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Invasive Glossy Buckthorn (*Frangula alnus*) Has Weak Impact on Native Understory Plant and Saprophagous Macroarthropod Communities

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Abstract: Glossy buckthorn (*Frangula alnus* Miller) is an invasive alien plant species (IAPS) rapidly expanding in North America but is largely understudied compared to the common buckthorn (*Rhamnus cathartica*). Our study investigated the effects of a 27-year-old *F. alnus* invasion on native understory plant and saprophagous macroarthropod communities in a wet deciduous woodland in Southern Québec, Canada. We hypothesized a decreased taxonomic diversity and a change in community composition of both indicator taxa with increasing *F. alnus* density. The understory plant and saprophagous macroarthropod communities were characterized, respectively, through vegetation surveys and pitfall trapping across a density gradient of 43 plots invaded by *F. alnus*. Our results demonstrated that *F. alnus* did not exert a strong influence on species community composition, although the homogenization of understory plant communities was observed. Despite several decades of *F. alnus* invasion at our study site, the consequences on the selected indicator taxa were overall relatively small, suggesting that the magnitude of effects is variable. We suggest that further investigation at a larger scale should be performed to evaluate the effect of *F. alnus* on a broad diversity of indicators and understand any context dependency.

Keywords: invasive plant species; Diplopoda; biodiversity; community ecology; millipede; Isopoda; woodlice

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Citation: Roberge, G.; Handa, I.T.; Juette, T.; Kneeshaw, D. Invasive Glossy Buckthorn (*Frangula alnus*) Has Weak Impact on Native Understory Plant and Saprophagous Macroarthropod Communities. *Diversity* **2024**, *16*, 584. https://doi.org/10.3390/d16090584

Academic Editors: Panayiotis G. Dimitrakopoulos and Bruce Osborne

Received: 26 June 2024
Revised: 2 September 2024
Accepted: 3 September 2024
Published: 14 September 2024

1. Introduction

Invasive alien plants species (IAPS) are defined as exotic plant species that are successfully established in a novel environment and are causing negative impacts on biodiversity, local ecosystems, human health, and ecosystem services [1]. Several have been recognized as being able to cause great and potentially irreversible biological disturbance to the ecosystems they invade [1–4]. IAPSs have strong competitive effects including advantageous reproductive mechanisms, earlier and later growth phenology, no (or few) natural predators, and the capacity to alter biotic and abiotic conditions in invaded ecosystems [1,5,6]. For instance, in Eastern North America, species such as *Phragmites australis* ssp. *australis* (Cav.) Steud. (common reed) propagate very rapidly by abundant seed and vegetative propagation and can form dense monocultures [7]. Some IAPS, like *Ailanthus altissima* (Mill.) Swingle, (tree of heaven) and *Rhamnus cathartica* L. (common buckthorn) have been reported to produce allelopathic substances, potentially inhibiting the survival of nearby plants [8–11]. Other IAPSs like *Rosa multiflora* Thunb. (Japanese rose) and *Berberis thunbergii* DC. (Japanese barberry) have dense foliage and form thickets, which greatly limit access to light for indigenous understory plants [12]. Given that the presence and impacts of IAPSs are projected to increase worldwide due to global trade and habitat modification [1], it is important to understand which species pose the greatest threat by understanding their interactions with local species [13].

The competitive ability of many IAPSs is postulated to negatively impact the diversity, relative abundance, and total abundance of companion species thus modifying community structure at multiple trophic levels as well as modifying food web interactions [14–17]. Changes in the plant community composition can lead to cascading effects through altered soil chemistry, leaf litter biomass, and leaf litter quality for detrital consumers thus affecting, in turn, microbial activity and community composition [18–20]. Earlier work has shown that ground-dwelling arthropod abundance, community structure, and diversity may be at risk due to IAPSs [21–23]. A decrease in resource diversity can lead to a decrease in consumer diversity [24], also referred to as the resource specialization hypothesis, whether taxonomically or functionally [25]. In their meta-analysis on the effect of plant invasions on arthropods, Litt et al. observed that total arthropod abundance decreased in 62% of the studies, but evidence varied depending on the functional groups that were evaluated [26]. Schuh and Larsen [27] documented a decrease in the abundance and diversity of crawling predatory insects, caused by the lack of prey in areas invaded by *R. cathartica*. Brousseau et al. [28] reported that the presence of *Reynoutria* spp. strongly decreased ground-dwelling arthropod richness and reduced correlations between feeding traits of predators and palatability traits of prey, suggesting that *Reynoutria* spp. disrupts functional linkages in the food web. In short, a loss of plant diversity due to IAPSs could lead to a diversity loss in ground-dwelling arthropods of both green (grazing) and brown (detrital) food webs [16,24,29].

The glossy buckthorn (*Frangula alnus* Miller) is a shrub in the buckthorn family (Rhamnaceae) and considered to be invasive in Eastern North America. Native to Asia and Europe, it was introduced in the late 1800s and was imported for its medicinal and ornamental properties [7,30]. Like other IAPS, the density of its foliage and thickets, as well as the late senescence of leaves in the fall and its rapid and effective reproduction mechanisms make it a strong competitor of understory plant species [7,31]. Its distribution has been increasing at a fast rate in Eastern North America since the mid-1900s [30,32,33]. However, studies on the impact of *F. alnus* on floral diversity are equivocal. Some research shows no effect on understory plant communities [34,35] or even an increase in shrub species richness [36]. Other studies have revealed negative relationships with certain groups of plants, such as a decrease in the density of native tree seedlings, herbaceous plant cover and richness, and changes in plant community structure in favor of shade-tolerant species [37,38]. In addition, Stokdyk and Hermann [39,40] observed that leaf extracts of *F. alnus* altered soil dynamics and total extractable nitrogen mineralization, causing changes in the microbial community functions and litter decomposition. Finally, the only known study assessing *F. alnus* and arthropod diversity found an increase in the abundance and diversity of generalist pollinating insects followed the removal of *F. alnus* [41].

Our goal was to study the impact of *F. alnus* invasion on two indicator communities, understory plants and saprophagous macroarthropods, to better assess the biodiversity risks associated with an *F. alnus* invasion in a wet deciduous woodland. Understory plants were selected as they are most likely to suffer from shading by *Frangula alnus* [3,7,37,38,42,43]. Moreover, saprophagous macroarthropods (detritus eaters larger than 5 mm) such as millipedes and woodlice were selected because they are known to be sensitive to disturbance [44,45] and are the first line of organic matter shredders in the brown food web playing an essential role in the decomposition of organic matter [46–49]. Despite the importance of saprophagous macroarthropods to ecosystem function [50,51], no study has assessed their relationship with *F. alnus*.

Using a density gradient of the *F. alnus* invaded plots, we hypothesized that the increase in the density of *F. alnus* will result in the following: (1) simplify the structure of plant species communities in the understory layer and (2) reduce species diversity. Additionally, we hypothesized that the increase in *F. alnus* density, as well as the diversity loss of native understory plant species would achieve the following: (3) alter species composition and (4) decrease species diversity of saprophagous macroarthropod communities.

2. Materials and Methods

The study site was located in the Boisé des Terres Noires nature reserve that covers 12 ha of deciduous forest in a 600 ha area, which comprised a diversity of habitats including wetlands, early succession woodlands, and peatlands [52]. These habitats are surrounded by agricultural land in L'Assomption, QC, Canada (45.81863, −73.4742) (Figure 1). Since 2016, a significant increase in *F. alnus* has been documented [53], but the invasion likely began following the commercial exploitation of peatland soil in 1996 [54].

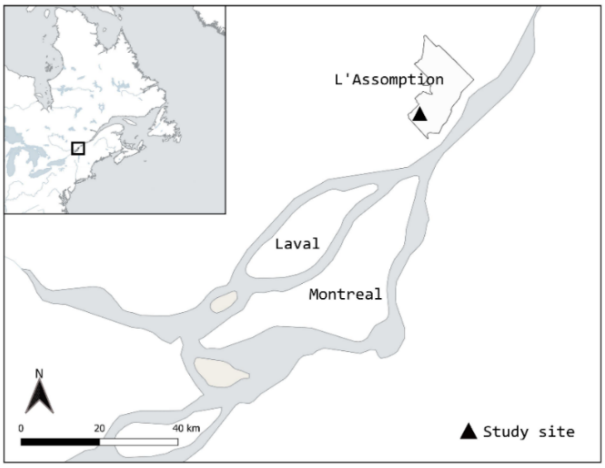

Figure 1. Location of the study site, in L'Assomption, Québec, Eastern Canada.

This invasion estimate was confirmed by coring the biggest individuals which were found to be around 27 years old (personal communication). The soil is acidic (average pH of 4.00 across the study site), which favors glossy buckthorn over common or European buckthorn [55]. Woodlands on the site were mainly dominated by pioneer trees, such as *Acer rubrum* L. (red maple), *Populus tremuloides* (Michx.) Á. Löve and D. Löve (quaking aspen), and *Betula populifolia* M. (gray birch). Several species of *Rubus* and ferns were also found in great abundance.

To assess the influence of *F. alnus* on native understory plant and saprophagous macroarthropod communities, we first visually estimated the percent cover of *F. alnus* (height > 1 m) along the transects perpendicular to an access trail. To prevent a border effect, all transects were started 10 m away from the trail. Based on this percent cover evaluation ranging from less than 5% to 100% cover of *F. alnus*, we established 43 sample plots, located at a minimum distance of 40 m from each other along the *F. alnus* density gradient. Stem density was then evaluated by counting individuals of *F. alnus* (height > 1 m) in 5 m^2 plots (high density) or in 50 m^2 plots (low density) and subsequently estimated per m^2.

2.1. Understory Plant Characterization

From 15 July to 25 August 2020, all vascular plants in the understory (height < 1 m) were identified and cover abundance was evaluated in 4 m^2 (four 1 m^2 circular plots) to the nearest 5% and then estimated per m^2. Unidentifiable plants in the field were sampled and photographed for further identification in the laboratory using identification keys [56]. A ratio of the cover abundance of each understory species to the total understory plant cover was calculated. Authorities were selected based on their use in North American and the most recent published work from the International Plant Name Index (IPNI) database [57].

2.2. Saprophagous Macroarthropod Sampling

Multi-Pher® pitfall traps (20.5 cm height and 10 cm in diameter) were used to collect saprophagous macroarthropods and were installed in the center of each plot in early June 2020, two weeks prior to activating traps, to minimize any disturbance related to digging [58]. The traps contained 100 mL of 50% ethanol for preservation, and the collected arthropods were then preserved in 80% ethanol in the laboratory. The traps were active for three periods during the summer of 2020—two 15-day periods and one 14-day period on 1 and 29 July and 27 August 2020, respectively, for a total trapping effort of 44 days. Data from five traps in the first sampling and three traps in the third sampling period were excluded from the analyses due to wildlife disturbance or technical issues that compromised the traps. Despite the shortcomings of this method [59–61], capture with the pitfall traps remains an effective and economical way to make a comparative assessment of edaphic arthropods [22,25,27,58,62]. All millipedes and woodlice were counted and identified to species [50,63–66], except for some juvenile Parajulidae (n = 5) whose species could not be identified because their secondary sexual characteristics (gonopods) were not developed. The average abundance of saprophagous macroarthropods was used to calculate diversity indices and analyze community structure.

2.3. Environmental Characterization

Environmental variables (soil temperature at ground level, soil humidity, soil pH, tree canopy cover, cover of woody debris, leaf litter biomass and composition) were measured given their potential impact on soil arthropod communities, understory plant communities, and potential relationship with *F. alnus* [27,42,67–69]. A HOBO data logger (Onset Computer Corporation, Bourne, MA, USA) was placed on the ground, under the leaf litter layer, in the center of 24 plots to record the temperature every 2 h from 11 June to 28 August 2020. Soil humidity was measured three times over the summer in each plot (at less than 1 m from the plot center) with a Field Scout TDR 300 moisture meter (Spectrum Technologies, Yellow Springs, OH, USA) with 7.6 cm rods. Care was taken to avoid rainfall events in the 24 h preceding soil humidity measurements. Soil pH was measured once (3 replicates) in the summer with a pHA10 Ecosens probe (YSI Inc., Bridgend, UK). Tree canopy cover (to the nearest 5%) and cover of woody debris (to the nearest 5%) were estimated for each plot. On 30 September 2020, three samples (15 cm × 15 cm × 5 cm) of the litter in the center of each plot were collected and dried at 35 °C. The leaf litter was sorted by species, and the total litter dry mass for each plot was determined. The average ambient air temperature for the summer of 2020 was 20.6 °C (±4.6 °C) [70]. Heavy rainfall (Max = 27 mm) occurred during the first arthropod sampling period from 23 to 24 June 2020. But generally, the trapping periods had little rain and were mostly sunny or cloudy [71].

2.4. Statistical Analysis

To obtain a general portrait of the environmental conditions at our site that corresponded to the gradient of *F. alnus* (range from 0 to >4 individuals m^{-2}), linear regression tests were carried out to test whether the density of *F. alnus* was correlated with soil temperature, soil humidity, leaf litter biomass, and the percentage of woody debris cover. We also used linear regression models to test whether canopy cover and soil pH influenced the density of *F. alnus*. Redundancy analyses (RDA) were used to explore community structures across plots for both understory plants and saprophagous macroarthropod communities. To analyze plant communities, rare species (<5% average cover and found in less than 5% of plots) were removed. Plant cover ratios were transformed using Hellinger's distance to minimize the effect of double zeros [72–74] and soil humidity, soil pH, and canopy cover were used as constraint variables. To assess saprophagous macroarthropod communities, the mean abundance of saprophagous macroarthropods was log-transformed to avoid the horseshoe effect [72]. Species with fewer than five individuals and unidentified juveniles were removed. Along with the density of *F. alnus*, other environmental factors that were likely to influence community structure, such as understory plant species, woody debris cover, and litter biomass were used as constraint variables and were standardized and centered on 0.

Community metrics such as species richness (*S*), species abundance, the effective number of species, Shannon–Wiener index (H'), and the evenness index (J') of the native understory plants (including rare plants) and saprophagous macroarthropod communities were calculated and tested as response variables in the linear regression models assessing the potential effect of *F. alnus* density. The Shannon–Wiener index was obtained from the following formula:

$$H' = -\sum_{i=1}^{S} PilnPi$$

where Pi corresponded to the proportion of species cover i on the total cover (for understory plants) or the proportion of species i individuals on the total number of individuals (for saprophagous macroarthropods). Evenness was calculated as follows:

$$J' = H'/\ln(S)$$

The effective number of species (eH') is an index based on the Shannon–Wiener index and was used to provide a more intuitive interpretation of diversity [75].

For native understory plants, the abundance and evenness index were square root transformed to meet linear model conditions. One extreme data point was removed for the evenness (plot L4) to fit conditions of normality. For saprophagous macroarthropods, the percentage of *F. alnus* leaves in the litter and the effective number of understory plant species were also used as explanatory variables, in addition to litter biomass (mg m^{-2}), pH, soil humidity (%) and woody debris (%)). All analyses and data processing were carried out with the R program version 4.0.4 [76] using the vegan library [77].

3. Results

3.1. Site Characteristics

In general, the environmental characteristics were stable across all 43 plots with no significant differences observed in soil humidity, leaf litter biomass, and soil temperature as a function of the density gradient of *F. alnus* (Table 1). However, woody debris cover increased significantly with *F. alnus* density (Table 1). Moreover, we observed that the density of *F. alnus* was not predicted significantly by tree canopy cover, but soil pH was a significant predictor (Table 1).

Table 1. Linear regression model output of the environmental variables associated with density gradient of *F. alnus* at the Boisé des Terres Noires study site. Variables that were most likely to influence the density of *F. alnus* were used as independent variables, such as tree canopy cover (%) and pH. Others that might be influenced by *F. alnus*, such as soil humidity (%), leaf litter biomass (g m^{-2}), ground-level temperature (°C), and woody debris cover (%) were used as dependent variables to test if they varied across the gradient of *F. alnus*.

Dependent Variable	Independent Variable	Mean ± SD	Estimate	±SE	T-Value	R^2	*p*-Value
F. alnus density (nb m^{-2})	Canopy cover (%)	58.95 ± 13.30	−0.009	0.006	−1.360	0.043	0.181
	pH	4.00 ± 0.40	−0.482	0.206	−2.344	0.118	<0.05 *
Humidity (%) [1]	*F. alnus* density (nb m^{-2})	20.46 ± 10.80	−0.034	0.092	−0.364	0.003	0.718
Leaf litter biomass (g m^{-2}) [1]		269.26 ± 65.90	0.238	0.267	0.893	0.019	0.377
Ground temperature (°C) [1]		20.15 ± 0.48	0.086	0.077	1.122	0.054	0.274
Woody debris cover (%) [1]		13.80 ± 6.50	0.510	0.083	6.16	0.481	<0.001 ***

[1] Square root transformation to fit the linear regression model conditions; * $p < 0.05$; *** $p < 0.001$.

3.2. Native Understory Plants

A total of 54 species of understory plants were found throughout the study site (Table 2). Among the most common species, saplings *A. rubrum* accounted for around 11%

of the total vegetation cover across all study plots, making it the second most abundant understory plant after *F. alnus*. The most abundant shrubs were ericaceous species such as *Rhododendron canadense* (L.) Torr., *Vaccinium angustifolium* A., and *Kalmia angustifolia* L., as well as *Aronia melanocarpa* (Willd.) Torr. (Rosaceae). Each of these species represented, on average, between 3% and 8% of total vegetation cover (Table 2). The most abundant herbaceous plant species was *Maianthemum canadense*, with an average cover of around 4%, as well as four species of pteridophytes, with a combined average cover of around 12% (*Dryopteris spinulosa* (Mull.) Watt., *Onoclea sensibilis* L., *Osmunda claytoniana* L., *Osmunda cinnamomea* L.). The rare species (n = 27) altogether accounted for, on average, less than 5% of the total vegetation cover. Other exotic plant species were also reported including *Phragmites australis* ssp. *australis* and *Galeopsis ladanum* L. These represented less than 3% of the vegetation cover and were found in less than 5% of the sampling stations. We also observed a general decrease in total native plant abundance across the gradient of *F. alnus*, where the highest abundance was observed when *F. alnus* was around two individuals m^{-2} ($R^2 = 0.11$, $p < 0.05$). On the site, with an average of 20.5%, Frangula alnus was the species with the largest percentage of total understory plant cover (Table 2).

Table 2. Dominant understory plant species: trees, shrubs, and herbaceous plants (>5% presence in plots and >5% vegetation cover) in all our 43 plots on our site. Shade tolerance, frequency (percentage of presence in plot) and average cover (percentage) of total vegetation for each of understory plant species.

Family	**Genre**	**Species**	**Shade Tolerance**	**Frequency (%)**	**Average Cover ± SE**
		Native and cosmopolite species			
		Trees			
Rosaceae	*Prunus*	*virginiana* L.	Tolerant	16.3	0.6 ± 0.3
Sapindaceae	*Acer*	*rubrum* L.	Medium	100	11.2 ± 1.4
Salicaceae	*Populus*	*tremuloides* M.	Intolerant	30.2	0.5 ± 0.1
		Shrubs			
Aquifoliaceae	*Ilex*	*mucronata* L.	Tolerant	34.9	1.4 ± 0.3
Caprifoliaceae	*Viburnum*	*cassinoides* L.	Tolerant	41.9	2.7 ± 0.7
Cornaceae	*Cornus*	*alternifolia* L.	Tolerant	7	1.1 ± 0.7
Ericaceae	*Kalmia*	*angustifolia* L.	Intolerant	48.8	3.4 ± 0.8
	Rhododendron	*canadense* L.	Tolerant	55.8	6.2 ± 1.4
	Vaccinium	*angustifolium* A.	Intolerant	58.1	6.2 ± 1.2
	Chamaedaphne	*calyculata* L.	Intolerant	9.3	0.3 ± 0.2
Rosaceae	*Aronia*	*melanocarpa* W.	Intolerant	88.4	8.3 ± 1.0
	Rubus	*occidentalis* L.	Tolerant	14	1.8 ± 1.2
	Rubus	*allegheniensis* P.	Intolerant	9.3	0.6 ± 0.3
	Rubus	*Pubescence* R.	Tolerant	44.1	5.1 ± 1.4
	Rubus	*hispidus* L.	Tolerant	16.3	1.8 ± 0.9
	Rubus	*idaeus* L.	Intolerant	16.3	2.3 ± 1.0
	Spiraea	*latifolia* A.	Medium	76.7	3.5 ± 0.6
		Herbs			
Asparagaceae	*Maianthemum*	*Canadense* D.	Medium	69.8	4.3 ± 0.9
Osmundaceae	*Osmunda*	*claytoniana* L.	Tolerant	7	0.7 ± 0.5
Polypodiaceae	*Dryopteris*	*spinulosa* M.	Tolerant	20.9	4.3 ± 1.9
	Onoclea	*sensibilis* L.	Medium	7	1.1 ± 1.0
	Osmunda	*cinnamomea* L.	Tolerant	11.6	1.2 ± 0.8
Primulaceae	*Lysimachia*	*borealis* R.	Tolerant	62.8	3.0 ± 0.8
Vitaceae	*Parthenocissus*	*quinquefolia* L.	Tolerant	23.3	1.8 ± 0.7

Table 2. *Cont.*

Family	Genre	Species	Shade Tolerance	Frequency (%)	Average Cover ± SE
		Exotic species			
Lamiaceae	*Galeopsis*	*ladanum* L.	Medium	2.3	<0.1
Poaceae	*Phragmites*	*australis* ssp. *australis* C.	Intolerant	4.7	<0.1
Rosaceae	***Frangula***	***alnus* M.**	**Tolerant**	**93**	**20.5 ± 3.0**
		***Rare species*: 27**			<5%
Richness of native species: 51					
Total richness: 54					

3.3. Native Understory Plant Communities

The redundancy analysis model for understory plant community composition only explained 14.3% of the variation along the two first axes (Figure 2). In plots with a high density of *F. alnus*, we observed shrub species such as *Cornus alternifolia* L., *Ilex mucronata* (L.) M.Powell, Savol. & S. Andrews, *Rubus occidentalis* L. the vine *Parthenocissus quinquefolia* (L.) Planch., herbaceous species like *M. canadense* and *Circaea lutetiana* L. and tree seedlings of *A. rubrum*. However, as the density of *F. alnus* only explained a small percentage of variation (4.4%) on the second axis, plant species composition was driven more strongly by other environmental factors, such as soil humidity and tree canopy cover, which were both associated with axis 1 and explained more than twice as much variation (9.9%).

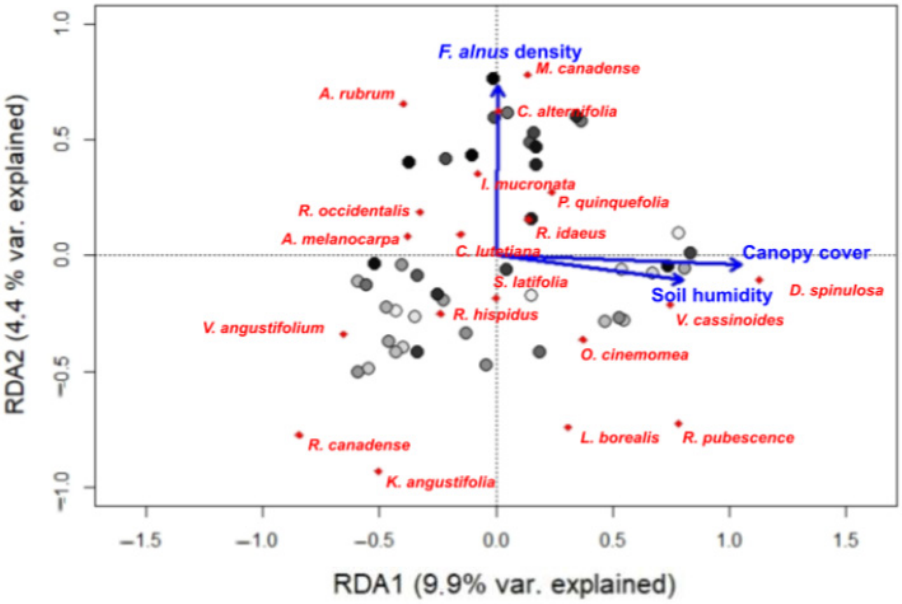

Figure 2. Redundancy analysis (see statistical output in Table S1) of percent cover of native understory plant species and environmental variables, according to each sampling plot (represented by dots). For each plot, density of *F. alnus* is represented by a gray gradient to visualize the degree of invasion, whereby pale plots have a lower density (0 individual m^{-2}) and gradually increase to dark for high density plots (>4 individual m^{-2}). Plant species, in red, have been centered and transformed (Hellinger). Significant constraint variables (canopy cover, soil humidity, soil pH and density of *F. alnus*), in blue, have also been standardized, centered on 0.

Surprisingly, shade-tolerant plant species were present on both ends (low and high density) of the *F. alnus* density gradient [56,78–80]. Conversely, peatland species like *K. angustifolia*, *R. canadense*, *V. angustifolium*, *Rubus hispidus* L., and *Spiraea latifolia* (A.) F.

Seym. were associated with plots with lower tree canopy cover and lower humidity. These species are mostly shade-intolerant, and they tend to prefer higher luminosity and soil humidity and more acidic organic soils [79,81].

Except for species richness (R^2 = 0.002, p = 0.78), we found a consistent negative, albeit weak, response of plant understory abundance and diversity measured with multiple diversity metrics along the gradient of *F. alnus* invasion (Table 3). The effective number of species (R^2 = 0.177, $p < 0.005$) and the Shannon–Wiener diversity index (R^2 = 0.21, $p < 0.005$) both decreased as *F. alnus* density increased, but the variation caused by *F. alnus* was not very strong [82]. The effective number of understory plant species variations was explained mostly by *F. alnus* density ($p < 0.01$) and leaf litter biomass ($p < 0.05$, R^2 = 0.2219, Table S3). Pielou's evenness in plant communities (R^2 = 0.26, p <0.001) still showed that when the density of *F. alnus* increased, understory plant communities tended to homogenize. Although the models showed a noticeable effect, the variation caused by the increasing density of *F. alnus* varied throughout the models.

Table 3. Linear regressions of density of *F. alnus* (individual m^{-2}) as a predictive variable on five diversity indices of understory native plant species (height < 1 m). Evenness index and total abundance were square root transformed to fit linear model conditions. All plant diversity indices were based on the ratio of mean species abundance (to the closest 5%, on 1 m^2) to total plant abundance (% cover).

	Descriptive Statistics		**Linear Model Output**				
Dependent Variable	**Mean ± SE**	**Median (Min–Max)**	**Estimate**	**SE**	**T-Value**	**R^2**	***p*-Value**
Specific richness (*S*)	11.4 ± 2.5	11 (7–17)	−0.093	0.331	−0.281	0.002	0.78
Effective number of species	7.1 ± 2.2	6.97 (2.60–12.9)	−0.783	0.264	−2.967	0.177	**<0.005 ****
Shannon-Weiner index (*H′*)	1.9 ± 0.3	1.94 (0.95–2.56)	−0.129	0.039	−3.316	0.211	**<0.005 ****
Evenness (*J′*) [1]	0.8 ± 0.11	0.80 (0.39–0.91)	−0.030	0.008	−3.731	0.272	**<0.001 *****
Total abundance of native understory plant species (%) [1]	38.3 ± 16.7	36.90 (9.5–79.45)	−0.392	0.172	−2.276	0.112	**<0.05 ***

[1] Square root transformation to fit the linear regression model conditions. * $p < 0.05$; ** $p < 0.005$; *** $p < 0.001$.

3.4. Saprophagous Macroarthropods

A total of 2566 saprophagous macroarthropods (millipedes and woodlice) were collected across all sampling periods, totaling nine species, and one which could only be identified to the genus level (*Cleidogona* sp.). Only one species of woodlice was captured, an exotic generalist species *Trachelipus rathkii* Brandt, 1833, that was many times more abundant than any other sampled species on the site (n = 1728) and known to be among one of the ten most abundant woodlouse species in North America [67]. All other eight species collected were diplopods; three of which were exotic (*Ophyiulus pilosus* Newport, 1842), *Choneiulus palmatus* Němec, 1895, and *Polydesmus inconstans* Latzel, 1884). *O. pilosus* abundance slightly increased along the gradient of *F. alnus*, whereas *C. palmatus* and *P. inconstans* were relatively stable (no significant relation to *F. alnus* density). Moreover, some species were only found in very low abundance, such as *Cleidogona* sp. (n = 2) and *Oriulus venustrus* Wood, 1864 (n = 6) (Table 4).

Table 4. Abundance, habitat, and origin (native/exotic) for each species of saprophagous macroarthropods (Diplopoda and Isopoda) captured in the 43 pitfall traps during the summer of 2020 on the Boisé des Terres Noires study site, in L'Assomption, Qc.

Class	Order	Family	Genre and Species	Total Abundance	Origin (Native/Exotic)	Habitat
Diplopoda	Chordeumatida	Cleidogonidae	*Cleidogona* sp.	2	Native	NA
	Julida	Blaniulidae	*Choneiulus palmatus* N.	56	Exotic	Urban, disturbed habitats
	Julida	Julidae	*Ophyiulus pilosus* N.	138	Exotic	Wetlands, Urban
	Julida	Parajulidae	*Uroblaniulus canadensis* N.	99	Native	Open woodland, mesic
	Julida	Parajulidae	*Oriulus venustus* W.	6	Native	Open woodland
	Julida	Parajulidae	*Parajulidae* sp.	5	Native	NA
	Polydesmida	Polydesmidae	*Polydesmus inconstans* L.	178	Exotic	Urban
	Polydesmida	Polydesmidae	*Pseudopolydesmus serratus* S.	266	Native	Mixed forests
	Spirobolida	Spirobolidae	*Narceus annularis* R.	88	Native	Woodland, Urban
Malacostraca	Isopoda	Trachelipodidae	*Trachelipus rathkii* B.	1728	Exotic	Terrestrial, generalist

3.5. Saprophagous Macroarthropod Community Composition

Overall, the selected variables generally predicted the composition of the saprophagous macroarthropod communities (Figure 3, 25.2% total var. explained). The density of *F. alnus* had a weak influence on the variation in community composition as it was associated mostly with axis 2 of the RDA (5.1%), compared to other vectors that were mostly associated with axis 1, such as native plant cover, woody debris cover, and soil humidity (20.1% var. explained). Nonetheless, some native species (*Uroblaniulus canadensis* Newport, 1844, *N. annularis* Raf. 1820, and *P. serratus* Say, 1821) [49] were associated with plots with higher native understory plant diversity and a lower *F. alnus* density. Species such as *P. inconstans* and *U. canadensis* were influenced by humidity and woody debris cover. Indeed, *U. canadensis* was associated with plots with lower humidity levels and more understory native plant diversity, whereas *P. inconstans* was mostly found where woody debris cover, and soil humidity were high. Exotic *Trachelipus rathkii* and *Choneiulus palmatus* [83] were also associated with these environmental vectors but to a lesser degree.

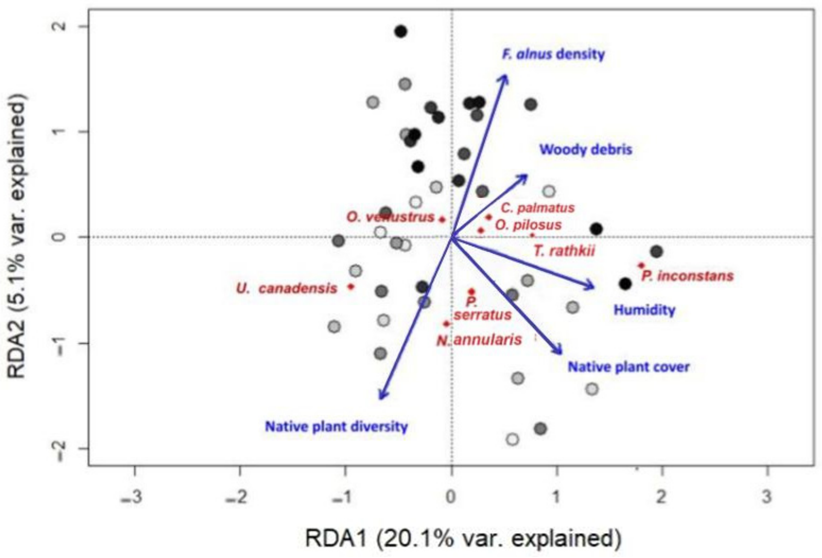

Figure 3. Redundancy analysis (see statistical output in Table S2) of average abundance of saprophagous macroarthropod communities and environmental variables across sampling plots

(represented by dots). For each plot, density of *F. alnus* is represented by a gray gradient to visualize the degree of invasion, whereby pale dots have a lower density (0 individual m^{-2}) and gradually increase to darker dots for high density plots (>4 individual m^{-2}). The species, in red, have been log-transformed to minimize the effect of very abundant species and the horseshoe effect. Significant constraint variables (soil humidity (%), woody debris cover (%), plant diversity (effective number of native plant species), and native understory plant cover (%)), in blue, were standardized, centered on 0, and vectors were scaled (×1.2) for better visualization.

No species were strongly associated with high *F. alnus* density as we observed that most of the species were present in plots where *F. alnus* density was lower. Similar to our observations with understory plants, these results suggest only a small influence of *F. alnus* density and a stronger influence of other measured environmental variables.

3.6. Saprophagous Macroarthropod Abundance and Diversity

Overall, the total abundance of the saprophagous macroarthropods did not vary across the gradient of *F. alnus* invasion, but the diversity metrics did vary significantly (Table 5). As with our observations on understory plants, an increase in *F. alnus* was associated with a decrease in all diversity indices of saprophagous macroarthropod communities (Table 5). Low diversity plots were homogenized by the dominance of *T. rathkii*. Plots with a higher density of *F. alnus* showed a decrease in the effective number of detritivore species ($R^2 = 0.10$, $p < 0.05$), the Shannon–Wiener index ($R^2 = 0.15$, $p < 0.02$), and evenness ($R^2 = 0.14$, $p < 0.02$). Similarly to understory plants, we observed a decrease in the diversity indices, but the variation was weakly explained by the density of *F. alnus* [82]. Species richness also was negatively impacted ($R^2 = 0.14$, $p < 0.02$), but since the total number of species per plot varied only from two to six, the data could not be normalized to fit model assumptions and therefore should be interpreted with caution.

Table 5. Descriptive statistics and linear regression outputs of density of *F. alnus* (individual m^{-2}) as a predictive variable on five community indices (effective number of species, Shannon-Wiener index, and evenness index) for saprophagous macroarthropod communities. Mean abundance of millipedes and woodlice were calculated across three trapping periods in summer 2020 and square root transformed to fit linear model conditions.

	Descriptive Statistics		**Linear Models Outputs**				
Dependent Variable	**Mean ± SE**	**Median (Min–Max)**	**Estimate**	**Std Error**	**T-Value**	**R^2**	***p*-Value**
Species richness (*S*)	4.47 ± 0.13	5 (2–6)	−0.27995	0.1070	−2.616	0.1431	**<0.02 ***
Effective number of species	2.59 ± 0.11	2.49 (1.24–4.14)	−0.19505	0.09306	−2.096	0.100	**<0.05 ***
Shannon-Wiener index (*H*′)	0.91 ± 0.04	0.914 (0.26–1.42)	−0.09680	0.03677	−2.633 7	0.1446	**<0.02 ***
Evenness index (*J*′)	0.60 ± 0.02	0.612 (0.216–0.881)	−0.05082	0.02005	−2.535	0.1355	**<0.02 ***
Mean abundance [1]	20.39 ± 1.8	20.3 (4.3–52.6)	0.2541	0.1696	1.498	0.05191	0.142

[1] Square root transformation to fit the linear regression model conditions. * $p < 0.05$.

Since the increase in density of *F. alnus* was associated with a decrease in saprophagous macroarthropod diversity, other environmental factors, such as the *F. alnus* ratio in the leaf litter and the understory plant diversity (effective number of species), were tested as possible predictors affecting saprophagous macroarthropod communities. Neither a reduction in the understory native plant diversity nor an increase in the *F. alnus* ratio in the leaf litter influenced saprophagous macroarthropod diversity.

4. Discussion

Contrary to our hypothesis that an increase in the density of *F. alnus* would alter community composition and lower the diversity of both indicator taxa, we did not find a strong alteration of the community composition due to increasing *F. alnus*, but our results did show a tendency towards homogenization indicated through negative, but generally weak, effects on the multiple diversity metrics for the native plant understory (Table 3) and saprophagous macroarthropod communities (Table 5).

Invasive alien species are one of the biggest causes of biodiversity loss worldwide [1,2], but results are equivocal as to the magnitude of the impacts on native ecosystems [35,38,84–89]. Our results demonstrate that the invasion by *F. alnus*, like other IAPSs, was associated with plant community changes and the loss of native plant diversity [36–38]. However, species richness and variation in other community indices were not strongly explained by an increasing density of *F. alnus* (Table 3), suggesting that glossy buckthorn may be less competitive than other IAPSs or that its effect may be scale-dependent [90].

Exceptional competitors are not ubiquitous among IAPSs. Hedja et al. [15], who assessed the potential effects of thirteen IAPSs on native diversity, showed that only a few caused an obvious adverse effect on native plant species (i.e., *Reynoutria* spp. and *Heracleum mantegazzianum*). Indeed, *Reynoutria* spp., have allelopathic properties and can reduce native species ten-fold [91]. Invasion by another strong competitor, *Centaurea maculosa*, can also lead to strong decreases in native plant abundance and diversity [92]. However, the case of *F. alnus* is not clearcut; previous studies have suggested that an increase in the density of *F. alnus* can lead to an increase in native plant species richness [34,36] or no significant effect on herbaceous plant communities [42,93]. It is thus not surprising that we only observed a weak, albeit significant, decrease in our measured diversity indices of native understory plants as the density of *F. alnus* increased. This pattern was driven in part by a decrease in shade-intolerant peatland species such as *V. angustifolium* and *K. angustifolia*.

Our data support the observation that not all groups of organisms nor ecosystems respond similarly to invasion by IAPSs [5,26,28,89]. We hypothesized that the loss of diversity and homogenization of plant species communities should, as a corollary, lower the diversity of the primary consumers [16,24–27]. Perhaps, because of the only slight decrease in understory plant diversity, we observed only a weak decrease in saprophagous macroarthropod diversity indices (Table 5). Moreover, we also observed that all exotic saprophagous macroarthropod species either increased in abundance or were unaffected when *F. alnus* increased in density. These exotic species are known to be generalist consumers and generally resilient to disturbance caused by changing plant communities and edaphic conditions [49,94]. We also observed that native species, such as *U. canadensis* and *N. annularis* were associated with plots that had a lower *F. alnus* density and a higher understory plant diversity, implying that these species were more sensitive to invasion by *F. alnus*. Soil humidity and woody debris were associated with saprophagous macroarthropod community structure, but no mechanisms responsible for the decrease in diversity could be identified within our selected variables, as neither the *F. alnus* ratio in the sampled leaf litter nor the native understory plant diversity explained saprophagous macroarthropod diversity loss in our study system (Table S4). Schuh and Larsen [27] also found an adverse impact on ground-dwelling arthropods following *R. cathartica* invasion but could not identify the causal mechanisms. While we understand that *F. alnus* can alter the pH, nitrogen mineralization, and microbial activity of soils [39,40], leaf litter traits were not assessed in detail in our study, which makes it difficult to speculate about the effect of changes to leaf litter quality on saprophagous macroarthropod consumers. Future investigations to understand cascading effects in ecosystems invaded by *F. alnus* and other IAPSs on saprophagous arthropods could benefit from a functional trait-based approach, given that there is frequently a covariance between detritus and detritivore traits [95–97].

Our results suggest that although *F. alnus* had a general moderate effect on the diversity of plant understory and a weak effect on saprophagous macroarthropod communities after

27 years, it may be a smaller threat for native biodiversity than other IAPSs. Its negative influence was stronger for understory plants than for saprophagous macroarthropods, as plots with a density of *F. alnus* higher than 1.5 individuals per m^2 decreased in the average effective number of plant species. Because older stems tend to occur in dense even-aged thickets, it may be that more significant decreases in biodiversity will occur at a higher density threshold or later in the invasion process, as observed for other invasive species [98]. Since Mills et al. [35] only observed a weak impact of *F. alnus* after 15 years in a similar ecosystem, we suspect that the threat to biodiversity posed by *F. alnus* occurs slowly. Despite success in colonizing and expanding its range, it appears that the invasiveness of *F. alnus*, although it seemed to interact with the species evenness, does not necessarily correlate with the severity of its impacts [86,87]. Nonetheless, we recommend pursuing research on the impacts of *F. alnus* on other indicator taxa and in different contexts, as some homogenization of plant and macroarthropod communities at our invaded site was observed.

Although the environmental variables that we monitored did not vary along our *F. alnus* gradient (Table 1), other relevant abiotic and biotic environmental variables may be influenced by *F. alnus*, making it difficult to understand the mechanisms at play following invasion [85]. Having multiple study sites could give us a better general understanding of the interaction of *F. alnus* with different indicator taxa as different sites and ecosystems can respond differently when invaded by the same IAPS [28,88], accounting in part for the lack of consistency in the scientific literature when it comes to assessing IAPSs [87,99,100]. A uniformized impact metric, as proposed by Barney et al. [99], could help to facilitate comparisons between the studies.

5. Conclusions

Our study demonstrated that *F. alnus* negatively influenced understory plant diversity and caused understory plant communities to homogenize, but the effect was not as strong as other IAPS. Consequently, the trophic level effects on saprophagous macroarthropods were not observed as much as expected. Nonetheless, our study supports the need for an ongoing re-evaluation and monitoring of IAPS as their mere presence may not be synonymous with strong negative effects on native biodiversity.

Supplementary Materials: The following supporting information can be downloaded at: https://www.mdpi.com/article/10.3390/d16090584/s1, Table S1. Statistical output of redundancy analysis (RDA) of environmental variables (standardized) associated with understory plants specific community (Hellinger transformation) between all 43 plots in our study site, at L'Assomption; Table S2. Statistical outputs of redundancy analysis (RDA) of constraint variables (standardized) that may be associated with specific variation in shredder detritivores communities (logarithmic transformation) between 43 sampling plots in study site, at L'Assomption; Table S3. The most explanatory multiple linear regressions models of the variation in the effective number of species of understory plants with several explanatory variables (*F. alnus* density, Litter biomass, pH). These models are derived by comparing several models and choosing those whose AICc are the lowest based on the MuMin package in R [101]; Table S4. Linear regressions models using *Frangula alnus* ratio in leaf litter and effective number of native understory plant species as predictive variables on different diversity index of saprophagous macroarthropods; Table S5. Linear regressions of density of *F. alnus* (per m^2), *F. alnus* in leaf litter (%) and effective number of plant species as predictive variables on five diversity indices of saprophagous macroarthropods species. Abundance of detritivores have been transformed (square roots) to fit linear model conditions. All arthropods' data are based on the average of three collects within summer 2020.

Author Contributions: G.R., D.K. and I.T.H. contributed to the study conception and design. G.R. prepared material and acquired data. Data analyses were carried out by G.R. and T.J. The first draft was written by G.R., with editorial support from D.K., I.T.H. and T.J. for the subsequent versions. All authors have read and agreed to the published version of the manuscript.

Funding: Financial support was provided by a Mitacs Accelerate partnership grant, as well as NSERC Discovery grants to D.K. and I.T.H.

Institutional Review Board Statement: Not applicable for this study.

Data Availability Statement: All data and codes are available on https://doi.org/10.17632/v7vjwph992.2.

Acknowledgments: We thank the members of Kneeshaw lab (C. Gabillot, M. Meyer, G. Bergen, P. McNie) and Handa lab members (R. Sepulveda-Mina, L. J. Raymond-Léonard, J. St-Pierre, E. Gagnon Koudji, F. Jaeger), for assisting in the data sampling, identification, and meaningful exchanges as well as the FRQNT-funded Center of Forest Research for their support. We are particularly grateful J. Campeau-Poirier for his assistance in the field work and sampling. Moreover, P.-M. Brousseau kindly helped confirm the identification of arthropods and provided advice on statistical analysis and data interpretation. We are also grateful to R. Dumas, M. Leboeuf and all members at the Fiducie des écosystèmes de Lanaudière for permission and support to work at the Boisé des Terres Noires field site. We thank C. Garceau and all members of the non-profit organization CANOPÉE for their partnership in the Mitacs Acceleration project. C. Garceau was a great contributor in realization of the methodology protocol. Finally, we thank S. Pellerin and C. Lavoie for their relevant feedback on an earlier draft.

Conflicts of Interest: First author, Gabrielle Roberge, and co-authors declare no financial and competing interest to disclose.

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