Overview

Parallel concepts and future opportunities across the biological control and invasion sciences

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Abstract

The biological control and invasion sciences are long-standing research fields that have accrued enormous fundamental and applied interest. However, their theoretical and practical integration remains in its infancy. Utilizing an expert elicitation process with participants spanning these sciences, we identify conceptual parallels and future opportunities to strengthen links and address future challenges in both fields. We found that the biocontrol and invasion sciences face pervasive context-dependencies that must be understood to improve outcome predictions, including climatic changes, spatiotemporal scales, and ‘ecological surprises’. Both sciences would further benefit from terminological streamlining to improve communication, sharing of emerging technologies, and mitigation of the taxonomic decline. The two fields are strongly affected by social perceptions and awareness by decision makers, requiring more effective engagement and translation efforts. Our exercise promotes cross-cutting interdisciplinary advances to improve understanding of fundamental ecological and evolutionary processes, socio-ecological challenges, and management efficacy across the biocontrol and invasion sciences.

Keywords

biological control, biological invasions, pest species, research prioritization, social science

Background

Biological control and biological invasions are enormous research fields with fundamental and applied components spanning natural and social sciences (Heimpel and Mills, 2017; Musseau et al., 2024). Biological control is largely an applied science that concerns the use of living organisms to suppress populations of weeds or animal pests through classical, augmentative, or conservation means (van Driesche and Bellows, 2014). Invasion science is centred on the fundamental process of biological invasion, whereby non-native organisms are introduced outside of their natural ranges by human activities, with a focus on drivers, impact, and management (Lockwood et al., 2013).

Both biocontrol and invasion sciences are thriving, with rapidly growing numbers of publications and a diversity of methods employed across world regions and habitat types (Faria et al., 2023; Galli et al., 2024). Moreover, both fields have transdisciplinary dimensions that are affected by myriad natural and social factors while affecting multisectoral stakeholders. These factors mediate the success of species and populations in novel and changing environments, and in turn inform practical management strategies and government policy. However, despite sharing many similar conceptual foundations and fundamental processes (Heimpel and Mills, 2017), and some authors integrating concepts and methods between the disciplines (e.g., Dick et al., 2014; Cuthbert et al., 2018), the fields have surprisingly thus far remained disjointed and lack full integration. Harmonising these sciences and identifying their parallels could better equip researchers and practitioners to achieve conservation targets, reduce redundancy in theory and practice, and more efficiently address global sustainability challenges through both sciences.

Biocontrol has a longstanding history spanning centuries (Huffaker and Messenger, 2012). One of the first applications was in 1865, when the cochineal insect *Dactylopius ceylonicus* was introduced from southern India into Ceylon for prickly pear cactus control. As a result of this longevity, biocontrol research paved the way for the development of fundamental theory underpinning consumer-resource interactions and ecological stability (Murdoch and

Briggs, 1996), by providing model trophic systems with strong management relevance. An increased emphasis on biocontrol was stimulated in recent decades by a greater awareness of the non-target harm and evolved resistance associated with unsustainable chemical control measures, contributing to alternative 'nature-based' approaches within the 'OneHealth' framework (Schaffner et al., 2024).

Although biological invasions have also been occurring for centuries, invasion science is a relatively young field, with research into the phenomenon accelerating decades after Elton's (1958) classic book, initiated by the seminal work by the SCOPE programme during the 1980s (Richardson and Pyšek, 2008). The rapid growth in invasion science research has provided further opportunities to test and apply broader ecological theories relating to eco-evolutionary dynamics, biogeography, and anthropogenic disturbance, among others, while also culminating in a plethora of terminology, metrics, and hypotheses (Enders et al., 2018; Soto et al., 2024). However, invasion science has sometimes been slow to integrate classical ecological theory and well-known biocontrol methodologies (Dick et al., 2014). Fundamental ecological and evolutionary mechanisms underpinning the success and impacts of biocontrol agents and biological invasions are exemplified in Boxes 1 and 2.

Box 1. Impact prediction approaches between biocontrol and invasion sciences.

Ecological impact prediction of introduced organisms is an essential component in both biocontrol and invasion sciences — often called "agents" and "invaders", respectively. Functional responses classically quantify feeding rates of consumers in relation to the availability of resources in their environment (Holling, 1959). This provides a foundation to characterize how consumers, such as predators and parasitoids, interact with and impact upon their resources, such as prey or hosts (Hassell, 1978). The form of functional response has implications for consumer-resource interactions; Type II interactions are deemed destabilizing towards e.g. prey populations owing to the absence of low-density refuge effects, with catastrophic eliminations possible; whereas Type III functional responses may be more stabilizing, reducing invasion impact, and also better suited for biocontrol agents to regulate rather than eliminate target organisms, and in doing so, the agents may remain extant themselves (Dick et al., 2014). The magnitude of the functional response and its parameters (e.g., maximum feeding rate) can be further harnessed quantitatively to compare species, populations, or individuals in both sciences.

Because of use in characterizing trophic interactions, for decades, functional responses have been pivotal in predicting the efficacy of biocontrol agents (Van Driesche and Bellows, 2012). The use of functional responses in invasion science is much more recent (Dick et al., 2014; Faria et al., 2023). In the last decade, invasion scientists have rapidly adopted functional response metrics to predict the impacts of existing and emerging invaders (Cuthbert et al., 2019) — a win for both sciences and an indication there might be other latent parallels and opportunities.

While the approach transcends both fields, recent syntheses have highlighted a discordance between biocontrol and invasion in their assessment of functional responses across contexts (Faria et al., 2023). This discrepancy may arise due to differences in the ecological roles and life histories of the species involved. For example, biocontrol efforts have typically focused on terrestrial parasitoids targeting specific pest species of agricultural importance, while invasion studies have most often assessed aquatic predators (Faria et al., 2023).

One limitation of comparative functional response studies is that they are inherently constrained to the per capita level. Fusing both the functional response and numerical response into a cohesive metric (i.e., the classic 'total response'; Holling, 1959) has improved predictions for both fields (Carrillo and Pena, 2012; Dick et al., 2017; Cuthbert et al., 2018).

Population-level data, such as consumer field abundance, total biomass, percentage cover, and other proxies, have recently been integrated with functional responses to form new metrics, namely the Relative Control Potential (RCP) and Relative Impact Potential (RIP) (Dick et al., 2017; Cuthbert et al., 2018; Dickey et al., 2020) (Figure A). These two metrics are based on almost identical frameworks, which permit the comparison of different agents, non-native species, and environmental conditions by fusing their functional response parameters (e.g., maximum feeding rate) and numerical response proxies (e.g., consumer field abundance). Furthermore, RCP and RIP allow for the incorporation of abiotic factors such as temperature changes, nutrient availability, habitat complexity, as well as biotic interactions including competition, commensalism, and resource reproduction (Cuthbert et al., 2019; South et al., 2022; but see Landi et al., 2022). The realisation that biocontrol operatives were routinely measuring functional and/or numerical responses to address questions essentially the same as invasion scientists, who had hitherto missed this method, is a lesson in how the two fields can be mutually beneficial.

One practical consideration to further bridge this gap is for better integration and availability of interaction strength and life history trait data. The FoRAGE database, which collates functional response data across a wide range of species and ecological conditions, exemplifies efforts to facilitate this integration (Uiterwaal et al., 2022). Further cross-fertilization of the two fields should explore the dynamics of functional response parameters with changing agent/invader density — known as ‘multiple predator effects’ (Wasserman et al., 2016) — which can be neutral, synergistic or antagonistic.

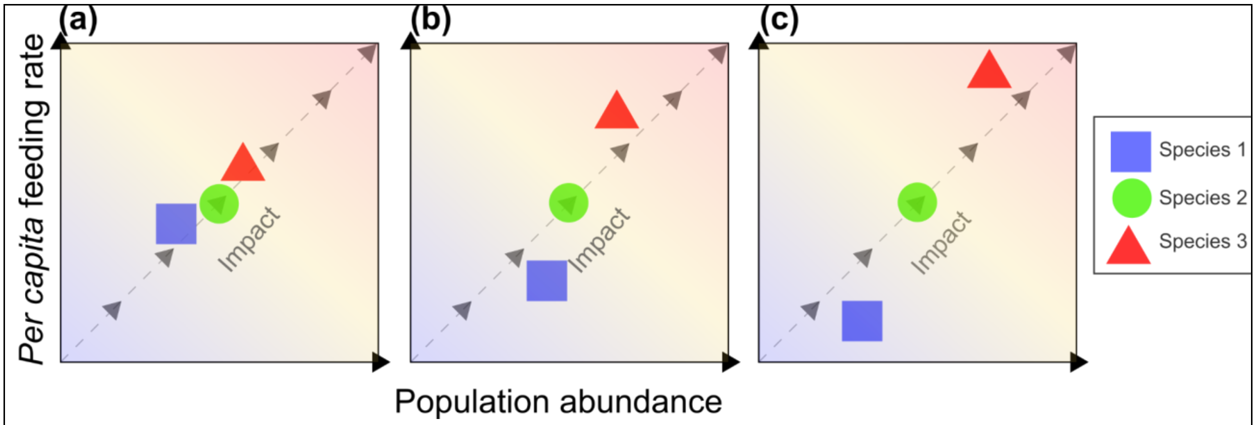

Figure A. Biplot showing variables underpinning the Relative Control Potential (RCP; biological control) and Relative Impact Potential (RIP; invasion science) metrics used to compare biocontrol agent efficacies and invasive species impacts, respectively. Consumer per capita effects (e.g., maximum feeding rates from functional response experiments) are scaled on the y-axis and population size of the consumer (e.g., field abundance, fecundity) on the x-axis. Impact increases diagonally by fusing these individual- and population-level metrics. Three scenarios are presented (panels a-c), with the three species compared therein having increasing impact dissimilarity from left to right.

Box 2. Understanding and predicting success of biocontrol agents and biological invasions.

Both fields have multiple commonalities with regards to the success of organisms in new environments. Population dynamics are very similar at the initial stages of both processes. Indeed, biocontrol can be viewed as a ‘planned invasion’, surpassing the critical transport and introduction stages and moving straight into establishment and spread (Abram and Moffat, 2018). This is parallel to the concept of “hard” and “soft” releases in invasion science, where establishment success is increased by releasing high quality individuals into suitable habitats (e.g., deer and bird releases). This field also side-steps the 'time-spent hypothesis', whereby plants with a longer residence time naturally accrue a greater diversity of natural enemies (Strong Jr, 1974). Therefore, there are valuable lessons to be learned from the well-described contexts which mediate the success of biocontrol agents, such as propagule pressure (ie., introduction effort) and genetic diversity, which also contribute to the success of biological invasions.

One of the key factors influencing the success of both biocontrol and biological invasion is propagule pressure, which is the number of individuals, frequency of introduction events, and viability of individuals introduced into a new environment. Similarities in biocontrol and invasion can be drawn because a sufficient number of biocontrol agent individuals must be released to establish a self-sustaining population and effectively suppress the target pest, while a high propagule pressure in terms of introduction events can increase the likelihood of establishment and subsequent spread of an introduced species (Shea and Possingham, 2000). High propagule pressure helps species to overcome demographic and environmental stochasticity (Grevstad, 1999; Memmott et al., 2005). Higher propagule pressure also increases the likelihood that the colonizing biocontrol agent possesses elevated genetic diversity and thus additive genetic variation. A key difference between biocontrol and biological invasion processes is that propagule pressure is typically known and controllable in the former, and often unknown and uncontrollable in the latter. Further, whilst biocontrol emphasizes agency viability (e.g. health, parasitism, fecundity), this is less frequently measured in invasion science; progress here is thus required, such as in the assessment of fitness of recently introduced individuals. Another parallel that has received little direct narrative is that biocontrol success can require initial trialing of many different agent species, while colonization pressure, a term favored by invasion science, follows the same mechanism, whereby the number of potential invader taxa can be correlated with eventual invasion success by one or a subset of them (MacIsaac and Johansson, 2017).

The double-edged sword of enemy release is another shared concept that is responsible for both biocontrol and invasion success. In biocontrol, this principle is harnessed to the advantage of biocontrol agents. By introducing host-specific natural enemies from the pest's native range, it is possible to leverage their ability to suppress the target species without harm to non-target species. In contrast, when non-native species are introduced into a new environment, they may escape their natural enemies, such as predators, parasites, and pathogens that usually regulate them in the native range (Keane and Crawley, 2002). This can lead to rapid population growth and ecological impacts (Baso et al., 2024). Concerns regarding unanticipated consequences of introducing a second non-native species to control a previously introduced pest species have been raised (Thomas and Reid, 2007). Therefore, it is paramount to validate the agent’s specificity for the target species with reliable experimental and native-range field data prior to release.

Among these three processes, propagule pressure is accepted in both fields, and is easier to study in an experimental setting. However, other aspects are difficult to isolate from confounding factors (e.g., biotic interactions, environmental variability, temporal changes). Today, there exist more rigorous protocols for the release of biocontrol agents in many areas globally, recognizing possible harm associated with unanticipated ecological effects (Abram and Moffatt, 2017). By carefully considering factors such as propagule pressure, colonization pressure, enemy release, and biotic resistance, it may be possible to mitigate risks associated with these practices while promoting the conservation of biodiversity.

Alongside this theoretical basis, from a management standpoint, biocontrol and biological invasions are closely aligned and interlinked. Biocontrol agents are often introduced as part of (integrated) efforts towards invasion management, but have occasionally become invasive in their own right, especially in early classical release programs that lacked rigorous pre-testing to ensure agent host specificity (e.g., Shine et al., 2020). Both fields are further underpinned by socio-economic context of the recipient human community. For example, globalization has facilitated the proliferation of 'unintentional biocontrol', through introductions that can harbor potential ecological impacts from introduced natural enemies (Fenn-Moltu et al., 2024). Similarly, biological invasions and their impacts can strongly resemble patterns in globalized trade and transport (Seebens et al., 2017; Hudgins et al., 2023). Public perceptions further influence the success of management strategies, monitoring, and decision making in both areas, with citizen science providing a useful avenue to augment management applications (Weaver et al., 2021). Furthermore, each field is set to benefit from the development of new technologies designed to predict population success and future trajectories, using resources such as machine learning, remote sensing, and environmental DNA (Fricke and Olden, 2023). Because both biocontrol and invasion science face similar future challenges and opportunities across natural and social dimensions, including context dependencies linked to climate change, eco-evolutionary context, and socio-cultural values, these sciences could bidirectionally benefit from cross-cutting and transdisciplinary perspectives, but these possibilities remain largely as yet underexplored.

We thus discuss a series of areas to better integrate biocontrol and invasion sciences, stemming from a workshop that elicited perceptions from a range of researchers and practitioners in both fields (Supplementary Material 1). We thus present these parallels and opportunities across natural, computational, and social axes, with the aim to foster improved discussion, collaboration, and knowledge exchange between these research areas.

Natural dimensions

Climate change

Global climate is rapidly shifting and increasing the severity of extreme weather events, as evidenced by increased incidence and intensity of heat waves, cold snaps, and flooding (Sun et al., 2020). Furthermore, chronic changes to temperature, precipitation, and salinity patterns are likely to directly mediate success and impacts of introduced populations, with effects from individual to ecosystem levels. The geographical range limit of biocontrol agents and invaders is dependent on their physiological tolerance to shifting environmental conditions, underpinning the need to incorporate thermal responses in biogeography. These climatic changes can also affect phenology between biocontrol agents and their targets, for example, with herbivore phenology progressing faster than that of plants owing to their higher thermal sensitivity (Korner and Basler, 2010). At the same time, thermally-driven biological invasions are projected to increase, presenting possible increasing risks to ecosystem services, socio-economies, and biodiversity, while biocontrol agent efficacy may also be affected. Species distribution models (SDMs) are valuable tools for understanding the current and future potential distribution of both biocontrol agents and invasives. These models help allocate and optimize tools and resources in border surveillance by understanding which geographic areas are most climatically suitable for a given species, determining future spread potential, and identifying suitable climate niches where taxa have a higher likelihood of establishment (Lantschner et al., 2019). However, evidence from biological invasions shows how niche shifts can compromise the transferability of these models (Liu et al., 2022).

Species distribution models such as MaxEnt (Phillips et al. 2006) have been routinely used to analyse climatic compatibility of biocontrol agents. For example, considering three parasitoids, *Megarhyssa nortoni*, *Ibalia leucospoides*, and *Rhyssa persuasoria*, that were introduced in the Southern Hemisphere for biocontrol of pine pest, *Sirex noctilio*. These models successfully predicted the establishment of *I. leucospoides* and *M. nortoni* in their current regions, demonstrating the importance of climatic factors in the success of biocontrol programmes (Mukherjee et al., 2021). Biocontrol agents with a strong climatic match between native and release locations establish more readily and become more effective than those with a weaker match (Sun et al., 2017). For example, Minghetti et al. (2020) used environmental niche models to identify areas within the introduced range of the shrub, *Solanum mauritianum* that are suitable for its biocontrol agent, *Gargaphia decoris.* Analyses demonstrated that the entire introduced range of *S. mauritianum* was suitable for *G. decoris* under current and future climatic scenarios, indicating a potential for successful control. Thus, climate matching proves valuable in identifying suitable regions for biocontrol agent release, and explains failures in establishment, informing both biocontrol and invasion science (Sun et al., 2017; Harms et al., 2021). Joint species distribution models have recently emerged as a novel analytical framework that can integrate species interactions into metacommunity and macroecology, providing a more realistic forecast of establishment likelihood (Pichler and Hartig, 2021).

Climate change can reshape invasion pathways by altering ecosystem abiotic conditions and biotic relationships. For example, melting sea ice opens new shipping routes, creating additional pathways for invasion, while warmer temperatures can facilitate warm-adapted invaders to further expand their distributions (Nong et al., 2019). The isotherm tracking hypothesis suggests that 'neo-native' species will also 'naturally' shift their ranges in response to changing temperature gradients. These shifts include poleward movement to higher latitudes for terrestrial organisms, upslope movement for terrestrial and freshwater species, and deeper habitat ranges for aquatic organisms (Rubenstein et al., 2023). Such changes are expected to influence trophic interactions and ecosystem structures in terrestrial and aquatic biomes, with wide-reaching implications for ecosystem resilience and function (Sun et al., 2020). Moreover, they can interact with other environmental changes within a multiple stressor framework, further complicating ecological outcomes. Lastly, climatic changes could also drive movements of natural enemies into invaded areas, thereby changing ecological outcomes.

Research scales

The scale at which ecological studies are conducted significantly influences the outcomes and applicability of findings (Tscharntke et al., 2007). Research conducted across different organizational, trophic, spatial, temporal, and geographical scales can yield varying results, impacting the interpretation of ecological interactions, species responses, and management strategies (Fortin et al., 2005; Tscharntke et al., 2007).

Biological control and biological invasion are intrinsically linked by scale, but also differ in important ways. Biocontrol efforts often start small by design (e.g., host-specificity trials in greenhouses or quarantine labs) but can scale dramatically when successful. Notably, the use of *Cactoblastis cactorum* against prickly pear (*Opuntia stricta*) in Australia is an example of biocontrol operating at an enormous scale, covering millions of hectares (Zimmermann et al., 2004). This means that biocontrol can be both hyper-local and broadly dispersed. Initial releases often occur at landscape or sub-landscape scales, followed by evaluation of agent establishment and spread. Success hinges on both spatial match with the target population and the broader landscape context, including climatic suitability. Similarly, invasion events often begin at small unnoticed scales (i.e., ‘sleeper populations’), arising from a single introduction, but can rapidly expand to continental or even global levels through natural dispersal, trait changes, and anthropogenic movements (Spear et al., 2021). In invasion science, research often focuses on broader global, national, or regional levels, while management solutions, including biocontrol options, are often implemented at a landscape level, resulting in discrepancies between theory and application (Esler et al., 2010). Like invasions, which may require multiple introductions from distinct populations to succeed, biocontrol often requires concerted effort over multiple releases to achieve establishment (Abram & Moffat, 2018).

Both biocontrol and invasion science research is disproportionately concentrated in developed countries, leaving Africa, parts of Asia, Central and South America, and many island nations underrepresented (Bellard and Jeschke, 2016; Pyšek et al., 2008). Biocontrol programs are often best funded and implemented in countries with existing regulatory and quarantine infrastructure, yet, many of the biodiversity hotspots most affected by invasive species remain underrepresented. This geographical bias stems from limited funding and, in some cases, underdeveloped academic and research systems (Pyšek et al., 2008). This leads to an imbalanced understanding of mechanisms and a lack of knowledge regarding regionally-specific biocontrol options and invasion dynamics (Pyšek et al., 2008). Since invasions do not adhere to political boundaries, this disparity can delay invader detection and management in vulnerable areas, potentially worsening invasion impacts (Bellard and Jeschke, 2016). Addressing this requires increased research funding in developing countries, promoting international collaboration, and strengthening of academic infrastructure.

Temporally, biocontrol programs often operate on extended timescales, spanning decades from discovery, testing, and release to population-level impact (van Lenteren, 2012). Some agents exhibit time lags before impacts are observable, leading to perceptions of inefficacy unless long-term monitoring is in place. However, when successful, biocontrol can provide enduring suppression and dynamic equilibrium, as seen with *C. cactorum* in Australia or *Uroplata girardi* against *Lantana camara* in South Africa (Zachariades et al., 2017). These long-term outcomes can contrast with invasion events, which often involve sudden and acute shifts. Nevertheless, biological invasions can also be associated with substantive time lags to proliferation and impact, with multi-decadal sigmoid population and impact dynamics identified across taxa (Soto et al., 2023). Environmental changes or arrival of new genetic material have been identified as catalysts for rapid surges in invasive populations and their potential impacts (Spear et al., 2021). While these processes likely also alter biocontrol agent efficacy, it is possible that population dynamics of biocontrol agents follow a shorter trajectory (i.e., reduced time lags) due to the intensity of pre-introduction trait selections that could prime performance immediately after introduction.

The spatio-temporal scale of biocontrol and invasion science research is often limited (Becker et al., 2019; Gonzalez et al., 2020). Spatially, biodiversity processes can differ between local and regional scales, as species interaction networks tend to be locally nested but regionally modular, reflecting distinct ecological and evolutionary dynamics (Delmas et al., 2019; Gonzalez et al., 2020). Temporally, long-term data are crucial for detecting patterns and mechanisms behind large-scale biodiversity changes, such as the global insect decline (Wagner et al., 2021; Zhou et al., 2023). However, limited funding, logistics, and deadlines often restrict the scope of research (Reynolds-Hogland and Mitchell, 2007). Consistent funding, stakeholder engagement, and collaborative efforts, such as combining datasets across studies, can help to overcome these constraints and expand the spatiotemporal scale of research (Heffernan et al., 2014). To fully understand invasion dynamics, research must consider these cross-scale interactions.

Biological invasions (including non-target effects from historic disastrous biocontrol releases) can impact biodiversity across various organizational scales, altering genetic, phylogenetic, taxonomic, and functional diversity. At the ecosystem level, they disrupt trophic networks that form the functional basis of ecological interactions. Invasions can permanently change trophic interaction strengths, modify connections, or cause species loss (Wainright et al., 2021). The efficacy of biocontrol releases and effects of invasion events are thus inherently multi-scaled, complex, and diverse. Both biocontrol and invasion science require research-scaling that aligns with the complex nature of ecological processes. Mismatches between study scale and management needs, as well as between management actions and ecosystem responses, along with geographical research biases, limit effective interventions. Addressing these mismatches requires embracing cross-scale thinking, such as integrating short-term trials with long-term monitoring, or local release data with regional invasion models. This requires uninterrupted budgets, as well as expanding research efforts across spatial, temporal, and organizational levels, particularly in underrepresented regions, to enhance our ability to predict, mitigate, and manage the impact of introduction events.

Ecological surprises

There is a rich potential for the development of theory that explains unexpected indirect impacts ('ecological surprises') of biocontrol agents. One important finding from invasion science is the immense potential scope of indirect effects of introduced species (e.g., Traveset and Richardson, 2006; Koel et al., 2019), which suggests that non-target effects of introduced biocontrol agents are far more diverse and frequent than is currently documented. A common conception is that non-target effects are almost always caused by generalist species with broad host repertoires, but some case studies challenge this view (Pearson and Callaway 2003). A classic example of cascading non-target impacts is the unauthorized introduction of *Myxoma* virus to the UK to control rabbits. Rabbit grazing creates patches of short grass, which favors ants that have a mutualistic relationship with caterpillars of a rare butterfly in the UK. The decline of the rabbit population thus ultimately contributed to the butterfly's extirpation (Elmes and Thomas, 1992). Similarly, gall flies released to the southwestern U.S. to control an invasive spotted knapweed (*Centaurea maculosa*) became abundant on the plants and thus provided a novel food source for deer mice (*Peromyscus maniculatus*) — a non-target species — which are the primary reservoir for hantavirus in the region (Pearson and Callaway, 2006). Infected deer mice became more abundant in the presence of gall flies, thereby increasing human disease risk.

The likelihood of cascading impacts could depend on the interaction strength between the agent and both target and non-target species (Pearson and Callaway, 2003). Interaction strength is context-dependent, subject to the influence of local environmental variables. A predictive understanding of context dependencies, and hence some of the factors and mechanisms contributing to unexpected impacts, could be enhanced through consideration of the Environmental Matching Hypothesis — a conceptual framework for experimental design and predictions (Ricciardi et al., 2013). The hypothesis is based on the premise that although myriad environmental variables can influence the performance of an introduced species, often only one or a few of them explain most variation in performance across space and time. This highlights the potential for an introduced biocontrol agent to have substantively different effects across a physically heterogeneous ecosystem or multiple ecosystems; for example, the same introduced species can be a superior intraguild predator at one site and an inferior predator in another site, along a physicochemical gradient (e.g., Kestrup and Ricciardi, 2009). A related concept is the 'sleeper cell' phenomenon, in which introduced species that are apparently innocuous for long periods of time are triggered to become invasive and damaging, owing to an environmental change (Spear et al., 2021).

It has been hypothesized that the risk of non-target impacts is higher in natural ecosystems versus human-disturbed ones because natural ecosystems can include species-rich communities with a higher diversity of non-target species and indirect interactions (Heimpel and Mills, 2017). One could expand this hypothesis to also consider the possibility of interactions with external stressors that could synergistically amplify the influence of the biocontrol agent. Conversely, invasion theory suggests that diverse systems might also have higher biotic resistance to the biocontrol agent and could plausibly dampen its effects through antagonistic interactions (Ricciardi et al., 2013). While species-rich systems offer greater opportunities for a generalist agent to expand its host repertoire, anthropogenically disturbed systems could impose selective pressures to increase the environmental tolerance of the agent such that it can increase its habitat range; the rationale for this outcome stems from the Anthropogenically Induced Adaptation to Invade (AIAI) hypothesis and the concept of the bridgehead effect — in which an introduced population undergoes evolution that increases its colonization potential and thus becomes the source of future invasions elsewhere (Hufbauer et al., 2012).

To improve risk assessment, both biocontrol and invasion sciences must address context dependence of indirect effects. Through invasion science, biocontrol science is offered insight into potential indirect impacts, as well as underexploited hypotheses and concepts (e.g. AIAI; Environmental Matching). Conversely, biocontrol science offers cases in which time-since-introduction, origin, genetics, propagule pressure, and colonization pressure of the introduced organism(s) are known and can be used in meta-analytical tests of hypotheses. Biocontrol also offers post-release evaluations; however, an important consideration is the timing of these evaluations. Delayed indirect effects, such as post-establishment evolution, invasion meltdowns, or environmental triggers that cause biocontrol agents to become invasive, may take years or decades to emerge (Spear et al., 2021). Therefore, risk assessments should incorporate long-term post-evaluations to identify any delayed indirect impacts of biological agents (Barrat et al., 2006, Carson et al., 2008).

Computational dimensions

Developing technologies

A crucial yet ever-changing aspect of biocontrol and invasion science is the development of technologies used to capture and measure raw data, monitor sites, process data, model results, and make usable predictions for future applications. Several key parallel developing technologies between the disciplines of biocontrol and invasion science include the application of high-throughput genetic sequencing, advanced remote sensing, machine learning, and improvements in data accessibility.

The application of molecular biology techniques, in particular genetic sequencing technologies, are commonplace in many biological fields, including biocontrol and biological invasion. Various genetic markers are routinely used to study population genetics, each of which offer differing degrees of variability and precision by targeting specific regions of DNA by PCR (i.e., mtDNA or cpDNA) or analyzing genomic characteristics using specific techniques such as restriction fragment length polymorphism analysis, amplified fragment length polymorphism analysis (Le Roux and Wieczorek, 2008), or microsatellites.

Fitzpatrick et al. (2012) highlighted the fact that in biological invasions (and similarly in the introduction of biocontrol agents), when considering the historical timescale of an invasion, the rate of mutation and genetic drift for most organisms may be insufficient. As such, this lack of required genetic resolution may leave many questions unresolved (Cuthbert et al., 2025). However, significant advances have been achieved in recent years in high-throughput genetic sequencing (Hu et al., 2021, Santam et al., 2023). This explosion in sequence data may enable the identification of novel methods for evaluating population genetics in the fields of biocontrol and biological invasion, providing the necessary resolution. Coupling these advancements to the array of novel applications these technologies bring, including but not limited to transcriptomics, epigenetics, and metagenomics (Santam et al., 2023), researchers may further identify novel research methods and approaches. It is important that the impact of high-throughput sequencing not be overestimated, but large data-driven science may provide valuable insight in future years when coupled with other developing technologies.

As with genetic information, collecting spatial data on biological invasions is important both for understanding occurrence and spread, as well as for guiding management interventions such as early detection and control. Despite long-standing challenges in remote sensing, such as limited image resolutions, continued improvements in sensor technology, increased data availability, and cloud-based computing platforms have increased the utility of remote sensing by providing synoptic, repeatable, and cost-effective monitoring solutions for invasion studies (Woodcock et al., 2020).

While utilized by both fields, remote sensing plays a more prominent role in invasion science, where it is used to map species distributions, monitor spread dynamics, and model habitat suitability (Vaz et al., 2019). In contrast, biocontrol research primarily relies on localized assessments of agent establishment and impact, with remote sensing playing a more indirect role, such as evaluating target species recovery post-agent release (Coetzee et al., 2022). Biocontrol stands to benefit from utilizing remote sensing in post-release monitoring by providing long-term, landscape-scale assessments of impact and control. For example, satellite-based remote sensing was used to monitor the extent and health of water hyacinth in Hartbeespoort Dam, South Africa, to evaluate the effectiveness of its biocontrol program (Coetzee et al., 2022). By integrating satellite-derived cover estimates with monthly field surveys, the study demonstrated how remote sensing information can provide historical and near-real-time insights into invasion dynamics while complementing field data collection, thereby enhancing assessments of biocontrol efficacy. Similarly, Herbert et al. (2024) highlighted the importance of early intervention and continuous remote sensing monitoring of the biological control program against *Salvinia molesta* using the biocontrol agent, *Cyrtobagous salviniae*, in Lake Ossa, Cameroon, where local livelihoods were threatened by the mats of weed covering the water surface, and where the endangered African manatee disappeared as a result of the invasion. They proposed that the integration of biological control and remote sensing technology is becoming more accessible and can be automated, and should therefore become a replicable model for future invasive weed programs around the world. Future research should therefore prioritize the integration of remotely sensed data with *in situ* monitoring to improve validation of control outcomes and inform adaptive management strategies.

More broadly, the application of data science and machine learning techniques in invasion science and biocontrol has shown promising results. For example, machine learning models can enhance biocontrol outcomes by identifying optimal release strategies, thereby improving resource allocation and implementation efficiency (White et al., 2022). Moreover, emerging opportunities around automatic monitoring and detection are harnessing deep-learning (informed by e.g., acoustics, eDNA, and image recognition) for improved population tracking (Fricke and Olden, 2023). Similarly, genetic data-driven approaches can enhance our understanding of invasion pathways and improve predictions (Brazier et al., 2022). These developing technologies, as in molecular biology and remote sensing, will facilitate better real-time monitoring, adaptive management, and improved ecological modelling across both disciplines.

Taxonomic imperative

Taxonomy is one of the oldest disciplines in science, and aims to describe and classify organisms into discrete categories (Britz et al., 2020). Historically, this was achieved primarily through the use of morphological characteristics to discern between evolutionary groups, while modern taxonomy tends towards an integrative approach that incorporates genetic, ecological, behavioral, and other informative data as additional independent lines of evidence (Karbstein et al., 2024). The importance of taxonomy cannot be overstated, considering that some biodiversity estimates have suggested that less than 20% of the extant species on Earth have been formally described (referred to as the "taxonomic impediment") (Costello et al., 2013; Liu et al., 2022). Taxonomic expertise is particularly relevant in the applied fields of conservation and biocontrol and invasion science, where the correct identification of target taxonomic groups lays the fundamental groundwork in research programs and management plans (Shimbori et al., 2023; Marvaldi, 2024).

The success of a biocontrol programme relies on the correct matching of target pests to their natural enemies, ensuring that the most damaging and host-specific control agent is selected (e.g., Barratt et al., 2018), and that post-release evaluations are accurate. Similarly, and often overlapping with biocontrol research, invasion science relies on accurate taxonomic identifications to assess factors such as the impacts of invasions on ecosystems, predictions of invasive potential, and the compilation of risk assessments and prioritization lists. Both disciplines face the difficulties associated with the practical applications of taxonomic classification methods, particularly with regards to the determination of inter-and intraspecific taxonomic boundaries and the choice of meaningful and consistent terminology to refer to distinct taxa at differential stages of evolutionary divergence (e.g., the use of terms such as populations, lineages, biotypes, species, and evolutionary units; see Downie, 2010). Additionally, the hybridization of invaders with native species, and between different biocontrol agent populations (or closely-related species), poses further challenges to identification and the unpredictable impacts on ecosystem dynamics, such as competition and feeding behavior. These impacts can significantly affect the performance of biocontrol agents, as well as the direct and indirect effects of invaders in novel environments.

The rapid growth of genetic technologies such as next-generation sequencing (NGS) platforms, and the overall shift towards genome-wide applications rather than conventional single-gene analyses (e.g., COI barcoding) is already changing the nature of research outputs in the domains of both biocontrol and invasion science. The recent uptake in RADseq methods exemplifies this, with a focus on much larger datasets for detecting population-level differences (e.g., single-nucleotide polymorphisms). This, in addition to the exponential advancements in artificial intelligence (AI) (e.g., image recognition tools and genome assembly methods), will continue to offer new opportunities and insights into taxonomic knowledge gaps (Karbstein et al., 2024). These technological advancements also offer greater opportunity for interdisciplinary collaboration between biocontrol practitioners, invasion scientists, taxonomists, programmers, modelers, and molecular biologists, to ensure that these advancements attain the full scope of their potential. The advancements of NGS and AI tools have, however, also contributed towards a growing shortage of well-trained taxonomists (Engel et al., 2021), with a relatively lower value placed on traditional taxonomic work (Agnarsson and Kuntner, 2007). Both biological disciplines should take notice of this emerging trend and emphasise the incorporation of integrative taxonomic approaches going forward. This presents a further opportunity for biocontrol and invasion science to promote and secure funding for traditional taxonomic work.

As we look further into the future, advanced genetic technologies such as CRISPR and gene drives may dramatically alter the landscape of biocontrol. CRISPR technology could be used to modify natural enemies, enhancing their effectiveness or ensuring that they exclusively target invaders without impacting non-target species. Gene drives, which propagate specific genes through populations, may offer a way to control or even eradicate invasions by altering their reproduction or survival traits (Ricciardi et al., 2017). However, the use of gene drives will require careful taxonomic consideration to ensure that gene-altered organisms do not negatively affect non-target species or ecosystems. The ethical and ecological implications of releasing genetically modified organisms into the wild highlight the continued importance of taxonomy in predicting and managing the potential risks associated with these new technologies. Taxonomy may be considered the foundation on which informed decisions by biocontrol practitioners and invasion scientists can be made, with many shared challenges and opportunities for their resolution that will result in enhancing the effectiveness of biocontrol as well as early detection rapid response programs.

Social dimensions

Public awareness and collaboration

Public awareness and robust collaboration form a focal point between biocontrol and invasion science, necessary for both scientific fields to progress and to manage biological invasions efficiently. Public engagement is essential to both disciplines to improve understanding, gather data, and generate support and potential funding for management strategies. The increasing awareness of the importance of reaching diverse audiences, including non-scientists, policymakers, and local communities, is a key parallel between the two fields (Jubase et al., 2021, Weaver et al., 2021). Both fields have to justify interventions, explain ecological risks and benefits, and gain public support for management actions. Conveying the importance of control efforts is necessary for achieving conservation goals (Pocock et al., 2022) and securing funding and access for research and application.

Both disciplines grapple with communication hurdles. Explaining the nuances of ecological interactions, potential non-target effects (in biocontrol), or the long-term impacts of invasions can be challenging. The overwhelming majority of contemporary science outreach is based on communication models that have been shown to be ineffective and can undermine public trust (Varner, 2014). Moreover, denialism about the severity of biological invasions and skepticism regarding the effectiveness of biocontrol interventions are widespread problems. Each field runs the risk of working in an 'ivory tower', losing touch with the public values and concerns, and ultimately limiting acceptance or engagement (Varner, 2014). Avoiding technical jargon and sharing findings in accessible formats are common imperatives.

Citizen science is a powerful tool that bridges both fields and can be effective for invasive species surveillance, management, and research, providing large datasets (Pocock et al., 2022, Gervazoni et al. 2023). Platforms like iNaturalist are increasingly used in invasion science to monitor species distributions and report new incursions, although user behavior and potential data biases require consideration (Pocock et al., 2022; Di Cecco et al., 2021). These tools offer open-source data valuable for tracking species distribution, monitoring control agent establishment, and identifying new invasions (August et al., 2020; Cock et al., 2025; Di Cecco et al., 2021). The first study of its kind in Argentina used citizen science to improve the known and potential distribution of *Iris pseudacorus* (a flowering plant), which is a significant wetland invader (Gervazoni et al. 2023). SDMs using different datasets, including GBIF data, citizen science data, as well as survey data, showed that the citizen science-tailored approach provided more data over a wider geographical extent compared to other data sources. In combination with survey data, these records were used to highlight the extent and potential further invasion by this highly invasive plant species.

A compelling example of successful community engagement, specifically within biocontrol, is the management of water hyacinth (*Pontederia crassipes*) at Hartbeespoort Dam, South Africa. Faced with overwhelming infestations, a community-driven initiative, supported by researchers, established satellite rearing stations for the biocontrol agent *Megamelus scutellaris* (Moffat et al., 2024). The continual and inundative releases of high numbers of agents, facilitated by mass-rearing efforts (Hill et al., 2020) that included community rearing stations, contributed significantly to the success in controlling water hyacinth at the Dam (Coetzee et al., 2022; Moffat et al., 2024). This collaboration demonstrably reduced water hyacinth cover, showcasing how public investment and agency can directly contribute to successful biocontrol outcomes (Moffat et al., 2024; Coetzee et al., 2022).

Significant opportunities exist for biocontrol and invasion science to collaborate more closely on public awareness and engagement strategies. Developing joint communication strategies could be highly effective. The fields can present a stronger, more consistent message by speaking with a more unified voice about the threats of invasions and the benefits of carefully managed biocontrol. This includes collaborative efforts targeting schools, utilizing social media effectively, and working with traditional media to counter misinformation and denialism using shared, accessible language (Weaver et al., 2021).

Future citizen science initiatives could be designed to serve both fields explicitly. Programs could train volunteers to monitor not only the presence and impact of invasive species but also the establishment and effectiveness of introduced biocontrol agents, as demonstrated by tracking agents using citizen science images and DNA barcodes (Cock et al., 2025; Pocock et al., 2022). This integrated approach would provide richer datasets for adaptive management and streamline public participation efforts.

Both fields recognize the imperative to work more closely with other disciplines, particularly the social sciences, communication experts, and economists, to better understand the socio-economic drivers and consequences of invasions and control actions, and to design more effective engagement approaches (Weaver et al., 2021). Recent efforts through the 'InvaCost' project that harnessed natural and social sciences globally have bolstered public and decision maker awareness by placing a monetary value on the economic costs of biological invasions, thereby making these effects more tangible (Diagne et al., 2021), while also considering the concurrence of beneficial effects between sectors (Carneiro et al., 2024). Using monetary costs and cost-benefit analyses considering interventions could be a useful means to improve support for biocontrol initiatives, given the negative consequences of invasions and potential low cost of long-term biocontrol. Furthermore, strengthening international collaboration, particularly between the Global North and South, is crucial. Joint efforts can help address the uneven distribution of research capacity and funding (Weaver et al., 2021), fill knowledge gaps in under-researched regions, facilitate access and benefit-sharing agreements, and leverage large databases of mutual relevance, potentially through greater co-development with public stakeholders globally (Pocock et al., 2022).

Moving beyond raising awareness, future efforts should focus on fostering public agency and co-designing solutions. The Hartbeespoort Dam example illustrates the power of community involvement in implementation of control methods through establishing a 'community of practice' (Moffat et al., 2024). Local stakeholders gain empowerment through collaborative projects, which enable them to actively monitor and make management decisions and evaluate different approaches, while building shared responsibility and stewardship. The collaboration involves joint work on tool development and application through transdisciplinary methods, which results in user-friendly tools that fulfil community requirements.

Unifying terminology and coordinating policy

Despite the overlap in their goals, biocontrol and invasion sciences have developed distinct terminologies, often leading to redundancy and confusion. Unifying terminology between these fields is essential to enhance communication and improve the effectiveness of research, policy and management strategies. The disjointed nature between the fields of biocontrol and invasion science is evident in the terminology used to describe similar concepts. For example, the hypothesis of how native species influence the establishment of non-native species is termed 'biotic interference' in biocontrol studies (Goeden and Louda, 1976) and 'biotic resistance' in invasion literature (Levine et al., 2004). Other examples include ‘inundative release’ vs ‘propagule pressure’, ‘multiple agents’ vs ‘colonization pressure’, ‘host specific’ vs ‘monophagous’, and ‘broad host range’ vs ‘polyphagous’, respectively, between biocontrol and invasion sciences. Discrepancies such as these complicate reviews and meta-analyses, as researchers must navigate and reconcile differing terms to synthesize findings effectively (Herrando-Pérez et al., 2014). Moreover, the lack of standardized terminology can lead to misunderstandings and misinterpretations of research outcomes, and potential misrepresentations in public science communication (Janovsky and Larson, 2019).

Creating a unified terminology for biocontrol and invasion offers several advantages. First, it reduces redundancy, ensuring that similar concepts are described consistently across studies. This improves the clarity and precision of scientific communication, facilitating more effective collaboration and knowledge sharing. Secondly, standardizing terms enhances the interpretability of statistical models and their coefficients, allowing for more accurate comparisons and integrations of research findings across the two fields (Soto et al., 2024). Despite the clear benefits, unifying terminology presents several challenges. One major obstacle is the inconsistent enforcement of top-down term changes by journals. For example, some journals have moved away from using the term 'alien' to describe non-native species, while others continue to use it (Occhipinti-Ambrogi and Galil, 2004; Robinson et al., 2016). This inconsistency is also common among regional policy nomenclature, further creating confusion and hampering efforts to standardize terminology and implement management (Soto et al., 2024; Ahmed et al., 2025). Another challenge is the need to include non-English terms in the unified glossary, ensuring that research from non-English-speaking regions is accurately represented and integrated.

To address these challenges, several solutions can be proposed. First, there should be a concerted effort to standardise key terms and definitions across the fields of biocontrol and invasion science. This can be achieved through collaborative efforts among researchers, journals, and institutions. Science communication articles should also be aware of the terminology used, and avoid overly emotive language.

Successful examples of unified terminology in other scientific fields can serve as valuable case studies. For example, the standardisation of terminologies in medical research has significantly improved the clarity and efficiency of scientific communication (Bodenreider, 2004). Similar strategies can be adopted in ecological research, with the potential to enhance the coherence and impact of studies on biocontrol and invasion. Researchers can also draw on examples from conservation biology, where consistent terminology has facilitated more effective policy-making and management practices (Salafsky et al., 2024). Applications in species delimitation exercises, and taxonomic classification more generally, provide further examples of the importance of the adoption of consistent terminology in the naming of taxa at varying levels of evolutionary distance (Downie, 2010).

Harmonization of terminology and actions could further allow for more cohesive policies to address biological invasions and promote effective biocontrol (e.g., within a 'OneHealth' framework; Schaffner et al., 2024). Government departments around the world are often separately assigned to biological invasions (e.g., conservation management for biodiversity and ecosystems) and biocontrol (e.g., integrated pest management for agriculture) issues, resulting in regulatory frameworks that are misaligned between the fields and potentially inefficient. Improved integration of policy towards management of invasions while considering biocontrol through natural enemies as a tool could thus reduce redundancy and improve efficiency in ecological management interventions. Although legislation on the prevention and management of biological invasions does exist, often the lack of financial and human resources to implement them on the ground makes it challenging to enforce regulations. Furthermore, it is important to coordinate the enforcement of actions against invasions in neighboring countries, a species that is being controlled or eradicated in one country might simply reinvade from an invaded neighboring country. An excellent example of regional legislative collaboration is the European and Mediterranean Plant Protection Organisation (EPPO), responsible for European cooperation in plant health. Its objectives are “to protect plants, to develop international strategies against the introduction and spread of dangerous pests and to promote safe and effective control methods”. The EPPO, which was founded in 1951 by 15 member states, has grown to today’s 51 member countries, including nearly every country in the European and Mediterranean region.

Lessons could also be learned from biocontrol practitioners concerning regulated biosafety protocols that must be adhered to when rearing agents, which could in turn inform biosecurity practices to contain non-native species, prevent spread, and improve proactivity. For both fields, it is also important that well-intentioned policy frameworks do not overburden researchers and practitioners to the extent that they stifle rapid management actions, such as early detection and rapid response protocols for invasions that could include biocontrol interventions.

Synthesis

Our perspective gives a structured overview of the current parallels and opportunities linking biocontrol and invasion sciences obtained through expert elicitation (Figure 1; Supplementary Material 1). Core areas of overlap span ecological mechanisms (e.g., propagule pressure, colonization pressure, functional responses and enemy release), ecological consequences (such as indirect effects and unexpected trophic cascades), anthropogenic disturbances and environmental drivers (such as climate change and biotic resistance), computational advances (including remote sensing and machine learning), research dimensions, such as taxonomic precision and scale mismatches, as well as societal engagement. These domains intersect through shared theoretical frameworks and practical challenges, revealing strong parallels in success metrics, impact pathways, and risks. Furthermore, these parallels suggest that more bidirectional engagement between fields is not only possible, but also necessary to resolve discrepancies and make progress. Mechanisms to foster this are exemplified by the co-development of functional response metrics (e.g., RCP and RIP; Dick et al., 2017; Cuthbert et al., 2018), with a particular future need to unify terminology, harmonize risk assessment protocols, and invest in interoperable data platforms and collaborative research agendas.

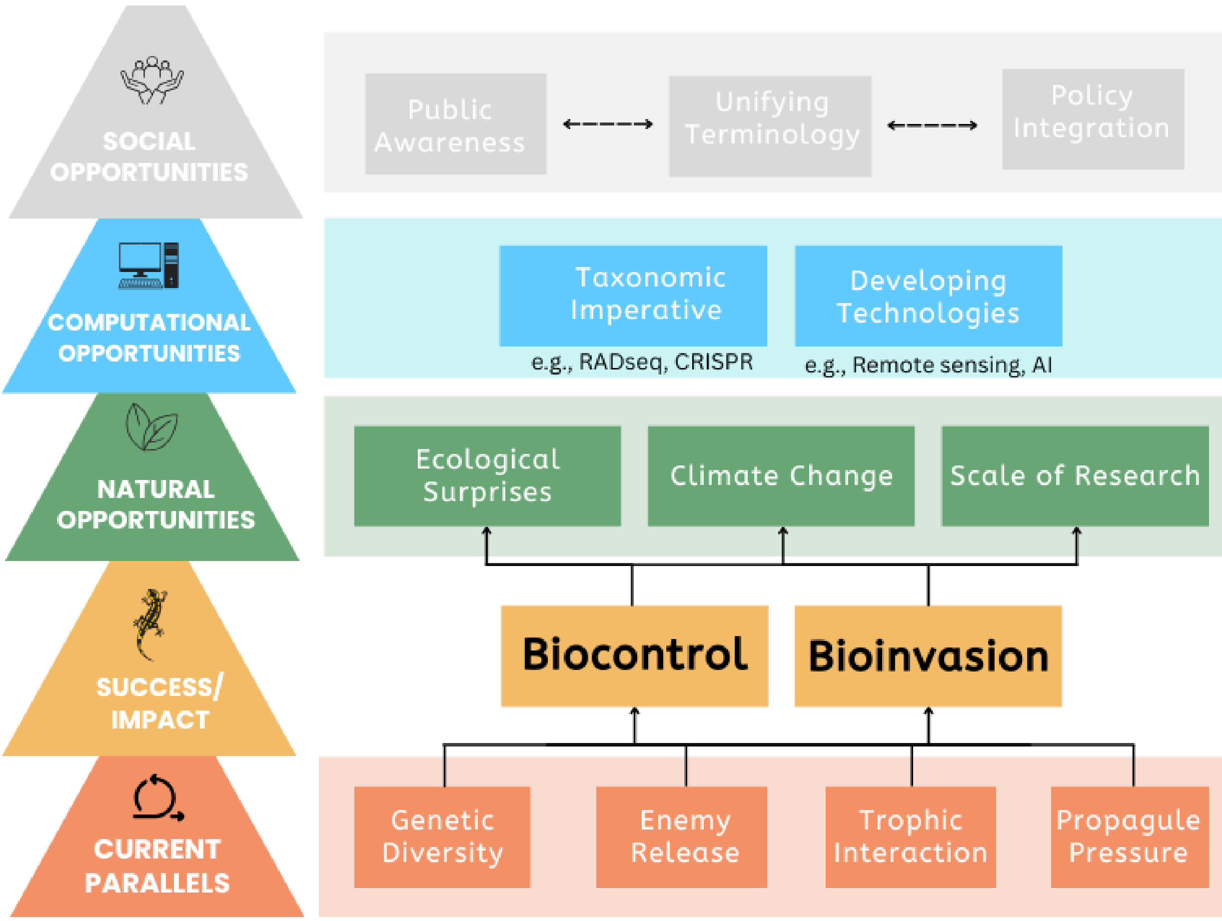

Figure 1. Graphic summary of parallel concepts and future opportunities of biocontrol and invasion sciences discussed in this perspective.

Integration of both research areas is particularly lacking within the socio-political dimension, neglecting key components such as the policy integration necessary for translating ecological findings into actionable frameworks across jurisdictions. Discussions on parallels on the socio-economic front, such as funding models, community livelihoods, and cost-benefit trade-offs, also require urgent development. Likewise, public awareness and collaboration, especially through citizen science and inclusive communication, are underrepresented, yet hold potential to bridge knowledge gaps and foster trust. Finally, broader anthropogenic disturbances beyond climate and habitat, such as urbanization, pollution, globalization, and infrastructure expansion, also require more explicit integration into future discussions, given their accelerating influence on species movement and ecosystem vulnerability.

Addressing these bidirectional areas is not just a matter of completeness, but of equity and sustainability. Research biases, whether geographic, taxonomic, or institutional, limit our collective capacity to respond to biodiversity challenges globally. Thus, tackling these biases by amplifying marginalized perspectives, investing in the Global South, and embracing diverse knowledge systems is crucial. By doing so, and by fostering a more integrated, inclusive, and responsive scientific dialogue, the biocontrol and invasion communities can meaningfully advance the sustainability agenda, ensuring environmental management strategies that are robust, just, and future-ready.

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References cited

Abram, P.K. and Moffat, C.E., 2018. Rethinking biological control programs as planned invasions. *Current Opinion in Insect Science 27*: 9-15.

Agnarsson, I., and Kuntner, M. 2007. Taxonomy in a changing world: seeking solutions for a science in crisis. *Systematic Biology* 56: 531-539.

Ahmed, D.A., Sousa, R., Bortolus, A., Aldemir, C., Angeli, N.F., Błońska, D., Briski, E., et al. 2025. Parallels and discrepancies between non-native species introductions and human migration. *Biological Reviews* 100: 1365-1395.

August, T.A., Pescott, O.L., Joly, A., and Bonnet, P. 2020. AI Naturalists Might Hold the Key to Unlocking Biodiversity Data in Social Media Imagery. *Patterns* 1: 100116.

Barratt, B. I. P., Cock, M. J. W., and Oberprieler, R. G. 2018. Weevils as targets for biological control, and the importance of taxonomy and phylogeny for efficacy and biosafety. *Diversity* 10: 73.

Baso, N.C., Bownes, A., Paynter, Q., Cartier, A., Hill, M.P. and Coetzee, J.A., 2024. Biogeographical comparison of *Lagarosiphon major* between native South Africa and invaded New Zealand: A natural enemy release case study? *Biological Control* 196: 105584.

Becker, D. J., Crowley, D. E., Washburne, A. D., and Plowright, R. K. 2019. Temporal and spatial limitations in global surveillance for bat filoviruses and henipaviruses. *Biology Letters* 15: 20190423.

Bellard, C., and Jeschke, J. M. (2016). A spatial mismatch between invader impacts and research publications. *Conservation Biology* 30: 230-232.

Bodenreider, O., 2004. The unified medical language system (UMLS): integrating biomedical terminology. *Nucleic Acids Research 32*: D267-D270.

Brazier, T., Cherif, E., Martin, J.F., Gilles, A., Blanchet, S., Zhao, Y., Combe, M., et al. 2022. The influence of native populations' genetic history on the reconstruction of invasion routes: the case of a highly invasive aquatic species. *Biological Invasions* 24: 2399-2420.

Britz, R., Hundsdorfer, A., and Fritz, U. 2020. Funding, training, permits—the three big challenges of taxonomy. *Megataxa* 1: 49-52.

Carneiro, L., Hulme, P.E., Cuthbert, R.N., Kourantidou, M., Bang, A., Haubrock, P.J., Bradshaw, C.J., et al. 2024. Benefits do not balance costs of biological invasions. *BioScience* 74: 340-344.

Carrillo, D., and Pena, J.E., 2012. Prey-stage preferences and functional and numerical responses of *Amblyseius largoensis* (Acari: Phytoseiidae) to *Raoiella indica* (Acari: Tenuipalpidae). *Experimental and Applied Acarology* 57: 361-372.

Cock, M.J.W., Day, M.D., Solis, M.A., and Winston, R.L. 2025. Publicly shared DNA barcodes and citizen science images provide new evidence on the establishment and spread of a lantana biological control agent, *Orphanostigma haemorrhoidalis* (Lepidoptera, Crambidae). *CABI Agriculture and Bioscience* 6: 0010.

Coetzee, J.A., Miller, B.E., Kinsler, D., Sebola, K., and Hill, M.P. 2022. It's a numbers game: inundative biological control of water hyacinth (*Pontederia crassipes*), using *Megamelus scutellaris* (Hemiptera: Delphacidae) yields success at a high elevation, hypertrophic reservoir in South Africa. *Biocontrol Science and Technology* 32: 1302-1311.

Costello, M. J., May, R. M., and Stork, N. E. (2013). Can we name Earth's species before they go extinct? *Science* 339: 413-416.

Cuthbert, R.N., Bodey, T.W., Briski, E., Capellini, I., Dick, J.T.A., Kourantidou, M., Ricciardi, A. and Pincheira-Donoso, D., 2025. Harnessing traits to predict economic impacts from biological invasions. *Trends in Ecology & Evolution* 40: 639-650.

Cuthbert, R.N., Dick, J.T.A., Callaghan, A. and Dickey, J.W., 2018. Biological control agent selection under environmental change using functional responses, abundances and fecundities; the Relative Control Potential (RCP) metric. *Biological Control* 121: 50-57.

Cuthbert, R.N., Dickey, J.W.E., Coughlan, N.E., Joyce, P.W. and Dick, J.T.A., 2019. The Functional Response Ratio (FRR): advancing comparative metrics for predicting the ecological impacts of invasive alien species. *Biological Invasions* 21: 2543-2547.

Delmas, E., Besson, M., Brice, M., Burkle, L. A., Dalla Riva, G. V., Fortin, M., Gravel, D., et al. 2019. Analysing ecological networks of species interactions. *Biological Reviews* 94: 16–36.

Diagne, C., Leroy, B., Vaissière, A.C., Gozlan, R.E., Roiz, D., Jarić, I., Salles, J.M., et al. F., 2021. High and rising economic costs of biological invasions worldwide. *Nature* 592: 571-576.

Di Cecco, G.J., Barve, V., Belitz, M.W., Stucky, B.J., Guralnick, R.P., and Hurlbert, A.H. 2021. Observing the Observers: How participants contribute data to iNaturalist and implications for biodiversity science. *BioScience* 71: 1179-1186.

Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B., Kumschick, S., et al. 2014. Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions* 16: 735-753.

Dick, J.T.A., Laverty, C., Lennon, J.J., Barrios-O'Neill, D., Mensink, P.J., Robert Britton, J., Médoc, V., et al. 2017. Invader Relative Impact Potential: a new metric to understand and predict the ecological impacts of existing, emerging and future invasive alien species. *Journal of Applied Ecology* 54: 1259-1267.

Dickey, J.W.E., Cuthbert, R.N., South, J., Britton, J.R., Caffrey, J., Chang, X., Crane, K., et al. 2020. On the RIP: using Relative Impact Potential to assess the ecological impacts of invasive alien species. *NeoBiota* 55: 27-60.

Downie, D.A. 2010. Baubles, bangles, and biotypes: a critical review of the use and abuse of the biotype concept. *Journal of Insect Science* 10: 176.

Elmes, G. W., and J. A. Thomas. 1992. Complexity of species conservation in managed habitats—interaction between *Maculinea* butterflies and their ant hosts. *Biodiversity and Conservation* 1: 155-169.

Enders, M., Hütt, M.T., and Jeschke, J.M. 2018. Drawing a map of invasion biology based on a network of hypotheses. *Ecosphere* 9: e02146.

Engel, M. S., Ceríaco, L. M., Daniel, G. M., Dellapé, P. M., Löbl, I., Marinov, M., Reis, R.E., et al. 2021. The taxonomic impediment: a shortage of taxonomists, not the lack of technical approaches. *Zoological Journal of the Linnean Society* 193: 381-387.

Esler, K. J., Prozesky, H., Sharma, G. P., and McGeoch, M. (2010). How wide is the “knowing-doing” gap in invasion biology? *Biological Invasions* 12: 4065-4075.

Faria, L., Cuthbert, R.N., Dickey, J.W., Jeschke, J.M., Ricciardi, A., Dick, J.T.A., and Vitule, J.R., 2023. The rise of the functional response in invasion science: a systematic review. *NeoBiota* 85: 43-79.

Fenn-Moltu, G., Liebhold, A.M., Weber, D.C. and Bertelsmeier, C., 2024. Pathways for accidental biocontrol: The human-mediated dispersal of insect predators and parasitoids. *Ecological Applications* 34: e3047.

Fitzpatrick, B.M., Fordyce, J.A., Niemiller, M.L., and Reynolds, R.G. 2012. What can DNA tell us about biological invasions? *Biological Invasions*, 14: 245-253.

Fortin, D., Beyer, H. L., Boyce, M. S., Smith, D. W., Duchesne, T., and Mao, J. S. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in yellowstone national park. *Ecology* 86: 132–1330.

Fricke, R.M., and Olden, J.D., 2023. Technological innovations enhance invasive species management in the Anthropocene. *BioScience* 73: 261–279.

Galli, M., Feldmann, F., Vogler, U.K., and Kogel, K.H., 2024. Can biocontrol be the game-changer in integrated pest management? A review of definitions, methods and strategies. *Journal of Plant Diseases and Protection* 131: 265–291.

Gervazoni, P., Minuti, G., Fuentes-Rodriguez, D., Coetzee, J., Sosa, A., Sabater, L., and Franceschini, C. 2023. Citizen science improves the known and potential distribution of a strong wetland invader: Implications for niche modeling and invasion management. *Environmental Management* 71: 1176–1187.

Goeden, R.D., and Louda, S.M., 1976. Biotic interference with insects imported for weed control. *Annual Review of Entomology* 21: 325–342.

Gonzalez, A., Germain, R. M., Srivastava, D. S., Filotas, E., Dee, L. E., Gravel, D., Thompson, P. L., et al. 2020. Scaling-up biodiversity-ecosystem functioning research. *Ecology Letters* 23: 757–776.

Grevstad, F.S., 1999. Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. *Biological Invasions* 1: 313–323.

Harms, N.E., Knight, I.A., Pratt, P.D., Reddy, A.M., Mukherjee, A., Gong, P., Coetzee, J., et al. 2021. Climate mismatch between introduced biological control agents and their invasive host plants: improving biological control of tropical weeds in temperate regions. *Insects* 12: 549.

Hassell, M.P., 1978. The dynamics of arthropod predator-prey systems. Princeton University Press.

Heffernan, J.B., Soranno, P.A., Angilletta, M.J., Buckley, L.B., Gruner, D.S., Keitt, T.H., Kellner, J.R., et al. 2014. Macrosystems ecology: Understanding ecological patterns and processes at continental scales. *Frontiers in Ecology and the Environment* 12: 5–14.

Heimpel, G.E., and N.J. Mills. 2017. Biological control: ecology and applications. Cambridge University Press.

Herbert, L., Zanga, A., Kinsler, D., Ayala, V., Kamla, A.T. and Diaz, R., 2024. Optimizing aquatic weed management in Lake Ossa, Cameroon: Harnessing the power of biological control and real-time satellite monitoring. *Biological Control* 199: 105650.

Herrando-Pérez, S., Brook, B.W. and Bradshaw, C.J., 2014. Ecology needs a convention of nomenclature. *BioScience* 64: 311–321.

Hill, M.P., Conlong, D., Zachariades, C., Coetzee, J.A., Paterson, I.D., Miller, B.E., Foxcroft, L. and Van Der Westhuizen, L., 2021. The role of mass-rearing in weed biological control projects in South Africa. *African Entomology* 29: 1030–1044.

Holling, C.S., 1959. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* 91: 385–398.

Hu, T., Chitnis, N., Monos, D., and Dinh, A., 2021. Next-generation sequencing technologies: An overview. *Human Immunology* 82: 801–811.

Hudgins, E.J., Cuthbert, R.N., Haubrock, P.J., Taylor, N.G., Kourantidou, M., Nguyen, D., Bang, A., et al., 2023. Unevenly distributed biological invasion costs among origin and recipient regions. *Nature Sustainability* 6: 1113–1124.

Hufbauer, R.A., Facon, B., Ravigne, V., Turgeon, J., Foucaud, J., Lee, C.E., Rey, O., and Estoup, A. 2012. Anthropogenically induced adaptation to invade (AIAI): contemporary adaptation to human-altered habitats within the native range can promote invasions. *Evolutionary Applications* 5: 89–101.

Huffaker, C.B., and Messenger, P.S., 2012. *Theory and practice of biological control*. Elsevier.

Janovsky, R.M., and Larson, E.R., 2019. Does invasive species research use more militaristic language than other ecology and conservation biology literature? *NeoBiota* 44: 27–38.

Jubase, N., Shackleton, R.T. and Measey, J., 2021. Public awareness and perceptions of invasive alien species in small towns. *Biology* 10: 1322.

Karbstein, K., Kösters, L., Hodač, L., Hofmann, M., Hörandl, E., Tomasello, S., Wagner, N.D., 2024. Species delimitation 4.0: integrative taxonomy meets artificial intelligence. *Trends in Ecology and Evolution* 39: 771–784.

Keane, R.M. and Crawley, M.J., 2002. Exotic plant invasions and the enemy release hypothesis. *Trends in Ecology and Evolution* 17: 164–170.

Kestrup, Ǻ.M., and A. Ricciardi., 2009. Environmental heterogeneity limits the local dominance of an invasive freshwater crustacean. *Biological Invasions* 11: 2095–2105.

Koel, T.M., Tronstad, L.M., Arnold, J.L., Gunther, K.A., Smith, D.W., Syslo, J.M., and White, P.J., 2019. Predatory fish invasion induces within and across ecosystem effects in Yellowstone National Park. *Science Advances* 5: eaav1139.

Korner, C., and Basler, D. 2010. Phenology under global warming. *Science* 327: 1461–1462.

Landi, P., McCoy, M.W., and Vonesh, J.R., 2022. Predicting invasive consumer impact via the comparative functional response approach: linking application to ecological theory. *Biological invasions* 24: 3565-3579.

Lantschner, M. V., de la Vega, G., and Corley, J. C. (2019). Predicting the distribution of harmful species and their natural enemies in agricultural, livestock and forestry systems: an overview. *International Journal of Pest Management* 65: 190-206.

Le Roux, J., and Wieczorek, A.M., 2009. Molecular systematics and population genetics of biological invasions: towards a better understanding of invasive species management. *Annals of Applied Biology* 154: 1-17.

Levine, J.M., Adler, P.B. and Yelenik, S.G., 2004. A meta-analysis of biotic resistance to exotic plant invasions. *Ecology Letters* 7: 975-989.

Liu, C., Wolter, C., Courchamp, F., Roura-Pascual, N., and Jeschke, J.M. 2022. Biological invasions reveal how niche change affects the transferability of species distribution models. *Ecology* 103: e3719.

Liu, J., Slik, F., Zheng, S., and Lindenmayer, D. B. (2022). Undescribed species have higher extinction risk than known species. *Conservation Letters* 15: e12876.

Lockwood, J.L., Hoopes, M.F. and Marchetti, M.P., 2013. Invasion ecology. John Wiley and Sons.

Marvaldi, A.E. (2024). Phylogenetic systematics and integrative taxonomy contribute to weed biological control. *Biological Control* 197: 105599.

MacIsaac, H.J. and Johansson, M.L., 2017. Higher colonization pressure increases the risk of sustaining invasion by invasive non-indigenous species. Aquatic *Ecosystem Health and Management* 20: 378-383.

Memmott, J., Craze, P.G., Harman, H.M., Syrett, P., and Fowler, S.V., 2005. The effect of propagule size on the invasion of an alien insect. *Journal of Animal Ecology* 74: 50-62.

Minghetti, E., Olivera, L., and Montemayor, S. I. (2020). Ecological niche modelling of *Gargaphia decoris* (Heteroptera), a biological control agent of the invasive tree *Solanum mauritianum* (Solanales: Solanaceae). *Pest Management Science* 76: 1273-1281.

Moffat, R., Weaver, K., Ngxande-Koza, S., Sebola, K., English, K., Kinsler, D., and Coetzee, J. (2024). Bridging boundaries: Six years of community engagement with biological control implementation and monitoring of water hyacinth on Hartbeespoort Dam, South Africa. *Biological Control* 194: 105544.

Mukherjee, A., Banerjee, A. K., and Raghu, S., 2021. Biological control of Parkinsonia aculeata: Using species distribution models to refine agent surveys and releases. *Biological Control* 159: 104630.

Murdoch, W.W., and Briggs, C.J., 1996. Theory for biological control: recent developments. *Ecology* 77: 2001-2013.

Musseau, C.L., Bernard-Verdier, M., Heger, T., Skopeteas, L.H., Strasiewsky, D., Mietchen, D. and Jeschke, J.M., 2024. A conceptual classification scheme of invasion science. *BioScience*, 74: 840-850.

Nong, D., Warziniack, T., Countryman, A.M., and Grey, E.K. 2019. Melting Arctic sea ice: Implications for nonindigenous species (NIS) spread in the United States. *Environmental Science and Policy* 91: 81-91.

Occhipinti-Ambrogi, A. and Galil, B.S., 2004. A uniform terminology on bioinvasions: a chimera or an operative tool?. *Marine Pollution Bulletin* 49: 688-694.

Pearson, D.E., and Callaway., R.M., 2003. Indirect effects of host-specific biological control agents. *Trends in Ecology and Evolution* 18: 456-461.

Phillips, S.J., Anderson, R.P., and Schapire, R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190: 231-259.

Pichler, M., and Hartig, F. 2021. A new joint species distribution model for faster and more accurate inference of species associations from big community data. *Methods in Ecology and Evolution* 12: 2159-2173.

Pocock, M.J., Adriaens, T., Bertolino, S., Eschen, R., Essl, F., Hulme, P.E., Jeschke, J.M., et al. 2024. Citizen science is a vital partnership for invasive alien species management and research. *iScience* 27: 108623.

Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Sixtová, Z.,, and Weber, E. (2008). Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution* 23: 237–244.

Reynolds-Hogland, M.J., and Mitchell, M.S. 2007. Three Axes of Ecological Studies: Matching Process and Time in Landscape Ecology. In: Bissonette, J.A., and Storch, I. (Eds.), *Temporal Dimensions of Landscape Ecology* (pp. 174–194). Springer.

Ricciardi, A., Blackburn, T.M., Carlton, J.T., Dick, J.T.A., Hulme, P.E., Iacarella, J.C., Jeschke, J.M., et al., 2017. Invasion science: a horizon scan of emerging challenges and opportunities. *Trends in Ecology and Evolution* 32: 464-474.

Ricciardi, A., M.F. Hoopes, M.P. Marchetti, and J.L. Lockwood. 2013. Progress toward understanding the ecological impacts of non-native species. *Ecological Monographs* 83: 263-282.

Ricciardi, A., Whoriskey, F.G., and Rasmussen, J.B., 1997. The role of the zebra mussel (*Dreissena polymorpha*) in structuring macroinvertebrate communities on hard substrata. *Canadian Journal of Fisheries and Aquatic Sciences* 54: 2596–2608.

Richardson, D.M., and Pyšek, P. 2008. Fifty years of invasion ecology–the legacy of Charles Elton. *Diversity and Distributions* 14: 161-168.

Robinson, T.B., Alexander, M.E., Simon, C.A., Griffiths, C.L., Peters, K., Sibanda, S., Miza, S., et al. 2016. Lost in translation? Standardising the terminology used in marine invasion biology and updating South African alien species lists. *African Journal of Marine Science* 38: 129-140.

Rubenstein, M.A., Weiskopf, S.R., Bertrand, R., Carter, S.L., Comte, L., Eaton, M.J., Johnson, C.G., et al. 2023. Climate change and the global redistribution of biodiversity: substantial variation in empirical support for expected range shifts. *Environmental Evidence* 12: 7.

Salafsky, N., Mejía Cortez, P., de Meyer, K., Dudley, N., Klimmek, H., Lewis, A., MacRae, D., et al. 2024. A standard lexicon of terms for area-based conservation version 1.0. *Conservation Biology* 38: e14269

Schaffner, U., Heimpel, G.E., Mills, N.J., Muriithi, B.W., Thomas, M.B., and Wyckhuys, K.A., 2024. Biological control for one health. S*cience of The Total Environment* 951: 175800.

Seebens, H., Blackburn, T.M., Dyer, E.E., Genovesi, P., Hulme, P.E., Jeschke, J.M., Pagad, S., et al., 2017. No saturation in the accumulation of alien species worldwide. *Nature Communications*, 8: 14435.

Shea, K., and Possingham, H.P., 2000. Optimal release strategies for biological control agents: an application of stochastic dynamic programming to population management. *Journal of Applied Ecology* 37: 77-86.

Shimbori, E.M., Querino, R.B., Costa, V.A., and Zucchi, R.A., 2023. Taxonomy and biological control: new challenges in an old relationship. *Neotropical Entomology* 52: 351-372.

Shine, R., Ward-Fear, G., and Brown, G.P., 2020. A famous failure: why were cane toads an ineffective biocontrol in Australia? *Conservation Science and Practice* 2: e296.

Soto, I., Ahmed, D.A., Balzani, P., Cuthbert, R.N., and Haubrock, P.J., 2023. Sigmoidal curves reflect impacts and dynamics of aquatic invasive species. *Science of the Total Environment* 872: 161818.

Soto, I., Balzani, P., Carneiro, L., Cuthbert, R.N., Macêdo, R., Serhan Tarkan, A., Ahmed, D.A., et al. 2024. Taming the terminological tempest in invasion science. *Biological Reviews* 99: 1357-1390.

South, J., Dickey, J.W.E., Cuthbert, R.N., and Dick, J.T.A., 2022. Combining resource population dynamics into impact assessments of native and invasive species under abiotic change. *Ecological Indicators* 142: 109260.

Spear, M.J., Walsh, J.R., Ricciardi, A., and Vander Zanden, M.J. 2021. The invasion ecology of sleeper populations: prevalence, persistence, and abrupt shifts. *BioScience* 71: 357-369.

Strong Jr, D.R., 1974. The insects of British trees: community equilibration in ecological time. *Annals of the Missouri Botanical Garden* 61: 692-701.

Sun, Y., Brönnimann, O., Roderick, G.K., Poltavsky, A., Lommen, S.T., and 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., and Keller, S.R. (2020). Biocontrol of invasive weeds under climate change: progress, challenges and management implications. *Current Opinion in Insect Science 38*: 72-78.

Thomas, M.B., and Reid, A.M., 2007. Are exotic natural enemies an effective way of controlling invasive plants?. *Trends in Ecology and Evolution 22*: 447-453.

Traveset, A., and Richardson, D.M. 2006. Biological invasions as disruptors of plant reproductive mutualisms. Trends in Ecology and Evolution 21: 208-216.

Tscharntke, T., Bommarco, R., Clough, Y., Crist, T. O., Kleijn, D., Rand, T. A., Tylianakis, J. M., et al. 2007. Conservation biological control and enemy diversity on a landscape scale. *Biological Control* 43: 294-309.

Uiterwaal, S.F., Lagerstrom, I.T., Lyon, S.R., and DeLong, J.P., 2022. FoRAGE database: A compilation of functional responses for consumers and parasitoids. *Ecology* 103: e3706.

Van Driesche, R., and Bellows Jr, T.S., 2012. Biological control. Springer Science and Business Media.

van Lenteren, J. C. (2012). The state of biological control. In Biological control: a global perspective (pp. 3-22). CABI.

van Steenderen, C.J.M., Mauda, E.V., Kirkman, W., Faulkner, K.T., and Sutton, G.F., 2024. The Asian Citrus Psyllid (*Diaphorina citri*) in Africa: using MaxEnt to predict current and future climatic suitability, with a focus on potential invasion routes. *African Entomology* 32: e18476.

Varner, J. 2014. Scientific outreach: toward effective public engagement with biological science. *BioScience* 64: 333-340.

Vaz, A.S., Alcaraz-Segura, D., Vicente, J.R., and Honrado, J.P. 2019. The many roles of remote sensing in invasion science. *Frontiers in Ecology and Evolution* 7: 370.

Wagner, D. L., Grames, E.M., Forister, M.L., Berenbaum, M.R., and Stopak, D., 2021. Insect decline in the Anthropocene: Death by a thousand cuts. *Proceedings of the National Academy of Sciences* 118: e2023989118.

Wainright, C.A., Muhlfeld, C.C., Elser, J.J., Bourret, S.L., and Devlin, S.P., 2021. Species invasion progressively disrupts the trophic structure of native food webs. *Proceedings of the National Academy of Sciences*, 118: e2102179118.

Wasserman, R.J., Alexander, M.E., Dalu, T., Ellender, B.R., Kaiser, H., and Weyl, O.L.F., 2016. Using functional responses to quantify interaction effects among predators. *Functional Ecology* 30: 1988-1998.

Weaver, K.N., Hill, M.P., Byrne, M.J., and Ivey, P. 2021. Efforts towards engaging communities to promote the benefits of biological control research and implementation in South Africa. *African Entomology* 29: 1045-1059.

White, D.T., Antoniou, T.M., Martin, J.M., Kmetz, W., and Twiss, M.R., 2022. A machine-learning approach to predict success of a biocontrol for invasive Eurasian watermilfoil reduction. *Ecological Applications* 32: e2625.

Woodcock, C.E., Loveland, T.R., Herold, M., and Bauer, M.E., 2020. Transitioning from change detection to monitoring with remote sensing: A paradigm shift. *Remote Sensing of Environment* 238: 111558.

Zachariades, C., Strathie, L.W., Kluge, R.L., and Hill, M.P., 2017. The biological control of weeds in South Africa. *African Entomology 25:* 177-191.

Zimmermann, H.G., Moran, V.C., and Hoffmann, J.H., 2004. Biological control of cactus weeds of the genus Opuntia in South Africa. *African Entomology* 12: 1-13.

Zhou, Y., Zhang, H., Liu, D., Khashaveh, A., Li, Q., Wyckhuys, K. A. G., and Wu, K., 2023. Long-term insect censuses capture progressive loss of ecosystem functioning in East Asia. *Science Advances 9*: eade9341.