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An Applied Empirical Framework for Invasion Science: Confronting Biological Invasion Through Collaborative Research Aimed at Tool Production

Gwylim S. Blackburn,[1,2,3,12] Pierre Bilodeau,[4] Tracey Cooke,[5] Mingming Cui,[1,6] Michel Cusson,[1,2] Richard C. Hamelin,[1,7] Melody A. Keena,[8] Sandrine Picq,[2] Amanda D. Roe,[9] Juan Shi,[10] Yunke Wu,[11] and Ilga Porth[1,6]

[1]Département des sciences du bois et de la forêt, Université Laval, 1030, Avenue de la Médecine, Quebec City, Québec, Canada G1V 0A6, [2]Laurentian Forestry Centre, Natural Resources Canada, 1055 du PEPS, Quebec City, Québec, Canada G1V 4C7, [3]Pacific Forestry Centre, 506 Burnside Rd W, Victoria, British Columbia, Canada V8Z 1M5, [4]Plant Health Science Directorate, Canadian Food Inspection Agency, 1400 Merivale Road, Ottawa, Ontario, Canada K19 0Y9, [5]Invasive Species Centre, 1219 Queen St E, Sault Ste. Marie, Ontario, Canada P6A 2E5, [6]Centre for Forest Research (CFR, CEF), Université Laval, 2405 Rue de la Terrasse, Quebec City, Québec, Canada G1V 0A6, [7]Department of Forest and Conservation Sciences, University of British Columbia, 2424 Main Mall, Vancouver, British Columbia, Canada V6T 1Z4, [8]United States Department of Agriculture, Forest Service, Northern Research Station, 51 Millpond Road, Hamden, CT 06514, [9]Great Lakes Forestry Centre, Natural Resources Canada, Government of Canada, 1219 Queen Street East, Sault Ste. Marie, Ontario, Canada P6A 2E5, [10]Key Laboratory for Silviculture and Conservation of Ministry of Education, Beijing Forestry University, Beijing, China 100083, [11]Otis Laboratory, Center for Plant Health, Science and Technology, Animal and Plant Health Inspection Service, Department of Agriculture, Buzzards Bay, MA 02542, and [12]Corresponding author, e-mail: gwylim.blackburn@canada.ca

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Abstract

Global ecosystem functions, services, and commodities are increasingly threatened by biological invasions. As a result, there is an urgent need to manage invasive species through global collaborative research. We propose an 'applied empirical framework' (AEF) to aggressively confront the current global biological invasion crisis. The AEF builds on existing models for invasion science that advocate 1) standardized research designs to reveal key aspects of biological invasion, and 2) collaborative research to facilitate the sharing of resources and information. The AEF further emphasizes the need for 3) the production of research 'tools' (e.g., data, methodologies, technical instruments) designed for direct uptake by agencies that manage biological invasion, and 4) a taxonomically targeted approach in which task forces conduct rapid, in-depth research on top-priority invasive species across their entire geographic range. We review collaborative science and the distinctive roles played by different collaborator types. We then provide an example of the AEF in action through the BioSAFE initiative (Biosurveillance of Alien Forest Enemies), a highly collaborative project aimed at developing genomic research tools to facilitate biosurveillance and intervention for forest invasive species. We illustrate the BioSAFE approach through our research on two polyphagous insect species: the wood-borer *Anoplophora glabripennis,* Motschusky (Coleoptera: Cerambycidae; Asian longhorned beetle) and the defoliator *Lymantria dispar*, Linnaeus spp. (Lepidoptera: Lymantriidae; gypsy moth). These examples illustrate how the AEF can focus and accelerate our response to the global biological invasion crisis by applying the resource capabilities of collaborative research groups to generate management tools for top-priority invasive species.

Key words: biological invasion, biosurveillance, collaborative science, gypsy moth, Asian longhorned beetle

Biological invasion involves the transportation, establishment, and spread of a species in a novel environment, with a subsequent negative impact on invaded ecosystems (reviewed in Blackburn et al. 2011, Flower and Gonzalez-Meler 2015, Budde et al. 2016). Biological invasion has resulted in the spread of invasive species from a diverse range of taxa around the globe (Seebens et al. 2017). Invasions have increased over the past century, with no predicted decline in the absence of rapid intervention (Seebens et al. 2017). Despite conflicting views on the relative costs and benefits of a substantial proportion of invasive species (Simberloff et al. 2013), many are widely acknowledged for their severe effects (e.g., *Spodoptera frugiperda*, Nagoshi et al. 2018: *Rhinella marina*, Russo et al. 2018, Shine 2018). Commodity losses and biological invasion control efforts alone are conservatively estimated to cost billions of dollars annually (Pimentel et al. 2000, 2005; Colautti et al. 2006; Aukema et al. 2011; Bradshaw et al. 2016). The impacts of invasive species are ecosystem-wide and can cause trophic cascades, altered nutrient cycles, modified habitat structure, and functional ecosystem shifts, and can also facilitate subsequent invasions (reviewed in Pimentel et al. 2000, Pejchar and Mooney 2009, Ehrenfeld 2010, Simberloff et al. 2013, Grebner et al. 2014, Millar and Stephenson 2015). Given these globally wide-ranging impacts, limiting biological invasion is one of the most urgent conservation and resource management challenges of the 21st century (The Strategic Plan for Biodiversity 2011–2020 and the Aichi Biodiversity Targets; Wingfield et al. 2015, Ricciardi et al. 2017, Seebens et al. 2017).

Formal regulatory frameworks for limiting biological invasion had their beginnings as early as the 1870s in response to individual invasive species (Kuijper 2010, Liebhold and Griffin 2016). However, broader, global-scale policies and research groups focused on invasive species did not develop until after the establishment of the United Nations in 1945. Since then, a constellation of international programs has emerged (reviewed in Ormsby and Brenton–Rule 2017). Key milestones include the establishment of guidelines for the prevention of invasive species under the Convention of Biological Diversity (CBD) in 1993, followed by the binding Application of Sanitary and Phytosanitary Measures (also called the 'SPS agreement') which entered into force under the World Trade Organization in 1995. Within the realm of plant-associated invasive species, National Plant Protection Organizations (NPPOs) commission research in order to set evidence-based standards that meet the SPS guidelines, which are administered by the International Plant Protection Convention (IPPC) of the United Nations. NPPOs also enforce existing policy at the national level by mobilizing regulatory agencies to implement surveillance (hereafter, 'biosurveillance') and intervention of invasive species (Box 1).

A number of issues currently limit the efficacy of existing biological invasion regulatory frameworks (summarized in Ormsby and Brenton–Rule (2017). One is the shortage of biological information available for effective biological invasion risk assessment (Shine 2018). In particular, the long-term consequences of potential invasive species on naïve ecosystems are inherently difficult to assess, due to ecological differences between sites and the possibility for delayed invasion impacts (Box 1). As a result, the SPS agreement permits phytosanitary decisions based on incomplete data, as well as a general precautionary approach to the implementation of sanitary and phytosanitary standards by individual countries. This is accompanied by an obligation to obtain missing data within a reasonable timeframe (Griffin 2000). A second complication for managing biological invasions stems from the multi-faceted role of humans in both their spread and control (Box 2). Overall, we must develop measures that can effectively curb invasion rates while permitting expanding global commerce. These measures must be brought about in the face of daunting constraints on research or regulation that stem from issues of sovereignty, conflicting political interests, varying social awareness or opinions of the impacts of introduced species, and imbalanced international resources or political infrastructure (e.g., Westing 1998, Kark et al. 2015).

We see several overarching needs for effectively confronting the current global biological invasion crisis in light of the points above. First, the global community must prioritize invasion science focused on biosurveillance and intervention (Box 1). The design of novel research solutions (for shorthand, 'tools'; e.g., data, methodologies, technical instruments) or support of existing methods for this purpose should be founded on detailed ecological or genetic data, and it should also appeal directly to regulatory policy (e.g., International Standards for Phytosanitary Measures, Leal et al. 2010, Wingfield et al. 2015). Second, we require international, interdisciplinary collaboration to meet the scale and complexity of biological invasion (Wingfield et al. 2015, Liebhold et al. 2017, Vaz et al. 2017, Abrahams et al. 2019). Collaboration can help integrate disparate views on biological invasion impacts across different stakeholder groups, in order to pursue realistic research tools for effective invasive species management. Collaboration is also logistically important for coordinating research across the entire geographic range of individual invasive species, and

Box 1. Biosurveillance and Intervention of Invasive Species

Direct responses to biological invasion involve biosurveillance and intervention. Biosurveillance involves the process of gathering, integrating, interpreting, and communicating essential information about invasive species and the risks they pose (Roe et al. 2018). Its purpose is to inform policy development aimed at minimizing the occurrence of biological invasion and to guide the actions of regulatory agencies in invasive species intervention. The data required for effective biosurveillance can be both costly and complex to gather (e.g., McGeoch et al. 2016). This includes active monitoring protocols along potential pathways of dispersal and detailed assessments of the ecological effects of candidate invasive species in both their native and invaded habitats (e.g., Packer et al. 2017). General ecological predictors of biological invasion ('general invasive traits', Whitney and Gabler 2008) have proven elusive, with empirical surveys collectively suggesting that biological invasion risk derives from varying qualities of both the introduced species and invaded habitat (Heger and Trepl 2003, Hayes and Barry 2008, Leffler et al. 2014, Ordonez 2014). The trajectories of new potential invasive species introductions are also difficult to predict because repeated introductions of the same species may exhibit different timescales or degrees of invasion (Crooks 2005, Aikio et al. 2010, Yelenik and D'Antonio 2013). These findings indicate that ecological assessments within a biosurveillance framework should ideally be based on taxon-specific rather than comparative data.

Progressing beyond biosurveillance, various intervention strategies may be employed when an invasive species is detected. These strategies exist along a continuum that ranges from the eradication of incipient invasions to population management in cases where the species has become irreversibly established (Epanchin-Niell and Hasting 2010). In general, the costs associated with intervention far surpass the preventative biosurveillance measures considered above (e.g., a documented average cost increase of 40 times across 58 invasive plant control projects, Harris and Timmins 2009; a projected cost increase of 10 times in one case of a disease-bearing mosquito, Vazquez-Prokopec et al. 2010; see also Simberloff et al. 2013)—entailing one or more complex strategies geared towards species removal, integrated pest management, long-term regional monitoring, mitigation of invasive species damage, and measures to comply with international phytosanitary trade regulations.

Box 2. The Human Element of the Biological Invasion Crisis

The roles of humans in both spreading and managing invasive species complicate the resolution of biological invasion on numerous fronts:

Human-mediated transport of goods is the primary cause of biological invasion, occurring via a multitude of transport mechanisms and pathways. These include deliberate species introductions (e.g., plants considered useful in their native range, crop and plantation species, biological control agents) and accidental introductions—trade in commodities (e.g., ornamental plants, grains, wood products), use of infested shipping material (e.g., shipping containers, crates, pallets, dunnage, ballast), and human movements of infested materials (e.g., firewood, equipment) (e.g., Leal et al. 2010, Humair et al. 2015, Ricciardi et al. 2017). Increased international commerce and human travel in the 19th century have resulted in sustained increases in biological invasion (Liebhold and Griffin 2016). These activities have allowed species to expand beyond otherwise strong natural geographic or ecological barriers (Seebens et al. 2015; Early et al. 2016). Repeated introductions have also enabled species to establish in cases where individual colonization events would typically fail (Simberloff 2009). Although curbing trade at least for some commodities offers one potential solution to human-mediated biological invasion, improved trade regulation is either more feasible or desirable in most cases (Liebhold et al. 2012, Roy et al. 2014).

Variable global commitment to curbing biological invasion exists at the international level, with limited investment or cooperation across nations and sectors in implementing invasive species management (Wingfield et al. 2015, Ormsby and Brenton-Rule 2017). For example, Latombe et al. (2017) report that in 2010 only 26% of 170 nations participating in the fourth National Reports to the Convention on Biological Diversity possessed operating biosurveillance programs. Lack of coordination or resources, particularly in developing countries, pose constraints on compliance with phytosanitary regulations and global coordination of invasion science (Wingfield et al. 2015, Ormsby and Brenton-Rule 2017).

Conflicting views of invasion risk or affect across different stakeholders may be based on differing cultural values, vested interest in financial compared to ecological trade-offs, or level of knowledge about an invasive species (Simberloff et al. 2013). Cases of deliberate introductions were traditionally made with the intention of enhancing local ecosystems in general (MacLeod et al. 2002, Liebhold and Griffin 2016), while commercial sectors have established introduced species for the purposes of enhancing commodity returns (Ewel et al. 1999). In either case, introductions not only alter local environments but also frequently bring an associated risk of invasion beyond the intended zone of introduction or introduction of accompanying species (e.g., Ewel et al. 1999, Garnas et al. 2012).

for amassing the necessary resources from diverse sectors to produce research tools. Finally, strong leadership by developed nations is necessary to counter the imbalanced international commitment or capacity to confront biological invasion. This leadership must be immediate and long-term, and it must seek to engage the complete set of nations affected by individual invasive species in question.

In this article, we propose the adoption of an 'applied empirical framework' (AEF) for invasion science that addresses the points outlined above. The AEF integrates key features of existing empirical frameworks concerning global collaboration and research design (Latombe et al. 2017, Packer et al. 2017). In addition, it explicitly links those features to existing regulatory frameworks through emphasis on the production of research solutions that are designed for direct application to invasive species management. Finally, the AEF prioritizes taxonomically targeted research efforts by collaborative task forces as a means to rapidly gather and synthesize the substantial information required to document biological invasion and generate ready-to-use tools. For background to the AEF, we first review the collaborative process in general, the distinctive roles played by different types of collaborators in the context of invasive species management, and current trends in collaboration within invasion science. We then present the AEF in detail and outline its influence on six major aspects of biological invasion research. Finally, we illustrate the AEF in action through case studies of two top-priority insect invasive species currently addressed by the BioSAFE initiative (Biosurveillance of Alien Forest Enemies; www.biosafegenomics.com)—a highly collaborative research project aimed at enabling genomics-based biosurveillance of forest invasive species.

Collaborative Science: Process, Participants, and Trends

The Nature of Collaborative Science

Collaboration reflects a natural process of resource sharing and partitioning when addressing complex or costly issues, or those with a broad relevance for a given field (Gui et al. 2018, Hall et al. 2018). Consequently, it is unsurprising that large-scale collaborations have been launched to address wide-ranging issues (e.g., disease control, World Health Organization; climate change, International Science Council) and are on the rise (reviewed in Leydesdorff and Wagner 2008; see also Ribeiro et al. 2018). The revolution in communication and transportation that has fostered globalization has undoubtedly also facilitated current collaborative trends (Hall et al. 2018) by weakening the geographic or cultural barriers that have historically inhibited the formation of large-scale collaborative groups (Gui et al. 2018).

Several meta-analyses have helped to clarify how collaborations evolve and the factors that predict their success. Collaborations often coalesce around partners associated with key local or national resources, such as infrastructure or financial support (Leydesdorff and Wagner 2008). As a result, a few privileged countries often serve as collaboration hubs. By contrast, collaborations can be constrained or impeded by political, legal, and administrative systems that feature conflicting or antiquated goals (Wagner and Leydesdorff 2005, Keenan et al. 2012, Hall et al. 2018). Successful collaborations share information easily among partners, which may be assisted by geographical, cultural, social, and technological proximity (Gui et al. 2018). Even so, the way that collaborations usually unfold is frequently comparable to adaptive systems comprised of self-interested participants (Leydesdorff and Wagner 2008, Kark et al. 2015) that vary in terms of resources, stakes, and investment in a given issue. Finally, collaborative group size influences the nature of their scientific contributions; large teams tend to meet large research goals, while small teams are more innovative (Wu et al. 2019). Collectively, these characteristics indicate that a collaborative research approach is needed to address the size, complexity, and mutual international relevance of the current global biological invasion crisis. They further suggest that the most successful ventures will take advantage of resources and expertise available from across a broad set of participants, while also sub-structuring the overall research effort as a means to promote innovation.

Contributions by Different Collaborator Types

Collaborators vary in their interests and operational approaches, and this affects the stage of invasion science research to which they contribute (Fig. 1), their motive to participate, and the type of resource that they offer (Table 1). Academic collaborators have a broad goal to advance scientific knowledge in general, so they can focus on fundamental research issues in invasion science. To pursue this motive, they can access distinct and substantial funding sources (e.g., government-sponsored academic grants, endowment funds), as well as technical personnel (e.g., students, post-doctoral fellows, research associates, technical staff and lab managers, project managers, accountants). By contrast, the research interests of governmental agencies reflect their responsibilities within invasive species management, such as facilitation, funding, research, policy development, or regulation. These responsibilities are accompanied by dedicated funding, access to data from monitoring programs (e.g., at ports of entry, eradication zones), and devoted research infrastructure (e.g., rearing facilities, collections). Research expertise within government takes numerous forms across departmental levels, ranging from political and analytical resources at the national level, to technical sampling expertise and knowledge of local biological variation within regional departments. Meanwhile, industry is motivated by the threat that invasive species pose to production or marketability of their products. With access to revenue to back this motive, industrial partners represent a valuable source of research funding, and can often contribute expertise on biological invasion risk, as well as technical infrastructure for the production of management tools. The product-oriented focus of industrial partners can also help to focus research on applied research solutions.

The same sets of motives and operational approaches outlined above bring a suite of limitations across collaborator types. In academia, funding is typically highly competitive and operates over short time cycles. Funding limitations can also affect government-sponsored research in cases where overarching research mandates change. The regulatory and political responsibilities of government agencies typically also bring a degree of information control, which can impede communication or impose restrictions on the type of data gathered or shared. Other potential governmental constraints include competing mandates among departments, unclear status of research results due to regulatory gaps, or unclear jurisdiction of research in cases where there is overlap or gaps in authority across different levels of government. Like government, industry can also impose constraints on information sharing, e.g., in situations where patents or other agreements are issued to protect research findings. The product-oriented nature of industrial research can also constrain the scope for broader research (e.g., long-term monitoring programs) only indirectly linked to tool production.

Non-governmental organizations (NGOs) are typically not-for-profit organizations that aim to generate or spread information about a cause (e.g., environment, conservation, invasive species). As such, they can help facilitate knowledge exchange and engagement with a diverse network of stakeholders, which can be critical for bridging the cultural gap between the research community and decision-makers (Crona and Parker 2012, Cook et al. 2013, Cvitanovic et al. 2015). They can also play a positive role in informing public views. The public itself plays an increasingly important collaborator role in invasion science (Box 3 describes the public role in detecting Asian longhorned beetle infestations). While public biosurveillance is typically passive—occurring through reports of 'chance' encounters with invasive species (Hester and Cacho 2017)—guided biosurveillance via citizen science, as well as crowd-funded projects are becoming more prevalent (e.g., brown marmorated stick bug, Maistrello et al. 2018; small cabbage white butterfly, Ryan et al. 2019). Importantly, public views often strongly affect the reception of biosurveillance or intervention of invasive species, which can shift government investment in those efforts (e.g., gypsy moth, Nealis 2009; emerald ash borer, Nourani et al. 2018; reviewed in van Eeden et al. 2017). In this sense, the public serves as a filter for invasion science research, ranging from crucial sources of consultation at the design phase to adjudicators of incipient tools. Given the wide variation in public science expertise, public opinion can be strongly influenced by educational campaigns but also by misinformation (Ricciardi et al. 2017, Pearson 2019).

Lessons From Different Collaborator Types

The characteristics of different collaborator types hold useful lessons for collaborative invasion science as a whole. First, early engagement with a diverse set of collaborators is likely to bring about the most fruitful project outcomes. Since collaborators can provide critical research resources and are key stakeholders (Table 1; we use 'stakeholder' in a broad sense to refer to groups with interests in any given research outcome), they provide valuable support and guidance throughout the duration of a project. For example, practitioners (e.g., policy analysts, regulators, manufacturers, technicians) are best positioned to identify conceptual or practical biosurveillance and intervention tools required to resolve biological invasion challenges, while research personnel from various sectors can determine the best research approach to generate those tools. In parallel to these technical roles, the public offers politically powerful cultural and societal values in their judgment of tool merit. Collectively, these diverse views strongly govern the ultimate success of a research tool through their influence on its design and uptake (e.g., Nealis 2009, Darling 2015).

The varied roles, strengths, and limitations across different collaborators (Table 1) also add insight to the overall advantages and disadvantages of collaboration. A large conservation science literature (reviewed in Kark et al. 2015) documents how collaboration often results in greater cost efficiency per unit effort or space (Kark et al. 2015) and how context-specific collaborator qualities (e.g., culture) can enhance or inhibit coordinated research (Bodin and Crona 2009). Our summary above reflects some of those broad qualities even at the finer scale of individual collaborator types, such as differences in research goals that are bound to arise due to inherently differing stakeholder interests. However, different collaborator qualities also highlight another dimension of this issue: the research approach or operational limits for each collaborator may enhance or constrain a research venture, even when there is broad consensus on project goals. With respect to research approach, this is reflected in the unique resources and expertise that different collaborators can supply. With respect to operational limits, this includes differences in 1) scope for unrestricted research direction or communication, ranging from high (e.g., public, academia) to low (e.g., government), 2) breadth or depth of knowledge and expertise, ranging from diverse (e.g., academia) to specific (e.g., NGOs), and from advanced (e.g., academia, government, industry) to variable (e.g., public), respectively, 3) continuity in stakeholder vision, ranging from long-term (e.g., academia, broad government mandate for invasive species management) to short-term (e.g., some species-specific government mandates, public views, industrial priorities), and 4) infrastructure to coordinate, ranging from relatively developed (e.g.,government,

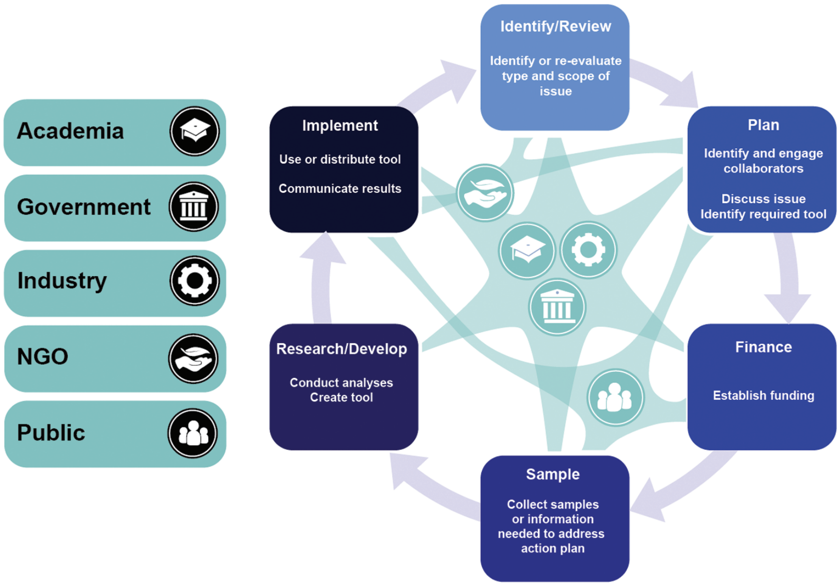


Fig. 1. Stages of invasion science research at which different collaborator types typically contribute. Arrows reflect the order of project phases and the fact that the overall process may be cyclical, leading from one project to another.

Table 1. Attributes of several major collaborator types within invasion science, summarizing their typical specific roles, their strengths and weaknesses within those roles, and their overall potential strength as collaborators

Collaborator	Role[a]	Strengths	Limitations	Potential
Academic	**Supplier**: identify, plan, finance, sample, research, implement **Facilitator**: networking, collaborative hub **Stakeholder**: increase knowledge	Freedom of research direction, communication Diverse knowledge and expertise	Short-term funding inhibits continuity	Bioinformatics and database hub
Government (Incl. NPPO)	**Supplier**: identify, plan, finance, sample, research, implement **Facilitator**: international engagement **Stakeholder**: tool uptake for policy ratification, regulation[b], and trade negotiation	Diverse expertise Knowledge of policy, biological invasion risk/impacts, knowledge gaps Internal funding Infrastructure for international governmental collaboration[c]	Restricted information sharing inhibits availability[d] or speed[e] Mandate changes inhibit continuity[f] Resistant to novel methods or discovery	Collaborative hub by sector and region Leadership in method development and application
Industry	**Supplier**: identify, plan, finance, sample, research, implement **Facilitator**: industrial coordination **Stakeholder**: uptake for optimal productivity	Diverse expertise Knowledge of biological invasion risk/impacts Internal funding Infrastructure for international industrial collaboration	Often narrow biological invasion interest[g] Priority changes inhibit continuity[h]	Leadership in novel method development and application
Nongovernmental organization	**Supplier**: identify, plan, implement **Facilitator**: stakeholder engagement, knowledge transfer, funding **Stakeholder**: increase knowledge	Freedom of research direction, communication	Short-term funding inhibits continuity	Collaborative hub across all collaborator types
Public	**Supplier**: plan, finance, sample, implement **Facilitator**: knowledge transfer **Stakeholder**: cultural and societal values	Freedom of research direction, communication	Inconsistent scientific knowledge Conflicting stakeholder visions hinder consensus	Citizen science as a major source of sampling Crowd sourcing as a major source of funding

[a]'Supplier' reflects resources contributed to project stages outlined in Fig. 1. 'Facilitator' reflects particular assets for facilitating one or more project stages. 'Stakeholder' reflects vested interest in a research issue or solution.

[b]Examples: detection, risk assessment, mitigation.

[c]Examples: controlled access data from port inspections, trapping programs, and eradication zones.

[d]Examples: data confidentiality, travel restrictions.

[e]Examples: procedural delays.

[f]Examples: novel invasive species priority, altered trade priorities.

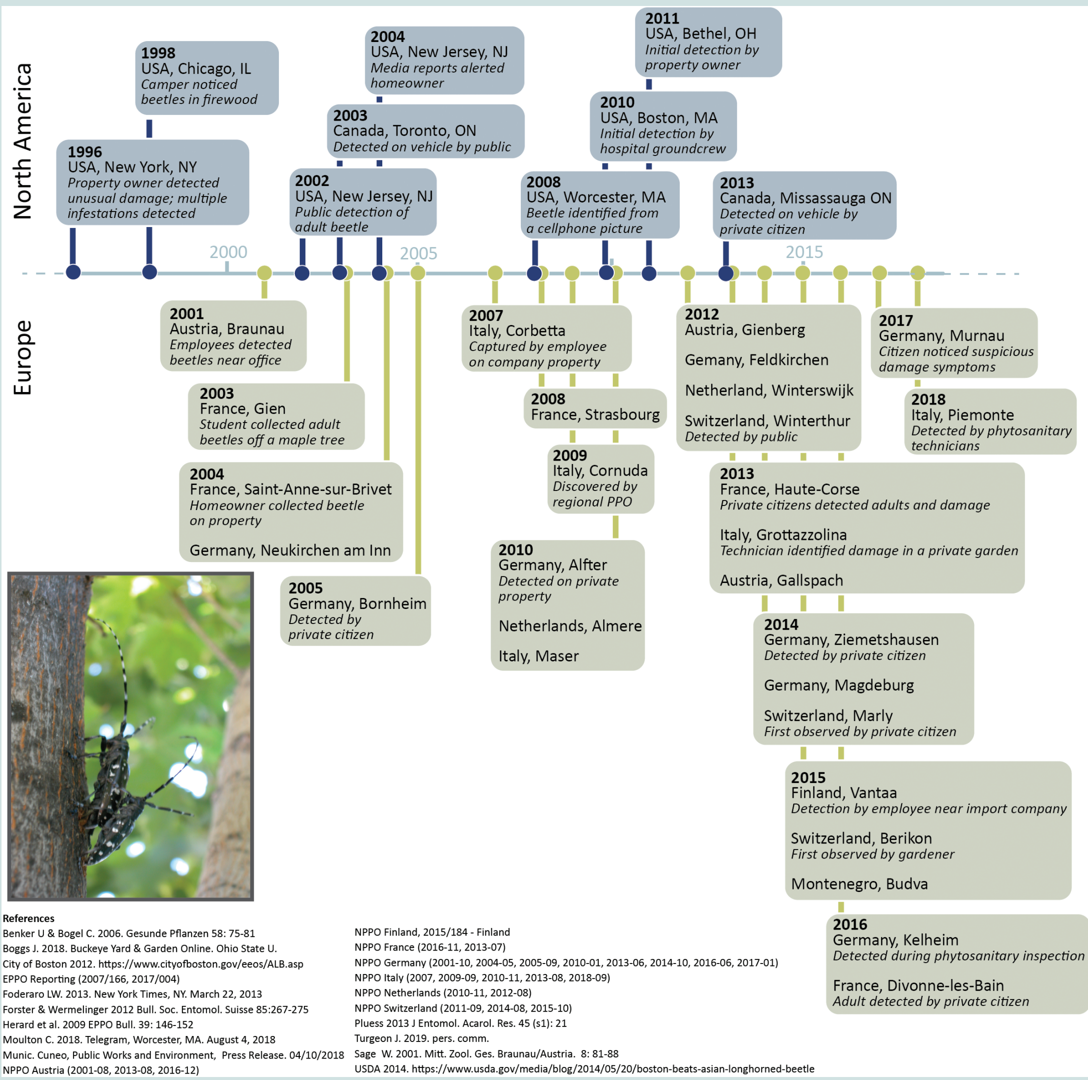
[g]Examples: post-establishment only, specific aspects of invasive species impact.

[h]Examples: changed cost/benefit analysis outcome, altered target market.

Box 3. Public Engagement for Detection of Asian Longhorned Beetle

The importance of passive surveillance has not been quantified, despite long-standing recognition of its contributions (Hester and Cacho 2017). In the case of the Asian longhorned beetle, public engagement has been a critical asset in the early detection of new invasions (Ciampitti and Cavagna 2014, Box 3 Fig. 1). Many Asian longhorned beetle infestations were initially reported by citizens, rather than focused surveillance efforts (Haack et al. 2010), and this has facilitated rapid interventions to new infestations. The initial Asian longhorned beetle infestation in North America was identified in New York City in 1996 by a concerned resident (Poland et al. 1998, Lingafelter and Hoebeke 2002). Following this initial find, additional infestations were detected in North America and Europe (Box 3 Fig. 1). In fact, most new Asian longhorned beetle detections are a direct result of an observant member of the general public (Box 3 Fig. 1). Upon detection, confirmation of Asian longhorned beetle relies on government authorities, which underscores the importance of public–government relationships and outreach.

Public outreach and media surrounding invasive species are key components of engagement and passive surveillance (Marchante et al. 2010). Asian longhorned beetle is a large beetle and makes distinctive boreholes in its tree hosts (Fig. 3), so visual detection is easier than for relatively inconspicuous invasive species. This feature has been used to great effect by regulatory organizations to create pest alerts or other information campaigns aimed at the public. Examples include pest fact sheets, pamphlets, media alerts, school curriculum material, and road signs (e.g., USDA, Natural Resources Canada, Canadian Food Inspection Agency). NGO organizations also help to transmit knowledge to the general public about Asian longhorned beetle (Forest invasives Canada, Invasive Species Centre). Social media is becoming more valuable in early detections and a number of users focus on invasive detection and scientific communication (e.g., @StopALB, @forestinvasives, @Invasivesnet, @InvSp). Media and programs targeting youth and educators (e.g., the BeetleBuster program) further extend the public outreach and education component. These resources fill an important knowledge gap between researchers and the general public.



Box 3, Fig. 1. Contributions of private citizens to the passive surveillance of ALB throughout its invasive range over 23 years of detections. Detection of major infestations are highlighted along a timeline from 1996 to 2018 for both North America and Europe.

industry) to undeveloped (e.g., public). The relevance of any particular collaborator quality varies across different research issues or contexts (Bodin and Crona 2009, Van Wilgen and Richardson 2014, Kark et al. 2015). Consequently, the planning stages for any invasion science project should involve an assessment of the value of collaboration in terms of both stakeholder interests and their collaborative strengths and limitations (Kark et al. 2015).

Current Trends in Collaborative Research

Despite the obvious benefits of collaborative research for invasion science (above; see also Margarey et al. 2010, Garnas et al. 2012, Keenan et al. 2012, Van Wilgen and Richardson 2014, Latombe et al. 2017, Liebhold et al. 2017, Packer et al. 2017), global-scale collaboration has been slow to develop. To assess this trend, we surveyed peered reviewed publications on insect invasive species listed within the Global Invasive Species Database (International Union for Conservation of Nature ['IUCN']; for detailed literature search methods, see Supp Materials [online only]). Insects represent a large proportion of invasive species worldwide (Seebens et al. 2017), so they offer useful insights for collaborative trends in invasion science. Our literature survey returned more than 4,000 articles for 81 terrestrial and aquatic insect species—an average of roughly 50 articles per species. The pattern of increasing institutional co-authorship over the past 20 yr in these articles (Fig. 2A), together with the large number of initiatives promoting research on invasive species and information exchange in general (e.g., more than 40 cited across reviews by Lucy et al. 2016, Latombe et al. 2017, Ormsby and Brenton–Rule 2017, Packer et al. 2017), indicates that the global scientific community is collectively mobilizing in response to the biological invasion crisis. However, median international co-authorship on individual projects shows no increase across the articles surveyed (Fig. 2B), suggesting that intensified collaboration has occurred chiefly at the national level. Moreover, while policy addressing biological invasion has expanded rapidly over the past 70 yr in the context of global trade, a formal framework for connecting research tools directly to policy is currently lacking (Ormsby and Brenton–Rule 2017). Despite these lags, we expect to see continued expansion of collaborative global invasion science networks in coming years, facilitated by frameworks for their implementation (discussed below). Clearly, given the global scale and rapid escalation of biological invasion, urgent effort is needed to accelerate this process.

An AEF for Invasion Science

We describe an AEF for invasion science that is aimed at accelerating and focusing invasion science to aggressively confront the current global biological invasion crisis. The framework builds on previously proposed models for global-scale invasion science that have emphasized: 1) standardized sample designs to reveal key aspects of biological invasion (Latombe et al. 2017), and 2) collaboration to facilitate information exchange between countries and different institutional organizations (Packer et al. 2017). The AEF further prioritizes 3) research that explicitly connects with existing regulatory policy (above; reviewed in Ormsby and Brenton–Rule 2017) through the production of research tools designed for direct uptake in invasive species management, and 4) a taxonomically targeted approach, in which task forces rapidly conduct in-depth research across the entire geographic range of top-priority invasive species to ensure successful tool production. Below, we summarize six critical facets of research within the AEF: 1) research goals, 2) focal species, 3) project design, 4) stakeholder engagement, 5) uptake of research tools, and 6) leadership in global collaboration. We then briefly discuss the aims of the AEF in relation to the framework presented by Latombe et al. (2017). Last, we present two case studies that exemplify the AEF.

Research Under the AEF

Research Goals

Critical knowledge gaps drive the study of biological invasion, and closing those gaps is key to developing innovative solutions for invasive species management. Latombe et al. (2017) propose a standardized research framework comprised of three 'Essential Variables for Invasion Monitoring': species' presence (essential variable 1, 'EV1'), species' alien status ('EV2'), and alien species' impact ('EV3'). The EV framework usefully ranks ecological data to illustrate how biosurveillance can move forward with minimal resources and maximum flexibility. Latombe et al. (2017) argue that only the first EV entails field data collection and is within the resource capabilities of all nations. They also stress that this first EV requires only simple, modular survey data, which would contribute positively to a global biosurveillance dataset regardless of the temporal or spatial scale of sampling. Finally, the approach accommodates any other extant data sources ('supplementary variables' such as invasion pathways or habitat characteristics, Latombe et al. 2017) that may broaden our understanding of biological invasion risk on a case-specific basis.

We view the EV approach as a valuable method to prioritize research needs, particularly for long-term monitoring across multiple nations (Latombe et al. 2017). However, we suggest that obtaining in-depth knowledge on the biological invasion process (e.g., origin, pathways, or tempo of invasion) and the traits that mediate it (e.g., invasive species host breadth, susceptibility to climatic variation) will typically require intensive, globally coordinated research that addresses most or all EVs and supplementary variables described by Latombe et al. (2017), and that also considers lagged or indirect ecological impacts (Box 1). There is substantial variation in the outcomes of biological invasion, both within and among species (Heger and Trepl 2003, Crooks 2005, Hayes and Barry 2008, Aikio et al. 2010, Yelenik and D'Antonio 2013, Leffler et al. 2014, Ordonez 2014). Consequently, research must, in general, be species-specific (we use 'species' throughout to signify any distinctive evolutionary lineage) rather than comparative, and should stress the importance of experimental verification of correlative patterns (e.g., Packer et al. 2017). While the investment required for this comprehensive approach can be substantial, taxonomically targeted research geared towards tool production (below) presents a means to concentrate the resources required to address these vital aspects of invasion science. By this approach, research goals can vary across projects to address unique aspects of the invasion biology, knowledge gaps, or research tools sought for focal invasive species, and to accommodate specific regulatory, political, or resource limitations.

Focal Species

Taxonomically targeted research is necessary to acquire the in-depth knowledge of biological invasion promoted by the AEF. Focal invasive species may be identified from national species lists relevant to individual collaborative initiatives, global lists (e.g., Global Invasive Species Database), or by species ranking schemes (Blackburn et al. 2014, Hawkins et al. 2015, McGeoch et al. 2016, Potter et al. 2019). The approach of choosing target invasive species does not downplay the importance of taxonomically broad biosurveillance (Latombe et al. 2017) or representation across invasion science (Packer et al. 2017), but it concentrates the most immediate and comprehensive research efforts on urgent biological invasion threats. We expect that the wide array of high-risk invasive species identified by the methods above will supply an ecologically and taxonomically varied range of potential 'model' species (Packer et al. 2017) across projects that will broaden our understanding of biological invasion in general when treated within the AEF. We also note that even projects aimed at developing focused tools are likely to generate incidental data that are broadly relevant to invasion science. In addition, targeted data collection and analysis efforts can often accommodate a taxonomically broad approach, at least within certain aspects of research. For example, monitoring surveys (EV1 in Latombe et al. 2017) and subsequent alien status (EV2) and impact (EV3) assessments are often conducive to multi-species data collection and downstream analyses.

Project Design

Merging knowledge of biological invasions across multiple research initiatives requires comparable methods and standards for data quality. Standardization of research design provides this comparability. Methods for research standardization are featured in the global monitoring framework of Latombe et al. (2017), and also the 'Global Networks for Invasion Science' (GNIS) proposed by Packer et al. (2017). Modular research designs (i.e., flexible in terms of depth and scope of data collection) further assist data comparability by accommodating both longitudinal data and varying research capacity over time or across research groups (Latombe et al. 2017). The ease of standardization varies among different types of projects. For example, sample design may often be precisely standardized in the case of survey approaches (e.g., EV1, EV2; Latombe et al. 2017). Conversely, species-specific research questions (e.g., addressing EV3 or other 'supplementary variables'; Latombe et al. 2017) may often require tailoring to specific objectives (e.g., precise hypotheses tested or biological details of the invasive species in question). Even here, common experimental methodologies (e.g., Packer et al. 2017), standardized metadata formats (Michener 2006), and high data quality standards will help reconcile findings across different species about biological invasion processes or invasive traits.

Stakeholder Engagement

Stakeholder engagement brings with it the cost of communication and reconciliation across potentially widely differing perspectives but it can benefit from sponsorship and stakeholder support for tools of predetermined utility (Nealis 2009, Van Wilgen and Richardson 2014, Richardson and Lefroy 2016). As a result, engagement of a broad array of stakeholders will strengthen invasive science projects from the research design phase (i.e., addressing knowledge gaps or techniques) through tool uptake. This should help to ensure public support for the research tools produced (Vaz et al. 2017, Shackleton et al. 2019), and to remedy the widely recognized limited uptake of tools by management agencies (e.g., Lauber et al. 2011, Darling 2015, Bilodeau et al. 2019, Nourani et al. 2018, Rohal et al. 2018). The actual choice of collaborators for a given project should capitalize on the strengths that they can contribute relative to the research challenge at hand, while also considering their accompanying limitations (e.g., Table 1). Kark et al. (2015) have proposed a detailed workflow for this selective process that also emphasizes how the costs and benefits for each potential collaborator affect project scope and viability.

Uptake of Research Tools and Data Sharing

The active stakeholder engagement outlined above, from project design through tool production, is aimed at ensuring rapid uptake of research results for invasive species management. Common data repositories featuring standardized metadata, data archiving, and long-term open access supply further resources that can make parallel data emerging from research projects more generally accessible and usable. Latombe et al. (2017) summarize several existing large-scale databases that may serve as efficient repositories to house and quality check data from across multiple projects. In addition, Lucy et al. (2016) propose INVASIVESNET (www.invasivesnet.org/), an association aimed at providing an information exchange hub for all sources of invasive species information. These may encompass or interface with other valuable information networks, such as the International Plant Sentinal Network (Giovani et al. 2015) and Q-bank (Bonants et al. 2013).

Leadership in Global Collaboration

Motivation to execute rapid, targeted research across the geographic range of focal invasive species is likely to remain internationally

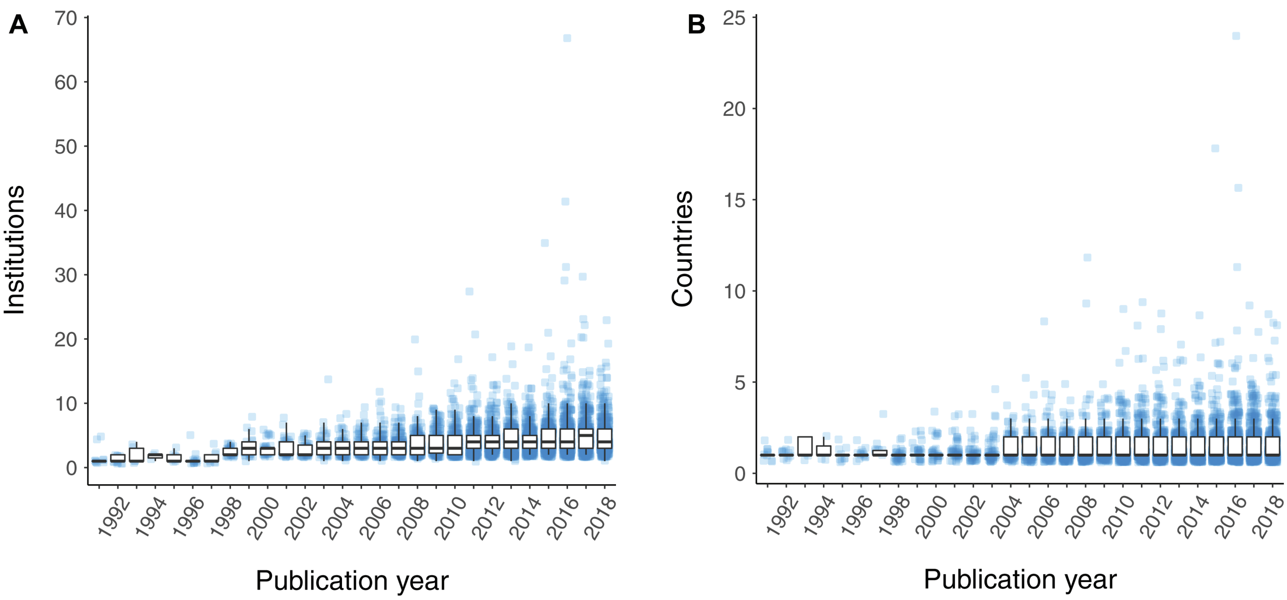


Fig. 2. Trends in international collaboration in insect biological invasion research, based on a literature search of invasive insect species for patterns of co-authorship, in terms of co-author affiliations by (A) institution (B) country. Results summarize 4,056 publications representing 81 species. Dots indicate individual publications; boxplots summarize quartiles of their distribution (thick horizontal line: median).

varied due to differences in perceived impacts of biological invasion, economic incentives, and infrastructure or politics (e.g., Westing 1998, Garnas et al. 2012). To accommodate this imbalance, we envision proactive leadership by economically privileged nations to engage in collaboration with the complete set of nations affected by focal invasive species. Packer et al. (2017) note that GNIS offer species-specific flexibility to take advantage of diverse funding opportunities, and that they can provide a relatively easy means to communicate with or adhere to relevant regulatory frameworks (above; reviewed in Ormsby and Brenton–Rule 2017). The Forest Health Division of the International Union of Forest Research Organizations presents one potential formal arena for initiating these types of collaborations. As improved and equilateral international commitment to biosurveillance and intervention develops over time, the collaborative efforts we suggest could easily transition toward a globally coordinated international invasion science program of any taxonomic breadth (e.g., Latombe et al. 2017).

The Vision of an AEF for Invasion Science

We view the approach for global monitoring of biological invasion by Latombe et al. (2017) as a broad form of AEF, given its aim to mobilize global-scale research for the sake of invasive species management and its accommodation of either taxonomically general or targeted research designs. In that respect, their framework encompasses the AEF that we propose here. The main thrust of the message of Latombe et al. (2017) is to promote a survey approach that prioritizes the acquisition of relatively accessible data, in order to encourage multinational collaborators to contribute towards a continuous, global, and taxonomically general monitoring scheme. We see that approach as vital for long-term, comprehensive invasive species management. However, in-depth, rapid research on top-priority invasive species is urgently needed, given the continued global escalation of biological invasion (Seebens et al. 2017), the lag in international commitment to coordinated invasion science (Wingfield et al. 2015, Latombe et al. 2017), and knowledge gaps regarding species-specific impacts (Simberloff et al. 2013, Wingfield et al. 2015, Ormsby and Brenton–Rule 2017). In our view, the extensive resources required to conduct comprehensive research geared toward tool production for direct uptake in invasive species management (funding, expertise, stakeholder representation, global research coordination) necessitate a highly collaborative and taxonomically targeted research approach. The AEF that we advocate here outlines key research design features characterizing that approach. It can facilitate the development of novel tools for invasive species management, which we demonstrate below in two case studies. It also contributes to long-term invasive species monitoring through both the establishment of transferable research designs and the development of in-depth knowledge that will shed light on interspecific trends and variation in biological invasion. As such, the AEF features the modular flexibility endorsed by Latombe et al. (2017)—supplying methodology and knowledge that will incrementally strengthen invasive species management overall. Moreover, it can easily transition (or contribute in parallel) to a taxonomically general, internationally coordinated, and long-term biological invasion management program as that knowledge accrues.

The AEF in Action: Case Studies From the BioSAFE Initiative

BioSAFE (initiated 2016; see Hamelin and Roe 2019) is a 4-yr collaborative biological invasion research project that exemplifies the key features of the AEF outlined above. Funded by the NGO Genome Canada and two provincial programs (Genome British Columbia and Genome Québec), the project aims to produce a genomics-informed biosurveillance pipeline (for shorthand, 'BioSAFE tool') enabling early detection and rapid, appropriate responses to forest invasive species. Next-generation sequencing (NGS) technology now brings genomic data within reach even for non-model organisms (reviewed in Roe et al. 2019; for applications in insects, see Jones et al. 2015, McKenna et al. 2016, Picq et al. 2018). Output from genomic analyses can often be assembled on a personal computer or even a smartphone, and can be used to assess species identity, global geographic origin, invasion pathways, and risk of establishment and spread (Lee 2002, Estoup and Guillemaud 2010, Handley et al. 2011, Kirk et al. 2013, Chown et al. 2016, Cristescu 2015, Rius et al. 2015, Wingfield et al. 2015, Sherman et al. 2016, Roe et al. 2019; for discussion of the boundaries of genomic applications, see Fitzpatrick et al. 2012, Bock et al. 2015). The BioSAFE tool aims to supply this information within species-specific workflows in order to help regulatory agencies predict biological invasion risk and the impact of intercepted invasive species.

BioSAFE is structured as a rapid, global-scale research effort that coordinates species-specific task forces with technical teams responsible for tool assembly. Project design involved engagement of regulatory agencies to gauge the need for a fast and reliable biosurveillance decision mechanism. The main anticipated components of the BioSAFE tool are next-generation sequencing panels, assignment algorithms, genomic databases, and a decision support system that interfaces with economic, pest, and genomic databases. Producing these components has entailed a multidisciplinary approach and collaboration from across many research fields (e.g., entomology, insect rearing, taxonomy, physiology, genomics, computing, bioinformatics, modeling, and economics; Table 2). The wide geographic distributions of the project's focal species (below) and their status as regulated invasive species has also entailed participation by various governmental agencies in order to undertake range-wide sampling efforts. Sub-structuring of the BioSAFE team has helped provide the independence needed to forge innovative solutions for the unique challenges that exist across different species or stages of tool assembly. More broadly, data sharing forms the basis for both the BioSAFE development phase and the final tool.

BioSAFE currently focuses on four global top-priority invasive species, of which two are insect pests: the wood-boring beetle *Anoplophora glabripennis*, Motschusky (Coleoptera: Cerambycidae; Asian longhorned beetle) and the defoliator moth *Lymantria dispar*, L. spp. (Lepidoptera: Lymantriidae; gypsy moth species complex) (Fig. 3). These species were selected to demonstrate that the BioSAFE tool can be applied across taxa with distinctive ecological and genomic characteristics. *Anoplophora glabripennis* and *L. dispar* spp. are both polyphagous insects listed among the most destructive invasive species in the world by the IUCN (see also Flower and Gonzalez-Meler 2015, Haack et al. 2009). In the following case studies, we summarize the invasion history of these two species, BioSAFE research goals for each one, and distinctive aspects of sampling or experimental design, in order to illustrate how current knowledge or the biology of each species have influenced the shared AEF features outlined above.

Case Study 1: Gypsy Moth

Gypsy moth is a species complex of serious forest pests. *Lymantria dispar* contains three recognized subspecies: the European gypsy moth, *L. dispar dispar*, and two Asian subspecies (AGM), *L. dispar asiatica* and *L. dispar japonica*, which are found across continental Asia and Japan, respectively (Pogue and Schaeffer 2007). All three subspecies are capable of feeding on hundreds of different deciduous and coniferous tree host species (Baranchikov 1989, Schaefer 1989, Liebhold et al. 1995; C. I. Keeling, M. A. Keena, and I. Porth, unpublished data). Population outbreaks can lead to significant defoliation of commercial and urban forest stands, causing substantial economic, ecological, and aesthetic losses (Bradshaw et al. 2016).

European gypsy moth was accidentally introduced from Europe to Massachusetts in 1869 (Liebhold et al. 1989). From here, it gradually spread north to Canada, south to Virginia and west to Wisconsin. Satellite populations of European gypsy moth are also regularly observed as far west as British Columbia, arriving through incidental transport of egg masses on vehicles. In the United States, the rate of European gypsy moth colonization has been reduced by implementation of the 'slow-the-spread' program (www.gmsts.org/), which uses aggressive eradication efforts to eliminate new populations that develop outside of the established range (Nealis 2009). NPPOs such as the Animal and Plant Health Inspection Service (APHIS, United States Department of Agriculture) and the Canadian Food Inspection Agency (CFIA) see the Asian subspecies as an even greater threat than European gypsy moth (Dumouchel 2010, USDA Pest Alert 2016). AGM have a broader host breadth than European gypsy moth (Baranchikov 1989), so they threaten a potentially wider range of hosts or habitats. Further, AGM females are flight-capable (unlike European gypsy moth females, reviewed in Keena et al. 2007), which may enable a relatively higher capacity for AGM population spread.

Although genomics-based tools developed from within our group are already used by the CFIA and APHIS to distinguish gypsy moth subspecies (Stewart et al. 2016, 2019), crucial details of the invasion history or local risk posed by intercepted samples are lacking, such as precise geographic origin, potential pathways of invasion, projected female flight capacity, or North American host breadth. The BioSAFE gypsy moth tool is designed to fill these gaps by providing an informative and rapidly employable genetic panel and decision system.

To establish a global AGM and European gypsy moth reference collection, we coordinated two collection campaigns in 2017 and 2018 that involved 37 colleagues stationed in 29 countries, as well as personal contacts or specialists in several additional countries (Table 2). Staff from national and provincial parks, CFIA, and APHIS further collaborated to obtain sample coverage within the regulated North American range of European gypsy moth. A key feature of outreach success was to provide participants with: 1) sufficient background information to understand the purpose of our project, and 2) all needed trap components, detailed information on trap assembly, and an option for prepaid package shipment by courier. The overall outreach effort returned over 15,000 individuals from pheromone traps deployed at 138 locations and from private collections. From these, we are currently processing approximately 1,500 representative moths to design genetic panels for profiling samples by geographic origin, flight ability, and host breadth.

Candidate gene searches for AGM flight ability and host breadth have involved controlled behavioral experiments on moths maintained in quarantine by the USDA Forest Service, along with genomic analyses conducted by collaborators at Canadian academic institutions and one agency of the Canadian government. The genes shortlisted from these experiments will permit profiling gypsy moth samples for potentially key invasive traits, while also offering potential targets for genetic manipulation or controlled breeding programs in the future.

Case Study 2: Asian Longhorned Beetle

The Asian longhorned beetle is a wood-boring insect that infests a wide range of hardwood trees, causing tree mortality due to extensive mining of the xylem. Asian longhorned beetle is native to China and Korea but has become established in Europe and North America. It has caused extensive economic and environmental damage to hardwood forests in each of these areas (Haack et al. 2009). Substantial resources have been invested to eradicate introduced Asian longhorned beetle populations. Although these efforts have been successful in several locations (e.g., Switzerland, the Netherlands, Chicago, New Jersey; Haack et al. 2009), new and persistent infestations exist in both the United States and Europe.

Previous research has sought to describe the genetic diversity of native and invasive Asian longhorned beetle populations using a range of molecular tools (Kethidi et al. 2003; Yulin et al. 2004; Carter et al. 2009; Ohbayashi et al. 2009; Carter et al. 2010; Javal et al. 2017, 2019; Wu et al. 2017). This work has provided insight into Asian longhorned beetle population structure, movement, and spread. However, it lacks the resolution needed to predict Asian longhorned beetle origin, secondary spread within an invaded range, or adaptation to new environments. On the latter front, cold hardiness of Asian longhorned beetle is one unexplored issue of relevance to the potential geographic range of Asian longhorned beetle invasion. The BioSAFE Asian longhorned beetle tool aims to address these knowledge gaps.

The demographic history of Asian longhorned beetle within its native range is complex, involving regional outbreaks, secondary spread, and genetic admixture between historically isolated populations (Carter et al. 2009, Javal et al. 2019). As a result, dense sampling of Asian longhorned beetle populations has been required to establish a reference collection suitable for profiling specimens in terms of geographic origin and cold hardiness. A second challenge is that there is no known long-range pheromone for this species (Haack et al. 2009), so sampling entails hand collection. Collaborations with Chinese and Korean partners have been critical to overcome these hurdles and adequately sample Asian longhorned beetle within its native range. Our current efforts to explore physiological traits related to Asian longhorned beetle invasive capacity have also relied heavily on these collaborations in order to undertake the permitting, collecting, securing, shipping, and rearing necessary to establish Asian longhorned beetle colonies within secure quarantine facilities. Obtaining samples from within the invasive range of Asian longhorned beetle has involved additional collaborative partnerships with regulatory agencies that are responsible for the eradication of Asian longhorned beetle populations. Here, it has been essential to ensure that their existing trapping protocols incorporate adequate sample preservation to ensure high-quality genomic specimens while maintaining effective eradication efforts.

A final level of sampling in the case of Asian longhorned beetle has been geared towards building a collection of other *Anoplophora* species, in order to distinguish *A. glabripennis* from its many congeners. There are at least 36 species in the genus, and these have diversified throughout Asia (Lingafelter and Hoebeke 2002). Although formally collecting reference samples for all *Anoplophora* species was beyond the scope of our current project, we have capitalized on the fact that many species are prized among insect collectors for their large size and striking coloration. This feature has allowed us to purchase specimens representing at least 15 species from online retailers. Despite the variable quality of DNA across the purchased samples, they have generally furnished sufficient genetic markers for species-level identification. Taxonomic expertise within government organizations has been crucial to morphologically verify species identity of the obtained samples.

Subsequent to sampling, research on Asian longhorned beetle thermal tolerance has proceeded through collaborative rearing

Table 2. Collaborators and their roles in the gypsy moth and Asian longhorned beetle projects within the BioSAFE initiative

Institution	Country	Collaborator type	Role
Gypsy moth			
Higher National Agronomic School	Algeria	Academic	Sample
University of Natural Resources and Life Sciences	Austria	Academic	Sample
Forest Research Institute	Bulgaria	Academic	Sample
Institute of Biodiversity and Ecosystem Research	Bulgaria	Academic	Sample
Canadian Centre for DNA Barcoding[a]	Canada	Academic	Sample
Canadian Food Inspection Agency (BC)[b]	Canada	Government, NPPO	Sample, implement
Canadian Food Inspection Agency (ON)[c]	Canada	Government, NPPO	Identify, plan, sample, implement
Department of Natural Resources of Nova Scotia	Canada	Government	Sample
Genome British Columbia	Canada	NGO	Finance
Genome Canada	Canada	NGO	Finance
Genome Québec	Canada	NGO	Finance
Laval University	Canada	Academic	Identify, plan, sample, R/D
Natural Resources Canada	Canada	Government	Sample, R/D, facilitate
Ontario Ministry of Natural Resources and Forestry	Canada	Government	Sample
University of British Columbia	Canada	Academic	Identify, plan, R/D, facilitate
Beijing Forestry University, Forestry College	China	Academic	Sample
Croatian Forest Research Institute	Croatia	Government	Sample
Institute of Forestry and Rural Engineering	Estonia	Government	Sample
National Institute of Agronomic Research – Val de Loire Center	France	Academic	Sample
Montpellier University	France	Academic	Sample
Forestry Competence Center	Germany	Academic	Sample
University of Sopron	Hungary	Academic	Sample
Agricultural Research Organization	Israel	Government	Sample
University of Padova	Italy	Academic	Sample
Council for Agricultural Research and Economics	Italy	Academic	Sample
University of Naples Federico II	Italy	Academic	Sample
University of Sassari	Italy	Academic	Sample
Museum of Natural History	Poland	Government	Sample
Siberian Branch of the Russian Academy of Science	Russia	Academic	Sample
Siberian Branch of the Russian Academy of Science	Russia	Academic	Sample
National Forest Centre	Slovakia	Government	Sample
National Institute of Forest Science	South Korea	Government	Sample
Institute of Subtropical and Mediterranean Horticulture 'La Mayora'	Spain	Academic	Sample
Karadeniz Technical University	Turkey	Academic	Sample
Animal and Plant Health Inspection Service (United States Department of Agriculture)[d]	United States	Government, NPPO	Sample, implement
United States Forest Service (United States Department of Agriculture)[e]	United States	Government	Sample, R/D
Asian longhorned beetle			
Private collectors	29 countries	Public	Sample
Canadian Food Inspection Agency	Canada	Government, NPPO	Identify, plan, sample, implement
Genome British Columbia	Canada	NGO	Finance
Genome Canada	Canada	NGO	Finance
Genome Québec	Canada	NGO	Finance
Laval University	Canada	Academia	Identify, plan, sample, R/D
McGill University	Canada	Academia	Sample
Natural Resources Canada	Canada	Government	Sample, facilitate
University of British Columbia	Canada	Academia	Identify, plan, sample, R/D, facilitate
Western University	Canada	Academia	Sample, R/D, facilitate
Beijing Forestry University	China	Academia	Sample, facilitate
National Institute of Agronomic Research[f]	France	Government	Sample
University of Hohenheim[g]	Germany	Academia	Sample, facilitate
Agricultural Research Service (United States Department of Agriculture)	United States	Government	Sample
Animal and Plant Health Inspection Service (United States Department of Agriculture)	United States	Government, NPPO	Sample, implement

Table 2. Continued

Institution	Country	Collaborator type	Role
United States Forest Service (United States Department of Agriculture)[h]	United States	Government	Sample

'Sample' role indicates collaborators who supplied insect samples. Country indicates institution location for all collaborator types. Country also indicates sample origin (except where noted) for those who supplied insect samples.

[a]Supplied samples from Russia.

[b]Supplied samples from Japan, Kosovo.

[c]Supplied samples from Russia, Iran, Japan, and Central Asia.

[d]Supplied samples from China, Germany, Japan, Slovakia, and Syria.

[e]Supplied samples from Bulgaria, China, Croatia, France, Germany, Greece, Japan, Lithuania, Poland, Russia, Slovak Republic, and United States.

[f]Supplied samples from Austria, China, France, and South Korea.

[g]Data sharing agreement.

[h]Supplied samples from China, South Korea.

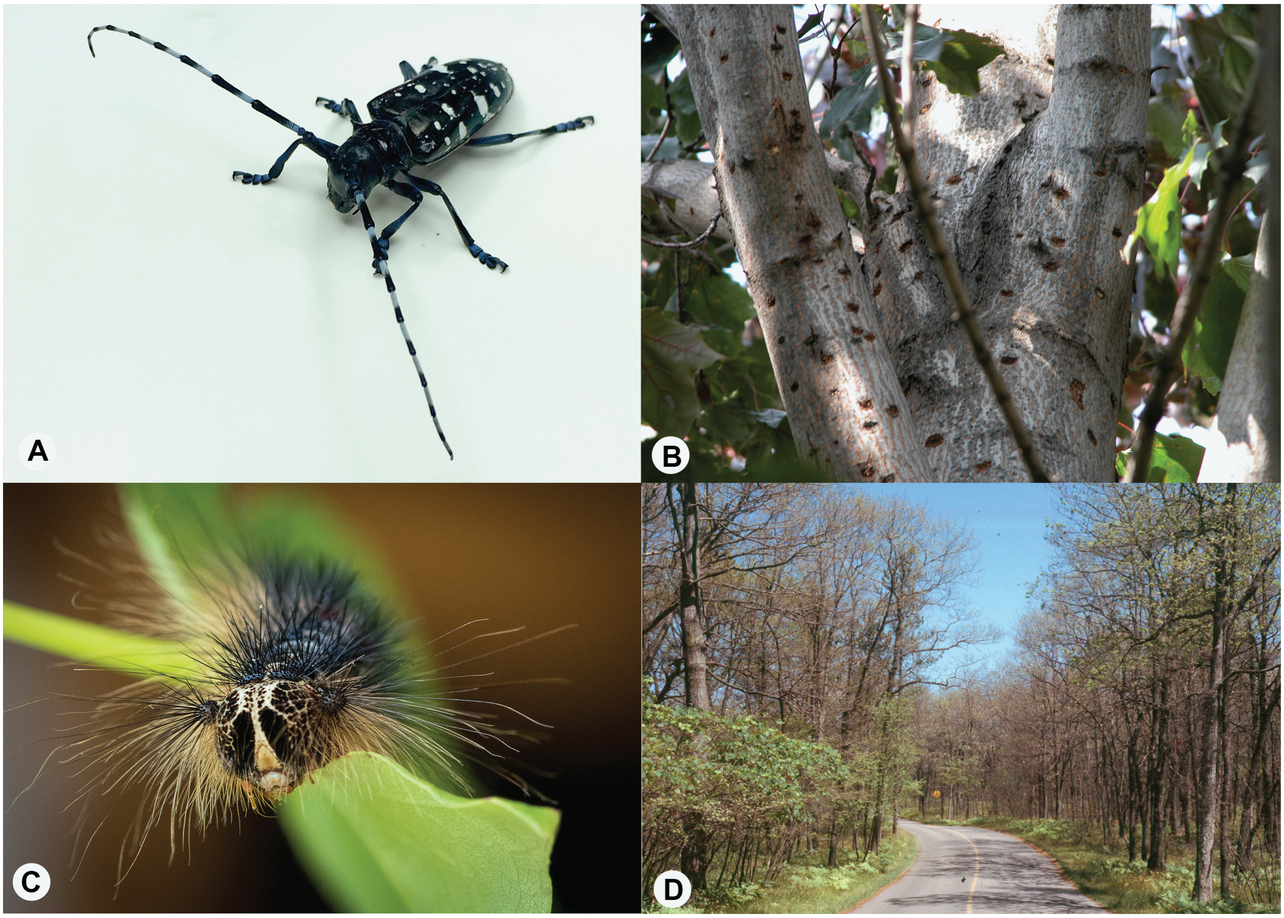


Fig. 3. Two focal invasive insect species of the BioSAFE initiative. (A) Adult female Asian longhorned beetle (*Anoplophora glabripennis*) (A. Roe); (B) Asian longhorned beetle oviposition scars and emergence holes in an infested maple (NRCan); (C) Larval gypsy moth (GM, *Lymantria dispar*) (C. Béliveau); (D) GM defoliation in a hardwood stand (NRCan).

experiments and genomic analyses between government and academic institutions in both Canada and the United States. This has entailed both manipulative experiments within quarantined colonies and gene-environment association studies based on natural sample collections and their accompanying ecological data. Similar to the AGM project, genetic information regarding the origin and potential invasion capacity of Asian longhorned beetle specimens is now feeding into the ongoing development of the identification and risk analysis pieces of the BioSAFE tool.

Conclusions

The components needed for global biosurveillance and intervention of biological invasion are now within reach (Wingfield et al. 2015). These include a means for prioritizing invasive species risk (e.g., Hawkins et al. 2015), a framework for flexible and feasible research design (Latombe et al. 2017, Packer et al. 2017), and ongoing development of global regulatory policies that reflect a general will to document and reduce biological invasion impacts (Ormsby and Brenton–Rule 2017, Packer et al. 2017). We argue that an AEF for invasion science is needed to directly integrate these components if we are to effectively address the global escalation of biological invasion.

The AEF emphasizes the need for task forces that invest adequate resources to rapidly research top-priority invasive species, as a means to confront key invasion threats while also broadening our understanding of biological invasion in general. It stresses that research should encompass both the native and invasive range of target species, and should address as closely as possible aspects of the biology of invasive species that are critical for understanding invasion risk (e.g., Chown et al. 2016, Roe et al. 2019), with the explicit aim to generate tools for direct uptake in biological invasion management. We have shown that collaboration is a crucial foundation for these aims, providing a means to gauge and reconcile the complex interests across stakeholders from the outset of project design, and to assemble the needed resources and expertise to bring an intensive research effort from the initial design phase through tool production and uptake. Strong leadership and support of collaborative research initiatives by economically developed nations will be important for implementing the AEF, given current imbalances in global commitment or capacity to address biological invasion.

Research design under the AEF is bound to vary across projects due to differing knowledge gaps, intended tools, and resource constraints across collaborative research projects. Moreover, progress in biological invasion management stemming from individual projects is likely to be incremental, with findings typically advancing our knowledge of biological invasion while also revealing new challenges (Fig. 1). The AEF simply aims to optimize invasion science within this context. Many research ventures reflect features of the AEF in terms of their biological, collaborative, or tool-oriented research scope (examples in Garnas et al. 2012, Packer et al. 2017, Nagoshi et al. 2018, Shine 2018). We think that research adopting the entire AEF will make the greatest progress in confronting the current global biological invasion crisis.

Supplementary Data

Supplementary data are available at *Annals of the Entomological Society of America* online.

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