Regional adaptation of integrated pest management to control invasive forest insects

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Globalization is increasing the threat of invasive forest insects to ecosystems. Control efforts against the same pest species progressively occur across distant jurisdictions as integrated pest management (IPM) programs or tactics developed in one region are adopted by another region. This knowledge exchange accelerates responses and collaboration; however, transplanted IPM programs can overlook preexisting or emerging differences between regions, which may explain their varying success. These differences include biological variation in the pest system, environmental conditions, issues of scale and capacity of the response, regulatory environment, and cultural context. We examine the role of these factors in the adoption and outcomes of IPM programs, drawing from case studies and an online survey of forestry IPM experts. To facilitate regional adaptation of IPM programs during their adoption and implementation in new regions, we propose an evaluation framework and recommend approaches to not only reduce risks but also maximize uptake, efficacy, and resilience.

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Invasive forest insect pests are a growing environmental challenge. Global trade is driving greater propagule pressure and establishment (Liebhold *et al*. 2017; Seebens *et al*. 2018), and plantings of nonnative tree species, particularly in plantations and cities, are contributing to biotic homogenization and ubiquity of suitable hosts (Hudgins *et al*. 2022). With these invasions come novel associations of invaders with host trees (Branco *et al*. 2015) and symbionts (Lu *et al*. 2016), which can result in tree decline and mortality (Wingfield *et al*. 2015). Climate change and other stressors are elevating the vulnerability of forests to insect pests, increasing the risk of new invasions by nonnative species (Pureswaran *et al*. 2022), as well as altering the distribution and impacts of native pests (Pureswaran *et al*. 2018; Lantschner and Corley 2023). The growing recognition of the role of forests in carbon sequestration and climate-change mitigation, in the maintenance of ecosystem services and biodiversity, and in promotion of human well-being (Felipe-Lucia *et al*. 2018) is reflected in demand for effective solutions to invasive forest insect pests.

In a nutshell:

- Increasingly, invasive insect pests affect multiple geographic areas, and integrated pest management (IPM) programs developed in one region are transplanted into others
- Overlooked differences in the pest system and IPM response, unique to each invasion, may impede control tactics and compromise their efficacy
- To successfully adapt to regional contexts and changing environments, IPM programs require proactive research, continued evaluation, and sharing of knowledge not limited to success stories

Integrated pest management (IPM) programs are increasingly being applied against the same invasive pest species in multiple regions and jurisdictions. Typically developed in one region, which may not be the first to have been impacted, IPM programs are often adopted by other regions in response to the shared pest. Reflecting the changing regulatory environment and societal expectations, most strategies to mitigate forest pest impacts now combine multiple tactics to identify, assess, mitigate, and monitor risks that can contribute to outbreaks and damage (ie risk-based management; Lovett *et al*. 2016). This approach contrasts with a historically more reactive style of management in which control tactics were implemented once outbreaks and/or damage occurred. Some instances of area-wide implementation of IPM programs, such as among municipalities and other jurisdictions, can improve control outcomes and lower the costs per unit area managed (Vreysen *et al*. 2007). Although management of invasive forest insects requires coordinated international action to limit their spread and impacts (Allison *et al*. 2021; Bonello *et al*. 2022; Carnegie *et al*. 2022; Nahrung *et al*. 2023), most decisions on responses to new pests—and the necessary funding—take place within national or regional borders.

Adoption of existing IPM programs carries obvious benefits. In some instances, knowledge exchange between regions accelerates control action by saving resources otherwise required for initial testing and development, and potentially

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mitigates the larger economic and ecological consequences of an invasion (Brockerhoff *et al*. 2010). Sharing expertise also encourages collaboration and training, as well as optimization of existing tactics or development of new tools (eg Roques *et al*. 2023). Importantly, early adoption of existing IPM programs enhances coordination of responses across jurisdictions, including area-wide management, promoting global solutions (Panzavolta *et al*. 2021; Nahrung *et al*. 2023). In the most proactive approach, invasions can even be anticipated prior to pest establishment to mobilize research and resources that may be needed for a future rapid response, such as through pre-screening and approval of biocontrol agents (Hoddle 2023). Once the pest is established, target outcomes of IPM will depend on the size and extent of its population(s). Objectives of an IPM program may include eradication of smaller, more localized populations, or suppression of more extensive, larger populations to not only reduce the pest's densities and damage but also inhibit its spread into neighboring regions—that may eventually adopt these IPM tactics.

However, adoption of a specific IPM program or its components in the unique context of one region does not guarantee successful control, and may not be feasible, in another region. In the absence of further research, unrecognized regional differences may reduce the efficacy of tactics, weaken support for the program, and even lead to its failure. Using case studies of invasive forest insect pests and feedback from an online survey of IPM experts, we examine a range of factors that may influence the success of IPM programs against shared pests. We also present a framework for modification—regional adaptation—of existing IPM programs for implementation in new regions and recommend strategies to promote information exchange and research to reduce risks and achieve desired outcomes.

Factors limiting IPM success

An implicit assumption is that an IPM program that has been successful in one region should produce similar results in another facing the same threat. However, many transplanted programs achieve only limited, if any, control. For example, biological control agents used to control pests in one region are often released into other regions invaded by the same pest (Cock *et al*. 2016). In some cases, levels of suppression are comparable (eg Slippers *et al*. 2015), but in others variable success of establishment or effects on the target pest have been observed (eg Gerber and Schaffner 2016). We surveyed experts in IPM of invasive forest insect pests across world regions (see Appendix S1: Panel S1 for methods) to obtain a diversified, qualitative assessment of adopted IPM programs and their control outcomes globally. In the online survey responses, only about half of the cases reported at least satisfactory outcomes, while others identified a variety of known—or suspected but not always investigated—factors underlying past or ongoing program challenges.

Here, we explore a spectrum of variables that should be considered when IPM programs are transplanted among regions or when control outcomes are unsatisfactory. Although the relative importance of these factors will vary among pests and regions, they could influence uptake, implementation, and efficacy of an adopted IPM tactic or program. We discuss five broad categories of factors in the context of forest insect pests, with specific examples from a globally important pest of pines, the woodwasp *Sirex noctilio* (Figure 1; Appendix S1: Panel S2). However, our framework can also apply to shared pests in agricultural systems, and more broadly to the management of invasive species spreading across multiple regions. Furthermore, many of the same

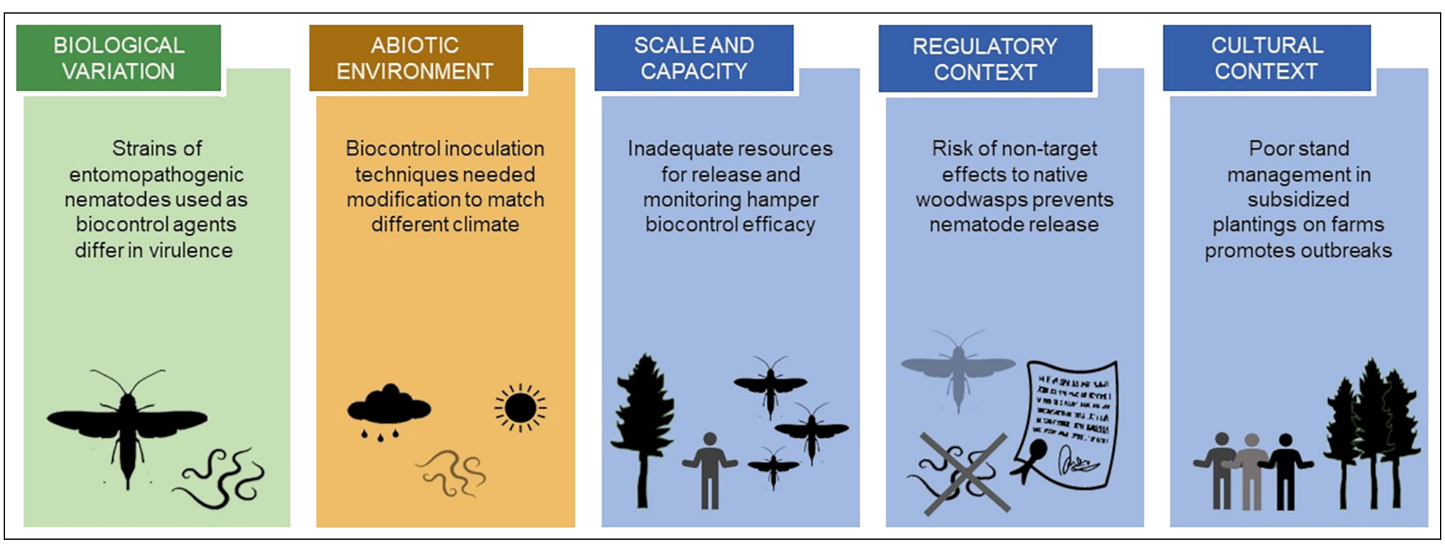

Figure 1. Examples of the challenges in the integrated pest management (IPM) program for the woodwasp *Sirex noctilio*, illustrating the differences across its invaded regions that have contributed to initial or continuing issues with implementation and/or pest control. See Appendix S1: Panel S2 for further details and references. Illustrations by Antonella Falconaro and Michael Stastny.

considerations are relevant to control programs involving native insect pests whose geographic distributions span different jurisdictions.

Biological variation in the pest system

Some invasive forest insects have broad distributions that include multiple hosts and climatic zones in their native range (Wingfield *et al*. 2015; Schröder *et al*. 2020), giving rise to considerable genetic variation among source populations for invasions. Preexisting or emergent differences in pest biology and ecology among invaded regions are often overlooked but could influence not only interactions with host trees, symbionts, and natural enemies (including biological control agents) but also pest population dynamics and resulting impacts—all of which could subsequently affect the outcomes of IPM tactics.

Population genetic studies of invasive species often reveal highly variable collections of genotypes or cryptic species, and recurrent introductions and hybridization among genotypes can increase variation over time (Garnas *et al*. 2016; Mutitu *et al*. 2020). Consequently, regions affected by the "same" insect pest may in fact be dealing with different ecotypes, subspecies, or even species. For example, eucalyptus snout beetles were originally all thought to be *Gonipterus scutellatus* (Schröder *et al*. 2020) but are now recognized as three distinct invasive pests from a cryptic complex of at least nine *Gonipterus* species. Biological characteristics of the pest may also be substantially altered after changes in the pest's symbionts, through microbiome shifts or acquisition of symbionts from native relatives or the new environment (Lu *et al*. 2016), with potential consequences for IPM tactics.

The efficacy of biological control may also be reduced by overlooked biological variation in the introduced natural enemies of the pest (Figure 1). For instance, variation in virulence among strains of the entomopathogenic nematode *Deladenus siricidicola*, the primary biocontrol agent of *S noctilio*, may explain its lower efficacy in some invaded regions (Figure 1; Morris *et al*. 2020). The strategy of intentionally releasing multiple provenances (ecotypes or biotypes) of a biocontrol agent—with the goal of increasing the likelihood of adapted populations with improved chances of success in a range of ecological conditions—carries the risks of introducing cryptic species and their subsequent hybridization (Clarke and Walter 1995; Stahlke *et al*. 2022).

Such complexity in the target pest or in its natural enemies may affect multiple IPM tactics. For instance, highly specific behavior-modifying semiochemicals, especially pheromones, are often used for surveillance and population monitoring, as well as for population suppression via removal of individuals, exposure to pathogens or insecticides, or mate disruption (Allison and Cardé 2016). While many species appear invariant in both pheromone signal and response traits throughout their range, others show geographic variation. This diversity is perhaps best recognized in moths (Allison and Cardé 2016), but differences in the aggregation pheromones of bark beetles have also been reported in the pine engraver *Ips pini* (Shumate *et al*. 2011) and the spruce beetle *Dendroctonus rufipennis* (Isitt *et al*. 2020). Unrecognized pheromone variation due to the existence of chemotypes or cryptic species may constrain the use of pheromones in IPM.

Ecological communities of the invaded regions likely differ in a myriad of attributes, some of which may have consequences for the pest problem and its management. Greater abundance or diversity of potential hosts, as well as species- or region-specific differences in their resistance, may alter the spread and population dynamics of the insect pest (Guo *et al*. 2019). Existing biotic stress on host trees by native or exotic insects or pathogens has been hypothesized to accelerate or amplify the impacts of the invader on tree health, or in turn be exacerbated or facilitated by the novel interaction (Santini and Battisti 2019). Native predators may help regulate populations of the invasive pest in some regions (Duan *et al*. 2015), but their effects may not be manifested until the establishment of a biocontrol agent (Broadley *et al*. 2022). Specific native biota may also preclude the release of biocontrol agents in that region due to the risk of nontarget effects (Figure 1).

Finally, rapid evolutionary change post-introduction or in response to management tactics may further influence a pest's susceptibility to control efforts. In addition to regional genetic differences that may arise from complex invasion pathways (Javal *et al*. 2019), adaptive phenotypic changes in the pest's biology in response to selection generated by IPM tactics (eg pesticides and biocontrol agents) can reduce their efficacy (Szűcs *et al*. 2019). On the other hand, evolutionary changes may also occur in biocontrol agents after their introduction and, in some cases, natural selection may enhance their establishment and impact on the target species (Phillips *et al*. 2008); these outcomes can also be actively pursued in biocontrol breeding programs through experimental evolution (Lirakis and Magalhães 2019).

Abiotic environment

Invaded regions often differ in environmental characteristics, especially climate, that may affect the biology of the pest system, mediate tree stress that may exacerbate the pest impacts, and alter the efficacy of control tactics. Population regulation of the pest due to abiotic factors (eg during overwintering) may be less pronounced in some regions, requiring increased efforts for pest control (McAvoy *et al*. 2017). The pest may also respond to climatic conditions by changing its phenology, potentially escaping control that targets certain life stages. In warmer regions, increased voltinism (the number of generations per year) can dramatically modify population dynamics and impacts (Corley and Bruzzone 2009). Requirements for climatic matching of biocontrol agents may preclude the use of specific source populations, natural enemy species, or protocols that have proven effective elsewhere (Fischbein *et al.* 2019). For instance, in South Africa, climatic differences initially contributed to suboptimal program performance to manage *S noctilio*: inoculation techniques that relied on entomopathogenic nematodes had originally been developed against the pest in a region with winter rainfall but had to be adapted for summer rainfall (Figure 1; Hurley *et al.* 2012).

Uncertainty in pest control outcomes due to environmental variation among regions is further exacerbated by ongoing climate change. With new climatic conditions and increased weather stochasticity, coupled with greater physiological stress on host trees, pest management may thus become problematic even for programs that have achieved satisfactory control (Jactel *et al.* 2019; Lehmann *et al.* 2020). In parallel, some native pests are displaying invasive-like characteristics due to geographic range expansion or unprecedented outbreaks, with predicted further spread and novel impacts, such as in the case of several species of bark beetles (Bentz *et al.* 2019; Ceriani-Nakamurakare *et al.* 2022). Periodic assessments and modifications may be required to ensure program resilience under future climate change and associated shifts in biotic disturbances and ecological interactions (Ayres and Lombardero 2000; Ricciardi *et al.* 2021).

Scale and capacity

IPM programs can be costly even after the completion of the research and development phases, restricting the scale at which an existing program can be adopted elsewhere. Costs of full adoption may be prohibitive, especially in cases where economic disparities exist among regions. The perceived magnitude of the pest problem and thus thresholds for intervention may also vary among jurisdictions that value the resource differently. These issues highlight links between public perception and allocation of resources for pest response (Morris *et al.* 2018), including unique considerations for invasive species management in urban ecosystems (Potgieter *et al.* 2022). Cost–benefit analyses of IPM strategies are further complicated by the fact that economic thresholds of damage, which likely vary among regions, are more difficult to define and apply in forest systems (Fox *et al.* 1997), especially in the case of non-timber tree species, as compared to crops in agroecosystems.

Due to global inequalities in the production and dissemination of knowledge and technologies (Backhouse *et al.* 2021), certain regions will inevitably be hindered in the scope of their response, and will lack the funding, capacity, or expertise for further research (Early *et al.* 2015; Hurley *et al.* 2017). Consequently, only some components of an existing IPM program may be adopted, its tactics may be poorly integrated, or the program may be scaled down in its implementation or further development—especially when limited resources impede ongoing monitoring and evaluation. For example, outbreaks of *S noctilio* in southern Argentina have continued despite nematode and parasitoid releases whose limited success may stem from a combination of reduced quality and quantity of biocontrol agents, and inadequate monitoring (Figure 1; Corley *et al.* 2019).

Regulatory context

Differences in the regulatory environment among jurisdictions may determine the feasibility and timelines of implementation of specific control tactics. Chemical control in particular is subject to stringent regulations that in some jurisdictions increasingly preclude the use of certain products or applications or delay their use until approved after an environmental impact risk assessment. For instance, the use of insecticides against the destructive hemlock woolly adelgid (*Adelges tsugae*) in eastern Canada has been restricted to a subset of the tools employed in the US, as Canadian legislation on neonicotinoids prohibits several application methods. Similarly, the importation of biological control agents may require jurisdiction-specific approvals (eg entomopathogenic nematodes; Abate *et al.* 2017). Additional stakeholder consultations (eg "duty to consult" Indigenous communities by provincial authorities in Canada) may be expected by jurisdictions on top of a national-level authorization; these processes can influence the pace and scope of control efforts. In addition, regulation to mitigate risk to nontarget organisms may constrain selection of suitable biological control agents; for instance, the nematode *D siricidicola* is not released in the US to control invasive *S noctilio* populations due in part to the presence of native species of woodwasps (Figure 1; Hajek *et al.* 2021). These region-specific contexts may lead to program modifications with unknown impacts on their overall efficacy, or hamper coordination of efforts to reduce further spread. Finally, pest responses in an exporting region can be dictated by the regulatory requirements imposed by the jurisdiction of the importing region—even if the specific pest is not a major problem in the former.

Cultural context

Human historical and societal environments can shape regional attitudes toward IPM programs (Figure 1). Differences in stakeholders' values, perspectives, and biases will influence the demand for and uptake or choice of IPM tactics, often highlighted by patterns of land ownership (Chang *et al.* 2009; Flint *et al.* 2009; Marzano *et al.* 2017). The spatial mosaic of stakeholders can complicate regional response and coordination and give rise to local differences in forest management and associated pest issues. In southwestern Argentina, for instance, subsidized but poorly managed pine plantations on farms are often associated with stand conditions that promote high populations of *S noctilio* (Villacide and Corley 2012). Historical examples of pest control—including indiscriminate use of toxic insecticides or instances of nontarget impacts in biocontrol—may underlie persistent resistance to demonstrably safer approaches (Crowley *et al.* 2017).

Cultural and socioeconomic divides may also affect outreach and communication, with poor uptake hindering effective implementation. These dimensions of IPM are better recognized in agricultural systems (Deguine *et al*. 2021) and are best addressed through involvement of social scientists. Issues surrounding the export of "postcolonial science" (Trisos *et al*. 2021), particularly in the face of global economic inequities, can also obstruct the adoption of IPM programs and, more broadly, coordination of policies on invasive pests.

Regional adaptation of IPM

In most cases of shared pests, each newly invaded region will have its own suite of unique circumstances and unknowns, some of which may factor in the success of IPM (Figure 2). Certain regional attributes, such as more effective stakeholder engagement or closer climatic matching of biocontrol agents, may indeed favor program success. In other instances, multiple unrelated or interacting factors could present unanticipated obstacles either prior to program adoption or much later. In our qualitative global survey (Appendix S1: Panel S1), IPM experts of invasive forest insect pests most frequently cited biological and environmental factors as challenges to the adoption or implementation of existing programs or in achieving desired outcomes (ranked among the top two factors in 22 out of 29 case studies), but issues of scale and capacity (15 case studies) and regulatory context (9 case studies) were recognized as other key impediments.

Depending on the pest and the impacted region, the IPM challenges reported in the survey were often interrelated; for instance, changes in the regulation of chemical control necessitated greater deployment of biocontrol agents, which, however, then struggled with establishment due to the region's climate. Given these difficulties, how can a program developed in another region be harnessed effectively to control the same pest in a new region? Existing information on the pest system and the invaded range should be examined to identify potentially important differences between regions that, along with knowledge gaps, will guide further research and evaluation to inform potential modifications—ideally prior to implementation (Figure 2). Biological and environmental variation are more likely to play a role when the pest has invaded distinct ecoregions; in contrast, factors related to scale and capacity, as well as regulatory or cultural context, may feature more prominently when the pest is affecting different jurisdictions within the same ecoregion. Ultimately, resource constraints and the relative urgency of the required response may restrict the scope of regional adaptations; initial IPM decisions should balance the anticipated efficacy of tactics and the greatest risks (unknowns) to the program.

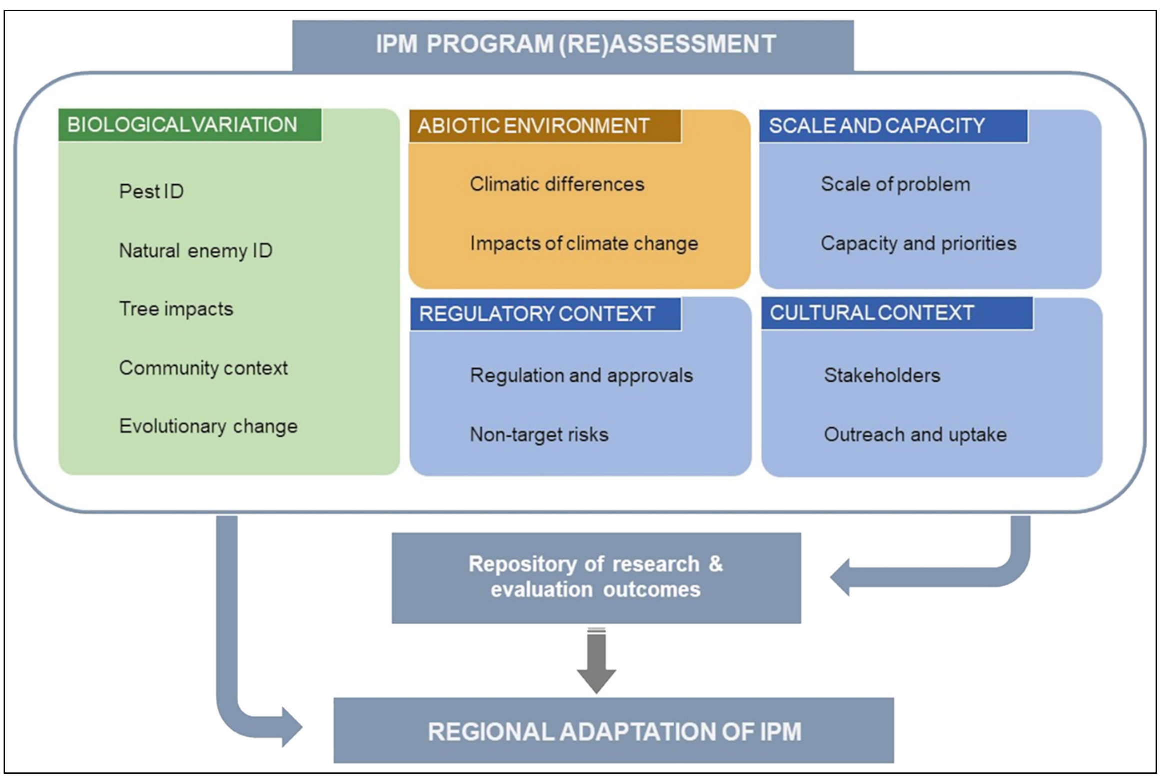

Figure 2. Synthesis of a framework for existing IPM programs to identify categories of potential factors that may require further research or modification to improve control outcomes and long-term program resilience. This assessment should occur before program adoption in a new region to guide regional adaptation and iteratively after program implementation as a periodic reassessment of efficacy over time. Observation and knowledge produced in this process would ideally be shared in an open repository compiling a diverse range of information on both successes and setbacks in program development and outcomes.

Is regional adaptation of IPM programs already occurring in forestry? In our survey of IPM experts, modifications to existing programs were common (21 of 32 cases) and often, though not always, based on examination of regional differences (15 of 21 cases). Overall, among programs that achieved satisfactory or complete control, most (12 of 15 cases) had undergone modifications, with the majority (10) reporting that the changes have led to critical or major impacts. However, in only half (5) of those cases did research specifically examine potential regional differences prior to the first evaluation of control outcomes. In other words, many IPM programs are implemented without adequate examination of variables that could determine their initial success. In our opinion, these patterns collectively reflect two related issues: (1) inadequate monitoring and evaluation and (2) insufficient sharing of knowledge about existing programs' trajectories, especially their challenges and failures.

Follow-up monitoring and evaluation are chronically underfunded components of IPM but are critical in the assessment of both ongoing efforts and new programs against shared pests, especially in the face of accelerating anthropogenic change (Figure 2). In addition to assessing control outcomes, they offer opportunities to examine the broader ecological and socioeconomic context of the pest system in the target region, track emerging issues or previously unrecognized complexities, and optimize or revise IPM tactics. Much of the development and implementation of IPM programs involves incremental accumulation of knowledge, series of setbacks, and seemingly trivial methodological improvements. However, this invaluable information is often not reported in the primary literature; at best, it is exchanged at research meetings (which involve other barriers to participation). Researchers and IPM practitioners would greatly benefit from an open-access outlet to encourage this knowledge sharing.

We propose establishment of a curated, publicly accessible, global repository to track information on existing and developing IPM programs, including knowledge gaps, emerging challenges, case studies of successful funding models, and operational and uptake strategies. One such format could involve a citable (digital object identifier [DOI]-assigned) platform, searchable by pest and host species. iBiocontrol (www.ibiocontrol.org), the open-access online catalog for worldwide biological control of weeds (Winston *et al.* 2024), is an example of a comprehensive, continually updated, jurisdiction-specific database of target and agent species, including unpublished assessments of outcomes. A similar catalog for IPM of invasive forest insects could, in addition, serve specifically as a repository of supplementary or partial information that does not warrant refereed publication and is often not disseminated, but that could help guide research and management decisions (Figure 2). Improved communication of IPM research and outcomes will facilitate more efficient adaptation of programs to regional contexts while enhancing coordination and resilience of control efforts against shared insect pests. This open-science model of information sharing could be applied to similar pest challenges in agricultural systems, and more generally to the management of invasive species.

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Data Availability Statement

Anonymized survey results are available on Zenodo at https://doi.org/10.5281/zenodo.13749152 (Stastny *et al.* 2024).

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Supporting Information

Additional material can be found online at http://onlinelibrary.wiley.com/doi/10.1002/fee.2829/suppinfo