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## Prospects for the biological control of *Iris pseudacorus* L. (Iridaceae)

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*Keywords:* yellow flag iris, weed biological control, native-range explorations, agent selection, invasive alien aquatic plants (IAAPs), North-South collaboration.

## Prospects for the biological control of *Iris pseudacorus* L. (Iridaceae)

### Abstract

Native to Europe, North Africa and western Asia, *Iris pseudacorus* L. (Iridaceae) has invaded natural and human-modified wetlands worldwide. This species is considered a noxious weed in several countries including Argentina, South Africa and New Zealand. Its broad ecological tolerance, high resilience and reproductive potential make current mechanical and chemical control measures cost-ineffective, and biological control is considered a suitable alternative. In order to prioritize candidate biocontrol agents, a list of organisms reported to attack the plant within its native range has been assembled, and information about their host-range and damaging potential gathered from the literature. Furthermore, surveys for natural enemies of the plant were conducted in Belgium and northern Italy. The insect fauna associated with *I. pseudacorus* at the sites surveyed comprised mostly incidental visitors and polyphagous feeders, with the exception of the sawfly *Rhadinoceraea micans* Klug (Hymenoptera: Tenthredinidae), the seed weevil *Mononychus punctumalbum* Herbst (Coleoptera: Curculionidae), and the flea beetle *Aphthona nonstriata* Goeze (Coleoptera: Chrysomelidae). The potential of these species for biocontrol was evaluated, and *A. nonstriata* was given highest priority. A population of this species was imported to quarantine in South Africa, where it is currently undergoing host-specificity testing. Importation of the two remaining candidates is expected shortly. In conclusion, the prospects for the biological control of *I. pseudacorus* appear promising.

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*Keywords:* yellow flag iris, weed biological control, native-range explorations, agent selection, invasive alien aquatic plants (IAAPs), North-South collaboration.

## 1. Introduction

Biological invasions are of great concern for biodiversity conservation and ecosystem integrity (Vilà et al., 2010), especially when it comes to wetlands, which are particularly vulnerable to invasive aquatic plants (Stiers et al., 2011; Hussner et al., 2017). Yellow flag, *Iris pseudacorus* L. (Iridaceae), is a herbaceous perennial, emergent macrophyte native to Europe, North Africa and western Asia, considered invasive in natural and human-modified wetlands worldwide. In the wild, this species is commonly found inhabiting swamps, marshes, and shallow waters along the shores of lakes, ponds or slow-flowing watercourses (Sutherland, 1990; Kavak, 2014). Exported internationally as an ornamental plant, escape from cultivation is presumably the main pathway of establishment of this species outside of its native range (Morgan et al., 2020).

To date, *I. pseudacorus* is considered naturalized and often invasive in Canada, the United States, Argentina, Chile, Uruguay, South Africa, Japan, Australia and New Zealand (Cody, 1961; Howell, 2008; Masciadri et al., 2010; Ugarte et al., 2011; USDA-APHIS, 2013; Jaca & Mkhize, 2015; Hayasaka et al., 2018). Although first records of establishment outside of its native range date as far back as 1771 (Wells & Brown, 2000), recognition of its invasive status is far more recent (USDA-APHIS, 2013). In Argentina and New Zealand, this species was first observed in the wild in the 1930s, but has since spread over a wide geographic range invading various ecozones and habitat types (McGrannachan & Barton, 2019; Gervazoni et al., 2020). In South Africa, *I. pseudacorus* was first recorded as naturalised in 2004 (Jaca & Mkhize, 2015), but since then further introductions and local dispersion through water systems rapidly expanded its range, leading to its listing as a category 1A emerging invader (NEMBA, 2014).

In most of its introduced range, *I. pseudacorus* has been linked to a variety of ecological and socio-economic impacts (Jacobs et al., 2011; Jaca & Mkhize, 2015; Gaskin et al., 2016; Hayasaka

et al., 2018). This plant's rapid vegetative growth allows it to form dense, monospecific stands, which outcompete the native wetland vegetation resulting in a reduction of plant diversity and the loss of natural habitats for fish and waterfowl (Jacobs et al., 2011; Morgan et al., 2020). Furthermore, its rhizome system traps the sediment, progressively compacting the soil and altering the hydrology and functioning of aquatic ecosystems, which slowly shift towards drier, species-poorer habitats (Jacobs et al., 2011; Morgan et al., 2020). In the United States, *I. pseudacorus* flowers were observed to attract long-tongued flies and bumblebees, reducing pollination of native flowering plants (Dieringer, 1982).

Being disturbance-adapted, *I. pseudacorus* is often found in human-modified habitats such as meadows, wet pastures and artificial wetlands (Thomas, 1980; Stone, 2009; Jaca & Mkhize, 2015). In these suburban settings, infestations clog up irrigation channels and drainage ditches, increasing the risk of flooding and resulting in agricultural losses and high maintenance costs (USDA-APHIS, 2013). Additionally, the plant may pose a threat to domestic animals, as its leaves and rhizomes contain high concentrations of glycosides making it poisonous if ingested (Jacobs et al., 2011).

*Iris pseudacorus* is a resilient weed: adapted to a variety of natural and disturbed environments, it can tolerate drought, submersion, salt stress, low pH and long-term anoxia (Schlüter & Crawford, 2001; Blokhina et al., 2003; Mopper et al., 2016). Its thick, tuberous rhizomes retain the ability to develop into new plants even after fragmentation (Jaca, 2013). Nonetheless, sexual reproduction plays an important role in its spread, both in the native and invasive range (Lamote et al., 2002; Gaskin et al., 2016). Its buoyant seeds, carried by flowing water and flood events, have been observed to survive desiccation and retain most of their viability for over two years (Authors, unpublished data). Altogether, these characteristics make *I. pseudacorus* a difficult target for manual or mechanical removal, which seldom, if ever, results in its eradication (Jaca & Mkhize,

2015; Hill & Coetzee, 2017). Chemical control using glyphosate is currently adopted to manage the weed in some countries (Jacobs et al., 2011). However, large-scale herbicide application is regarded as environmentally undesirable, especially in proximity of water systems (Myers et al., 2016).

Following these considerations, classical biological control is considered a viable alternative for the long-term management of *I. pseudacorus* invasions. In 2016, the first biocontrol programme for this species was initiated in South Africa (Hill & Coetzee, 2017), and the option is now under consideration by other countries such as New Zealand and Argentina (McGrannachan & Barton, 2019; Gervazoni et al., 2020). Field surveys conducted throughout the South African invaded range found no specialized natural enemies attacking *I. pseudacorus* in the wild, whereas generalist insects were observed to cause only minor damage to the plant, leaving most herbivore niches unexploited (Authors, unpublished data). This supports the hypothesis that a lack of specialist herbivores may be among the factors determining the enhanced competitive ability of invasive *I. pseudacorus* populations in its invaded range, emphasizing the potential of biocontrol as a management option for this species (Blossey & Nötzold, 1995; Keane & Crawley, 2002). In this regard, the main objective of this study was to compile a list of organisms reported to attack *I. pseudacorus* within its native range, and conduct surveys of the insect fauna associated with the plant in an attempt to prioritize natural enemies as candidate biocontrol agents.

## **2. Materials & Methods**

### ***2.1 Literature review***

A comprehensive list of insect species reported to be associated with *I. pseudacorus* within its native range was compiled. Google, Google Scholar, Web of Science and CABI Invasive Species Compendium were searched using different combinations of the terms '*Iris pseudacorus*', 'yellow

flag iris', 'natural enemies', 'invertebrates', 'herbivores' and 'damage'. For each species, information regarding its geographic distribution, host-range and damage was gathered from the available literature and relevant online databases (Robinson et al., 2010; Pocock et al., 2015; Ellis, 2020).

## **2.2. Field surveys**

*Iris pseudacorus* has a widespread distribution in Europe and western Asia, being a common element of wetland ecosystems across different bioregions and climate types (Kavak, 2014). In the absence of specific information regarding the genetic and geographic origin of invasive *I. pseudacorus* populations, native range surveys followed an eco-climatic approach (Wapshere, 1985). In the invaded range, this species is found along the coasts of North America, southern Chile, north-eastern Argentina, Uruguay, South Africa, Japan, south-east Australia and New Zealand (GBIF, 2019), showing a marked preference for warm temperate climates (Cfa and Cfb for the greatest part, Csa and Cwb in minor proportions; Kottek et al., 2006). Accordingly, our surveys focused on humid areas of Belgium and northern Italy, as these share a similar climate to that invaded by the plant (Cfa and Cfb; Kottek et al., 2006). A total of 12 sites, spread across a variety of natural and human-modified habitats (IUCN, 2012), were visited multiple times between 2017 and 2018, covering different phenological phases of the plant (Table 1).

[Table 1 near here]

At each site, three *I. pseudacorus* plots (1m<sup>2</sup> each, at least 10m apart from each other) were sampled as replicates. Wetland plant species co-occurring with *I. pseudacorus* were identified within a 9m<sup>2</sup> quadrat around each sampling plot, and their contribution to the vegetation matrix was estimated following the DAFOR scale (Kent & Coker, 1992). Each quadrat was monitored

closely for 30 minutes, during which the insects found on *I. pseudacorus* were collected and observations were made on their presence on the co-occurring plant species.

Where possible, all parts of the plant (*i.e.* leaves, rhizomes, roots, flowers and seed capsules) were inspected. Insects were collected using aspirators, fine-mesh nets and soft tweezers. Samples of various plant parts were gathered for subsequent dissection and placed into Berlese funnels to facilitate invertebrates extraction. An attempt was made to rear immature insects to the adult stage in emergence boxes. All specimens were preserved in 90% ethanol and stored at 4°C in the dark. Identification was conducted via consultation with expert entomologists and taxonomists from the Royal Belgian Institute of Natural Sciences (RBINS). Finally, a population of a flea beetle species found feeding on *I. pseudacorus* in the field was reared in controlled conditions to observe its feeding behaviour and development on the plant.

### ***2.3. Species Accumulation Curves***

A species accumulation curve (SAC) represents the number of species present in a particular area or habitat as a function of the effort required to observe them (Colwell et al., 2004). As native range surveys for natural enemies are often prone to geographical and temporal limitations, SACs can be used as an informative tool to evaluate the adequacy of the sampling effort and highlight the need for further investigations (Hortal et al., 2006). We constructed a SAC using a subset of herbivorous insects collected on *I. pseudacorus* during our surveys. Species occurring at only one sampling site and determined (from direct observations or literature review) not to feed on the plant were considered incidental visitors and excluded from the analyses.

Individual-based rarefaction curves were generated using the software EstimateS<sup>®</sup> (Version 9.1.0; Colwell, 2013). Non-parametric, incidence-based estimators were adopted to predict true species richness and evaluate the adequacy of our sampling effort. The Chao2 estimator classifies



rare species as occurring in exactly 1 (*uniques*) or 2 (*duplicates*) sampling units; the corresponding incidence-based coverage estimator (ICE) adds information based on species found in 10 or fewer units; whereas the Michaelis-Menten is an asymptotic estimator calculated as the mean score after 100 randomization (Chao et al., 2005; Hortal et al., 2006). These estimators were chosen as they are known to perform well in studies with small sample size (Hortal et al., 2006). A statistical extrapolation of the obtained species accumulation curve to three times its empirical size was also computed using a likelihood-based estimator with 95% bootstrap confidence intervals (Colwell et al., 2004).

#### ***2.4. Candidate(s) prioritization***

*Geographic distribution.* It was assumed that organisms with a broad native distribution, ranging across different climate zones and habitat types, would be able to adapt to a broader suite of environmental conditions and therefore be more likely to establish upon introduction in the invaded range (Blossey, 1995; Paynter et al., 2017). Accordingly, species known from literature to be widespread throughout *I. pseudacorus* native range, and that were observed to be most abundant during our sampling, were given higher priority.

*Damage type, timing and extent.* In order to achieve substantial control over time, biocontrol agents should be able to decrease the density of their host and increase its susceptibility to biotic and abiotic stressors (Harris, 1973). *Iris pseudacorus* shows high stress-tolerance and competitive abilities, but studies investigating the mechanisms behind its competitiveness are scarce. This plant exhibits a fast foliar growth in early spring (Sutherland, 1990), which some authors have linked with overshadowing of smaller plants (Hayasaka et al., 2018). During summer, when leaves reach maximum height and photosynthetic activity peaks, resources are allocated to rhizomes and roots growth (Sutherland, 1990). Belowground biomass constitutes the greatest part of the total biomass,

and has been observed to reach over 99% in plants grown in controlled conditions (Mopper et al., 2016). This characteristic, often linked with the resilience of this species (Sutherland, 1990), could enhance its ability to compete for space and resources. Degradation of the rhizome, typically occurring after 6-15 years, was observed to be strongly accelerated by mechanical damage, especially in wet soils (Sutherland, 1990). Following these considerations, priority was given to organism able to exert a significant pressure on newly emerged leaves and rhizomes of the plant, either by being individually damaging or through high and sustained infestation levels (Wapshere, 1985). Nonetheless, as *I. pseudacorus* is known to disperse both clonally and sexually, attention was paid to select also enemies attacking its reproductive structures. Candidates were classified based on damage type, timing and extent, which were assessed qualitatively in the field and verified from literature sources, when available.

*Inferred host-range.* The family Iridaceae differentiated during the late Cretaceous or early Tertiary and appears phylogenetically isolated within the order Asparagales (Goldblatt, 2000). The genus *Iris* (sub-family Iridoideae) diversified from the sub-Saharan African clades of the tribe Iridae (*i.e.* *Dietes*, *Bobartia*, *Ferraria* and *Moraea*) ca. 45mya, and its distribution is now restricted to temperate regions of the Northern Hemisphere (Goldblatt et al., 2008). Australian and Neotropical Iridaceae show an even higher degree of phylogenetic separation from *I. pseudacorus* (Goldblatt et al., 2008), putting them at a lower risk from strictly host-specific biocontrol agents (Briese, 2005). Information regarding the host-range of each organism reported or observed attacking *I. pseudacorus* within its native range was gathered from the literature and supplemented with field observations. Organisms recorded uniquely on species within the genus *Iris* were selected as potential biocontrol agents, and priority was given to those believed to feed and develop solely on *I. pseudacorus*.

### 3. Results

#### 3.1. Literature review

Sutherland (1990) reports 22 invertebrates and 11 pathogens reported to attack *I. pseudacorus* from the literature. This list was updated by McGrannachan & Barton (2019) to include records of 36 arthropods and 67 fungi worldwide. Our review focused only on invertebrates, finding 42 insect species associated with *I. pseudacorus* within its native range (Table 2). The majority of these species are reported to be polyphagous and were therefore considered unsuitable as potential biocontrol agents. A total of 11 species were however given further consideration based on their known host-range and damage potential (Table 2). These were the thrips *Iridothrips iridis* Watson (Thysanoptera: Thripidae); the aphid *Aphis newtonii* Theobald (Hemiptera: Aphididae); the flea beetle *Aphthona nonstriata* Goeze (Coleoptera: Chrysomelidae); the seed weevil *Mononychus punctumalbum* Herbst (Coleoptera: Curculionidae); the sawfly *Rhadinoceraea micans* Klug (Hymenoptera: Tenthredinidae); the scarce marsh neb *Monochroa divisella* Douglas (Lepidoptera: Gelechiidae); the noctuid moths *Amphipoea crinanensis* Burrows and *Oxytripia orbiculosa* Esper (Lepidoptera: Noctuidae); the leaf-mining flies *Cerodontha iraeos* Robineau-Desvoidy and *C. iridis* Hendel (Diptera: Agromyzidae); and the gall midge *Dicerura iridis* Kaltenbach (Diptera: Cecidomyiidae).

[Table 2 near here]

#### 3.2. Field surveys

The surveys for natural enemies of *I. pseudacorus* took place during the spring and summer months in Europe, at sites where the plant was growing naturally. The sites surveyed were located mostly within marshes, swamps and lentic systems (natural and artificial ponds and lakes), with

only a few occurring on the shores of streams or canals. In the field, *I. pseudacorus* was observed in isolated patches and in admixture with native wetland plants (Table 1).

A total of 34 herbivorous insect species were recorded on *I. pseudacorus* during our surveys (Table 3). These comprised five orders: Coleoptera (15 spp.), Hemiptera (8 spp.), Orthoptera (5 spp.), Lepidoptera (4 spp.) and Hymenoptera (2 spp.). The majority (ca. 65%) of these species were found dwelling on the leaves of the plant, whereas the remaining were recorded on flowers and fruits. Only one species emerged from the seed capsules collected in the field. Although no endophagous root feeders were recovered during our surveys, rhizome inspection highlighted the presence of feeding damage that was later attributed to the larvae of *A. nonstriata*, a flea beetle commonly associated with *I. pseudacorus* (see below, Section 3.4.).

[Table 3 near here]

### **3.3. *Species accumulation curves***

Of the 34 herbivorous species collected, 20 were encountered only at one sampling site and therefore considered incidental visitors. The remaining 14 species (used to compute species accumulation curves) made up between 64 and 93% of the total richness predicted by ICE (15 spp.), Chao 2 (14-17 spp.) and Michaelis-Menten (22 spp.) estimators (Figure 1). The S(est) curve nearly reached the asymptote at 14 spp., with statistical extrapolations indicating that a 3-fold increase in sampling effort would only yield 2 additional species. This suggests that ICE and Chao 2 predictions might represent better accuracy than Michaelis-Menten estimates, as observed in other studies dealing with small sample size (Hortal et al., 2006).

[Figure 1 near here]

### **3.4. *Candidate(s) prioritization***

Almost 80% (11 spp.) of the herbivorous insect species consistently associated with *I. pseudacorus* during our surveys were determined to be polyphagous and thus excluded from the prioritization process (Table 3). The three remaining species were the iris sawfly *Rhadinoceraea micans* Klug (Hymenoptera: Tenthredinidae), the seed weevil *Mononychus punctumalbum* Herbst (Coleoptera: Curculionidae), and the flea beetle *Aphthona nonstriata* Goeze (Coleoptera: Chrysomelidae) (Figure 2).

*Rhadinoceraea micans* larvae were recorded at two pond sites in Belgium. Despite the low abundance, individual feeding was associated with severe defoliation of the target plant, whereas no damage was observed on the neighbouring vegetation. To date, the host range of this species is believed to be restricted to *I. pseudacorus* (Price et al., 2005), although larval feeding is reported on other *Iris* species (Ellis, 2020). Native to central and northern Europe, *R. micans* adult females lay their eggs between the leaf sheaths of *I. pseudacorus* in spring, showing a preference for waterside plants (Halstead & Henricot, 2010). The larvae can be found feeding on the plant during a 3-4 week period in early summer, after which they burrow into the soil to overwinter at the prepupal stage (Boevé et al., 2013).

*Mononychus punctumalbum* was recorded at all sites visited during *I. pseudacorus*' flowering season in Belgium. Adults were observed feeding on flowers and fruits, perforating them with their rostrum and causing significant damage. Some of the holes in the fruits harboured pale-white eggs, covered in frass. After hatching, larvae consume the seeds of the plant and then pupate within the mature fruit. New adults exit the fruit in late summer, then crawl into the soil to overwinter (Gültekin & Korotyayev, 2012). This species has a wide distribution in the central and western Palearctic region, where it is recognized as an important factor limiting *Iris* spp. populations (Skuhrovec et al., 2017). All *Mononychus* species are known to develop exclusively on *Iris* spp.

and *M. punctumalbum* is reported to use *I. pseudacorus*, *I. germanica* L. and *I. spuria* L. as host plants, although adult feeding is recorded on other species within the genus (Gültekin & Korotyayev, 2012).

*Aphthona nonstriata* was the most common and abundant insect species encountered during our surveys. Present both in Belgium and northern Italy, adult flea beetles were observed across all habitat types surveyed. The presence of this species was associated with tangible levels of damage on *I. pseudacorus* leaves, especially evident during early spring when the population reaches the highest densities (Authors, pers. obs.). The peculiar furrow-like damage left behind by *A. nonstriata* adults is easily recognizable, and no other plant species showed signs that could be attributed to the feeding pattern of this species. *Aphthona nonstriata* is commonly found in wetland habitats of Europe and western Asia, but only reported in association with *I. pseudacorus* (Hubble, 2010; Baviera & Biondi, 2015). In controlled conditions, oviposition by adult females occurred a few centimetres below the soil surface, in close proximity to the plant stem. After hatching, larvae were observed to mine the plant stem downward, boring the external parts of the rhizomes and feeding within it (Figure 2). *I. pseudacorus* plants used to rear the flea beetles often suffered secondary infections and eventual rotting of the rhizome system (Authors, pers. obs.). At completed development, larvae exited the plant roots and pupated in the soil. New adults emerge gradually during the summer months (Steinhausen, 2005), exerting a low but sustained feeding pressure on the plant. These adults are believed to overwinter at the end of the summer (Biondi, pers. comm.). However, under controlled conditions, summer adults were able to oviposit and conclude another generation, indicating that warmer temperatures might allow the species to be multivoltine.

[Figure 2 near here]

#### **4. Discussion**

The native range of *I. pseudacorus* is vast, extending through most of Europe all the way to western Siberia, the Caucasus and the Middle East (Kavak, 2014). Our surveys, focused on wetland areas within the Atlantic and Continental bioregions of Europe, were intended to be a first, exploratory study of the insect fauna associated with this species. To our knowledge, field surveys to identify natural enemies of *I. pseudacorus* have not been conducted elsewhere within the native range of the plant. Given the geographical and temporal limitations of our study, further investigations should be carried across the species' native range to include other biogeographic regions (e.g. Mediterranean), climate types and habitats, as these are known to influence insect diversity (Goolsby et al., 2006). Research is already underway to elucidate the genetic origin of invasive *I. pseudacorus* populations and guide future studies. Our surveys found only a portion of the specialist natural enemies reported from the literature to attack *I. pseudacorus* within its native range. Among other factors, this could be attributed to i) the small geographic scale of the study; ii) asynchrony between sampling moments and period of activity of some species; or iii) the inability to access all parts of the plant at some locations. Nonetheless, the results of our SAC indicate that a significant proportion of the non-incident herbivorous insects predicted to occur on *I. pseudacorus* at the localities visited were encountered during our surveys, confirming the validity of our sampling effort.

Most of the herbivorous insect species recorded on *I. pseudacorus* were incidental visitors, polyphagous feeders or species associated with other plants occurring at the site (e.g. the loosestrife flower weevil *Nanophyes marmoratus* Goeze and the rush sawfly *Dolerus ferrugatus* Serville). After excluding them from the prioritization process, three remaining species were evaluated as potential biocontrol agents. Preliminary surveys of the insect fauna associated with *I. pseudacorus*

in South Africa found no sign of these species (Authors, unpublished data), but further analyses are needed to assess the presence of native analogues (Paynter et al., 2010).

The criteria applied for the prioritization of our agents have been employed in other studies (Paynter et al., 2017; Egli & Olckers, 2020) and are known to be good preliminary indicators of chances of establishment, potential level of control and risk of non-target attack (Goolsby et al., 2006). The three prioritized candidates possess several characteristics suggesting their potential as biocontrol agents. Larvae of the sawfly *R. micans*, despite being active only for a short period of time, are individually highly damaging and able to completely defoliate their host. By feeding on the leaves of *I. pseudacorus*, these larvae are believed to sequester secondary plant metabolites which are stored in the haemolymph as defence against predators (Boevé et al., 2013). This characteristic suggests a high acquired specificity and lower predicted chances of attack from generalist predators in the invaded range (Sheppard, 2002). However, toxicity testing should be considered to determine if these metabolites could pose a risk to domestic animals or wildlife upon ingestion (Boevé et al., 2018). Additionally, *R. micans* larvae bear a strongly hydrophobic cuticle which allows them to move on the water's surface to reach new plants (Voigt et al., 2011). This detail, coupled with the oviposition preference shown by adult females, makes them an interesting option for release in extremely wet regions invaded by *I. pseudacorus* (e.g. wetlands of Argentina; Gervazoni et al., 2020), where other species might have a problem establishing (Van Driesche et al., 2009).

The weevil *M. punctumalbum* is the only candidate that attacks the reproductive structures of the plant. Its capacity to limit *I. pseudacorus* seed production (Skuhrovec et al., 2017) is regarded as a valuable asset for halting the spread of the weed in the invaded range. Although seed-destruction alone is not expected to cause a decline in the current density or distribution of the



weed, long-term pressure by seed weevils was observed to reduce the hosts' reproductive fitness, hindering dispersal and limiting the insurgence of new invasions (Impson & Hoffmann, 2019). Future studies should investigate the seed production and field germination rates of *I. pseudacorus* across different ranges, in order to determine the potential of the weevil to control its spread (Clewley et al., 2012).

The flea beetle *A. nonstriata* was given highest priority in our study. The ability of root-feeding beetles to impact both the foliar and rhizome systems of their target is considered a fundamental resource to reduce invasiveness (Simelane, 2010). Other *Aphthona* spp. have been used in the biological control of leafy spurge (*Euphorbia esula* L.) in the U.S. and Canada, where root-boring larvae were observed to cause significant damage to the plant, sometimes leading to secondary fungal and bacterial infections (Caesar, 2003; Bouchier et al., 2006). Further research should investigate potential interactions between *A. nonstriata* and plant pathogens, as these could contribute to the effectiveness of biocontrol (Willsey et al., 2017).

In some instances, cumulative stress exerted by multiple agents was observed to greatly increase the level of control achieved on the target weed (Hoffmann & Moran, 1998). The organisms presented in this study are deemed complementary in attacking different parts of the plant at different times, decreasing its competitiveness and increasing susceptibility to external stressors. All three candidates are thus advised for further investigations, prioritizing *A. nonstriata* based on its widespread distribution, broad period of activity, damage duality and suspected monophagy. In 2017, a population of this species was collected from the Snoekengracht Nature Reserve (Verrijck - Belgium) and imported to the quarantine facility of the Centre for Biological Control, Rhodes University (Makhanda, South Africa), where it is currently undergoing host-specificity testing.

Although emerging invaders such as *I. pseudacorus* are often not the focus of biological control programmes, there have been significant successes against incipient weeds in the past (Olckers, 2004). The effectiveness of these programmes highlights the potential of implementing biocontrol during early stages of invasion, minimizing the impact of the weed and the costs required for its control (Mgidi et al., 2007). International cooperation and joint research projects strongly contribute to the success of these programs by allowing research to be conducted concomitantly within the native and invasive range of the weed (Olckers, 2004). In this perspective, the current project fits within a broader collaboration between research institutes in Belgium (Vrije Universiteit Brussel), South Africa (Centre for Biological Control, Rhodes University), Argentina (Centro de Ecología Aplicada del Litoral and Fundación para el Estudio de Especies Invasivas) and New Zealand (Landcare Research). Because of the global extent of *I. pseudacorus* invasion, the results obtained through this collaboration will contribute substantially to the implementation of sustainable management plans aimed at alleviating the impact of this species on wetland ecosystems worldwide.

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### Disclosure statement

No potential conflict of interest was reported by the authors.

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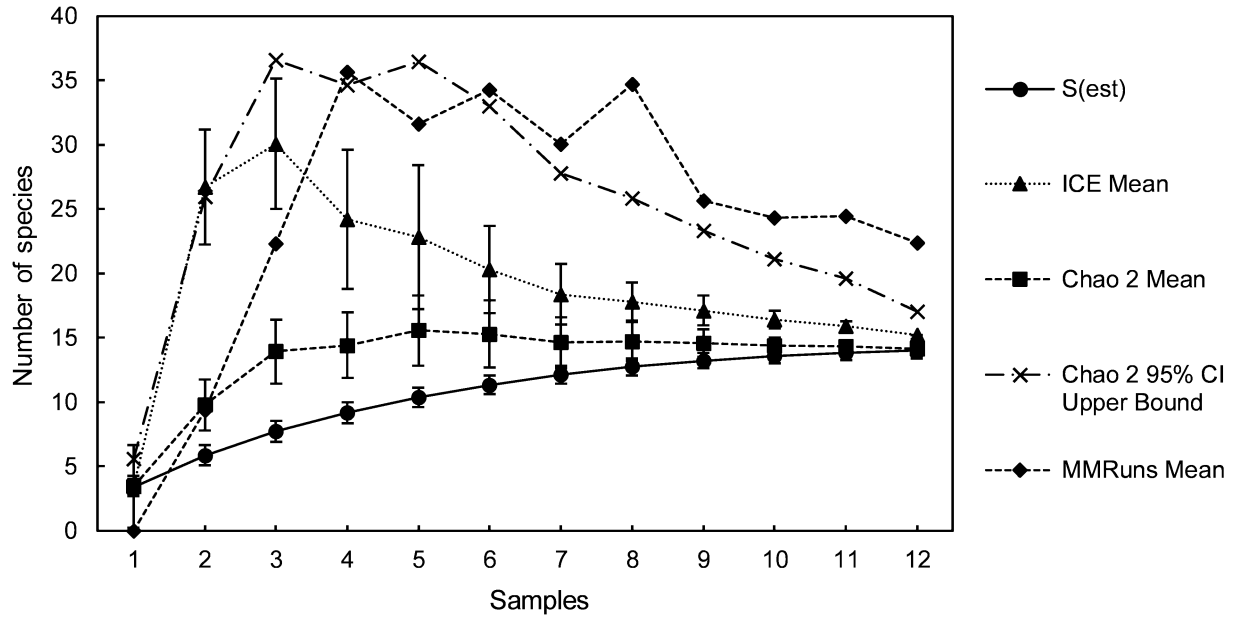
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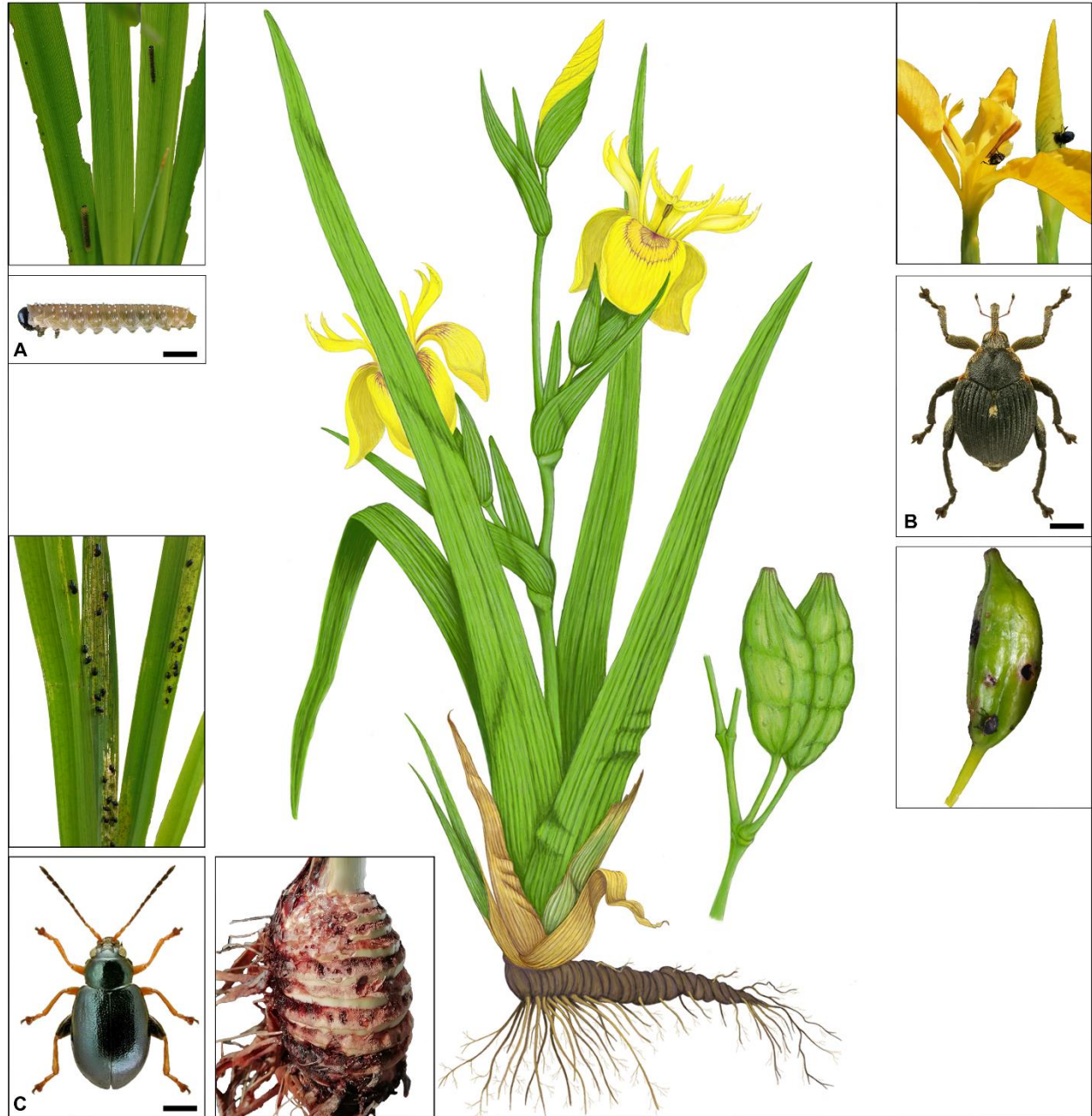
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# **Prospects for the biological control of *Iris pseudacorus* L. (Iridaceae)**

## **Figures & Tables**



**Figure 1.** Species accumulation curve of non-incidental herbivorous insect species associated with *Iris pseudacorus* at the sites surveyed in Belgium and northern Italy. Incidence-based Coverage Estimator (ICE Mean), bias-corrected Chao 2 (Mean and 95% CI Upper Bound) and Michaelis-Menten (MMRuns Mean) estimates are shown (error bars indicate standard deviation). When the rarefaction curve  $S(est)$  and the estimators converge at the highest observed richness, estimates can be considered as representative (Longino et al., 2002).



**Figure 2.** Schematic representation of the damage caused to *Iris pseudacorus* by the three agents prioritized in the present study. **A:** *Rhadinoceraea micans* larvae (bottom panel) feeding on *I. pseudacorus* leaves (top panel); **B:** *Mononychus punctumalbum* (central panel) damaging the flowers of the plant (top panel) and new adults emerging from the seed capsules (bottom panel); **C:** *Aphthona nonstriata* adult (central panel) feeding on the leaves of the plant (top panel) and holes bored in the rhizomes by its larvae (right panel). Size bars: A = 5mm; B = 1mm; and C = 0.5mm. Illustration of *I. pseudacorus* by Federico Banfi; iconographies of *A. nonstriata* and *M. punctumalbum* by Lech Borowiec; other pictures are property of the authors.

**Table 1.** Sites surveyed for natural enemies of *Iris pseudacorus* in the native range. Habitat types follow the IUCN Habitats Classification Scheme (IUCN, 2012). Common plant species (> 30% cover) co-occurring with *I. pseudacorus* at each site are listed from the most to the least abundant.

Country	Site coordinates	Habitat type	Visited	Plant species†
Belgium	50.835917, 4.435583	Artificial pond (15.2)	Jul 2017; Jun 2018	<i>Pa; Ls; Le</i>
Belgium	50.838000, 4.435583	Permanent stream (5.1)	Jul 2017; Jun 2018	<i>Eq; Ca; Tl</i>
Belgium	50.877417, 4.466611	Artificial pond (15.2)	Jul 2017; May 2018	<i>Ca; Tl; Ma; Ls</i>
Belgium	50.833889, 4.836417	Marsh (5.4)	Jul 2017; Apr 2018	<i>Ca; Ma; Eq; Tl; Pa</i>
Belgium	50.984889, 5.100417	Natural pond (5.7)	Jul 2017; May 2018	<i>Eq; Tl</i>
Belgium	51.088444, 5.306583	Permanent river (5.1)	Jul 2017; Apr 2018	<i>Eq; Tl</i>
Italy	45.885389, 8.794333	Swamp (5.7)	Aug 2017	<i>Pa; Ca</i>
Italy	45.800944, 8.783139	Lake shore (5.5)	Aug 2017	<i>Ca; Pa; Le</i>
Italy	45.912639, 8.825500	Lake shore (5.5)	Aug 2017	<i>Ls; Ma</i>
Italy	45.810750, 8.607944	Lake shore (5.5)	Aug 2017	<i>Ca; Pa; Ls; Le</i>
Italy	45.752889, 8.678722	Lake shore (5.5)	Aug 2017	<i>Pa; Ca; Le; Po; Eq</i>
Italy	45.898028, 8.827528	Swamp (5.7)	Aug 2017	<i>Pa; Ca</i>

† *Ca* = *Carex* spp.; *Eq* = *Equisetum* spp.; *Le* = *Lycopus europaeus*; *Ls* = *Lythrum salicaria*; *Ma* = *Mentha aquatica*; *Pa* = *Phragmites australis*; *Tl* = *Typha latifolia*.

**Table 2.** List of insect species reported to attack *Iris pseudacorus* within its native range (adapted from McGrannachan & Barton, 2019). Information regarding geographic distribution (de Jong et al., 2014), known host-range and damage type are provided.

Species	Distribution	Host-range	Damage
<b>THYSANOPTERA</b>			
<b>Thripidae</b>			
<i>Frankliniella intonsa</i> Trybom, 1895	Widespread in Europe	Polyphagous on herbs (Ellis, 2020)	Found mainly on flowers, larvae feed on the content of epidermal cells (Ellis, 2020)
† <i>Iridothrips iridis</i> Watson, 1924	Central and northern Europe	Only recorded on <i>I. pseudacorus</i> (Jenser, 2013)	Feeds and reproduces within submerged leaf sheaths of the plant (Jenser, 2013)
<i>Thrips flavus</i> von Schrank, 1776	Widespread in Europe	Polyphagous (Ellis, 2020)	Larvae and adults feed on flower buds (Ellis, 2020)
<b>HEMIPTERA</b>			
<b>Aphididae</b>			
<i>Aphis fabae</i> Scopoli, 1763	Widespread in Europe	Broadly polyphagous (Ellis, 2020)	Forms large colonies that can cause leaf deformation and eventual death (Ellis, 2020)
† <i>Aphis newtoni</i> Theobald, 1927	Widespread in Europe	Reported only on <i>Iris</i> spp. (Ellis, 2020)	Forms ant-attended colonies feeding at the base of the leaves and on the inflorescence (Ellis, 2020)
<i>Dysaphis tulipae</i> Boyer de Fonscolombe, 1841	Cosmopolitan	Polyphagous. <i>Iris</i> spp. being the most common hosts (Stekolshchikov, 2008)	Form colonies on leaves, flowers and fruits, later infest rhizomes (Stekolshchikov, 2008)
<i>Macrosiphum euphorbiae</i> Thomas, 1878	Cosmopolitan	Polyphagous. Considered a pest of various greenhouse and field crops (CABI, 2020)	Large infestations lead to stunted leaf growth, distortion, necrotic spots, etc. (CABI, 2020)
<i>Myzus ascalonicus</i> Doncaster, 1946	Cosmopolitan	Polyphagous (Blackman & Eastop, 2020)	Vector of plant viruses (Blackman & Eastop, 2020)
<b>Cicadellidae</b>			
<i>Metalimnus formosus</i> Boheman, 1845	Widespread in Europe	Recorded on <i>I. pseudacorus</i> , <i>Glyceria</i> , <i>Carex</i> and <i>Sphagnum</i> (Pocock et al., 2015)	No information available
<b>Cymidae</b>			
<i>Cymus glandicolor</i> Hahn, 1831	Europe and west Asia	Polyphagous. Associated with <i>Carex</i> spp. (Poelen et al., 2014)	No information available
<b>Myridae</b>			
<i>Adelphocoris ticinensis</i> Meyer-Dur, 1843	Europe and the Middle East	Polyphagous. Associated with <i>Lythrum</i> spp. and <i>Achillea</i> spp. (Hoessini, 2014)	No information available
<b>Rhyparochromidae</b>			
<i>Pachybrachius fracticollis</i> Schilling, 1829	Europe and west Asia	Polyphagous. Associated with <i>Carex</i> spp. (Poelen et al., 2014)	No information available

Species	Distribution	Host-range	Damage
<b>COLEOPTERA</b>			
<b>Chrysomelidae</b>			
† <i>Aphthona nonstriata</i> Goeze, 1777	Widespread in Europe and western Asia	Monophagous on <i>I. pseudacorus</i> (Baviera & Biondi, 2015)	Adults consume strips of epidermis parallel to the leaf nerves. Larvae descend as stem miners down to the rhizome where they continue as borers (Ellis, 2020)
<i>Plateumaris sericea</i> Linnaeus, 1758	Widespread in Europe and western Asia	Polyphagous. <i>Sparganium</i> spp. indicated as main hosts, but adults observed on a variety of wetland plants (Bukejs, 2010)	Adults often found on flower heads, so believed to be pollen feeders. Larvae feed on root-parts of the host plants (Ellis, 2020)
<b>Curculionidae</b>			
† <i>Mononychus punctumalbum</i> Herbst, 1784	Widespread in Europe and western Asia	<i>Iris pseudacorus</i> , <i>I. x germanica</i> L. and <i>I. spuria</i> L. reported as main hosts (Gültekin & Korotyaev, 2012)	Adults feed on flowers and fruits, causing visible deformations. Larvae develop within the fruit, feeding on the seeds (Skuhrovec et al., 2017)
<b>HYMENOPTERA</b>			
<b>Tenthredinidae</b>			
† <i>Rhadinoceraea micans</i> Klug, 1816	Restricted to central and northern Europe	<i>Iris pseudacorus</i> indicated as main host (Price et al., 2005), although larval feeding observed on other <i>Iris</i> spp. (Ellis, 2020)	Larvae are voracious leaf feeders that may cause severe defoliation (Halstead & Henricot, 2010)
<b>LEPIDOPTERA</b>			
<b>Erebidae</b>			
<i>Rhyarioides metelkana</i> Lederer, 1861	Central Europe	Polyphagous. Hosts include <i>Caltha</i> and <i>Mentha</i> spp. (Kučinić et al., 2014)	No information available
<i>Spilosoma urticae</i> Esper, 1786	Widespread in Europe	Polyphagous (de Prins et al., 2020)	Larvae are defoliators (de Prins et al., 2020)
<b>Gelechiidae</b>			
† <i>Monochroa divisella</i> Douglas, 1850	Central Europe	Reported only on <i>Iris</i> spp., primarily on <i>I. pseudacorus</i> (de Prins et al., 2020)	Larvae are leaf miners (Ellis, 2020)
<b>Geometridae</b>			
<i>Lycia zonaria</i> Schiffmuller, 1775	Central Europe	Polyphagous (Poelen et al., 2014)	Larvae are defoliators (de Prins et al., 2020)
<b>Glyphipterigidae</b>			
<i>Orthotelia sparganella</i> Thunberg, 1788	Widespread in Europe	Polyphagous. Hosts include <i>Sparganium</i> , <i>Glyceria</i> and <i>Typha</i> spp. (Ellis, 2020)	Larvae are leaf and stem miners (Ellis, 2020)
<b>Noctuidae</b>			
<i>Acronicta rumicis</i>	Widespread in Europe	Polyphagous (Poelen et al., 2014)	Larvae are defoliators (de Prins et al., 2020)

Species	Distribution	Host-range	Damage
Linnaeus, 1758			
† <i>Amphipoea crinanensis</i> Burrows, 1908	Central and northern Europe	<i>Iris pseudacorus</i> indicated as main host (Robinson et al., 2010)	Larvae are reported to feed inside the stems of the plant (Robinson et al., 2010)
<i>Celaena leucostigma</i> Hubner, 1808	Widespread in Europe	Polyphagous on helophytes (Ellis, 2020)	Larvae are leaf miners and stem/roots borers (de Prins et al., 2020)
<i>Globia algae</i> Esper, 1789	Widespread in Europe	Polyphagous on helophytes (Ellis, 2020)	Larvae are leaf miners and stem borers (Ellis, 2020)
<i>Globia sparganii</i> Esper, 1790	Widespread in Europe	Polyphagous on helophytes (Ellis, 2020)	Larvae are leaf miner and stem borers (Ellis, 2020)
<i>Hydraecia micacea</i> Esper, 1789	Widespread in Europe	Highly polyphagous (de Prins et al., 2020)	Larvae are stem and root borers (Ellis, 2020)
† <i>Oxytripia orbiculosa</i> Esper, 1799	Disjunct in southern and eastern Europe	Restricted to <i>Iris</i> spp., in particular <i>I.</i> <i>pumila</i> and <i>I. pseudacorus</i> (Ellis, 2020)	Larvae are leaf miner and later bore into the rhizomes (Ellis, 2020)
<i>Plusia festucae</i> Linnaeus, 1758	Widespread in Europe	Polyphagous (de Prins et al., 2020)	Larvae are defoliators (Pocock et al, 2015)
<i>Plusia putnami</i> Grote, 1873	Widespread in Europe	Polyphagous (Poelen et al., 2014)	Larvae are defoliators (Pocock et al, 2015)
<i>Xylena exsoleta</i> Linnaeus, 1758	Widespread in Europe	Polyphagous (Wagner, 2020)	No information available
<i>Xylena vetusta</i> Hubner, 1813	Widespread in Europe	Polyphagous (de Prins et al., 2020)	Larvae are defoliators (Pocock et al, 2015)
<b>Nymphalidae</b>			
<i>Coenonympha oedippus</i> Fabricius, 1787	Central Europe	Polyphagous. <i>Carex</i> and <i>Molina</i> spp. indicated as hosts (Bräu et al., 2010)	Larvae are defoliators (Bräu et al., 2010)
<b>Tortricidae</b>			
<i>Aphelia paleana</i> (Hübner, 1793)	Widespread in Europe	Polyphagous (Poelen et al., 2014)	Larvae are defoliators (Ellis, 2020)
<i>Clepsis spectrana</i> Treitschke, 1830	Widespread in Europe	Highly polyphagous (Ellis, 2020)	Larvae are defoliators (de Prins et al., 2020)
<i>Paramesia gnomana</i> Clerck, 1759	Widespread in Europe	Polyphagous (Poelen et al., 2014)	Larvae are defoliators (Ellis, 2020)
<i>Sparganothis pilleriana</i> Schiffermuller, 1775	Widespread in Europe	Polyphagous (de Prins et al., 2020)	Larvae are defoliators (de Prins et al., 2020)
<b>DIPTERA</b>			
<b>Agromyzidae</b>			



Species	Distribution	Host-range	Damage
† <i>Cerodontha iraeos</i> Robineau-Desvoidy, 1851	Widespread in Europe	<i>Iris pseudacorus</i> indicated as primary host. Larval mines reported on <i>Iris</i> , <i>Belamcanda</i> and <i>Gladiolus</i> spp. (Spencer, 1990)	Larvae create a short mine in the leaf blade, where pupation occurs (Spencer, 1990)
† <i>Cerodontha iridis</i> Hendel, 1928	Widespread in Europe	<i>Iris foetidissima</i> indicated as primary host. Larval mines reported on <i>I. pseudacorus</i> , <i>I. spuria</i> and <i>I. orientalis</i> (Spencer, 1990)	Larvae create a short mine in the leaf blade, where pupation occurs (Spencer, 1990)
<b>Cecidomyiidae</b>			
† <i>Dicerura iridis</i> Kaltenbach, 1873	Central and Northern Europe	Reported only on <i>I. pseudacorus</i> (Ellis, 2020)	Larvae feed through external digestion, causing a light discolouration of the leaf tissue (Ellis, 2020)
<b>Ceratopogonidae</b>			
<i>Atrichopogon pollinivorous</i> Downes, 1955	Central Europe	<i>Lonicera</i> spp. are indicated as primary hosts (Downes, 1955)	Adults are pollen feeders. Little is known on the feeding habits of the larvae (Downes, 1955)
<b>Syrphidae</b>			
<i>Eumerus strigatus</i> Fallen, 1817	Widespread in Europe	Polyphagous. Considered a pest of flowering plants (Ricarte et al., 2017)	Adults are pollinivorous. Larvae feed on bulbs and rhizomes causing rot (Kizil et al., 2008)

† Species to be given further consideration as potential biocontrol agents based on currently known host-range and damage type.

**Table 3.** List of herbivorous insect species recorded on *Iris pseudacorus* during surveys in Belgium and northern Italy. Incidence is expressed as percentage of sites at which the species was found. Abundance is the total number of individuals encountered during the survey. Position of the insect on the plant, life stage and known plant associations of each species are also indicated.

Species	Incidence	Abundance	Position	Life stage	Known plant associations
<b>ORTHOPTERA</b>					
<b>Tetrigidae</b>					
<i>Tetrix subulata</i> L.	8.3	2	Leaves	Adult	Polyphagous (Bellmann & Luquet, 2009)
<b>Tettigoniidae</b>					
<i>Barbitistes alpinus</i> Fruhstorfer	8.3	1	Leaves	Adult	Polyphagous (Wagner, 2020)
<i>Leptophyes laticauda</i> Frivaldsky	8.3	2	Leaves	Nymph	Polyphagous (Wagner, 2020)
<i>Miramella alpina</i> Kollar	8.3	14	Leaves	Adult	Polyphagous (Asshoff & Hättenschwiler, 2005)
<i>Phaneroptera nana</i> Fieber	16.7	2	Leaves	Adult	Polyphagous (Davis, 1989)
<b>HEMIPTERA</b>					
<b>Cicadellidae</b>					
<i>Cicadella viridis</i> L.	25	6	Leaves	Adult	Polyphagous (Nickel & Remane, 2002)
<b>Cixiidae</b>					
<i>Cixius</i> sp.	8.3	1	Leaves	Adult	-
<b>Coreidae</b>					
<i>Coreus marginatus</i> L.	8.3	1	Fruits	Adult	Polyphagous (Ding et al., 2004)
<b>Miridae</b>					
<i>Adelphocoris</i> sp.	8.3	2	Leaves	Adult	-
<b>Pentatomidae</b>					
<i>Eysarcoris aeneus</i> Scopoli	8.3	1	Fruits	Adult	Polyphagous (Paik et al., 2007)
<i>Halyomorpha halys</i> Stål	25	5	Fruits	Adult	Polyphagous (Leskey et al., 2012)
<i>Nezara viridula</i> L.	8.3	1	Fruits	Adult	Polyphagous (Todd, 1989)
<i>Palomena prasina</i> L.	16.7	3	Fruits	Adult	Polyphagous (Ozsahin et al., 2014)
<b>COLEOPTERA</b>					
<b>Chrysomelidae</b>					
<i>Altica palustris</i> Weise	8.3	1	Leaves	Adult	<i>Lythrum salicaria</i> (Fuss et al., 2005)
† <i>Aphthona nonstriata</i> Goeze	66.7	187	Leaves	Adult	<i>Iris pseudacorus</i> (Baviera & Biondi, 2015)
<i>Cassida viridis</i> L.	8.3	1	Leaves	Adult	Lamiaceae (Borowiec & Więtojańska, 2018)
<i>Chrysolina geminata</i> Paykull	8.3	1	Leaves	Adult	<i>Hypericum</i> spp. (Jolivet & Petitpierre, 1976)

Species	Incidence	Abundance	Position	Life stage	Known plant associations
<i>Chrysolina polita</i> L.	8.3	1	Leaves	Adult	Lamiaceae (Jolivet & Petitpierre, 1976)
<i>Donacia vulgaris</i> Zschach	8.3	2	Leaves	Adult	Ord. Poales (Kölsch & Pedersen, 2008)
<i>Exosoma</i> sp.	16.7	2	Flowers	Adult	-
<i>Gastrophysa viridula</i> De Geer	8.3	1	Leaves	Adult	<i>Rumex</i> spp. (Smith & Whittaker, 1980)
<i>Phyllobrotica quadrimaculata</i> L.	8.3	1	Leaves	Adult	<i>Scutellaria</i> spp. (Mitter et al., 1991)
<i>Plateumaris sericea</i> L.	16.7	3	Flowers	Adult	Polyphagous (Bukejs, 2010)
<b>Curculionidae</b>					
† <i>Mononychus punctumalbum</i> Herbst	50	91	Flowers Fruits	Adult	<i>Iris</i> spp. (Gültekin & Korotyaev, 2012)
<i>Nanophyes marmoratus</i> Goeze	16.7	7	Flowers	Adult	<i>L. salicaria</i> (Blossey & Schroeder, 1995)
<b>Meloidae</b>					
<i>Lytta vesicatoria</i> L.	16.7	2	Leaves	Adult	Polyphagous (Schlager, 2004)
<b>Nitidulidae</b>					
<i>Brassicogethes aeneus</i> Fabricius	33.3	8	Flowers	Adult	Brassicaceae (Ekbom & Borg, 1996)
<b>Tenebrionidae</b>					
<i>Lagria hirta</i> L.	25	3	Leaves	Adult	Polyphagous (Szujecki, 2012)
<b>HYMENOPTERA</b>					
<b>Tenthredinidae</b>					
<i>Dolerus ferrugatus</i> Serville	16.7	4	Leaves	Larva	<i>Juncus effusus</i> (Borowski & Marczak, 2017)
† <i>Rhadinoceraea micans</i> Klug	16.7	23	Leaves	Larva	<i>Iris</i> spp. (Halstead & Henricot, 2010)
<b>LEPIDOPTERA</b>					
<b>Crambidae</b>					
<i>Anania hortulata</i> L.	8.3	1	Flowers	Adult	Polyphagous (Groenteman et al., 2017)
<i>Pyrausta aurata</i> Scopoli	8.3	1	Flowers	Adult	Lamiaceae (Dirimanov, 1970)
<b>Noctuidae</b>					
<i>Plusia festucae</i> L.	8.3	3	Leaves	Larva	Poaceae (Zahiri & Fibiger, 2008)
<b>Tortricidae</b>					
<i>Pandemis corylana</i> Fabricius	8.3	1	Leaves	Adult	Polyphagous (Ellis, 2020)

† Species prioritized as candidate biocontrol agents in this study.