Biological Conservation 268 (2022) 109506

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Perspective

# Fighting neobiota with neobiota: Consider it more often and do it more rigorously

Yan Sun [a], Heinz Müller-Schärer [b,*], Urs Schaffner [c]

[a] College of Resources and Environment, Huazhong Agricultural University, 430070 Wuhan, China
[b] Department of Biology, University of Fribourg, CH-1700 Fribourg, Switzerland
[c] CABI, CH-2800 Delémont, Switzerland

ARTICLE INFO

*Keywords:*
Importation or classical biological weed control
Invasive non-native plants
Sustainable management
*Ambrosia artemisiifolia*
Invasive trees

ABSTRACT

Invasive non-native plants (INNP) cause severe impacts on nature and human well-being, and these are predicted to increase. While management tools have been developed to control early-stage invasions or to clean particular sites from INNP, they are only rarely available to halt and reduce large-scale invasions. Importation biological weed control (IBWC; also termed classical biological weed control) offers a potentially effective tool, especially when combined with other land management interventions. Here, we aim to bridge the gap between IBWC advocates and critics by providing a state of the art of IBWC and exploring untapped opportunities and new ideas to further increase efficacy and safety of this tool. We first present a decision tree to identify the circumstances under which IBWC should be considered, either alone or as part of an integrated weed management approach. We then address concerns raised against IBWC by contrasting historical approaches with recently suggested improvements and outline a path forward. With two case studies, we emphasize that successful reduction of weed densities using IBWC will specifically also contribute to environmental health and human well-being by restoring ecosystem services without pesticide input and reaching areas with otherwise no INNP management options. We hope that our compilation helps to reconcile advocates and critics of IBWC and lead to a more constructive discourse and hopefully closer collaboration between the two groups. A joint effort is needed to further improve IBWC and to consider it more often, as the increasing threats imposed by INNP are urgently awaiting sustainable and affordable solutions.

## 1. Invasive non-native plants and their (unsuccessful) management

Biological invasions are among the most pervasive drivers of global change and arise from accidental or, notably for plants, from deliberate introductions in areas outside their native range (van Kleunen et al., 2020), with subsequent establishment and spread. Despite widespread implementation of prevention policies, rates of introduction and establishment of non-native species across taxa are rising globally and show no sign of abating (Seebens et al., 2017). Invasive non-native species are a major threat to rare and endemic native species and protected areas, alter ecological food webs, impact the provision of ecosystem services, and can impair human health (Vilà and Hulme, 2017).

Invasion science has developed into a rapidly expanding discipline within general ecology over the past decades (Richardson, 2011), yet little progress has been made with regard to developing and implementing sustainable and integrated management solutions, particularly against invasive non-native plants (INNP) (Müller-Schärer et al., 2018). Furthermore, the fact that INNP often have been deliberately introduced for expected benefits, e.g., as ornamentals, for erosion control, wood, forage or fodder (van Kleunen et al., 2020), may in general have delayed the awareness of a potential threat and thus also the development and implementation of management interventions, as compared to other non-native taxa. Moreover, while conservationists, rangeland managers and other stakeholders confronted with large-scale plant invasions possess tools to clear or reduce weed cover on a piece of land, they are often left without cost-effective, environmentally friendly, and sustainable management tools to manage the invasion process at the landscape scale (e.g., several ten or hundred thousand ha). Experiences from large-scale INNP management programmes show that implementation of manual and/or chemical clearing at the landscape level are difficult both from a financial and logistical perspective (see Box 1, Case

* Corresponding author.
*E-mail address:* heinz.mueller@unifr.ch (H. Müller-Schärer).

https://doi.org/10.1016/j.biocon.2022.109506
Received 27 December 2021; Received in revised form 19 February 2022; Accepted 26 February 2022
Available online 11 March 2022

Study 1). This is especially true for INNP found in natural areas (Foxcroft et al., 2013) or in areas with low-yield semi-natural habitats, such as dry rangeland (Griffith and Lacey, 1991; Fig. 1). An uncontrolled spread of INNP in rangeland is also critical from a conservation point of view; for example, in Kenya, the rangeland managed by Community Conservancies harbours higher total numbers of wildlife than all National Parks together (https://kwcakenya.com/conservancies/). A further complication arises from the fact that INNP are often spread over a mosaic of various land-use and habitat types that are managed by different stakeholders with different management imperatives (Box 1: Case Study 2). Lack of coordination among stakeholders will greatly hamper effective management at the landscape or regional scale, as failing management by one will affect all (Müller-Schärer et al., 2018).

## 2. There is a tool for managing large-scale plant invasions

Thus, persons or institutions involved in environmental protection or natural resource management are often left with few options to manage plant invasion processes at the landscape scale, and countries are unable to meet the Aichi Biodiversity Targets addressing invasive species, or the respective targets of the UNs' Sustainable Development Goals. As a last resort, importation biological weed control (IBWC) (also referred to as classical biological control) measures are sometimes proposed and implemented, involving the deliberate release of specialist natural enemies, mostly arthropods and pathogens, from the weed's native range. Here, we use the more recently proposed approach-based term 'importation biological control' as being more self-explanatory (Heimpel and Mills, 2017). In contrast to other INNP management interventions, the costs for developing and implementing IBWC are usually covered by public funding and can thus be considered as a public good, with the land users and society at large as beneficiaries (Naranjo et al., 2015).

While fighting fire with fire constitutes a well-approved remedy, fighting invasive non-natives with non-natives remains confronted with tenacious and continued critique, even from some invasion scientists (see Table 1 for references), despite the widely reported impacts of IBWC on the target INNP (Hinz et al., 2020; Fig. 2; cf. below). Here, we provide a state of the art of IBWC, emphasizing the opportunities and needs for IBWC, identifying yet untapped opportunities and reviewing new ideas to further increase efficacy and safety of this approach. We primarily focus on terrestrial habitats, but our general considerations also apply for aquatic habitats, given the increased stakeholder demand for IBWC and other non-chemical INNP management, and the highly successful IBWC projects, of aquatic plants (Hill and Coetzee, 2017; Pratt et al., 2021). We first present a decision tree to assign management goals and approaches to the various stages and other aspects of INNP invasions, and to specifically identify conditions under which IBWC is particularly likely to lead to cost-effective and sustainable INNP management. We then explore why IBWC, either alone or in combination with other management measures, is not used more often. For this, we list some of the often-cited concerns raised against this management tool, respond by contrasting historical approaches with recent improvements, and

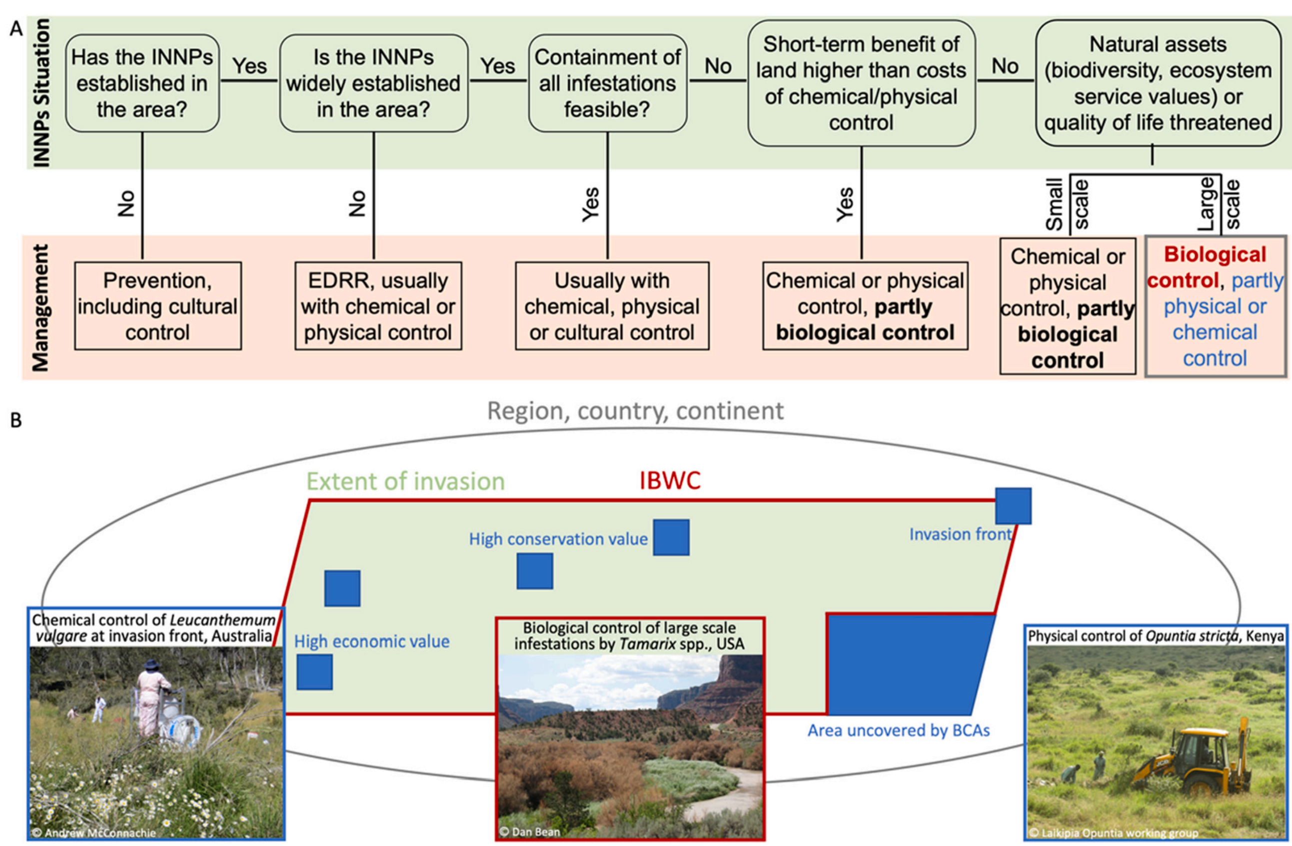


**Fig. 1.** Decision tree to prioritise invasive non-native plant management approaches.
Priority consideration of invasive non-native plant (INNP) management approaches (A) along the invasion process, building on the three-tiered management tactic (i) prevention, (ii) early detection and rapid response and (iii) control, and (B) in the context of a spatially explicit management strategy, which integrates diverse management approaches to achieve different management objectives (e.g., biological control to reduce INNP densities or seed production at large scale [red area]; chemical or physical control to slow down the spread of the INNP or to protect areas of high conservation or economic value [blue squares]). Note that the decision tree serves to determine which management approach(es) should be considered first under which circumstances; the ultimate decision whether a particular approach can and should be implemented depends on additional criteria, including characteristics of the target weed and of the invaded landscape. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

**Table 1**

Concerns raised against importation biological weed control (IBWC), historical approaches to conduct pre-release and post-release studies and recent methodological improvements. BCA: biological control agents; INNP: invasive non-native plants; EDRR: early detection rapid response; (1) Augustinus & Sun et al. 2020; (2) Dauer et al. 2012; (3) Caton et al. 2016; (4) Ehlers et al. 2020; (5): Havens et al. 2019; (6) Hinz et al. 2019; (7) Louda et al. 2003; (8) Lukey and Hall 2020; (9) Moran et al. 2021; (10) Müller-Schärer et al. 2020; (11) Müller-Schärer and Schaffner 2020; (12) NPCSC 2021; (13) Ollivier et al. 2020; (14) Schaffner et al. 2020; (15) Shaw et al. 2018; (16) Simberloff 2012; (17) van Wilgen et al. 2020b; (18) Wapshere 1974.

| | | Concerns (5,7,16) | Historical approaches | Recently addressed improvements |
|---|---|---|---|---|
| Pre-release | A | IBWC lacks scientific foundation and scrutiny ("try and see") | Close ties between practitioners and academia since the 1960s resulted in the development of guidelines for pre-release assessment of non-target risks in IBWC (18). | International and interdisciplinary research teams composed of both practitioners and academia continuously refine and improve these procedures by contributing to, and testing theory of, basic ecology and evolution (11). |
| | B | Uncertain projections of direct non-target effects | Test plant lists are established based on phylogenetic relationships and chemotaxonomy and in close collaboration with the various stakeholders and authorities involved. Pre-release testing predictions for non-target attack were more than 99% accurate (6). | Host-specificity tests are made at the population level of the BCA. Novel pre-release tests have been suggested and done to include selection studies that combine -omics tools with behavioural bioassays to explore the potential for evolutionary adaptations in the BCA to novel host plants (10). |
| | C | Uncertain projections of indirect non-target effects | Undesirable indirect non-target impact has been detected in some IBWC programmes. In-depth systematic searches for such impacts of released agents have not regularly been done in the past. | It has recently been proposed to assess indirect effects pre-release using comparative biogeographic studies in the native and the introduced range and network ecology to predict BCA impact on food webs (13). |
| | D | Low and uncertain projection for the efficacy of IBWC agents | Compared to host-specificity tests, efficacy assessments of BCA have been given less emphasis in pre-release studies. Attention was given to agents that are expected to reduce the most sensitive transition in the life cycle of the target plant (2,3). | Novel pre-release approaches include experimental evolution studies to assess the potential of the BCA to select for resistant/tolerant plant genotypes and to adapt to environmental conditions (10). Demographic models are used to identify where an IBWC agent can build up high densities (1). |
| | E | IBWC should be better regulated | New world countries that widely adopted IBWC, such as Australia, New Zealand, South Africa, and USA have well-established review processes for release of weed biocontrol agents (4,8). | Regulations are currently underway also in countries in Asia, Africa and Europe. They should include a thorough consultation with stakeholders within and outside federal and tribal government (12,15). |
| Post-release | F | Insufficient monitoring of the efficacy and non-target effects of released BCA | Presently, quantitative post-release monitoring remains sporadic as most of the investment is spent on screening and developing new BCA. | Demographic studies ensuring the efficacy of the release agent and discerning the severity of nontarget impacts have been developed and applied. A system for categorizing the degree of success of biocontrol has recently been described (9). |
| | G | Missing post-release environmental, social, and economic analyses | Past studies, mainly from Australia and South Africa, indicate that IBWC delivers benefit-to-cost ratios ranging from 8:1 to over 3000:1, with increasing benefits over time as the value of avoided impacts and/or managent costs accumulates (17). | There is increasing evidence for the economic benefits of successful IBWC and for its impacts on the provision of ecosystem services, including effects on water supply, human health, and tourism and recreation (9,14). |

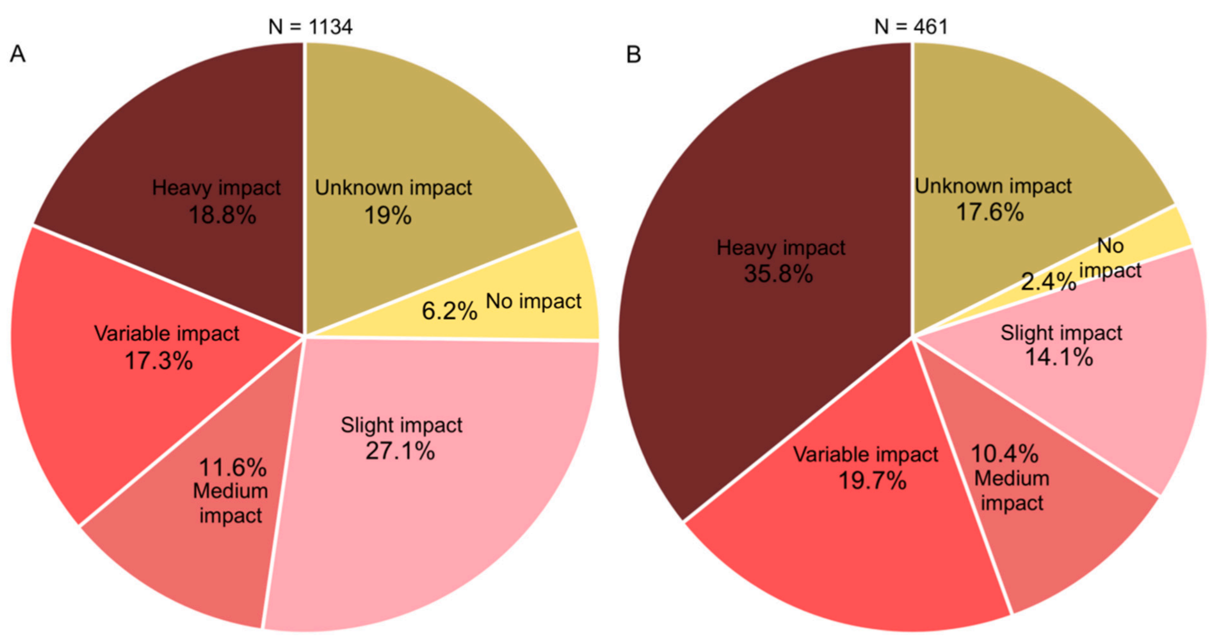


**Fig. 2.** (A) Published outcomes of releases of biological control agents (BCA) on invasive non-native plants (INNP) per country with established releases and (B) counts of the published highest impact level for each INNP and country with BCA released and established. Numbers above the pies give the total number of events. All unpublished impact records in the database are shown as "Unknown impact". Analyses that also considered both published and unpublished impact records are given in the Supporting Information Fig. S1. Data were retrieved from the weed biocontrol catalogue (Winston et al., 2021), see SI for details.

then outline a path forward to further increase efficacy and safety in future IBWC projects. Finally, we describe two case studies to emphasize and illustrate that successful IBWC will specifically also promote environmental health and human well-being and thus affect multiple sectors. By this, we aim to reconcile the advocates and critics of IBWC and hope that this will lead to a more constructive discourse and closer collaboration between the two groups to further improve IBWC, and to consider and apply it more often, as the increasing threats imposed by INNP are urgently awaiting sustainable and affordable solutions.

## 3. IBWC: where and when to do it

INNP management usually follows a three-tiered management approach: (i) prevention; (ii) early detection and rapid response (EDRR); and (iii) control. When designing EDRR to eradicate recently established INNP in a defined area, chemical or physical control practices are to be prioritized (Fig. 1). Also, when INNP have already well established, but so far have colonized only part of the suitable range in the new region, chemical, physical, or cultural (e.g., restriction of livestock movement) control measures may be implemented as a containment measure at the invasion front to slow down or stop the further spread of the target weed (Grice et al., 2011). With increasing INNP densities and areas invaded, chemical and physical control practices reach their limits to control the invasion process, but they continue to be useful tools for managing particular sites invaded by an INNP, e.g., sites of high conservation or economic value (Fig. 1). However, the management of an INNP at the regional, national or landscape scales increasingly requires an approach that i) reduces the population density and/or spread of the INNP across multiple or all invaded habitats, and that is ii) affordable for land users, iii) self-sustainable, and iv) environmentally friendly. The overall value of semi-natural or natural areas, such as grasslands, also comprises biodiversity conservation and ecosystem service values, which may not generate short-term economic benefits to land users, or are not marketable at all, but are of importance for other beneficiary groups (e.g., Reyers et al., 2013). If these values are threatened by INNP, as e.g., in the case of plant invasions in South Africa (van Wilgen et al., 2008; Box 1: Case Study 1) or Ethiopia (Shiferaw et al., 2019), the IBWC approach becomes even more important (Fig. 1). Payment-for-ecosystem services like the 'Working-For-Water' programme in South Africa can financially support INNP management at a large scale, but such expensive programmes cannot be easily set up in low-income countries. Moreover, evaluation of the 'Working-For-Water' programme indicates that even well-funded INNP management programmes should emphasize IBWC as a key component of an integrated management approach (Box 1: Case Study 1). With regard to managing woody plant invasions on Robinson Crusoe Island, globally the fourth most invaded island for woody species, Smith-Ramírez et al. (2017) concluded that mechanical and chemical control of invasive species seemed to be insufficient to prevent biodiversity loss; thus, they recommended that developing alternatives like IBWC is indispensable on this island, which is part of a World Biosphere Reserve.

Besides the extent of invasion and economic and environmental considerations, the selection of suitable management practices also depends on the characteristics of the target INNP species (Paynter et al., 2012). However, species characteristics do not a priori preclude the use of biological control practices, as there are examples of successful IBWC management of species with a wide range of characteristics (annuals/perennials, clonal/sexual, ruderal/competitive, monocots/dicots, trees/shrubs/herbs, taxonomically isolated/not isolated, genetically diverse/uniform populations) (Winston et al., 2021). However, species characteristics are used for prioritizing species for certain management practices or for designing individual management measures (e.g., seed-feeding vs. root-feeding biological control agent) or integrated management approaches to specifically target critical plant vital rates, such as e.g., survival and reproduction (Havens et al., 2019).

In most cases where widely established INNP cause serious environmental or socio-economic impacts, or the invaded ecosystem has even undergone a regime shift (Shackleton et al., 2020), returning the system to some historical condition is not a realistic objective. However, adopting a 'novel ecosystem' approach should not be confounded with taking no action to mitigate the negative impacts of INNP. If an uncontrolled population build-up and spread of INNP threatens key ecosystem services (e.g., biodiversity, water availability; Box 1: Case Study 1), food production (fisheries, pasture land, crops) or public health (caused by allergenic plants; Box 1: Case Study 2), then management tools such as IBWC should be seriously considered, together with attempts to adapt to the novel ecosystem (Morse et al., 2014). A combination of mitigation and adaptation measures is already routine in the combat against other drivers of global change, including climate change (Smith et al., 2020).

## 4. Addressing concerns raised against IBWC and its historical approach

Critiques of IBWC that have been repeatedly put forward include its lacking efficacy and being too risky, taking too long to meet public expectation and being too expensive (e.g., Louda et al., 2003; Simberloff, 2012; Havens et al., 2019; Table 1A). Admittedly, while chemical and mechanical control management can be stopped, this is hardly possible with biological control that involves the release of non-native organisms. This, however, also holds true for biological invasions that do not stop at national borders and also most often cannot be reversed. Therefore, risks and benefits associated with IBWC interventions need to be assessed relative to the risks and benefits of an unregulated invasion of the target INNP or to those of alternative management measures (Downey and Paterson, 2016; Müller-Schärer et al., 2018; Hanley and Roberts, 2019). In Table 1 we address some of the concerns raised against IBWC and contrast its historical approaches with how science and policy have addressed them more recently. IBWC of plant invaders has a history dating back over 150 years. From the late 1960s onwards, it has developed in conjunction with fundamental research on antagonist-plant relations to the benefit of both (Müller-Schärer and Schaffner, 2020; Table 1A). This led to the development of guidelines for pre-release assessment of non-target risks in IBWC, which are based on co-evolutionary processes between plants and their antagonists, and on chemotaxonomy (Wapshere, 1974), and more recently also on insights derived from applying -omics tools (Müller-Schärer and Schaffner, 2020, cf. below and Table 1B). As a result, IBWC has reached a high level of efficacy and safety with substantial returns on investment. Hinz et al. (2020) reported that of the 313 established biological control agent (BCA) species recorded until 2012 and for which impact could be assessed, pre-release testing predictions for non-target attack are more than 99% accurate (Table 1B). Re-analysing all available data for control efficacy from the weed biocontrol catalogue (Winston et al., 2021; https://www.ibiocontrol.org/catalog/) by treating unpublished impact records in the database as unknown outcome, we found that more than 75% of releases that led to establishment resulted in at least slight impact (Fig. 2A). These results are very similar to earlier published records that also included unpublished impact data (Hinz et al., 2019, 2020) (Fig. S1). Focussing on the target weed and taking the highest impact level per target weed and country where at least one of the IBWC agent releases led to establishment, we found that 85% of INNP experienced at least a slight impact and 35.8% experienced heavy impact (Fig. 1B; details on the method, impact definitions and data source are given in the Supporting Information).

## 5. Recent improvements in IBWC and as-yet untapped opportunities

Two special journal issues have recently reviewed and reported the developments reached so far in making biological control more safe, effective and sustainable, one on next generation biological control

**Box 1**

***Case Study 1: Invasive non-native tree species in South Africa***

Invader impact on multiple sectors

South Africa is one of the countries most seriously affected by INNP (Fig. 3). For example, South Africa has more invasive non-native tree species recorded per unit area than anywhere else in the world (Richardson et al., 2020). In 1995, South Africa established the large 'Working-for-Water' programme to meet the dual demands of poverty alleviation and conservation (van Wilgen and Wannenburgh, 2016). The main environmental reason why this programme has been supported by significant and continuous governmental funding was that it aimed to reduce the loss of surface and ground water to INNP. Nationwide, INNP were estimated to reduce annual water runoff by approx. 3.3 million $m^3$, thereby also affecting Cape Town's water security (Le Maitre et al., 2020). In addition, economic losses due to INNP in South Africa are attributable to grazing and to other biodiversity-related values (van Wilgen and De Lange, 2011).

IBWC and its importance in integrated weed management

South Africa is also one of the five nations that have been – and continue to be – at the forefront of development in IBWC (together with Australia, Canada, New Zealand and the United States of America; Moran and Hoffmann, 2015). As of 2018, South African scientists have tested and released IBWC agents against 69 INNP, and 87 agents established on 66 of the target weeds (Zachariades, 2018; Moran et al., 2021). Those responsible for managing and implementing the 'Working-for-Water' programme have long recognized the importance of biological control and have set aside a significant proportion of funding to support the identification, testing and release of new biological control agents against a range of invasive plant species (van Wilgen, 2020). This has resulted in numerous successes in reducing the invasiveness and impacts of several major weed species (Hill et al., 2020). For example, Henderson and Wilson (2017) found that during the first 23 years of the programme the increase in invasion range of those INNP against which IBWC was successfully incorporated in the management toolbox has slowed down, and in a few cases even led to range contractions. In contrast, other interventions had no detectable effect on the target INNP range expansion. When considering those 54 INNP that have been targeted for IBWC and on which agents have been established for at least 10 years, in 28% biological control has been assessed as being very successful with the weed suppressed below a tolerable threshold for all parameters considered (density, biomass, area and rate of spread) and in all habitats in which the target weed occurs. In 46% of the cases, biological control has resulted in a mix of various degrees of success for different parameters and habitats, and 26% of the cases are considered to be least successful or failures (Moran et al., 2021).

Collaboration between academia and practitioners

A large number of well-designed post-release studies to assess the impacts of released IBWC agents on the target weed, as well as changes in ecosystem functioning and the provision of ecosystem services, have been conducted in South Africa (e.g., Hoffmann et al., 2020). In contrast to many other countries implementing IBWC, post-release evaluation became the focus of several research teams in South Africa. Before the involvement of the 'Working for Water' programme, post-release monitoring conducted at the universities was largely funded through the National Research Foundation. More recently, the 'Working for Water' programme has also allocated significant funding to post-release monitoring (van Wilgen et al., 2020a). To date, no significant non-target effects have been reported from the IBWC agents released in South Africa (Hill et al., 2020).


**Fig. 3.** (A, B) Invasion of non-native tree species in South Africa and integrated weed management, including (C) biological, (D) chemical and (E) mechanical control.

***Case Study 2: Common ragweed, Ambrosia artemisiifolia, in Europe and China***

Invader impact on multiple sectors

Native to North America, *Ambrosia artemisiifolia* L. (*Ambrosia* in the following) has invaded different parts of the world and its spread and impact are likely to increase with changing climate (Sun et al., 2017; Fig. 4). It has particularly raised awareness due to its production of a large number of highly allergenic pollen grains, resulting in huge health costs, and as a major agricultural weed, especially in spring-sown crops (Müller-Schärer et al., 2018). A recent case study of its effects on public health reports that some 13.5 million persons suffer from *Ambrosia*-induced allergies in Europe, causing costs of € 7.4 billion annually (Schaffner et al., 2020).

IBWC and its importance in integrated weed management

There is a long history of IBWC attempts against *A. artemisiifolia* in different parts of the world, including eastern Europe (Russia, former Yugoslavia, Georgia, Ukraine), Australia and Asia (China and Kazakhstan) (Gerber et al., 2011).

*Europe:* IBWC of *Ambrosia* outside the native range started in the former Soviet Union in the 1960s, when more than 30 insect species from North America were introduced into quarantine, of which only a few were released and only two established, but both have been unsuccessful as BCA (Gerber et al., 2011). The North American native chrysomelid beetle *Ophraella communa* LeSage (*Ophraella* in the following) was first observed in Europe in 2013 (Müller-Schärer et al., 2014). Field studies in Italy proved evidence that *Ophraella* can reduce *Ambrosia* pollen production by 82%. A recent study projected that once the leaf beetle has colonized its environmental niche, it will reduce the number of patients by 2.3 million and the health costs by Euro 1.1 billion per year. Augmentative biological control through mass rearing and targeted releases of *Ophraella*, together with the importation of other agents might be needed to cover cooler regions with expected lower number of *Ophraella* generations and thus reduced impact of IBWC. Habitat- and region-specific *Ambrosia* management interventions have been developed to combine IBWC by *Ophraella* with establishing a competitive grass-legume vegetation (Cardarelli et al., 2018) and to identify when to mow *Ambrosia*-infested vegetation most cost-effectively (Lommen et al., 2018). Extensive host-specificity studies have been carried out in Europe and China, showing no negative effect on sunflower production and no evidence of substantial non-target effects on native European plant species (Kim and Lee, 2019; Augustinus et al., 2020a, 2020b). Further host-specificity tests are presently under way in Europe, possibly leading to deliberate releases in areas where *Ophraella* has not yet spread to naturally.

*China*: Five insect herbivores were introduced into China from 1987 to 1989 for managing *Ambrosia*, but only the tortricid moth *Epiblema strenuana* (Walker) (*Epiblema* in the following) established (Wan et al., 2005). *Ophraella*, which was introduced accidentally, was first discovered in Eastern China in 2001. In an augmentative strategy, 32 mass producing centres were established with an annual mass-producing of 800 million insects (*Ophraella* and *Epiblema*) which were subsequently released in 16 provinces in China. Release densities of 0.7 *Ophraella/Ambrosia* and 0.4 *Epiblema/Ambrosia* reduce *Ambrosia* density by >90% when assessed 70 days after release (Zhou et al., 2015).

International and interdisciplinary network

The successful EU-COST-SMARTER research programme illustrates the inherent demand for an interdisciplinary and international approach interconnecting experts in weed management, plant distribution monitoring, plant invasion biology, aerobiology, public health, and economics (Müller-Schärer et al., 2018). This international research programme, together with the fast spread and use of *Ophraella* as a most successful BCA of *Ambrosia* in Asia, greatly boosted studies on the *Ophraella-Ambrosia* interaction, mirrored by 16 publications before 2010, but 82 publications after 2010 (WOS with the term "*Ophraella communa*"). By this, it has become a research model for exploring aspects of both basic ecology and evolution, but also for its application in IBWC, either alone or as a part of integrated weed management. This specifically resulted in new approaches for improving pre-release studies to better predict safety and effectiveness (e.g. Sun et al., 2020a, 2020b, 2020c), including novel experimental evolution studies (e.g., Müller-Schärer et al., 2020), as well as post-release studies to estimate benefits (e.g., Sun et al., 2017; Mouttet et al., 2018; Schaffner et al., 2020) and to better understand and enhance spread and impact (e.g., Wan et al., 2019; Zhao et al., 2018; Augustinus et al., 2020a, 2020b; Litto et al., 2021; Zhang et al., 2021), also under climate change conditions (Sun et al., 2020a, 2020b, 2020c) (cf. also Tables 1, 2).

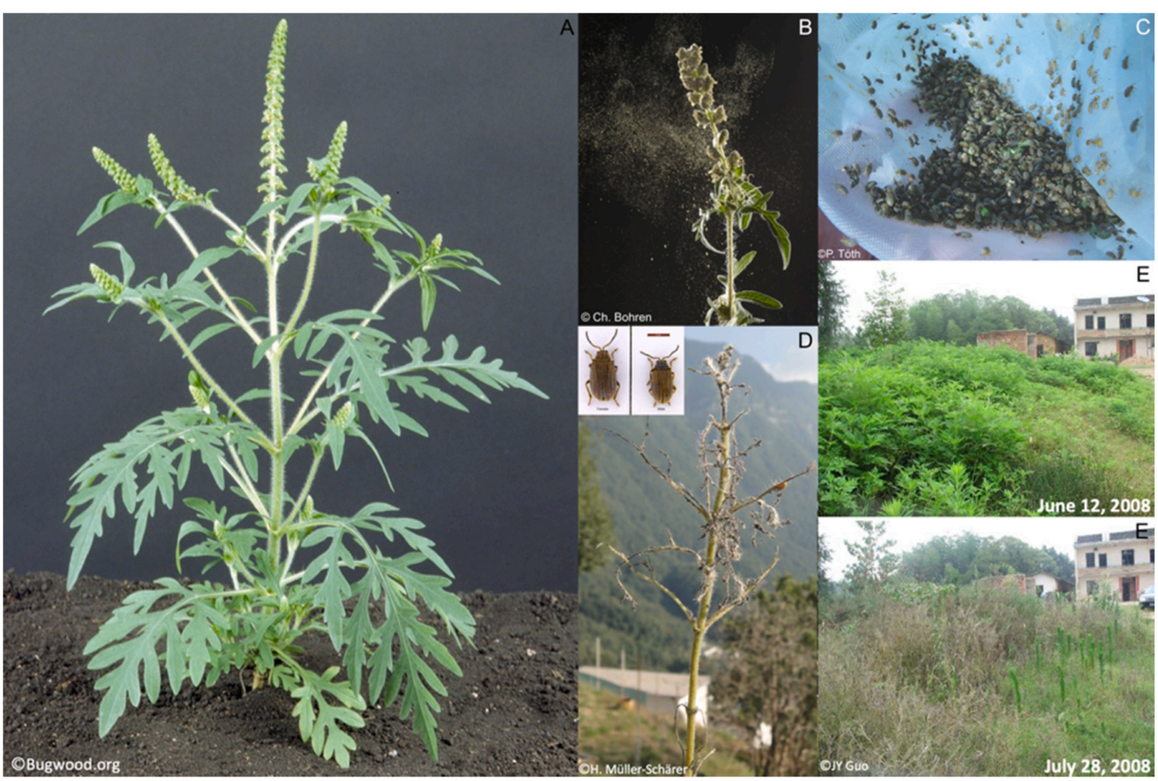


**Fig. 4.** (A) Common ragweed, *Ambrosia artemisiifolia* whole plant; (B) highly allergenic pollen; (C) its BCA *Ophraella communa* collected in north Italy; (D) damage on an individual plant; (E) rapid control using IBWC in China.

(editorial overview by Le Hesran et al., 2019) and one specifically on the biological control of plant invaders (editorial overview by Müller-Schärer and Schaffner, 2020). These extensive literature reviews are a follow-up of two international conferences and provide evidence for the continuous refinement and improvement of IBWC measures (Table 1A). Molecular technologies are now routinely incorporated in IBWC projects to identify the genetic diversity in the target weed both in its native and introduced ranges, to detect invasions of cryptic INNP species and of potential BCA (Paterson et al., 2019; Kumaran et al., 2020), as well as for developing molecular phylogenies to establish more relevant and meaningful test plant lists and to better interpret results of host-specificity tests (Table 1B). Further improvements are proposed by conducting pre-release experimental evolution studies that combine field selection experiments with molecular analyses and bioassays to anticipate potential evolutionary outcomes of the intended species interactions (Müller-Schärer et al., 2020; Sun et al., 2020b) and to select better BCA (Lirakis and Magalhães, 2019) (Table 1B). Also, studies on network ecology have recently been proposed to decipher tri-trophic interactions in both the native and the introduced ranges to minimize risks of indirect non-target effects (Ollivier et al., 2020), and various approaches have been elaborated to better predict the impact of climate change on species interactions and thus on future IBWC efficacy (Sun et al., 2020c; Table 1C). Demographic models are not only used to identify most sensitive transitions in the life cycle of the target weed that can be targeted by BCA (Dauer et al., 2012; Catton et al., 2016, Table 1D), but they are especially important also to monitor biocontrol effectiveness and impact post-release (Havens et al., 2019) (Table 1F; cf. also below and Table 2). Furthermore, demographic models for BCA also have been used in combination with species distribution models to identify where an IBWC agent can build up high densities (Augustinus et al., 2020a, 2020b; Table 1D). In the past, among-population variation in ecological traits of BCA was exploited to increase genetic diversity by collecting BCA from distinct populations in their native range. They were subsequently combined to promote adaptation post-release and increase establishment and control efficacy. Modern guidelines for IBWC no longer allow this practice and further insist that single populations are separately assessed for potential efficacy and safety before their introduction (USDA-APHIS/TAG, 2021; Müller-Schärer et al., 2020; Sun et al., 2020a; Table 1D). While some countries with a long history of biological invasions, such as Australia, New Zealand, South Africa, United States or Canada, have well-established review processes for the release of BCA (Ehlers et al., 2020; Lukey and Hall, 2020), such regulations are only now underway in most other countries, e.g., in Asia, Africa, and Europe (Shaw et al., 2018; NPCSC-Standing Committee of the National People's Congress, 2021; Table 1E).

As emphasized by both critics and advocates of IBWC, there remains an urgent need for more well-designed post-release studies monitoring the realized non-target effects by the introduced BCA, their population dynamics and impacts on the target weed, as well as changes in ecosystem functioning and the provision of ecosystem services (Carson et al., 2008; Havens et al., 2019; Schaffner et al., 2020) (Table 1F). Demographic models have been used to analyze in parallel both the effectiveness of the BCA on the target weed and on non-target species at risk (Catton et al., 2016) (Table 1F), but clearly such studies need to become an integral part of a modern post-release monitoring programme (cf. below and Table 2). There is agreement by both biological control experts (McFadyen, 1998; Blossey, 1999; Delfosse, 2005) and the broader scientific community (Carson et al., 2008; Maron et al., 2010) that well-designed post-release studies are essential to monitor and interpret the outcomes of IBWC, both for target and non-target impact, as well as for changes in ecosystem functioning and the provision of ecosystem services. A more rigorous system for categorizing the degree of success of biocontrol has been proposed by Hoffmann et al.

**Table 2**
Steps in a modern importation biological weed control (IBWC) programme and the ways forward to increase efficacy, safety, and outcome evaluation (adapted from Müller-Schärer and Schaffner 2008).

| | Steps in a IBWC programme | Proposed outline of future IBWC projects |
|---|---|---|
| Pre-release | Setting goals | At onset of project, define goals of overall invasive weed management and the contribution of IBWC, and formulate science-based working hypotheses. |
| Pre-release | Target weed ecology | Perform detailed taxonomic, demographic, population genetic and species distribution studies both in the native and introduced range to account for ecological and evolutionary changes post-introduction and to efficiently search for suitable BCA. |
| Pre-release | Exploration of potential BCA | Conduct biogeographic studies on trophic interactions and use network theory to make predictions regarding indirect non-target effects of the BCA in the target region. |
| Pre-release | Selection of efficient BCA | Consider genotype by genotype interactions in view of selecting the most efficient populations for introductions and release on specific target INNP populations in novel environments. |
| Pre-release | Host specificity testing of BCA | Combine host-specificity tests in containment with (multiple) carefully designed open-field tests in the native range to assess target fidelity under natural conditions and consider bioassays and -omics tools to explore evolvability of non-target use. |
| Pre-release | Predict BCA efficacy | Develop physiology-based demographic models to predict under which conditions the BCA will affect weed population densities. |
| Pre-release | Petition | Petition for field release includes falsifiable predictions regarding efficacy and non-target effects of the BCA in the new environment, and indicators to be included in post-release monitoring. |
| Post-release | Release preparation | Strengthen coordination at the regional/ continental level (e.g., in Europe or Africa) to account for natural spread of released BCA. Collect environmental, social and economic baseline data in the target region prior to the release of the BCA. |
| Post-release | Agent release & redistribution | Experimental releases (varying genotypes/ populations, number of releases and sites) at replicated sites across target habitats should routinely be initiated and monitored. Consider setting up control plots where BCA is excluded. Establish a thorough EDRR system for BCA. |
| Post-release | Agent and impact evaluation | Carefully design post-release studies to monitor the BCA's population dynamics and impacts on the target weed, its realized non-target effects and changes in ecosystem functioning and the provision of ecosystem services. For this, demographic analyses of the BCA, the target INNP and of non-target plants potentially at risk must become an integral part of a modern post-release monitoring programme. This will allow predictions made pre-release to be tested, for more quantitative evaluations of biocontrol projects and to better understand the underlying reasons for spatial or temporal variation in outcomes. |

(2019) and recently implemented by Moran et al. (2021). This will not only allow for more quantitative economic evaluations of biocontrol outcomes, but also help to better understand the underlying reasons for spatial or temporal variation in biocontrol outcomes, to test hypotheses based on pre-release studies and to assess when IBWC can be effective by itself and when it should be combined with other management options (Schaffner et al., 2020; van Wilgen et al., 2020b; Table 1G).

## 6. An outline for future IBWC projects as a path forward to increase their efficacy and safety

The framework of an IBWC project generally consists of a clear sequence of stages ranging from target weed ecology and genetics, exploration for potential control agents, testing for efficacy and safety up to agent releases and agent evaluation (Table 2). On each of these topics, a large body of literature has accumulated over the past 150-year history of IBWC. Acknowledging the concerns raised against IBWC and considering the most recent improvements and the yet untapped opportunities (Table 1), we list key points to be considered more rigorously for each step. By this, we propose an outline for future IBWC projects to further improve efficacy and safety (Table 2). Besides the need for more detailed post-release monitoring to evaluate efficacy and potential non-target impacts and retrospective socio-economic analyses, pre-release benefit-to-cost estimates are also still lacking but need to be established to raise public awareness and compel policymakers to ensure appropriate funding. We acknowledge that specialist knowledge and appropriate funding for implementing IBWC may not always be available in resource-poor countries, but knowledge transfer and capacity building can be achieved through international cooperation and support by international funding agencies (e.g., Mersie et al., 2019).

## 7. Successful IBWC: beyond reducing target weed densities

The goal of sustainably managing INNP is firstly to reduce weed densities or slow down their spread and thereby to restore or conserve the provision of ecosystem services, including food production and biodiversity, and to halt land degradation, thereby addressing several of the targets of the UN Sustainable Development Goal No 15 ‘Life on land’. Beyond this and most importantly, successful biological control, including IBWC, has significant indirect effects to further contribute to environmental health by, e.g., reducing synthetic pesticides with their negative environmental impact on biodiversity, and on soil and water quality (van Lenteren et al., 2018). Moreover, it can offer solutions that promote environmental or human health in situations where chemical or physical control is unlikely to be implemented at a large scale (cf. Case Studies below). In essence, IBWC and other forms of biological control greatly contribute to the ‘One Health’ concept, which is based on the recognition that the health of people is closely connected to the health of animals, plants, and our shared environment, and which has regained special attention in the era of global change (Essack, 2018).

Two ongoing case studies (Box 1) highlight (i) the above-mentioned effect of IBWC on multiple sectors, and (ii) the crucial role of IBWC in integrated weed management. They also demonstrate the benefit, but also the need for (iii) international and interdisciplinary networks and (iv) collaborations between academia and practitioners.

## 8. IBWC: do it more rigorously and more often

IBWC directly addresses a main anthropogenic driver of global change, i.e., biological invasions. It has an excellent track record for safety, but both IBWC advocates and critics agree that post-introduction monitoring clearly needs to be improved for both target and non-target impact, as well as for changes in ecosystem functioning and the provision of ecosystem services. This is a great, but yet largely untapped opportunity to strengthen the scientific basis of IBWC by testing hypotheses based on pre-release studies. As a management tool, IBWC has proven to be highly effective, but obviously not in all cases, as based on published records, only little more than one third of the targeted INNP in a given country experienced ‘heavy impact’, i.e., when the need for other control methods was stated as greatly reduced or no longer necessary. Our analysis is based on the impact of single BSA, but many INNP have multiple BCA established on them and thus, the combined impact of all BCA species on a single INNP may be higher (see Moran et al., 2021). Recent reports clearly highlight that the sustainable management of INNP is often only achievable if IBWC is part of an integrated management approach (van Wilgen et al., 2020a; Box 1: Case Study 1); however, there was no recent increase in number of studies integrating IBWC studies with other management measures worldwide (Lake and Minteer, 2018). We hope that our compilation helps to reconcile the supporters and critics of IBWC and lead to a more constructive discourse and hopefully closer collaboration between the two groups, as concerns raised against IBWC need be taken up jointly by the scientific community and the IBWC practitioners to continuously improve this crucial tool in INNP management (Tables 1, 2), not to forbear in doing it.

## CRediT authorship contribution statement

All three authors wrote the manuscript together.

## Declaration of competing interest

We have no conflict of interest to declare.

## Acknowledgments

We are grateful to Rachel Winston and Hariet Hinz for providing the updated records of the weed biocontrol catalogue (Winston et al., 2021). We acknowledge the constructive comments by John Maron, Mark van Kleunen and David M. Richardson on earlier versions of this manuscript, and the Novartis Foundation (#17B083 to HMS and YS), the Swiss National Science Foundation (project number 31003A_166448 to HMS) and the Scientific Research Foundation for Returned Scholars, Huazhong Agricultural University (11042110026 to YS) for funding. HMS thanks the ‘Center of Excellence of Weed and Invasive Plant Management under Climate Change’ of the University of Tehran for support. US was supported by the Swiss National Science Foundation and the Swiss Agency for Development and Cooperation as part of the Swiss Programme for Research on Global Issues for Development (r4d), for the project “Woody invasive alien species in East Africa: Assessing and mitigating their negative impact on ecosystem services and rural livelihoods” (Grant Number: 400440_152085) and by CABI with core financial support from its member countries (see https://www.cabi.org/about-cabi/who-we-work-with/key-donors/).

## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109506.

## References

Augustinus, B.A., Gentili, R., Horvath, D., Naderi, R., Sun, Y., Tournet, A.M.T.E., Schaffner, U., Müller-Schärer, H., 2020a. Assessing the risks of non-target feeding by the accidentally introduced ragweed leaf beetle, Ophraella communa, to native European plant species. Biol. Control 150, 104356.

Augustinus, B., Sun, Y., Beuchat, C., Schaffner, U., Müller-Schärer, H., 2020b. Predicting impact of a biocontrol agent: integrating distribution modelling with climate-dependent vital rates. Ecol. Appl. 30, e02003.

Blossey, B., 1999. Before, during and after: the need for long-term monitoring in invasive plant species management. Biol. Invasions 1, 301–311.

Cardarelli, E., Musacchio, A., Montagnani, C., Bogliani, G., Citterio, S., Gentili, R., 2018. Ambrosia artemisiifolia control in agricultural areas: effect of grassland seeding and herbivory by the exotic leaf beetle Ophraella communa. NeoBiota 38, 1–22.

Carson, W.P., Hovick, S.M., Baumert, A.J., Bunker, D.E., Pendergast, T.H., 2008. Evaluating the post-release efficacy of invasive plant biocontrol by insects: a comprehensive approach. Arthropod Plant Interact. 2, 77–86.

Catton, H.A., Lalonde, R.G., Buckley, Y.M., De Clerck-Floate, R.A., 2016. Biocontrol insect impacts population growth of its target plant species but not an incidentally used nontarget. Ecosphere 7, e01280.

Dauer, J.T., McEvoy, P.B., Van Sickle, J., 2012. Controlling a plant invader by targeted disruption of its life cycle. J. Appl. Ecol. 49, 322–330.

Delfosse, E.S., 2005. Risk and ethics in biological control. Biol. Control 35, 319–329.

Downey, P.O., Paterson, I.D., 2016. Encompassing the relative non-target risks from agents and their alien plant targets in biological control assessments. BioControl 61, 615–630.

Ehlers, G.C., Caradus, J.R., Fowler, S.V., 2020. The regulatory process and costs to seek approval for the development and release of new biological control agents in New Zealand. BioControl 65, 1–12.

Essack, S.Y., 2018. Environment: the neglected component of the one health triad. Lancet Planet. Health 2, e238–e239.

Foxcroft, L.C., Witt, A., Lotter, W.D., 2013. Icons in peril: Invasive alien plants in African protected areas. In: Foxcroft, L.C., Richardson, Pyšek P., DM, Genovesi P. (Eds.), Plant Invasions in Protected Areas: Patterns, Problems and Challenges. Springer, Netherlands, Dordrecht, pp. 117–143.

Gerber, E., Schaffner, U., Gassmann, A., Hinz, H.L., Seier, M., Müller-Schärer, H., 2011. Prospects for biological control of Ambrosia artemisiifolia in Europe: learning from the past. Weed Res. 51, 559–573.

Grice, A., Clarkson, J., Calvert, M., 2011. Geographic differentiation of management objectives for invasive species: a case study of Hymenachne amplexicaulis in Australia. Environ. Sci. Pollut. 14, 986–997.

Griffith, D., Lacey, J.R., 1991. Economic evaluation of spotted knapweed Centaurea maculosa control using picloram. J. Range Manag. 44, 43–47.

Hanley, N., Roberts, M., 2019. The economic benefits of invasive species management. People Nat. 1, 124–137.

Havens, K., Jolls, C.L., Knight, T.M., Vitt, P., 2019. Risks and rewards: assessing the effectiveness and safety of classical invasive plant biocontrol by arthropods. Bioscience 69, 247–258.

Heimpel, G.E., Mills, N.J., 2017. Biological Control: Ecology and Applications. Cambridge University Press.

Henderson, L., Wilson, J.R., 2017. Changes in the composition and distribution of alien plants in South Africa: an update from the southern African plant invaders atlas. Bothalia 47, 1–26.

Hill, M.P., Coetzee, J., 2017. The biological control of aquatic weeds in South Africa: current status and future challenges. Bothalia 47, a2152.

Hill, M.P., Moran, V.C., Hoffmann, J.H., Neser, S., Zimmermann, H.G., Simelane, D.O., Klein, H., Zachariades, C., Wood, A.R., Byrne, M.J., Paterson, I.D., 2020. More than a century of biological control against invasive alien plants in South Africa: a synoptic view of what has been accomplished. In: van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A. (Eds.), Biological Invasions in South Africa. Springer International Publishing, Cham, pp. 553–572.

Hinz, H.L., Winston, R.L., Schwarzländer, M., 2019. How safe is weed biological control? A global review of direct nontarget attack. Q. Rev. Biol. 94, 1–27.

Hinz, H.L., Winston, R.L., Schwarzländer, M., 2020. A global review of target impact and direct nontarget effects of classical weed biological control. Curr. Opin. Insect. Sci. 38, 48–54.

Hoffmann, J.H., Moran, V.C., Hill, M.P., 2019. Conceptualizing, categorizing and recording the outcomes of biological control of invasive plant species, at a population level. Biol. Control 133, 134–137.

Hoffmann, J.H., Moran, V.C., Zimmermann, H.G., Impson, F.A., 2020. Biocontrol of a prickly pear cactus in South Africa: reinterpreting the analogous, renowned case in Australia. J. Appl. Ecol. 57, 2475–2484.

Kim, H.G., Lee, D.H., 2019. Review of the biology and ecology of a ragweed leaf beetle, Ophraella communa (Coleoptera: Chrysomelidae), which is a biological control agent of an invasive common ragweed, Ambrosia artemisiifolia (Asterales: Asteraceae). Biocontrol Sci. Tech. 29, 185–200.

Kumaran, N., Choudhary, A., Legros, M., Sheppard, A.W., Barrett, L.G., Gardiner, D.M., Raghu, S., 2020. Gene technologies in weed management: a technical feasibility analysis. Curr. Opin. Insect. Sci. 38, 6–14.

Lake, E.C., Minteer, C.R., 2018. A review of the integration of classical biological control with other techniques to manage invasive weeds in natural areas and rangelands. BioControl 63, 71–86.

Le Hesran, S., Ras, E., Wajnberg, E., Beukeboom, L.W., 2019. Next generation biological control–an introduction. Entomol. Exp. Appl. 167, 579–583.

Le Maitre, D.C., Blignaut, J.N., Clulow, A., Dzikiti, S., Everson, C.S., Görgens, A.H., Gush, M.B., 2020. Impacts of plant invasions on terrestrial water flows in South Africa. In: van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T. A. (Eds.), Biological Invasions in South Africa. Springer International Publishing, Cham, pp. 431–457.

Lirakis, M., Magalhães, S., 2019. Does experimental evolution produce better biological control agents? A critical review of the evidence. Entomol. Exp. Appl. 167, 584–597.

Lommen, S.T., Jongejans, E., Leitsch-Vitalos, M., Tokarska-Guzik, B., Zalai, M., Müller-Schärer, H., Karrer, G., 2018. Time to cut: population models reveal how to mow invasive common ragweed cost-effectively. NeoBiota 39, 53–78.

Louda, S.M., Pemberton, R., Johnson, M., Follett, P., 2003. Nontarget effects—the Achilles' heel of biological control? Retrospective analyses to reduce risk associated with biocontrol introductions. Annu. Rev. Entomol. 48, 365–396.

Litto, M., Bouchemousse, S., Schaffner, U., Müller-Schärer, H., 2021. Population differentiation in response to temperature in *Ophraella communa*: implication for the biological control of *Ambrosia artemisiifolia*. Biol. Control 164, 104777.

Lukey, P., Hall, J., 2020. Biological invasion policy and legislation development and implementation in South Africa. In: van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A. (Eds.), Biological Invasions in South Africa. Springer International Publishing, Cham, pp. 515–551.

Maron, J.L., Pearson, D.E., Hovick, S.M., Carson, W.P., 2010. Funding needed for assessments of weed biological control. Front. Ecol. Environ. 8, 122–123.

McFadyen, R.E.C., 1998. Biological control of weeds. Annu. Rev. Entomol. 43, 369–393.

Mersie, W., Alemayehu, L., Strathie, L., McConnachie, A., Terefe, S., Negeri, M., Zewdie, K., 2019. Host range evaluation of the leaf-feeding beetle, Zygogramma bicolorata and the stem-boring weevil, Listronotus setosipennis demonstrates their suitability for biological control of the invasive weed, Parthenium hysterophorus in Ethiopia. Biocontrol Sci. Tech. 29, 239–251.

Moran, V., Hoffmann, J., 2015. The fourteen international symposia on biological control of weeds, 1969–2014: delegates, demographics and inferences from the debate on non-target effects. Biol. Control 87, 23–31.

Moran, V.C., Zachariades, C., Hoffmann, J.H., 2021. Implementing a system in South Africa for categorizing the outcomes of weed biological control. Biol. Control 153, 104431.

Morse, N.B., Pellissier, P.A., Cianciola, E.N., Brereton, R.L., Sullivan, M.M., Shonka, N.K., Wheeler, T.B., McDowell, W.H., 2014. Novel ecosystems in the anthropocene: a revision of the novel ecosystem concept for pragmatic applications. Ecol. Soc. 19, 12.

Mouttet, R., Augustinus, B.A., Bonini, M., Chauvel, B., Desneux, N., Gachet, E., Le Bourgeois, T., Müller-Schärer, H., Thibaudon, M., Schaffner, U., 2018. Estimating economic benefits of biological control of *Ambrosia artemisiifolia* by *Ophraella communa* in southeastern France. Basic Appl. Ecol. 33, 14–24. https://doi.org/10.1016/j.baae.2018.08.002.

Müller-Schärer, H., Schaffner, U., 2008. Classical biological control: exploiting enemy escape to manage plant invasions. Biol. Invasions 10, 859–874. https://doi.org/10.1007/s10530-008-9238-x.

Müller-Schärer, H., Bouchemousse, S., Litto, M., McEvoy, P.B., Roderick, G.K., Sun, Y., 2020. How to better predict long-term benefits and risks in weed biocontrol: an evolutionary perspective. Curr. Opin. Insect. Sci. 38, 84–91.

Müller-Schärer, H., Lommen, S.T.E., Rossinelli, M., Bonini, M., Boriani, M., Bosio, G., et al., 2014. Ophraella communa, the ragweed leaf beetle, has successfully landed in Europe: fortunate coincidence or threat? Weed Res. 54, 109–119.

Müller-Schärer, H., Schaffner, U., 2020. Editorial overview: biological control of plant invaders: a continued stimulus and yet untapped potential to link and advance applied and basic research. Curr. Opin. Insect. Sci. 38, v-viii.

Müller-Schärer, H., Sun, Y., Chauvel, B., Karrer, G., Kazinczi, G., Kudsk, P., Oude, A.L., Schaffner, U., Skjoth, C., Smith, M., 2018. Cross-fertilizing weed science and plant invasion science to improve efficient management: a European challenge. Basic Appl. Ecol. 33, 1–13.

Naranjo, S.E., Ellsworth, P.C., Frisvold, G.B., 2015. Economic value of biological control in integrated pest management of managed plant systems. Annu. Rev. Entomol. 60, 621–645.

NPCSC. (Standing Committee of the National People's Congress), 2021. Biosecurity Law of the People's Republic of China (中华人民共和国生物安全法). Order No. 56 of the President of the People's Republic of China (主席令13届第56号). Standing Committee of the National People's Congress (全国人民代表大会).

Ollivier, M., Lesieur, V., Raghu, S., Martin, J.F., 2020. Characterizing ecological interaction networks to support risk assessment in classical biological control of weeds. Curr. Opin. Insect. Sci. 38, 40–47.

Paterson, I.D., Coetzee, J.A., Weyl, P., Griffith, T.C., Voogt, N., Hill, M.P., 2019. Cryptic species of a water hyacinth biological control agent revealed in South Africa: host specificity, impact, and thermal tolerance. Entomol. Exp. Appl. 167, 682–691.

Paynter, Q., Overton, J.M., Hill, R.L., Bellgard, S.E., Dawson, M.I., 2012. Plant traits predict the success of weed biocontrol. J. Appl. Ecol. 49, 1140–1148.

Pratt, P.D., Moran, P.J., Pitcairn, M., Reddy, A.M., O'Brien, J., 2021. Biological control of invasive plants in California's Delta: past, present, and future. J. Aquat. Plant Manag. 59s, 55–66.

Reyers, B., Biggs, R., Cumming, G.S., Elmqvist, T., Hejnowicz, A.P., Polasky, S., 2013. Getting the measure of ecosystem services: a social–ecological approach. Front. Ecol. Environ. 11, 268–273.

Richardson, D.M., 2011. Invasion science: the roads travelled and the roads ahead. In: Richardson, D.M. (Ed.), Fifty Years of Invasion Ecology: The Legacy of Charles Elton. Blackwell Publishing Ltd, pp. 397–407.

Richardson, D.M., Foxcroft, L.C., Latombe, G., Le Maitre, D.C., Rouget, M., Wilson, J.R., 2020. The biogeography of South African terrestrial plant invasions. In: van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A. (Eds.), Biological Invasions in South Africa. Springer International Publishing, Cham, pp. 67–96.

Schaffner, U., Steinbach, S., Sun, Y., Skjøth, C., Weger, L.Ad., Lommen, S.T., Augustinus, B.A., Bonini, M., Karrer, G., Šikoparija, B., Thibaudon, M., Müller-Schärer, H., 2020. Biological weed control to relieve millions of allergy sufferers in Europe. Nat. Commun. 11, 1745.

Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., Pyšek, P., Winter, M., Arianoutsou, M., 2017. No saturation in the accumulation of alien species worldwide. Nat. Commun. 8, 14435.

Shackleton, R.T., Foxcroft, L.C., Pyšek, P., Wood, L.E., Richardson, D.M., 2020. Assessing biological invasions in protected areas after 30 years: revisiting nature reserves targeted by the 1980s SCOPE programme. Biol. Conserv. 243, 108424.

Shaw, R.H., Ellison, C.A., Marchante, H., Pratt, C.F., Schaffner, U., Sforza, R.F., Deltoro, V., 2018. Weed biological control in the European Union: from serendipity to strategy. BioControl 63, 333–347.

Shiferaw, H., Bewket, W., Alamirew, T., Zeleke, G., Teketay, D., Bekele, K., Schaffner, U., Eckert, S., 2019. Implications of land use/land cover dynamics and prosopis invasion

on ecosystem service values in Afar region, Ethiopia. Sci. Total Environ. 675, 354–366.
Simberloff, D., 2012. Risks of biological control for conservation purposes. BioControl 57, 263–276.
Smith, P., Calvin, K., Nkem, J., Campbell, D., Cherubini, F., Grassi, G., Korotkov, V., Le Hoang, A., Lwasa, S., McElwee, P., Nkonya, E., 2020. Which practices co-deliver food security, climate change mitigation and adaptation, and combat land degradation and desertification? Glob. Chang. Biol. 26, 1532–1575.
Smith-Ramírez, C., Vargas, R., Castillo, J., Mora, J.P., Arellano-Cataldo, G., 2017. Woody plant invasions and restoration in forests of island ecosystems: lessons from Robinson Crusoe Island, Chile. Biodivers. Conserv. 26, 1507–1524.
Sun, Y., Beuchat, C., Müller-Schärer, H., 2020a. Is biocontrol efficacy rather driven by the plant or the antagonist genotypes?A conceptual bioassay approach. NeoBiota 63, 81.
Sun, Y., Bossdorf, O., Grados, R.D., Liao, Z., Müller-Schärer, H., 2020b. Rapid genomic and phenotypic change in response to climate warming in a widespread plant invader. Glob. Chang. Biol. 26, 6511–6522.
Sun, Y., Brönnimann, O., Roderick, G.K., Poltavsky, A., Lommen, S.T., Müller-Schärer, H., 2017. Climatic suitability ranking of biological control candidates: a biogeographic approach for ragweed management in Europe. Ecosphere 8, e01731.
Sun, Y., Ding, J., Siemann, E., Keller, S.R., 2020c. Biocontrol of invasive weeds under climate change: progress, challenges and management implications. Curr. Opin. Insect. Sci. 38, 72–78.
USDA-APHIS/TAG, 2021. Reviewer's Manual for the Technical Advisory Group for Biological Control of Weeds: Guidelines for Evaluating the Safety of Candidate Biological Control Agents. Retrieved from, Second edition. https://www.aphis.usda.gov/import_export/plants/manuals/domestic/downloads/tag-bcaw-manual.pdf.
van Kleunen, M., Xu, X., Yang, Q., Maurel, N., Zhang, Z., Dawson, W., Essl, F., Kreft, H., Pergl, J., Pyšek, P., 2020. Economic use of plants is key to their naturalization success. Nat. Commun. 11, 1–12.
van Lenteren, J.C., Bolckmans, K., Köhl, J., Ravensberg, W.J., Urbaneja, A., 2018. Biological control using invertebrates and microorganisms: plenty of new opportunities. BioControl 63, 39–59.
van Wilgen, B.W., 2020. A brief, selective history of researchers and research initiatives related to biological invasions in South Africa. In: van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A. (Eds.), Biological Invasions in South Africa. Springer International Publishing, Cham, pp. 31–63.
van Wilgen, B.W., De Lange, W.J., 2011. The costs and benefits of invasive alien plant biological control in South Africa. Afr. Entomol. 19, 504–514.
van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A., 2020a. Biological invasions in South Africa: an overview. In: van Wilgen, B.W., Measey, J., Richardson, D.M., Wilson, J.R., Zengeya, T.A. (Eds.), Biological Invasions in South Africa. Springer International Publishing, Cham, pp. 3–31.
van Wilgen, B.W., Reyers, B., Le Maitre, D.C., Richardson, D.M., Schonegevel, L., 2008. A biome-scale assessment of the impact of invasive alien plants on ecosystem services in South Africa. J. Environ. Manag. 89, 336–349.
van Wilgen, B.W., Raghu, S., Sheppard, A.W., Schaffner, U., 2020. Quantifying the social and economic benefits of the biological control of invasive alien plants in natural ecosystems. Current Opinion in Insect Science 38, 1–5.
van Wilgen, B.W., Wannenburgh, A., 2016. Co-facilitating invasive species control, water conservation and poverty relief: achievements and challenges in South Africa's working for water programme. Curr. Opin. Environ. Sustain. 19, 7–17.
Vilà, M., Hulme, P.E. (Eds.), 2017. Impact of Biological Invasions on Ecosystem Services. Springer International Publishing, Cham.
Wan, F.H., Liu, W.X., Ma, J., Guo, J.Y., 2005. Ambrosia artemisiifolia and A. trifida. In: Wan, F., Zheng, X., Guo, J. (Eds.), Biology and Management of Invasive Alien Species in Agriculture and Forestry. Science Press, Beijing, China, pp. 662–688.
Wan, J., Huang, B., Yu, H., Peng, S., 2019. Reassociation of an invasive plant with its specialist herbivore provides a test of the shifting defence hypothesis. J. Ecol. 107, 361–371.
Wapshere, A.J., 1974. A strategy for evaluating the safety of organisms for biological weed control. Ann. Appl. Biol. 77, 201–211.
Winston, R.L., Schwarzlander, M., Hinz, H.L., Day, M.D., MJW, Cock, Julien, M.H., 2021. Biological Control of Weeds: A World Catalogue of Agents and Their Target Weeds. Based on FHTET-2014-04. Available online at. USDA Forest Service, Forest Health Technology Enterprise Team. https://www.ibiocontrol.org/catalog/. (Accessed 20 August 2019).
Zachariades, C., 2018. Biological Control of Invasive Alien Plants in South Africa: A List of All Insects, Mites and Pathogens Released as Biological Control Agents From 1913–2018. https://www.arc.agric.za/arc-ppri/Documents/Table1-NaturalEnemiesAll.pdf.
Zhang, Y., Zhao, C., Ma, W., Cui, S., Chen, H., Ma, C., Guo, J., Wan, F., Zhou, Z., 2021. Larger males facilitate population expansion in *Ophraella communa*. J. Anim. Ecol. 90 (12), 2782–2792.
Zhao, C., Ma, F., Chen, H., Wan, F., Guo, J., Zhou, Z., 2018. Heritability and evolutionary potential drive cold hardiness in the overwintering Ophraella communa beetles. Front. Physiol. 9, 666.
Zhou, Z.S., Guo, J.Y., Wan, F.H., 2015. Review on management of Ambrosia artemisiifolia using natural enemy insects. Chin. J. Biol. Control 31, 657–665.

## Further Reading

Zhou, Z.S., Rasmann, S., Li, M., Guo, J.Y., Chen, H.S., Wan, F.H., 2013. Cold temperatures increase cold hardiness in the next generation Ophraella communa beetles. PloS one 8, e74760.