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Opinion

How do we know when invasive species control strategies work?

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Controlling invasive species is costly and difficult but can have major ecological, economic, and health benefits. Researchers commonly compare the efficacy of specific control methods. However, invasive species control programs vary greatly in overarching goals and often occur over large areas, long timeframes, and varied environmental and social contexts. The success of these programs likely hinges on factors including organizational structures, concurrent restoration activities, geographic and temporal scope of control, and the invasive species' biology. To enable assessment of the relative influence of these common features, we propose clearer definitions of success in invasive species control and explicit comparisons among control programs. Post hoc assessment of existing programs' success will complement system-specific studies to guide strategies that work in real-world situations.

Highlights

Invasive species pose a major threat to ecosystems, economies, and human health with global economic damage alone estimated at over US$400 billion annually.

Invasive species control programs are taking on increasingly ambitious strategies to eradicate or reduce the abundance of invasive species. However, the success of invasive species control programs is highly variable.

Accurately measuring success of invasive species control is complicated but hinges primarily on measuring the environmental gains achieved by control programs and the longevity of those gains.

We develop a framework to assess the success of invasive species control and hypotheses about what determines success.

Explicitly comparing the successes and failures of invasive species control projects is critical to anticipate the scale and durability of potential control efforts and improve future programs.

The control of invasive species

Stories of **invasive species** (see Glossary) control often evoke comparisons to classical epic tragedies. Control efforts are framed as futile Sisyphean tasks, invasive species as many-headed hydras, and efforts of invasive species managers as Herculean in magnitude [1,2]. These strong terms reflect the urgency in curbing the negative effects of invasive species [3] and skepticism about whether we are up to the task. Undoubtedly, the control of invasive species is difficult, and many attempts to do so fall short of their initial promise [4]. And yet, there are clear success stories where the control of invasive species has a strong net benefit (Box 1) that can yield some of the highest rewards of all conservation actions [12]. The reality is likely less hyperbolic: when assessed, the success of **invasive species control programs**, from small-scale projects to national initiatives, is highly variable. Within that variability, there is opportunity for improvement.

A strong connection between invasion biology research and on-the-ground invasive species management is essential for creating successful **control actions** and **control strategies**. The efficacy of control actions (e.g., pesticides, **biocontrol** agents, and traps) is typically evaluated at the local scale (e.g., [13]), while the plausibility of control strategies is commonly evaluated using theoretical models [14,15]. However, **invasive species management success** is complex and depends on myriad features, from species and ecosystem attributes to methodological effectiveness and administrative characteristics [16]. We lack broad-scale comparisons of which attributes of invasive species control programs best predict their success. Related fields, such as conservation biology and restoration biology [12,17,18], have embraced a comparative approach to assessing the success of on-the-ground projects, and invasion biology has recently drawn important lessons from this approach (Table 1). We suggest that comparisons among

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Box 1. Examples of invasive species control programs that have achieved success toward different goals

'Asset protection': successful programs in the Hawaiian Islands have combined invasive species control with restoration efforts in biodiversity hotspots. For example, at the high-elevation Hakalau Forest National Wildlife Refuge (Figure IA), managers combine invasive plant control, fencing, and ungulate control with a multidecadal investment in restoration within former pasture lands situated above intact forest [5]. Reforestation, primarily with koa (*Acacia koa*), created corridors of native plants from low- to high-elevation areas that have achieved a major conservation objective by creating habitat for threatened and endangered native birds [5]. Avian populations are increasing in restored areas where invasive plant control is prioritized, but are declining elsewhere, coincident with increased climatic suitability for the mosquito that transmits avian malaria [6].

'Minimize spread and impacts': control of the sea lamprey (*P. marinus*; Figure IB) in the North American Great Lakes has been one of the largest and longest-running success stories in aquatic invasive species control. The success of this program has been attributed to significant, long-term investment by broad stakeholder groups, combined with effective control methods and ongoing research to improve control tools [7].

Eradication: eradication programs achieve the highest success rates on islands and at the earliest stages of invasion [**8,9**]. For example, invasive mammals have been eradicated from numerous islands to protect sensitive wildlife [9] (Figure IC).

'Environmental control': giant salvinia (*Salvinia molesta*; Figure ID), native to South America, was accidentally introduced via the aquarium industry into freshwater bodies throughout the world, where it clogs waterways and drastically reduces aquatic biodiversity. Control of this weed was considered intractable until the development and release of the host-specific weevil *Cyrtobagous salviniae* as a biocontrol agent in Queensland, Australia, in 1980 [10]. In Australia, the weevil does not eradicate salvinia but reduces its abundance to levels where its negative impacts are not apparent [10]. The beetle has had subsequent successes against salvinia infestations globally, for example, in a biocontrol project in Lake Ossa, Cameroon, that restored fishing and African manatee (*Trichechus senegalensis*) habitat by removing salvinia mats [11].

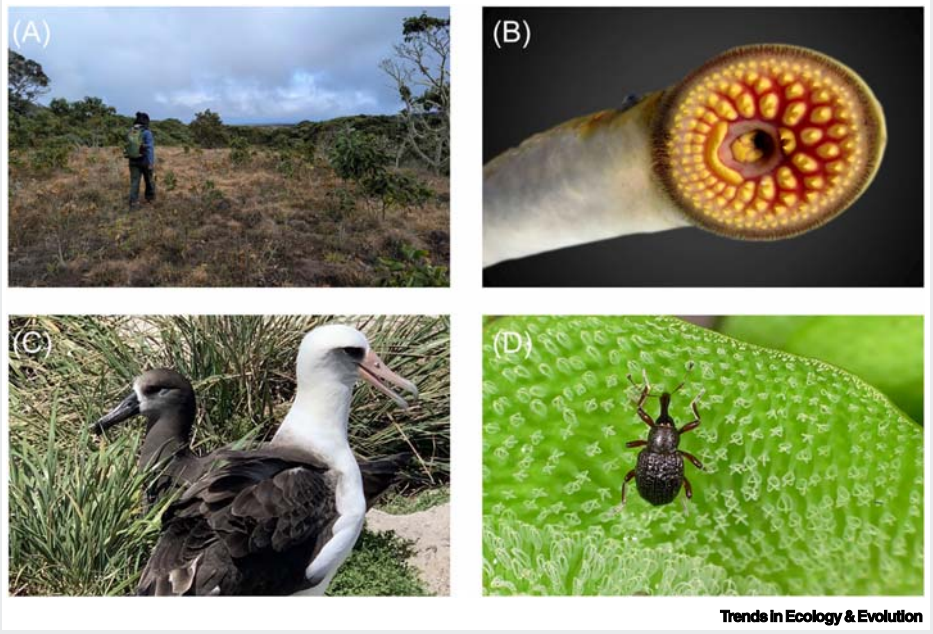


Figure I. (A) Invasive plant control and native plant restoration in Hakalau Forest National Wildlife Refuge. (B) An invasive lamprey (*P. marinus*) from the North American Great Lakes. (C) Laysan albatross (*Phoebastria immutabilis*) and black-footed albatross (*Phoebastria nigripes*) nest on Pacific Islands with mammal eradication programs. (D) *C. salviniae*, a host-specific weevil introduced to control the invasive plant giant salvinia (*S. molesta*) in Cameroon. Photo credits: A. Lauren Smith, B. Andrea Miehls, C. Helen Sofaer, D. Rodrigo Diaz, Victoria Ayala, and Aristide Kamla.

existing invasive species control projects yield valuable lessons that can guide invasive species management toward success, and we provide insights into how to make those comparisons to test critical hypotheses.

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Table 1. Major findings of comparative studies of invasive species control

Major findings	Invasive taxa	Geography	Experimental or program-based	Key response(s)	Refs
Ecosystem properties improve with invasive species control when habitats are undisturbed, isolated, and lack other invaders.	Multiple	Global	Program-based	Qualitative assessment of ecosystem effects	[4]
Chemical methods marginally outperform mechanical methods; effects from small-scale studies may not reflect those of large-scale actions.	Plants	Global	Experimental	Reduction in invasive species; increase of native species	[13]
Control methods unevenly applied across different countries.	Plants	Global	Program-based	Implementation of control actions	[18]
Few studies measure ecosystem benefits. Most biocontrol agents reduced growth or abundance of target plant species.	Plants	South Africa	Program-based	Qualitative assessment of reduction in invasive and ecosystem effects	[19]
Greater control of invasive plants by biocontrol when the plant is perennial, aquatic, or riparian and when biocontrol agent is multivoltine, external feeding, and plant-feeding as both larva and adult	Plants	North America	Program-based	Qualitative assessment of reduction in invasive species	[20]
The native vegetation has the potential to recover to a preinvasion target state.	Plants	Global	Experimental	Reduction of invasive species; recovery of native plants.	[21]
Biocontrol agents successfully reduce invasive plant mass and seed production, and increase diversity of nontarget plants.	Plants	Global	Experimental	Reduction of invasive species; recovery of native plants.	[22]
Eradication more successful at smaller sites.	Aquatic plants and animals	North America	Program-based	Eradication of invasive species	[23]
Individual manager characteristics predict success of post-tamarisk removal revegetation	*Tamarix* sp. (plant)	Western North America	Program-based	Ordinal scale of ecosystem recovery	[24]
Successful control of mammals on islands has increased.	Vertebrates	Islands	Program-based	Eradication of invasive species	[9]
Substantial improvements in native species demographic rates due to invasive mammal eradication	Mammals	Islands	Program-based	Ecosystem effects attributable to eradications	[8]
Early eradications on confined areas more successful. Eradications of pathogens slightly more successful than insects.	Herbivorous invertebrates and plant pathogens	Europe	Program-based	Eradication of invasive species	[25]

Defining the success of invasive species control

Clear definitions and measures of success are needed to guide environmental management projects, and these measures will vary depending on project context and goals (Figures 1 and 2) [26,27]. The success of invasive species control is easily conflated with complete

Glossary

Asset protection: the local suppression of invasive species to protect a finite resource, such as a population of an endangered species or a land unit of particularly high value.
Biocontrol: the suppression of an invasive or undesirable species using live specialist natural enemies, usually introduced from the same native range as the target invasive species ('classical' biocontrol).
Control action: a measure intended to reduce the abundance, distribution, or impacts of an invasive species, for example, trapping, spraying herbicide, or releasing a biological control agent.
Control strategy: a set of coordinated actions, prioritized over time and space, to reduce the abundance, distribution, or impact of an invasive species.
Cost–benefit analysis: the balancing of the gains and losses of an action, often forming the basis for determining whether the positive outcomes of invasive species control outweigh the expenses.
Durability: the length of time over which a control action or strategy suppresses the abundance, distribution, or impact of an invasive species.
Early detection and rapid response (EDRR): the process of finding invasive species at the beginning of their establishment, before substantial spread occurs, and implementing eradication or containment efforts to minimize invasive species' impacts and long-term control costs.
Environmental control: the indirect reduction of the abundance, distribution, or impacts of invasive species by altering biotic and abiotic factors to disfavor the invasive species, for example, by restoring competitors or predators (biocontrol) or modifying ecosystem properties such as soil fertility or water quality.
Eradication: complete removal of an invasive species from an area.
Impact curve: the relationship between time and the cumulative abundance of the invader within an area, congruent with the processes of introduction, establishment, and spread of an invasive species.
Integrated pest management: an adaptive approach to invasive species control, focusing on maximizing the benefits of suppression while minimizing both economic and environmental costs.

eradication; however, in many cases, eradication is not feasible or necessary to reduce **invasive species impacts** and achieve **positive ecosystem outcomes** [28]. We describe the components of successful invasive species control based on four factors related to project goals: how success is measured (Figure 1), level of control, **durability** of control (Figure 2), and geographic scale of control (Figure 2).

'How success is measured': invasive species management projects evaluate their success by focusing on different outcomes (Figure 1, referred to as the 'evaluation stage' in [13]), including the following: successful implementation of the action itself (e.g., hectares treated and volunteers recruited), successful control of the target species (e.g., reduction in infestation density or area), or success in achieving positive ecosystem outcomes (e.g., increased abundance of an imperiled native species). Later metrics of success—positive ecosystem outcomes—best align with the goals of natural resource management [29]. However, earlier metrics, such as area treated, are most commonly measured and reported [27], leading to a gap in understanding of whether management is meeting its ultimate goals [4].

'Level of control': projects differ substantially in the level of control they hope to achieve. For example, keeping invasive cheatgrass (*Bromus tectorum*) below 5% cover prevents the worst ecosystem consequences of increased fire risk [30]. Some techniques are best suited to specific control levels. For example, classical biological control aims to reduce the abundance and spread of an invasive species rather than eradicate it [31].

'Durability': some invasive species management actions provide long-term control while others only temporarily reduce abundance or spread, thus requiring persistent treatment (Figure 2). Durable control is achieved either by eradicating the invasive species or by restoring the processes that limit invasion without future interventions (**environmental control**) [32,33]. While durable control is often the desired outcome, temporary control may be a reasonable goal when a longer-lasting solution is not feasible and the invasive species has severe negative impacts. For example, repeated temporary control of invasive mosquitoes is necessary to protect endangered birds in Hawaii, USA, from the devastating effects of mosquito-borne avian malaria [6,34].

'Geographic scale': there is clear evidence that eradication is more costly and less likely to succeed in larger invaded areas [23,25,35,36]. However, the spatial scaling of the success of noneradication methods (i.e., treatments to suppress an invasive species) is less clear. In particular, it remains unclear whether an increase in necessary effort scales linearly with area or whether nonlinearities (e.g., 'tipping points' or 'economies of scale') can be leveraged to reduce control costs per unit area. Finally, the benefits of control measures may also increase with geographic area, but it is unclear at what rate those benefits accrue relative to the cost of control. One strategy employed against a variety of focal invasive taxa is to create barriers to dispersal, effectively creating multiple smaller patches in which eradication and control programs can be more successful [37,38].

Optimizing control strategies based on models

The most comprehensive assessment of **invasive species control efficiency** is the balance between the benefit of control, by alleviating damage from the invasive species (Figure 1), and the costs of that control (Box 2). This logic is made explicit in bioeconomic models (e.g., **cost–benefit analysis**, return on investment models, optimization models, and agronomic economic threshold models) that calculate the 'net value' of a control action [14,43]. These models give valuable insights into optimal control strategies [15], but they struggle with the shortcomings in the valuation of ecosystem properties [44,45] and coping with vast uncertainties in the efficacy

Invasion curve: the relationship between time and the area infested, representing the process of introduction, establishment, and spread of an invasive species.
Invasive species: a subset of established nonnative species that spread and have a negative impact on biodiversity and local ecosystems.
Invasive species control efficiency: a positive benefit–cost analysis of controlling invasive species.
Invasive species control program: a coordinated effort to reduce the abundance, distribution, or impact of an invasive species.
Invasive species impacts: the measurable effects of an invasive species on organismal, population, community, landscape, or ecosystem properties.
Invasive species management success: the implementation of a control strategy that results in environmental, health, and economic gains due to a reduction in damage caused by invasive species.
Minimizing spread and impacts: a strategy for the nondurable suppression of an invasive species across large geographic areas to reduce its negative effects.
Positive ecosystem outcomes: beneficial environmental consequences of invasive species management.

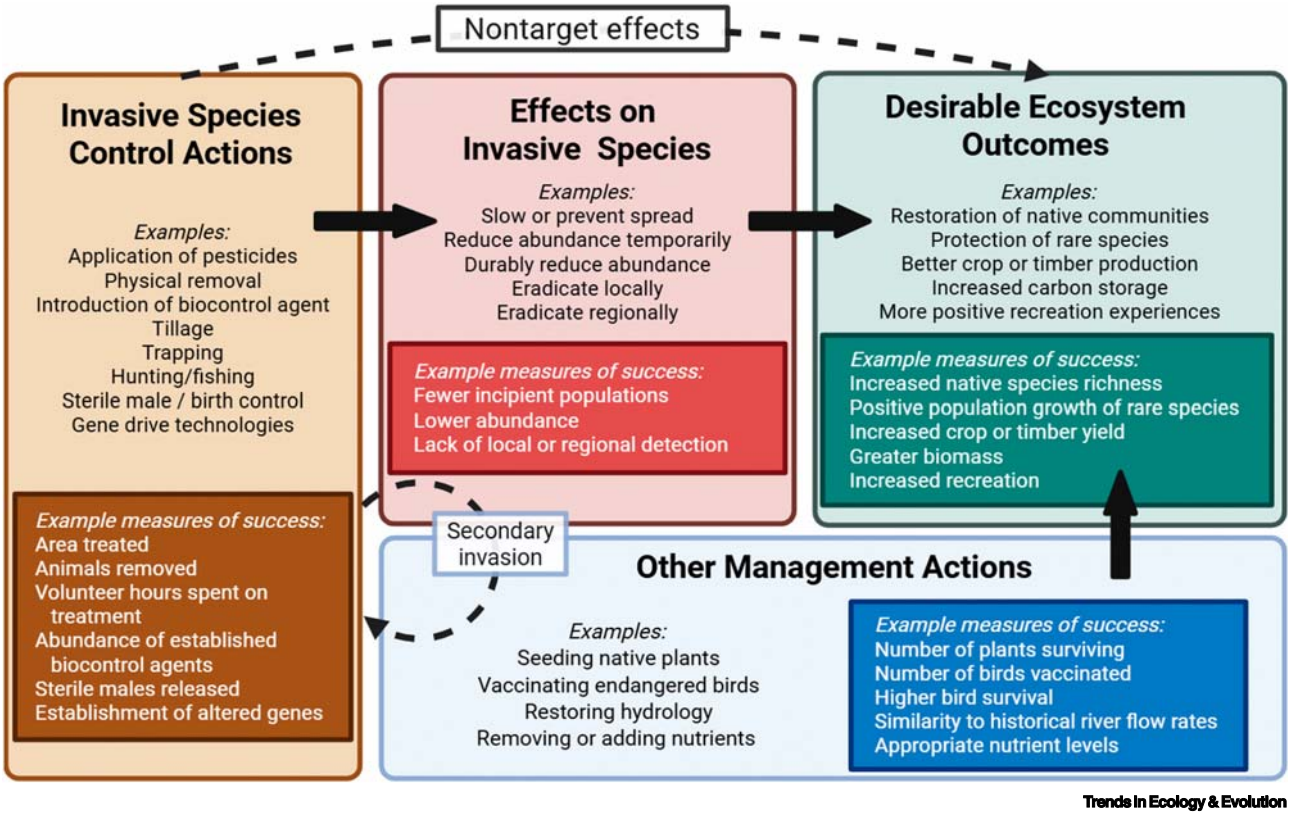


Figure 1. Measuring the success of invasive species management projects requires clear objectives. Invasive species control actions achieve project goals by creating desirable ecosystem outcomes through the reduction or elimination of the invasive species. Invasive species control actions are often a component of larger environmental management actions aimed at creating those outcomes. Arrows indicate the intended (solid) and unintended (dotted) consequences of management actions.

of control and the potential impact and spread of the invasive species [43,46,47]. For example, an economic analysis of control and prevention efforts for marine invaders in Australia concluded largely with concerns about uncertainties in biology and in valuing the benefits of control [48], and it is inappropriate to evaluate the persistence of Hawaiian birds and Great Lakes fisheries purely on economics (Box 1). Qualitative assessments of returns on investment can inform decision-making even where costs and benefits are not placed in common economic terms. This logic forms the backbone of decision support tools used to guide control strategies [49] and provides the basis for categorizing control strategies.

Categorization of control strategies

When invasions cover a small area and control tools are effective, eradication is often the optimal strategy because even if costs of surveillance and treatment are high, eradication avoids future costs that would accrue in perpetuity (Figure 2). In practice, campaigns to eradicate invasive species on islands have a success rate of 88% (Box 1; [8,9]), and there have been broad successes in eradication early in the **invasion curve** [25,50] or the **impact curve** [51]. However, **early detection and rapid response (EDRR)** demands high investment in surveillance and decisive action once a species is detected, for eradication to remain feasible [50]. For example, the yellow-legged hornet (*Vespa velutina*), a honeybee predator and a threat to human health, is now widespread in South Korea and mainland Europe, where eradication is considered infeasible; however, it has been successfully interdicted and eradicated in Great Britain and Japan due

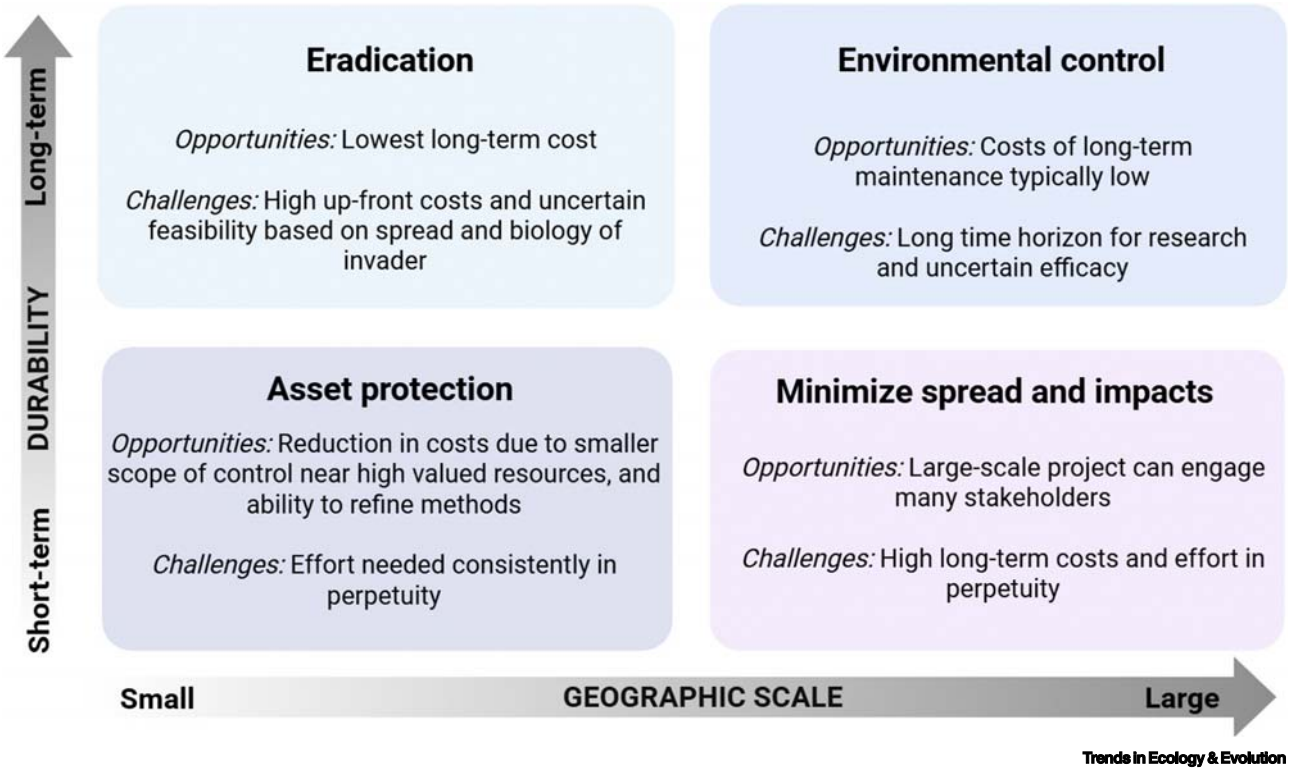


Figure 2. Project goals may require control of invasive species across different geographic (small to large) and temporal (temporary to permanent durability) scales. Goals arrayed along these axes are better suited to some techniques than others and encounter different opportunities and challenges. Figure created using BioRender (HYPERLINK "http://biorender.com/" http://biorender.com/).

to early detection efforts [52]. Because there are repeated introductions of this species globally (https://agr.wa.gov/about-wsda/news-and-media-relations/news-releases?article=46922), extensive monitoring and vigilance are needed to prevent its eventual establishment.

At larger spatial scales, durable control to suppress the abundance and negative impacts of an invader can sometimes be achieved by environmental controls, restoring or altering ecosystem processes that disfavor the invader without seeking eradication (Box 1). Again, these programs achieve long-term gains by reducing or eliminating the need for future control, and they typically come with large upfront costs. Nevertheless, cost–benefit analyses find these investments to be cost-efficient [53]. For example, large-scale control of many invasive plants and insects has been achieved by classical biocontrol. Major successes include the control of glassy-winged sharp-shooter (*Homalodisca vitripennis*) in Tahiti [54], the cassava mealybug (*Phenacoccus manihoti*) in Benin [55], and giant salvinia from freshwater ponds on multiple continents (Box 1). Similarly, indirect approaches such as the restoration of fire regimes in the Brazilian Cerrado [56], water flows in the Southwestern USA [57], depleted soil nutrient levels [58], and competitors in Puerto Rican forests [59] have each reduced the abundance and impacts of invasive species, though these examples occur alongside other control activities. Restoring ecosystem function could also necessitate fostering novel communities. In a heavily invaded Hawaiian lowland forest, the intractable management of nonnative plants led researchers and managers to conclude that restoring native community composition was not feasible [60]. They instead decided to restore the landscape with a combination of native and nonnative, noninvasive species to resist future invasions and shape ecosystem processes [61].

Box 2. How to measure success of invasive species control

For an invasive species manager, there are inevitable trade-offs between conducting control and measuring its success. Idealized designs measure success by calculating cost–benefit ratios of control, documenting control actions and their costs, and estimating the reduction in damages. However, there are limitations to enumerating both costs and benefits of invasive species control. Therefore, many programs, reaching beyond implementation success, measure reductions in the invasive species, assess ecosystem (or other) gains, or use qualitative self-assessments. These measures improve our understanding of when invasive species control is successful.

'Documenting control costs': control costs include materials used in control and the workforce involved in planning and implementation. Participatory science, volunteers, and actions (e.g., prescribed burns) aimed at both invasive species control and other purposes can considerably reduce costs and can be difficult to account for [39].

'Documenting ecosystem gains': before–after control–impact (BACI) monitoring designs clearly document the effects of invasive species control. A BACI design is difficult or impossible in many cases (for instance, when it is undesirable to leave uncontrolled reference plots), and comparisons between control-action plots and reference plots, or before-after treatment measurements, also provide evidence of success. Replication is needed to demonstrate the environmental gains within a project, and the durability of the effects is a critical feature.

'Documenting and valuing the decline of invasive species': often, projects document, via BACI or other designs, the decline of invasive species without measuring positive environmental effects. When available, we can translate declines in invasive species to presumed ecosystem gains based on other sources (e.g., other studies that assess the relationship between the abundance of the invasive species and impact [40]). The shape of the abundance–impact relationship (i.e., whether it is linear, accelerating, or decelerating) can strongly affect the value of invasive species control [41], and examples of each relationship have been documented [42].

'Qualitative assessments': even if no objective measures of success are recorded, many invasive species projects include some form of self-assessment documenting perceived successes and limitations. When conducted earnestly, though clearly subjective, these self-assessments provide insights into the strengths and limitations of a project.

When control of an invasive species is not durable, the costs of control accrue in perpetuity, leading some authors to describe those costs as 'an infinite financial commitment' [35]. However, the damage caused by invasive species is similarly persistent, so the commitment to control is still efficient when the annual economic and ecological benefits outweigh annual costs. When faced with a widespread invasive species, an effective strategy is **asset protection.** For instance, in the Hawaiian Islands, invasive species removal projects protect the remaining habitat patches and corridors that are the sole habitats for imperiled plant and bird species (Box 1). One benefit of spatial prioritization and local-scale action is the ability to control multiple environmental threats simultaneously and create multiple benefits within a focal area (Box 1).

At large spatial scales, nondurable control can still be successful in **minimizing spread and impacts** if organizations invest in it consistently over the long-term. For instance, in the Great Lakes of North America, invasive sea lampreys (*Petromyzon marinus*) have been controlled since the 1950s through dams and lampricides to maintain critical Great Lakes fisheries and ecosystems (Box 1). Even short periods of weakened control measures [such as those that occurred during the COVID-19 (coronavirus disease 2019) pandemic] result in a marked increase in fish attacks by lampreys [62].

Hypotheses about what drives the success of invasive control

Invasive species control programs are multifaceted, complex human affairs that deal with vastly different organisms, geographies, and tools. What rules might be important in predicting their success? We hypothesize predictors of success that fall broadly into five categories: viable goals, biological features, site features, control methods, and organizational structures. These hypotheses are testable by comparing the outcomes of established projects.

'Viable goals': for a project to be successful, it must set realistic goals [16] with clear links to desirable ecosystem outcomes (Figure 1). Projects that initially conduct a feasibility study or use decision support tools are more likely to meet their goals than those that do not [63]. Viable goals enable success across stages, from implementation to ecosystem outcomes, and match available resources to the spatial and temporal scope. Some projects, often due to societal pressures [64], outline goals that are clearly outside their capacity (i.e., in the wrong quadrant of Figure 2). These projects are less likely to meet their stated goals but may make considerable headway toward alternative goals (e.g., protecting assets instead of eradicating invasives). Timing is key to many actions; for example, EDRR programs must be fast and decisive.

'Biological features': it is likely that the traits that predict invasive status, for example, rapid growth and high reproductive rate (e.g., [65]), also contribute to the difficulty of invasive species control. However, other traits (e.g., rooting below tillage depth, tolerance to pesticides, and cryptic lifestyles) may stymie control efforts even if they are not associated with invasiveness *per se*. Thus, biological features shape the success of control for a given implementation effort, as well as ecosystem outcomes. Trait-based perspectives may be useful in determining suites of organisms that might be managed in a similar way; for example, restoration and environmental control may be effective for minimizing threats from multiple invasive species with fast life history strategies adapted for disturbed environments [66].

'Site features': invasive species control will likely be more successful at sites with limited ongoing propagule pressure (e.g., small lakes vs. connected aquatic habitats), less anthropogenic disturbance [4], fewer available resources for the invader (e.g., nutrient-poor vs. rich habitat), and more antagonistic biotic interactions (e.g., species-rich vs. depauperate sites).

'Control methods': for individual invasive species, there is often robust, detailed literature on the efficacy of control methods (e.g., chemical, mechanical, biological, and environmental manipulations, such as burning or altering hydrological regimes; and physical barriers, such as fences or dams). For example, chemical control methods tend to have greater short-term efficacy than mechanical control for invasive plants [13,18]. However, the paradigm of **integrated pest management** stresses the need for multiple synergistic control methods that are often context-dependent [67]. Overall, we expect the efficacies of control methods to be important predictors of control success and durability, but these will be system-specific.

'Organizational structure and effort': invasive species control programs are human undertakings, so their degrees of success may relate to human interactions and structures. For example, successful control of invasive tamarisk (*Tamarix* spp.) and subsequent recovery of native vegetation at 40 North American riparian sites were less related to biology or geography and more related to attributes of stakeholders involved in the project. Highly collaborative approaches guided by shared information led to success in this example [24] and are common among successful, high-profile invasive species control efforts [7,10]. In other cases, successful management has been attributed to clear accountability by a major organization [68], as piecemeal land ownership can result in differing priorities among land units [69]. Thus, we predict that programs in which accountability for control is clear, that invest in information gathering and sharing, and that operate under simple land-ownership or social structures will achieve greater success.

Likewise, many successful invasive species management programs have relied on large, inexpensive labor forces [70], and invasive species managers cite inadequate resources as the largest barrier to success [29]. Capital investment (in terms of expenditure or personnel) and

continuity of funding may predict ongoing implementation success irrespective of organizational structure.

Concluding remarks

Assessing invasive species control programs, and disseminating those assessments, can improve the success and efficiency of invasive species management. Successes and costs can be evaluated among different projects aiming to control a single species, within habitat types, and among disparate programs managing the many invasive species throughout the world. Such syntheses may take the form of meta-analyses of existing data, comparisons within broad data collection efforts, and preplanned experiments to guide future control efforts. Existing comparative projects have yielded valuable insights into best practices for eradication, methods for invasive plant control, organizational limitations, likely targets for biocontrol, and challenges posed by invasive species in plant restorations (Table 1). A living repository for the outcomes of invasive species control programs would aid these comparisons. The major challenge in these comparisons is measuring degrees of success in ways that balance objectivity with logistical constraints and the multifaceted goals typical of environmental management (Box 2). Our ability to generalize about the factors that predict success will be driven by the ingenuity of researchers formulating ways to make valid comparisons and by practitioners who document the degree of success of their own work (see Outstanding questions). Learning from past successes and failures can guide our epic adventures in invasive species control and perhaps avert some tragedies.

Outstanding questions

How can goals of invasive species management be tailored to best create positive outcomes?

How do the costs and benefits of invasive species control scale as programs take on larger geographic or temporal scopes?

Does collaboration through communities of practice result in greater success in invasive species control?

What aspects of invasive species biology, site attributes, control methods, and management organization structures predict the success of invasive species control?

Which dimensions of invasive species control success are most predictive of long-term ecological outcomes? For example, are early-stage metrics (e.g., hectares treated and reduction in abundance) reliable proxies for later ecosystem recovery?

How frequently do invasive species control efforts generate unintended ecological consequences? Under what conditions do these trade-offs undermine net benefits?

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Declaration of interests

The authors declare no competing interests.

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