

Research Article

Raw wool as an important vector for plant introductions: insights from the 2021 floods in the Vesdre River valley (Belgium)

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Citation: Verloove F, Gonggrijp S, Valentini S, Barker R, Gwynne-Evans D, Planchuelo AM, Vandeloek F, Leliaert F, Dana ED (2026) Raw wool as an important vector for plant introductions: insights from the 2021 floods in the Vesdre River valley (Belgium). *Management of Biological Invasions* 17(2): 343–362, <https://doi.org/10.3391/mbi.2026.17.2.08>

Received: 7 February 2025

Accepted: 14 November 2025

Published: 9 February 2026

Handling editor: Ileana Herrera

Thematic editor: Ana Novoa

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Abstract

The Vesdre River valley (province of Liège, Belgium) was historically home to an important wool-processing industry. Raw wool was mostly imported from Australia, South Africa, and South America and contained numerous seeds and fruits. After cleaning the wool (“scouring”), the wastewater was discharged into the river, where the seeds germinated downstream of the mills, forming the so-called “wool aliens”. As a result of changed production processes (in particular: wastewater was no longer discharged) and the (almost) demise of this industry, the wool alien plants disappeared in the mid-20th century. In July 2021, the valley faced unprecedented floods, as a result of which the entire valley was destroyed. The banks of the river, for decades overgrown with the invasive weed *Reynoutria japonica*, were exposed again. In 2022 and 2023, seeds from the long buried sediment, which were thus introduced many decades ago, germinated. 178 wool alien taxa were identified, most of them from Australia and South Africa, the main suppliers of wool. Five families accounted for more than 87% of the taxa (in order of importance: Malvaceae, Fabaceae, Juncaceae, Geraniaceae and Convolvulaceae). Species-rich families like Asteraceae and Poaceae were completely lacking because their seeds likely did not survive the wool-processing or, more likely, were short-lived. The diversity of Malvaceae (71 taxa; 11 species of *Abutilon* and 15 of *Sida*) was quite remarkable. Almost 40% (68 taxa) of all taxa found had not been observed in Europe before (or even outside their sometimes limited native range), despite the fact that the wool alien floras were extensively studied in the past. More than 80% (143 taxa) are considered weeds at least somewhere in the world. Wool therefore appears to be a very efficient vector for the unintended introduction of foreign seeds, including those of invasive species. Given the increasing use of wool waste as fertilizer, inspection or certification measures may need to be considered to limit the risk of introducing new weeds.

Key words: invasion, Malvaceae, non-native plants, seed bank, wool industry

Introduction

Biological invasions are a major driver of biodiversity loss worldwide, often facilitated by global trade and transport networks. A well-documented but underexplored pathway for the unintentional introduction of non-native plants is the international wool trade. During the industrial era, raw wool was shipped across continents and frequently carried diaspores—seeds, fruits, and dung—originating from the native pastures where sheep grazed (Mitchell 1982; Stace and Crawley 2015). These propagules, embedded in fleece or excreted in dung, represent a striking example of human-mediated dispersal.

Recent assessments, such as Chapter 3 of the IPBES Global Report on Invasive Alien Species (Hulme et al. 2024), emphasize the complex interactions between direct drivers (trade, transport, land-use change) and indirect socio-economic factors that underpin species introductions. Among historical trade goods, wool stands out as a highly effective though poorly quantified vector, capable of transporting viable diaspores over long distances (Hayward and Druce 1919; Probst 1949).

In Europe, several industrial regions with wool-processing facilities developed unique floras of so-called “wool aliens” – non-native plant species introduced through raw wool (Thellung 1912; Kloos 1939; Probst 1949; Lousley 1961; Bernard and Fabre 1977). One such region is the Vesdre River valley in eastern Belgium, which emerged as a key centre for wool scouring from the 19th century onwards. Wool was imported from a wide range of regions, including Australia, New Zealand, South America, and South Africa (Visé 1942, 1958), exposing the Vesdre valley to diaspores from both temperate and subtropical floras. The scouring process discharged seed-rich wastewater into the river, leading to the germination of non-native plants along the banks (Visé 1942, 1958; Lambinon et al. 1959).

The collapse of the international wool industry in the late 20th century caused many wool mills to close (Supplementary material Figure S1), and the sharp decline in the supply of wool, combined with stricter environmental regulations, led to the complete disappearance of the wool alien flora (Verloove 2006). Nevertheless, recent observations along the Meuse River in the Netherlands—downstream of the Vesdre—suggest that viable diaspores from historical wool imports may still emerge under the right disturbance regimes, such as major excavations (Verloove et al. 2025).

Following the catastrophic floods of July 2021, which severely disturbed vegetation and soil along the Vesdre valley (Journée et al. 2023; de Goër de Herve and Pot 2024), conditions emerged that resemble those favouring wool alien establishment in the past. This event provided a rare opportunity to investigate whether dormant diaspores might re-emerge after decades of dormancy.

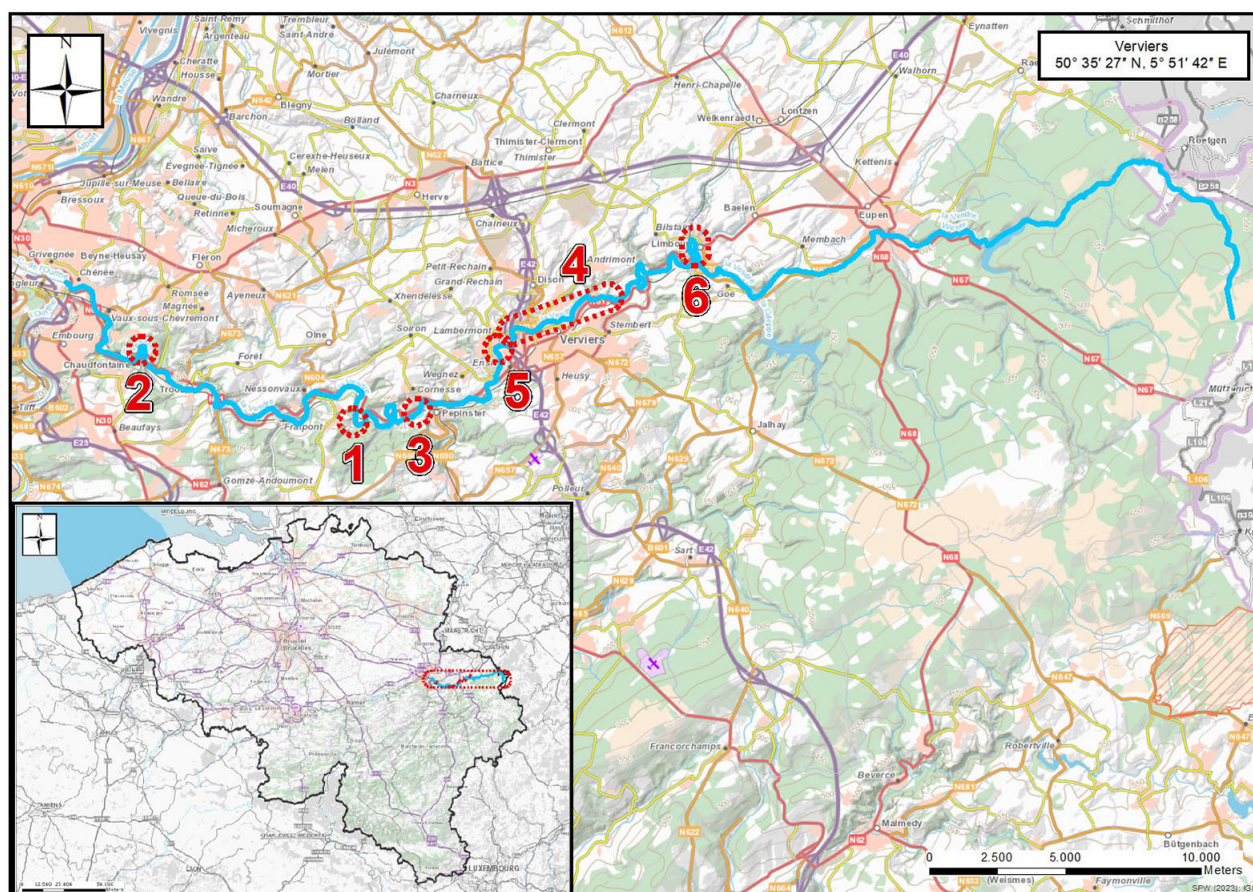


Figure 1. Study area: the Vesdre valley in Belgium (blue color), province of Liège, indicating the most important collection locations: 1. Goffontaine, 2. Chaudfontaine, 3. Pepinster, 4. Verviers, 5. Ensival and 6. Dolhain. In total, approximately 50 sites were surveyed throughout the valley, but only the most important ones are shown here to maintain map readability. Source: ©SPW ©CartoWeb.be ©ArcMap.

This study focuses on the Vesdre valley as a historical and contemporary hotspot of unintentional plant introductions via wool processing. By combining archival data with recent floristic surveys conducted after the 2021 floods, we aim to:

1. Reconstruct the geographic origins and composition of wool alien floras historically associated with the Vesdre.
2. Identify newly emerging wool aliens in the post-flood landscape.
3. Examine the field establishment and reproductive success of recorded taxa to assess their potential for local persistence.

Through this case study, we seek to shed light on the long-term ecological legacies of trade-related plant introductions and demonstrate how historical pathways remain relevant under modern disturbance scenarios.

Materials and methods

Study area

The Vesdre River is about 70 km long and forms the northern border of the Ardennes. It belongs to the basin of the Meuse River and runs almost entirely through the province of Liège (eastern Belgium) (Figure 1). Its main

tributaries are the Ghete, the Helle, the Gileppe and the Hoëgne. The river successively crosses cities such as Eupen, Limbourg, Verviers, Pepinster, Trooz, and Chaudfontaine and finally flows into the Ourthe in Chênée near Liège. About three kilometers further on, the Ourthe flows into the Meuse. The Vesdre rises in the Fagnes de Steinley at an altitude of 605 m and flows into the Ourthe at an altitude of 70 m. The basin covers about 700 km² and the population density is 429 people/km² (Gettel et al. 2011). The Vesdre valley is a mosaic of urbanized zones, industrial relics, and semi-natural riverbank habitats. Land use is dominated by urban development in Verviers and surrounding towns, with patches of abandoned industrial sites and transitional zones along the river. These are often colonized by ruderal and pioneer vegetation. The floodplain features gravel and sand bars, riparian thickets, and disturbed soils – conditions particularly favourable to the germination of buried diaspores.

The Vesdre River valley has a temperate oceanic climate (a Cfb climate type), featuring cool to warm summers and cool to mild winters, with a relatively narrow annual temperature range and few extremes of temperature. In Verviers—the main town in the valley—mean annual temperature (1991–2020) was 10.2 °C, with average maxima and minima of 14.1 °C and 6.4 °C, respectively (www.meteo.be). On average, there are 8.4 days per year with maximum temperatures below 0 °C, and 56.4 days with minimums below freezing. The last and first frost dates average 14 April and 6 November. There are 6.5 hot days (≥ 30 °C) per year. Annual precipitation totals 1,002.5 mm, spread over 148.7 days, and is evenly distributed throughout the year.

Fieldwork

Fieldwork was conducted between July and December 2022 and from April to October 2023. Approximately 50 sites were surveyed, selected in a targeted manner using recent aerial imagery, Google Maps, and local knowledge. Selection was based on the likelihood of finding wool aliens, i.e. locations that had been significantly disturbed by the 2021 floods and where conditions favoured seed germination – particularly the presence of exposed sandy or gravelly substrates. Heavily wooded stretches or undisturbed valley sections were excluded from the survey, as they were considered unlikely to yield results. The study area focused on the river stretch downstream from the former wool-processing industries, from Goé (Limbourg) to the Vesdre's confluence with the Ourthe near Liège, covering more than 40 km. Additionally, a few temporary debris storage areas—located outside the main survey zone, such as in Eupen and Theux (along the Hoëgne River)—were also inspected (Figure S2). The locations that yielded the most species were the following:

- 1) Goffontaine (Pepinster): recently developed nature reserve, after excavating soil, on the left bank of the river, right in front of the water treatment plant (Figures S3–S4);
- 2) Chaudfontaine: leveled soil at the former swimming pool, right bank of the river;
- 3) Pepinster (Les Mazures): a vacant piece of land along the river of over 12,000 m² on which waste, including river sediment, was dumped after the floods;
- 4) Verviers: several localities in the city (e.g., quai de la Vesdre, upstream of rue Renier, rue de l'Épargne, etc.; Figure S5). The site of the Traitex wool mill, the only one that is left that is still active, was also visited (Figure S6);
- 5) Ensival (Verviers): demolition site of the former manufacturer of textile machinery Houget-Duesberg-Bosson, located next to the river;
- 6) Dolhain (Limbourg): muddy bank of the river.

Taxon selection and definition of “wool aliens”

A taxon was considered a putative wool alien if it met the following criteria: 1) seed ecology (long-lived or dormancy-prone seeds capable of surviving in fleece, dung, or sediment), 2) historical precedent (documented as a wool alien in the Vesdre valley or similar regions in Europe), and 3) biogeography (native to regions historically exporting wool to Belgium and known to occur in sheep pastures). Species introduced through other pathways (e.g., ornamental horticulture) or lacking plausible links to wool trade were excluded. Species were considered non-native if their presence in the study area was due to human-mediated dispersal beyond their native range.

Identification and taxonomic verification

Most specimens were identified by the authors using regional floras or taxonomic monographs relevant to the species' presumed native range. Where needed, expert consultations were conducted (see Acknowledgements). In selected cases, molecular identification (DNA barcoding) was applied to confirm uncertain identities.

Taxonomic names were checked and standardized using Plants of the World Online (POWO 2024). Synonyms were harmonized, and accepted names are used consistently in the manuscript and Table S1.

Data recording and specimen collection

Nearly all taxa were collected as herbarium specimens and deposited in the herbarium of Meise Botanic Garden (BR). Records were also registered in the observations.be citizen science platform (<https://observations.be/>). Plants were typically collected at flowering or fruiting stage. Where only a

single individual was present, or if flowering was unlikely due to seasonal timing or herbivory (e.g., by *Sus scrofa*, *Capreolus capreolus*, or *Branta canadensis*), specimens were carefully excavated for ex situ cultivation.

Data compilation and analysis

A complete list of all recorded taxa is provided in Table S1, along with key biological, geographical, and ecological attributes. These include: accepted species names (primarily based on POWO 2024), relevant synonyms, taxonomic authorities, plant families (following APG IV 2016), and biogeographic origin (natural and introduced range). Maximum life stage observed (vegetative, flowering, fruiting), including ex situ development if applicable, is also reported.

Non-native status was assessed based on documented occurrence as a wool alien in Belgium, Central Europe, and the UK (Probst 1949; Clement and Foster 1994; Verloove 2006), and on previous records as a non-native species elsewhere in Europe (based on GBIF).

Randall's (2017) *Global Compendium of Weeds* was used as the primary source for weed status because it is the only available, comprehensive global database that systematically lists all species ever recorded as weeds—regardless of context or severity—anywhere in the world. While broad in scope, it provides a standardized reference point for assessing global weed recognition across diverse regions and sectors. This inclusive definition does not align directly with ecological frameworks of invasiveness (e.g., Richardson et al. 2000; Blackburn et al. 2011; Soto et al. 2024).

For biogeographic classification, taxa were assigned to regions using the World Geographical Scheme for Recording Plant Distributions (Brummitt 2001), with manual correction of known inconsistencies in distribution records.

A comparative analysis was then performed to identify dominant biogeographic source regions and taxonomic patterns among the recorded wool aliens in the Vesdre valley.

Results

We identified 178 taxa from 16 families (Table S1; Figure 2A). Some species not previously recorded as wool aliens in Europe are illustrated in Figure 3A–J.

The most represented family was Malvaceae (71 taxa, 40% of all taxa), followed by Fabaceae (48 taxa, 27%), together accounting for nearly 70% of all recorded taxa. Other families with notable numbers of taxa included Juncaceae (15 taxa, 8%), Geraniaceae (12 taxa, 7%), and Convolvulaceae (10 taxa, 6%). The remaining families were represented by fewer than 10 taxa each.

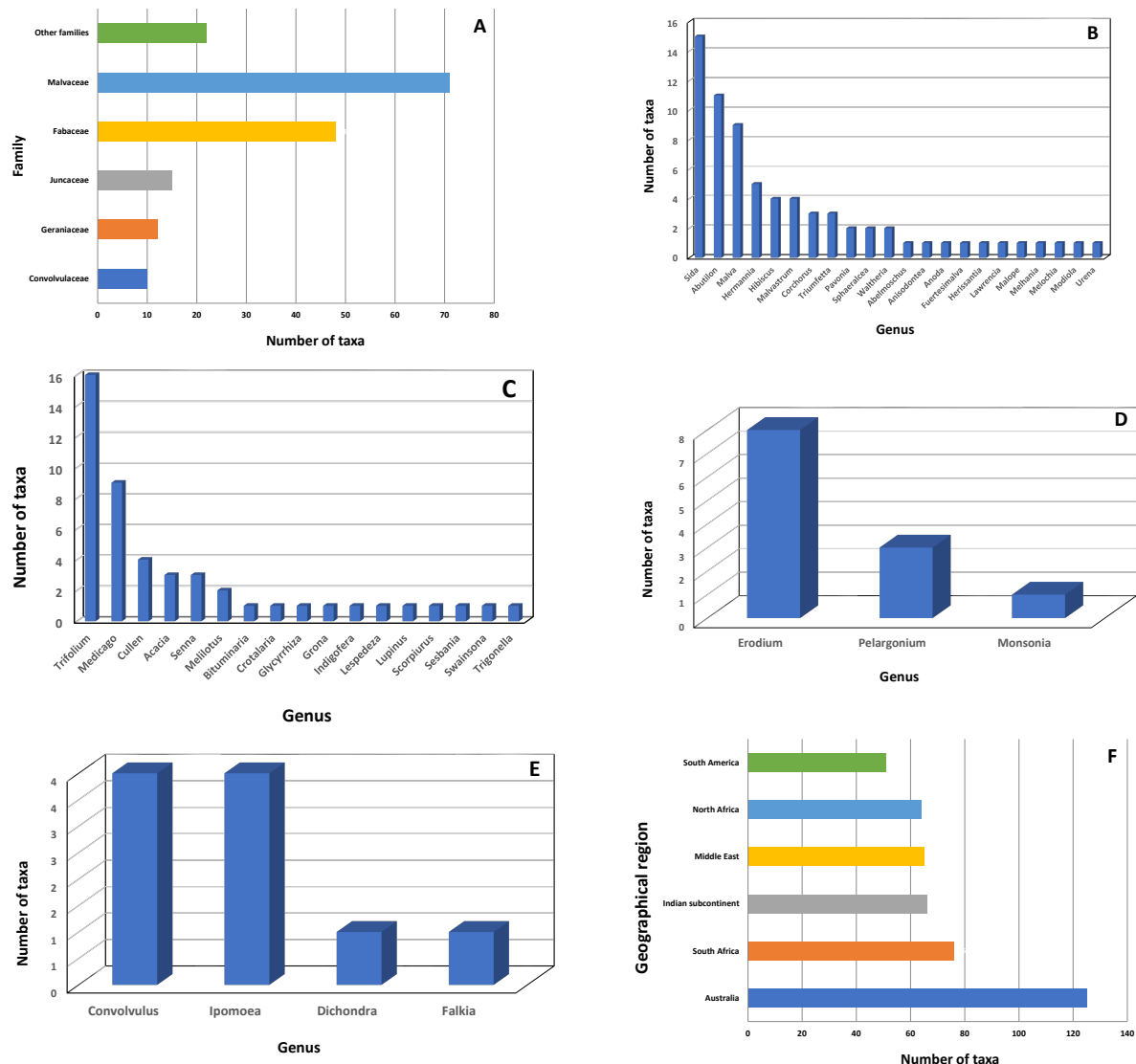


Figure 2. A. Taxonomic structure of the wool alien flora from the Vesdre River (Belgium) after the 2021 floods. B–E. Number of taxa per genus found as wool alien along the Vesdre River after the 2021 floods: Malvaceae (B), Fabaceae (C), Geraniaceae (D) and Convolvulaceae (E). F. Biogeographical origin of the wool alien flora from the Vesdre River after the 2021 floods, based on the World Geographical Scheme for Recording Plant Distributions (Brummitt 2001).

At the genus level, 22 genera were identified within Malvaceae, with *Sida* (15 taxa) and *Abutilon* (11 taxa) particularly well represented (Figure 2B). Fabaceae included 17 genera, of which *Trifolium* (16 taxa) and *Medicago* (9 taxa) were most numerous (Figure 2C). Juncaceae was represented solely by *Juncus* (15 taxa), Geraniaceae by three genera with *Erodium* (8 taxa) being dominant (Figure 2D), and Convolvulaceae by four genera, with *Convolvulus* and *Ipomoea* accounting for four taxa each (Figure 2E).

Regarding geographic origins, the majority of taxa are native to or widely naturalized in multiple regions. Australia was the most frequent source (125 taxa, 70%), followed by South Africa (76 taxa, 43%). Other regions of origin include the Indian subcontinent (66 taxa, 37%), the Middle East (65 taxa, 37%), North Africa (64 taxa, 36%), and South America—particularly Argentina, Chile, Paraguay, and Uruguay—with 51 taxa (29%) (Figure 2F). Overlapping distributions across regions were common.

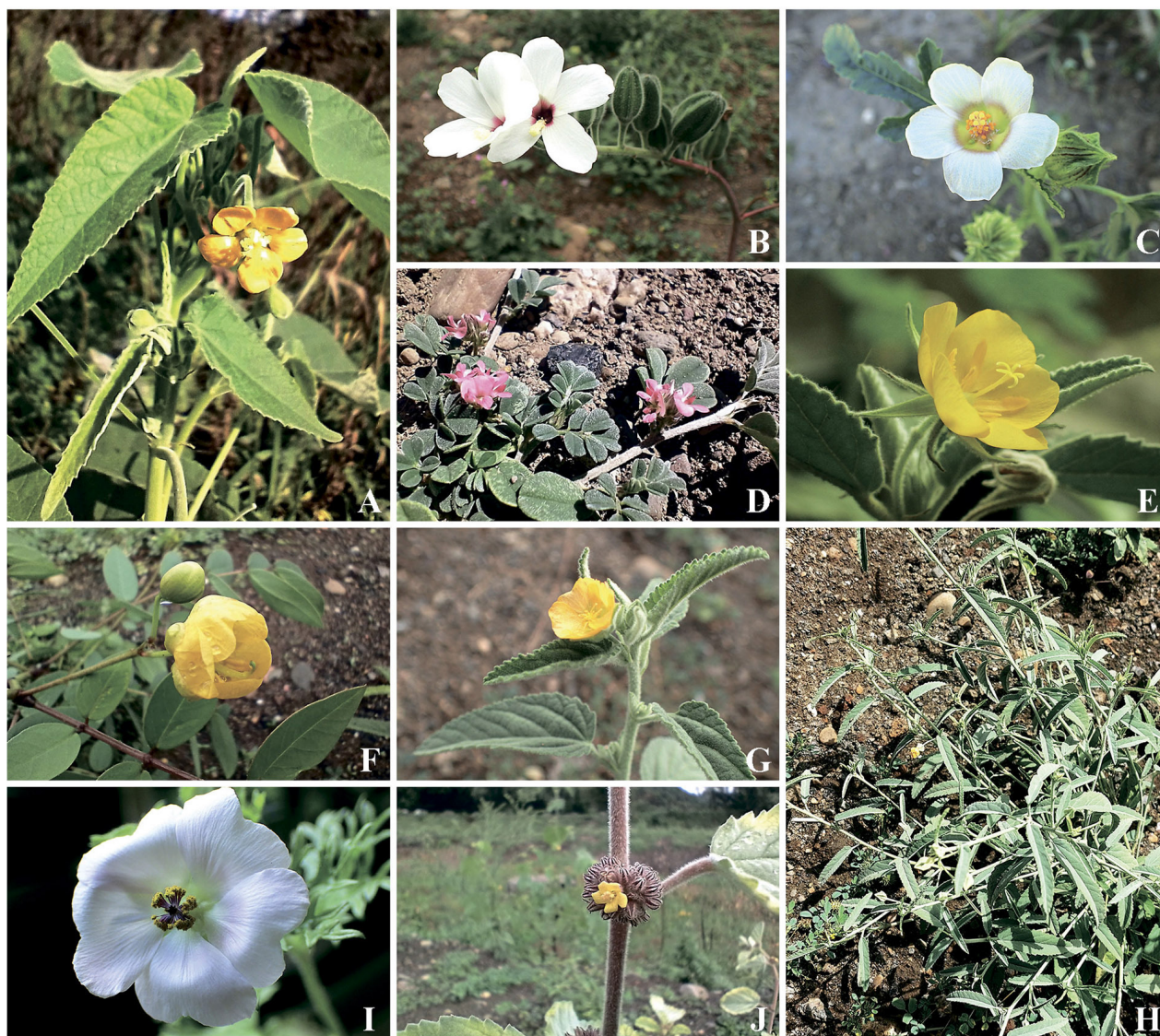


Figure 3. Wool aliens recorded in Goffontaine (Belgium) in late summer 2022: (A) *Abutilon oxycarpum*; (B) *Abelmoschus ficulneus*; (C) *Hibiscus verdcourtii*; (D) *Indigofera linnaei*; (E) *Melhania oblongifolia*; (F) *Senna planitiicola*; (G) *Sida atherophora*; (H) *Sida rohlenae*; (I) *Sphaeralcea purpurata*; (J) *Waltheria rotundifolia*. Photos by F. Verloove, S. Gonggrijp, and S. Valentini.

Of the 178 taxa recorded, 68 (38%) had never previously been reported in the wild in Europe. 113 taxa (63%) had not been recorded as wool aliens in Central Europe, and 127 taxa (71%) were previously unrecorded as wool aliens in Belgium.

The recorded taxa varied widely in ecological behaviour, but over 80% (143 species) are listed as weeds somewhere in the world, according to Randall's (2017) *Global Compendium of Weeds*. This includes both invasive species and taxa considered minor nuisances in agricultural or disturbed habitats.

Of the 178 recorded taxa, 110 (62%) reached reproductive maturity and produced seeds under field conditions. These include both annuals and perennials, with flowering and fruiting observed between July 2022 and October 2023.

Discussion

Taxonomic structure

A total of 178 wool alien taxa belonging to 16 families were identified. The family-level composition reflects a combination of ecological traits and historical processes. Five families (in order of importance: Malvaceae, Fabaceae, Juncaceae, Geraniaceae, and Convolvulaceae) accounted for the vast majority of taxa, with the Malvaceae (represented by 71 taxa) being particularly diverse.

All these families, except the Juncaceae, typically have species with water-impermeable “hard” seeds (Baskin et al. 2000). Seeds of species of Fabaceae, Malvaceae, Geraniaceae, and Juncaceae are known to be dispersed via epizoochory (e.g. Fischer et al. 1996; Benthien et al. 2016) and often form persistent soil seed banks (Thompson et al. 1997). Their predominance is consistent with the durability of their seeds, which are known to survive extreme conditions such as ingestion by animals (D’hondt and Hoffmann 2011), pathogen attack (Halloin 1983; Kremer et al. 1984), or high temperatures and chemical exposure during wool scouring. This resilience likely explains why many of these seeds remained viable for decades in sediment and germinated after the mechanical disturbance of the 2021 floods.

In contrast, no taxa were recorded from Asteraceae or Poaceae, the historically most species-rich families of European wool alien floras (Pyšek 2005), nor from other characteristic groups such as Apiaceae (Fabri and Lambinon 1991) or genera including *Acaena* (Yeo 1973), *Crassula* (Ryves 1975), and *Lepidium* (Ryves 1976–1977). The absence of these taxa most likely reflects the short-lived nature of their seeds, which—despite being common among historical wool aliens—did not persist in the seed bank long enough to reappear.

Within the Malvaceae, diversity was exceptional compared with historical data. Genera such as *Abutilon* (11 taxa; e.g. Figure 3A) and *Sida* (15 taxa; e.g. Figure 3G–H) far exceeded previous records from Central Europe and the British Isles, where only a few taxa of each were known (Probst 1949; Clement and Foster 1994). Particularly remarkable was the presence of five African *Hermannia* species, two of which likely represent undescribed taxa and none of which had ever been recorded in Europe before.

For other families, genus-level representation was broadly consistent with earlier surveys: *Erodium*, *Medicago*, and *Trifolium* were also well represented in historical wool alien floras in Belgium and elsewhere in Europe (Visé 1942, 1958; Clement and Foster 1994).

Seed survival and introduction pathways

The presence of the recorded species likely reflects a combination of source floras, seed traits, and the nature of the wool industry. The recorded species were present in the original source floras of the regions from which

the wool originated. Many of the taxa are known to occur in sheep pastures in Australia, South Africa, the Mediterranean, and other source regions.

Species with adaptations to epizoochory were likely overrepresented, as seeds transported in fleeces with spiny, hooked, or adhesive diaspores had a higher chance of being carried over long distances and deposited during wool-processing. Seeds also had to withstand the wool scouring process, which involved high temperatures and chemical treatments (Hayward and Druce 1919). Many species—particularly those with hard, protective seed coats—appear to have survived this procedure.

Furthermore, these seeds remained viable in the soil seed bank for decades. Direct discharge of wastewater into the Vesdre ceased in the second half of the 20th century, and the taxa observed in this study therefore likely originated from seeds buried in sediment for at least 50 years.

Following the 2021 floods, untreated wastewater from Traitex, the last operational wool mill, was temporarily discharged into the river. The absence of short-lived wool aliens, such as grasses and composites, suggests that these recent discharges did not contribute substantially to the flora. Several factors support this interpretation. First, the volume of imported wool today is negligible compared to historical levels. Second, although some preliminary cleaning may take place in the countries of origin, wool is still mainly scoured in Europe. Traitex currently processes almost exclusively European wool, primarily from the UK, France, Germany, and Italy (<https://www.traitek.be/>). Third, modern grazing systems involve fenced, intensively managed pastures with reduced botanical diversity due to herbicide and fertilizer use, competitive forage grasses, and overgrazing.

Together, these considerations indicate that the observed flora primarily emerged from long-lived diaspores in the historical seed bank rather than from recent contamination. The absence of short-lived wool aliens further supports this view.

Several non-native species were excluded because their seeds probably did not arise from the seed bank, e.g. *Xanthium* spp., whose short-lived seeds (Wapshere 1974) are thought to persist only temporarily in the environment or to have arrived through other pathways. Similarly, birdseed aliens [e.g. *Guizotia abyssinica* (L. f.) Cass., and less common species like *G. scabra* (Vis.) Chiov., *Ipomoea purpurea* (L.) Roth or *Setaria faberi* R.A.W. Herrm.], food refuse aliens [e.g. *Physalis grisea* (Waterf.) M. Martínez, *P. peruviana* L., *P. philadelphica* Lam., *Salvia hispanica* L., *Solanum lycopersicum* L., etc.], and escaped garden ornamentals [e.g. *Alcea rosea* L., *Papaver atlanticum* (Ball) Coss., *Verbena bonariensis* L.] were not included.

Conversely, some taxa recorded are native to Belgium but probably do not occur naturally in the study area, such as *Lythrum hyssopifolia* L. and certain *Medicago* and *Trifolium* species (Verloove and Van Rossum 2024).

Phenological and ecological constraints

Some long-lived taxa were underrepresented relative to other well-studied regions. For example, only a few Cyperaceae ($n = 7$) were recorded, with no *Carex* species at all and only five *Cyperus* species, compared to 11 and 21 species, respectively, reported as British wool aliens (Clement and Foster 1994). Many of these species are perennial and do not flower until the second year or later, and their habitats—muddy riverbanks subject to flooding and harsh winter conditions—may have limited survival and germination.

Even among taxa with long-lived seeds, some genera remained scarce or absent without clear explanation; for instance, *Trigonella* and *Vicia*, which are common wool aliens elsewhere (Probst 1949; Clement and Foster 1994), were largely missing.

Comparison between locations

In addition to phenological and ecological constraints, spatial variation within the study area also influenced species occurrences. Approximately 50 locations were surveyed across the study area, of which six were particularly species-rich and selected for more detailed observation (see Materials and Methods and Figure 1). These six locations encompassed a range of habitat types and land uses, including a recently developed nature reserve (Goffontaine), leveled soils (Chaudfontaine), river debris deposition areas (Pepinster, Les Mazures), urban riverbanks (Verviers), demolition sites (Ensival), and muddy riverbanks with characteristic Juncaceae and Cyperaceae vegetation (Dolhain).

Overall, the composition of non-native taxa was broadly similar across the six sites. Minor differences were mostly related to habitat-specific microenvironments – for example, muddy banks favoured sedges and rushes, while disturbed soils in urban or debris-deposition sites hosted a wider mix of herbaceous taxa. Goffontaine yielded a substantially higher number of taxa and included several taxa not recorded at other sites. This higher richness likely reflects a combination of factors: the excavation of a small valley created both moist and dry microhabitats, and additional soil removal during the development of the nature reserve may have exposed a larger portion of the long-lived seed bank than at other sites, where soil disturbance was more superficial. These findings highlight how local habitat heterogeneity and disturbance intensity can influence the emergence of wool alien taxa, even when species composition is largely similar across sites.

Biogeographical origin

The majority of observed wool aliens are native to or widely naturalized in Australia and South Africa (70 and 43% of all taxa, respectively), followed by species from the Indian subcontinent, the Middle East, North Africa,

and South America (particularly Argentina, Chile, Paraguay, and Uruguay). Notably, 46 taxa (26%) are endemic to Australia and/or New Zealand and not naturalized elsewhere, and 12 taxa to South Africa, confirming these regions as the principal sources of introduction.

Biogeographical origin was determined from current native and introduced ranges (POWO 2024) and assigned to global regions following the World Geographical Scheme for Recording Plant Distributions (Brummitt 2001). Current ranges do not necessarily reflect the original wool source or dispersal routes, and some attributions involve uncertainty. For example, several taxa occur in India, yet historical data indicate limited wool imports from the Indian subcontinent. Actual sources may lie elsewhere within broader native or naturalized ranges, or result from cross-contamination during storage and transport.

A few species are difficult to explain biogeographically. *Dracocephalum parviflorum* (North America) and *Erodium stephanianum* (Central Asia) originate from regions for which Visé (1942) explicitly asserted there was no wool import into the Vesdre valley during his period of activity. To our knowledge, there are no archival or trade-data sources confirming substantial wool shipments from North America prior to or in the early 20th century. Nonetheless, the identification of these species is reliable, and both have previously been recorded as wool contaminants in other parts of the world (e.g., Clement and Foster 1994; Angelo and Boufford 2014).

These cases might result from several, non-exclusive scenarios: cross-contamination during storage or shipment of wool sourced from multiple countries; later introductions via other pathways; or mislabelling or misreporting of origins in archival records. For instance, agricultural or garden soil, grain imports, or trade in other raw materials might have allowed small numbers of diaspores to reach the Vesdre valley.

While the wool industry historically dominated the region, other sectors such as grain milling were also active, as evidenced by the occasional presence of grain aliens (e.g., van Ooststroom and Reichgelt 1961). Small quantities of diaspores could have entered via agricultural commodities, eventually joining the buried seed bank. We consider such alternative routes exceptional, but acknowledge them as possible hypotheses in absence of direct proof.

Comparison with historical European wool alien floras

Approximately 1,600 wool alien species have been recorded in Europe over the past century (Sukopp 1972, largely based on Probst 1949). In the British Isles alone, the number is estimated to be around 800 taxa (Stace and Crawley 2015). It is important to note that historical surveys covered a long time span and captured a broad range of species, including those with short-lived diaspores. In contrast, the taxa recorded in the present study

were limited to those with particularly resilient, long-lived diaspores. Despite this constraint, the diversity we recorded in just two growing seasons (2022–2023) is striking. In total, 178 taxa were recovered (see Results), many of which had not previously been recognized as wool aliens in Europe. Several species were even entirely new to the European wild flora, while others had only been introduced via different pathways such as contaminated grain. This indicates that the wool pathway still harboured considerable undocumented diversity.

Compared to historical studies, our results suggest that past wool alien floras may have been underdocumented. Earlier surveys, though extensive, relied mainly on observations shortly after introduction. The excavation and disturbance of sediments in the Vesdre valley exposed diaspores that had persisted for decades, allowing a unique window into a “hidden archive” of non-native propagules. This highlights the importance of considering seed longevity when reconstructing introduction histories.

Weediness and invasion risk

The majority of the taxa recorded are listed as weeds somewhere in the world according to Randall’s (2017) *Global Compendium of Weeds*. This classification is broad and heterogeneous, encompassing both highly invasive species and taxa that are only minor nuisances in agricultural or disturbed environments (cf. Soto et al. 2024). As such, it does not equate to invasiveness per se, but rather signals that these species have demonstrated weedy behaviour under certain conditions.

Nevertheless, the high proportion of weedy taxa underscores the risks associated with wool as a historical introduction pathway. Among the recorded taxa, some are well-known invaders with significant ecological or economic impacts. *Acacia mearnsii* De Wild. (de Wit et al. 2001), for instance, is one of the world’s worst invasive trees, and *Lespedeza juncea* (L.f.) Pers. is currently listed as an invasive species of Union Concern (Verloove et al. 2023). Others are more modest in impact, occurring only locally or under specific environmental conditions.

This pattern aligns with broader invasion biology frameworks. According to the IPBES (2023) assessment, unintentional transport via trade and raw materials is a major driver of species introductions, with propagule pressure and disturbance being key determinants of establishment success. The Vesdre case provides a clear illustration: wool unintentionally carried a diverse and risk-prone seed load, and large-scale soil disturbance following the floods created the conditions for their emergence.

Importantly, it should be noted that more than 100 of the recorded taxa ($n = 110$; Table S1) successfully produced seeds in situ. This suggests that even in the absence of new introductions, several wool alien taxa could persist locally through seed banks. This also underlines the importance of post-disturbance monitoring, even when historical introduction pathways have ceased.

While this specific pathway has now become obsolete in western Europe, similar risks persist wherever unprocessed wool or other raw commodities are traded internationally (EPPO 2009).

Narrow endemics and undescribed taxa

In addition to widespread weedy taxa, a subset of the flora consists of narrow-range endemics or species that had not yet been formally described at the time of their introduction. These findings are particularly relevant from a biogeographical and historical perspective, as they offer direct evidence of the specificity of wool trade connections with remote source areas.

An examples includes *Abutilon nobile* Domin, endemic to central Queensland. Even more remarkable are taxa completely unknown to science at the time they were introduced. *Sida sivarajanii* Tambde, Sardesai & A.K. Pandey, a narrowly distributed species of the Indian subcontinent, was only recently formally described (Tambde et al. 2020). These also include e.g. *Hibiscus verdcourtii* (Craven et al. 2011), several *Convolvulus* and *Juncus* species from Australasia, as well as *Sida brachypoda* (Holland and Reynolds 1988). The same pattern was historically observed in the UK and elsewhere: a number of wool aliens were described as new species solely based on their presence in imported material (e.g., *Chenopodium auricomiforme* Murr & Thell., *Lepidium fallax* Ryves, *L. peregrinum* Thell., *L. pseudodidymum* Thell., *Millotia depauperata* Stapf, *Stipa brachychaeta* Godr. [now *Amelichloa brachychaeta* (Godr.) Arriaga & Barkworth] or *Thellungia advena* Stapf (Godron 1853; Stapf 1910; Thellung 1913; Murr and Thellung 1915; Stapf 1920; Ryves 1976–1977). Such records indicate that sheep grazed not only in common pasturelands but also in botanically unique, often isolated ecosystems – sometimes beyond easy human reach.

Interestingly, similar observations were made in the present study, where several taxa appear to be undescribed: a *Medicago* likely originating from the Middle East, and two South African species of *Hermannia*. These discoveries demonstrate the unexpected floristic value of historical industrial seed banks and justify further taxonomic investigation.

While this material is now dormant in most former wool-processing regions, the Vesdre valley provides a rare opportunity to reconstruct the hidden diversity of past trade networks and the diaspores they carried.

Morphological traits

As expected, many taxa are susceptible to epizoochory, i.e. they are adapted for dispersal by hairy animals. They either have needle-like fruits (e.g. *Erodium*, *Monsonia*, *Pelargonium*), fruits or mericarps bearing spines, often barbed or with hooked apices (e.g. *Medicago*, *Pavonia urens*, *Sida*, *Triumfetta*), bristly or spiny fruiting heads that stick to animal fur in their entirety (e.g. *Datura*, *Ibicella*, *Trifolium*), mucilaginous seeds (all species of

Juncus but also e.g. *Acacia*, *Melochia corchorifolia*) or sticky vegetative parts (e.g. *Glycyrrhiza*).

However, some species lack obvious dispersal armature. Hayward and Druce (1919) suggested that such species relied upon the easily dehiscent fruit and the smallness and abundance of their seeds which readily adhere to the greasy wool. Stace and Crawley (2015) added that seeds could also enter wool via dried dung from sheep grazing pasture plants. Thus, epizoochory explains only part of the introduction; species without specialized dispersal traits could also become contaminants, provided seeds remained undigested after grazing. These were typically hard seeds with water-impermeable coats, known to resist digestion and survive long-term in soil seed banks (D'hondt and Hoffmann 2011).

Wool aliens: an obsolete pathway, or a hidden risk?

Historical relevance

During the peak of the wool-processing industry in the Vesdre valley (late 19th to mid-20th century), raw wool acted as a significant vector for the introduction of non-native plant species. Containing diaspores entangled in fibres or present in dried dung, wool waste was directly released into the river during the scouring process, facilitating large-scale unintentional introductions. The present study confirms the legacy of this pathway through the persistence of non-native taxa, some of which may still emerge from the seed bank under favourable conditions.

Current situation

Under present conditions, this introduction route appears largely inactive. Modern wastewater treatment facilities effectively eliminate diaspores, and direct discharge of untreated industrial water—once common—is no longer permitted. The sole remaining wool-processing facility in the area (Traitex) no longer poses a sustained introduction risk, although a brief exception occurred during the 2021 floods when untreated effluent may have entered the river. However, no evidence exists for new species introductions via this event.

Potential reactivation of related pathways

Although the traditional wool-based pathway is obsolete in western Europe, the unintentional spread of plant diaspores through organic materials remains a contemporary concern. Historically, wool waste (“shoddy”) was widely used as fertilizer, especially in orchards and gardens, and played a documented role in the introduction of non-native species, notably in the UK (Lousley 1961; Shimwell 2006).

Today, the use of wool by-products in agriculture and horticulture is once again being promoted for its nutrient value and slow-release properties (Zheljaskov et al. 2009; Górecki and Górecki 2010; Bradshaw and Hagen 2022; Broda et al. 2023). Most commercial applications involve processed materials such as wool pellets, which likely undergo treatments that destroy seeds. However, anecdotal reports and promotional materials suggest that raw or minimally processed wool may still be used in some settings.

While this observation requires further verification, it raises the hypothesis that raw wool could again function as a vector – though not along riverbanks, but in gardens or agricultural fields, echoing earlier patterns. We stress that no direct evidence of contemporary introductions was found in this study, and the relevance of this pathway today remains speculative.

Implications for monitoring and management

The case of wool aliens provides a rare historical example of an industrial seed bank acting as a driver of non-native plant establishment. Although the specific pathway is no longer active, the broader lesson remains relevant: any raw organic material moved across biogeographic boundaries—be it wool, compost, or biofertilizer—has the potential to carry viable diaspores. This underlines the need for:

- Rigorous treatment and inspection protocols for organic amendments;
- Awareness of historical pathways that may resurface under new conditions;
- Early detection and monitoring strategies tailored to emerging introduction vectors.

In this sense, the Vesdre valley serves not only as a site of botanical curiosity but also as a cautionary case study in the long-term ecological implications of global trade in raw materials.

Concluding remarks

The reappearance of 178 wool alien taxa on the banks of the Vesdre River—decades after the cessation of wool-related seed input—provides rare and compelling evidence of the efficiency of wool as a historical vector for plant dispersal. The extraordinary taxonomic richness recovered highlights how the global wool trade acted as a powerful driver of species introductions, connecting remote source areas with European industrial landscapes.

Equally striking is the role of the long-lived soil seed bank. All of the observed taxa had persisted for more than half a century, with germination triggered only by the large-scale disturbance caused by the 2021 floods. This demonstrates how industrial diaspores can remain viable long after

their introduction, challenging assumptions about the completeness of past floristic surveys and emphasizing the importance of seed longevity in invasion dynamics.

Under current conditions, reintroduction of wool aliens via traditional industrial pathways is highly unlikely. Wool-processing in the region is now minimal, tightly regulated, and restricted to largely European sources. The historical seed bank thus remains a substantial reservoir for future germination, that has now been supplemented by recent seed production, ensuring its continued viability under favourable conditions.

Nevertheless, contemporary practices may recreate elements of this risk. Renewed promotion of wool waste as a natural fertilizer, whether in agriculture or horticulture, has the potential to reintroduce diaspores into new environments. While processed products such as pellets may be safe, the direct use of unprocessed wool could once again facilitate the spread of non-native taxa – this time not near textile mills, but across fields, orchards, and gardens.

Taken together, these findings underscore three key messages: wool was historically one of the most effective unintentional vectors of non-native plant dispersal; persistent seed banks can act as long-term legacies of past introductions; and modern practices, if poorly regulated, risk reactivating this pathway. Ongoing monitoring, research, and clear regulatory frameworks will be essential to prevent repeating the botanical consequences of the past.

Authors' contribution

Research conceptualization: FV, SG; sample design and methodology: FV, SG; investigation and data collection: FV, SG, SV; data analysis and interpretation: FV, SG, SV, RB, DGE, AP, FVDL, FL, ED; writing: original draft: FV; writing: review and editing: SG, SV, RB, DGE, AP, FVDL, FL, ED.

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Acknowledgements

The authors are indebted to the following people who confirmed or helped with the identification of particular species: Bill Barker (*Lawrenzia*; Australia), Massimo Bovini (*Sida*; Brazil), Thales Coutinho (*Waltheria*; Brazil), Robert Davis (*Swainsona*; Australia), Antoine Gazeix (*Lythrum*; France), David Halford (*Corchorus* and *Triumfetta*; Australia), Héctor Keller (*Sida*; Argentina), Phillip Kodela (*Acacia*; Australia), Isabel Larridon (*Afroscirpoides*; England), Marianne LeRoux (*Pelargonium*; South Africa), Bruce Maslin (*Acacia*; Australia), Daniel McNair (*Herissantia*; U.S.A.), Daniel Murphey (*Acacia*; Australia), Hiroyoshi Ohashi (*Desmodium* s.l.; Japan), Ashton Ruiters (*Pavonia*; South Africa), Matija Strlic (*Pelargonium*; South Africa) and Karen Wilson (*Juncus*; Australia). Otakar Šída (curator of the PR herbarium in Prague, Czech Republic) sent relevant images from the Domin herbarium and Julia Percy-Bower from the PERTH herbarium (Australia). Olivier Baltus and Philippe Guillaume (Service public de Wallonie) are thanked for providing useful information about potentially interesting localities for wool alien plants in the Vesdre River valley. The authors thank the anonymous reviewers for their constructive comments, which considerably improved a previous version of this manuscript. We thank Liliane Tytens (Meise Botanic Garden, Belgium) for preparing the photographic plate and improving the quality of the images. Finally, Mathieu Schmetz, a retired worker from the local wool mills, is thanked for sharing useful first-hand information.

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Supplementary material

The following supplementary material is available for this article:

Figure S1. Dolhain, abandoned wool mill on the banks of the Vesdre River, 6 September 2022, S. Valentini.

Figure S2. Pepinster, Forges Thiry, 6 September 2022, S. Valentini.

Figure S3. Goffontaine, 6 August 2022, F. Verloove.

Figure S4. Goffontaine, 6 August 2022, F. Verloove.

Figure S5. Verviers, the Vesdre River near Rue Renier, 16 July 2023, S. Gonggrijp.

Figure S6. Verviers, Traitex, view of wool bales, 4 August 2023, F. Verloove.

Table S1. Wool alien taxa observed after the 2021 floods on the banks of the Vesdre River (Belgium).

This material is available as part of online article from:

http://www.reabic.net/journals/mbi/2026/Supplements/MBI_2026_Verloove_etal_SupplementaryTables.xlsx

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