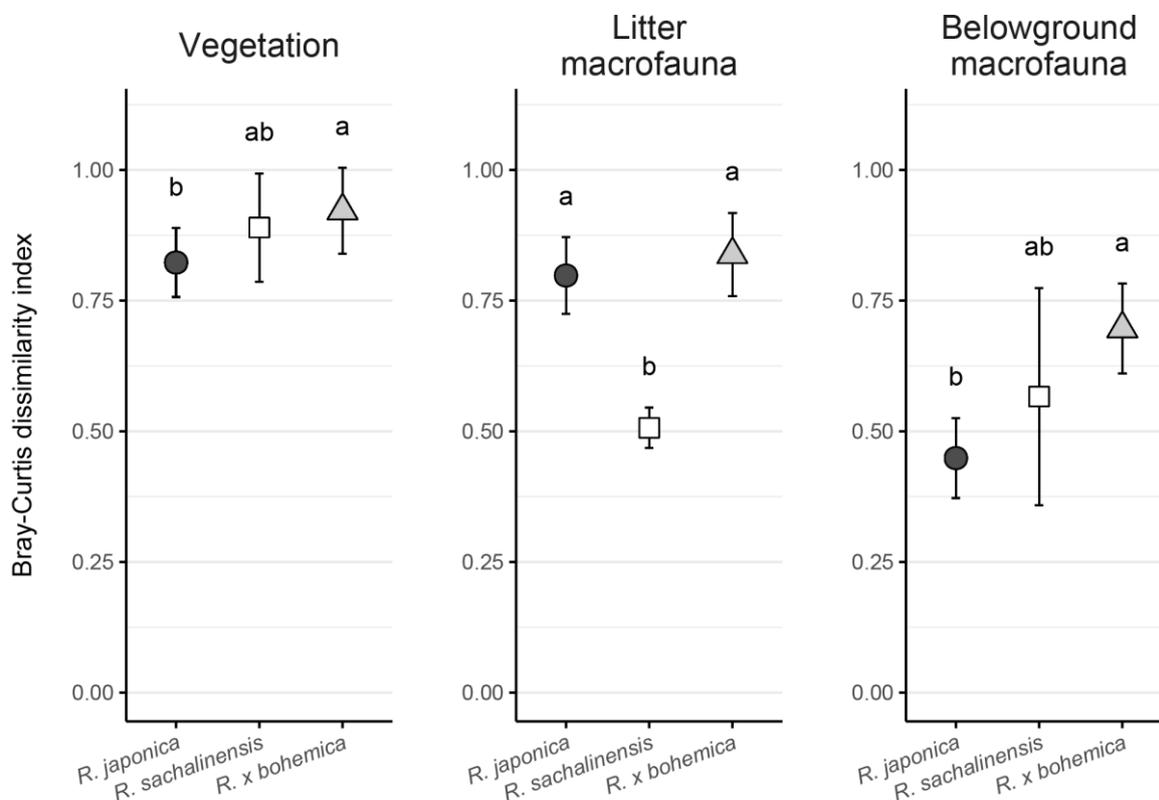


Figure 2. Bray-Curtis dissimilarity index of invaded communities compared to the native communities. Within each of the three compartments, differences between the *Reynoutria* species are labelled with the group-letters from a Kruskal-Wallis test ($\alpha = 0.05$).

Taxonomic composition of litter-dwelling macroinvertebrate communities was also strongly modified by knotweed invasion, with an average dissimilarity of 0.78 ± 0.17 between invaded and uninvaded communities. Impacts caused by *R. japonica* (0.86 ± 0.10) and *R. × bohemica* (0.84 ± 0.08) were significantly higher (K.-W. test; $n = 4$, $p = 0.01$) than those due to *R. sachalinensis* (0.5 ± 0.04) (Figure 2).

For belowground macroinvertebrate communities, taxonomic composition displayed an overall dissimilarity of 0.60 ± 0.16 between invaded and uninvaded areas. Invasion by *R. × bohemica* caused a dissimilarity between invaded and uninvaded areas of 0.69 ± 0.09 , which was significantly higher (K.-W. test; $n = 5$, $p = 0.02$) than the dissimilarity caused by *R. japonica* (0.45 ± 0.08) (Figure 2). The level of dissimilarities caused by the invasion of *R. sachalinensis* is intermediate compared to those of the two other species (0.57 ± 0.21) and does not differ significantly from either of them.

Finally, a strong correlation was found between the Bray-Curtis dissimilarity values of each knotweed species for plant communities and for belowground macroinvertebrate communities (Pearson test; $r = 0.86$, $p = 0.01$). However, the dissimilarity values for litter-macroinvertebrates communities were not correlated to dissimilarity values from either of the two other compartments.

4. Discussion

4.1. Effects of Asian Knotweed Invasion on Native Plant Communities

To describe the impact of invasion by the Asian knotweeds on native communities of plants, above- and belowground macroinvertebrates, we compared these communities of areas invaded by the three species *R. japonica*, *R. sachalinensis* and *R. × bohemica* to communities of uninvaded areas in close vicinity. We observed a reduction of up to 93.3% of plant species richness in invaded herbaceous communities, which is in agreement with a previous, consistent body of literature [52,68]. This loss of plant species richness was accompanied by a strong alteration of community composition, capable of reaching a complete dissimilarity between native and invaded assemblages in some instances.

Among the knotweed species studied here, the impacts of *R. japonica* on native vegetation appear to be significantly exceeded by those of *R. × bohemica*, while also being slightly below those of *R. sachalinensis*. This could be connected to *R. japonica*'s lower regeneration from rhizomes [35] and lower competitive ability [69]. A lower inhibitory effect of *R. japonica* on the germination of native seeds through allelopathy has also been described [6,70]. Also, invasion by hybrid *R. × bohemica* leads to the strongest loss of plant richness amongst the three knotweed species, while impacts on the richness of invaded communities were weaker and similar for *R. japonica* and *R. sachalinensis*. The hybrid knotweed's increased impacts on native plant communities have also been documented in former studies: Chmura et al. [8] showed that *R. × bohemica* had the strongest negative effect on the productivity of native vegetation, and Parepa et al. [36] observed a higher biomass production of the hybrid species compared to its parent species, making the former even more competitive. Indeed, *R. × bohemica* has been reported to display the highest regeneration rate from rhizomes [47,59] as well as a strong phytotoxic effect on native plants, prone to inhibit germination of native species and therefore reducing the local species pool [6]. Also, through higher productivity, *R. × bohemica* stands can cause the accumulation of more litter than the other knotweed species, reducing the amount of sunlight reaching the soil [71] and thus limit the germination and establishment of native species [72]. The litter of all three knotweed species is generally of lower quality than the litter of the displaced plant species, thus potentially altering the nutrient cycling of the invaded ecosystems [38,73,74]. Moreover, recent evidence points to inconsistent phytotoxic abilities of knotweed litter over time, leading to competition or facilitation interactions which may alter invaded ecosystems even more [75].

Our results contrast with the findings of Hejda et al. [76], who reported lower effects of *R. × bohemica* on species richness and dissimilarity between native and invaded plots compared to *R. japonica* and *R. sachalinensis*. This discrepancy might be explained by homogeneous vegetation cover of the invasives in the plots of our study (ranging from 90% to 100% for the three species) while covers in Hejda et al. [76] varied with the identity of the invasive knotweed species (from 40% to 100% for *R. × bohemica* plots, and from 70% to 100% for *R. japonica* and *R. sachalinensis*), suggesting that some of these *R. × bohemica* patches were either managed, or in an earlier colonization process, possibly blurring the signal of the hybrid's impact compared to the other two species. The regionality of our study, allowing for similar conditions across all sites, may also contribute to its discrepancy with Hejda et al.'s [76] results, which involve a variety of invaded meadows (from lowland alluvial to sub-alpine) sampled all across the Czech Republic. Further research is required to conclude on the relative effects of these three knotweed species on the plant compartment.

4.2. Effects of Asian Knotweeds on Aboveground Macroinvertebrate Communities

Plant communities and soil fauna are closely connected and take part in ecosystem stability through numerous trophic interactions and nutrient cycling [21,77], for instance a higher diversity of plant species can lead to a higher diversity of trophic resources [78,79], higher productivity of plant communities [80] and higher stability of belowground food

webs [21]. The disruptive effects of Asian knotweed on native vegetation are therefore prone to spread through trophic levels, and to impact indirectly the associated soil fauna.

The sampling of litter-dwelling macroinvertebrates led to rather heterogeneous results. The overall impact of knotweed invasion on taxonomic richness varied from -76.7% to $+288\%$, suggesting that knotweed invasion is not the prevalent factor driving litter-dwelling macroinvertebrate taxonomic richness, or that the invasion effect may be strongly counterbalanced by environmental conditions. Strong differential effects related to the identity of the invasive knotweed species appeared. The presence of *R. japonica* promoted taxonomic richness, while heavily modifying community composition. The hybrid *R. × bohemica* had similar effects on community composition, but its overall positive effect on species richness was more variable. On the contrary, invasion by *R. sachalinensis* was responsible for a loss of taxonomic richness and a weaker alteration of the invaded communities.

Our study highlights two contrasting drivers of aboveground macroinvertebrate diversity. On the one hand, it has been shown that knotweed invasions lead to a reduction of trophic resource diversity and quality due to poor knotweed litter quality [14], as well as to a structural simplification of the litter habitat, both contributing to a lower diversity of herbivores [12]. That loss of herbivorous preys can, in turn, lower the diversity of predators [11] through cascading effect, as soil food webs are mostly governed by bottom-up control [81]. On the other hand, detritivores have conversely been shown to benefit from the high productivity of knotweed stands [53,82]. The strong difference between native and invaded macroinvertebrate communities we described here supports this evidence. Invasion by an Asian knotweed created a novel litter habitat that was scarce or absent in native, uninvaded vegetation at all study sites, and this might explain the dramatic increase of macroinvertebrate richness observed under *R. japonica* and *R. × bohemica*. This observation also matches a shift in trophic structure, such as described by Haddad et al. [20], where a reduction of plant species richness through invasion would theoretically be followed by a shift from a predator-dominated invertebrate community to an herbivore-dominated community.

Unexpectedly, the impact of *R. sachalinensis* on taxonomic richness and community composition of native litter-dwelling macroinvertebrate communities was significantly lower (and largely negative) than those of the other two Asian knotweeds. Upon closer examination of the study sites, the native aboveground macroinvertebrate communities under *R. sachalinensis* also appeared to be the richest in taxa; it is therefore likely that the reduction of trophic resources following *R. sachalinensis*' colonisation had acted as a filter, possibly resulting in the exclusion of specialist herbivores associated with native plants which were eliminated during the invasion process. This would support the plant functional diversity hypothesis [83]. Hence, invasion by *R. sachalinensis* appears to have modified the structure of existing, complex litter-dwelling macroinvertebrate communities, whereas the two other species seemed to have recruited new taxa in communities that were originally much poorer taxonomically. Another explanation of *R. sachalinensis*' weaker impact might be its higher susceptibility to generalist herbivores through a higher leaf palatability [37], thus potentially producing more palatable litter than the other two species, resulting in less litter accumulation.

4.3. Effects of Asian Knotweeds on Belowground Macroinvertebrates

The influence of plant community composition on belowground soil fauna has been described before [84–86], and has also been studied with invasive plants [23,28,87,88]. As stated above, the diversity of available food resources is the key factor in the linkage of plant and soil communities [88,89]. However, the effects of invasive plants on soil communities were found to be mostly case-specific [90,91].

Our study revealed that the three Asian knotweed taxa had negative effects on belowground macroinvertebrate richness and community composition, with a significantly higher impact of the hybrid *R. × bohemica* than of *R. japonica*. A comparable reduction of

25% of belowground invertebrate richness under *R. japonica* and *R. × bohemica* was observed by Gerber et al. [11], also reporting a positive correlation between native plant richness and invertebrate taxonomic richness. In our study as well, overall impacts of the three knotweeds on belowground macroinvertebrate community composition were positively correlated with their impacts on native plant community composition, suggesting an indirect effect of knotweed colonisation on belowground macroinvertebrates through the alteration of vegetation, possibly due to the reduction of trophic resource diversity. Interestingly, there was no such relation between above-ground and belowground macroinvertebrate communities, implying a disruption of the trophic link between those two compartments of our study sites through knotweed invasion. Such a difference between responses of invaded soil compartments has been described for other invasive plants such as *Arundo donax* L., 1753 and *Impatiens glandulifera* Royle [22,92]. Furthermore, a meta-analysis by Zhang et al. [27] showed that the effects of invasive plants could be separated into litter-based effects and rhizosphere effects, even though both compartments can facilitate plant invasion through positive feedback of nutrient cycling in soil systems. According to their research, invasive plant litter increases the abundance of aboveground decomposers, while the roots of the invasives have a negative impact on belowground herbivores and predators. The latter are also undergoing changes in habitat structure due to the knotweed's rhizomes [59]. Our observations here fit this pattern, and further allelopathic effects on soil biota through root exudates or leaf leachates can be expected.

5. Conclusions

Invasion by the Asian knotweed species complex is a well-studied phenomenon, with documented impacts on vegetation, fauna and nutrient cycling, as well as soil parameters. In this regional study, we have highlighted the potential direct and indirect effects of knotweed invasion throughout seven invaded ecosystems, with observed changes in vegetation as well as above- and belowground macroinvertebrates. We found a dramatic reduction of plant species richness and heavily modified plant communities, which were positively correlated to the changes in belowground macroinvertebrate communities and presented the same order of magnitude. The response of the litter compartment presented very heterogeneous results but were mostly positive in terms of taxonomic richness and unrelated to the alteration of vegetation or belowground macroinvertebrates. Additional research is needed to disentangle and quantify the consequences of knotweed invasion on the litter and belowground compartments (ideally on a greater geographical scale), and to describe the alteration of trophic networks in the invaded ecosystems. Furthermore, we found that the negative impact of the hybrid *R. × bohemica* on native vegetation and belowground macroinvertebrates was generally stronger than those of *R. japonica* and *R. sachalinensis*, confirming the results of numerous previous studies. The hybrid knotweed appears therefore to pose an even larger threat to invaded ecosystems than its two parent species. Knowing that its actual spread is insufficiently documented, it appears necessary to increase efforts to monitor its dispersion (especially with the hybrid's ability to reproduce sexually), and to describe the differences between knotweed taxa in greater detail in order to devise adapted management techniques.

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Abbreviations

The following abbreviations are used in this manuscript:

MDPI	Multidisciplinary Digital Publishing Institute
DOAJ	Directory of open access journals
TLA	Three letter acronym
LD	linear dichroism

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