Advances in understanding the ecology of invasive crop insect pests and their impact on IPM

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1 Introduction

Invasive species remain one of the greatest threats to the productivity and sustainability of agriculture, forests, prairies and wetlands (Lovett et al., 2016; Paini et al., 2016). By definition these species are alien (i.e. non-native) to some ecosystems in which they now occur. In their adventive geographic range, they lack co-evolutionary history with the native flora and fauna. As a result, hosts are bereft of specific resistance mechanisms, and no specialized co-evolved natural enemies occur to regulate pest population growth. Alien species become invasive when they cause, or are likely to cause, economic, ecological or social (including human health) harms. Indeed, most insect pests of agriculture and forestry are non-native and efforts to control them dominate applied entomology (Liebhold and Griffin, 2016). The most recent update to the National Road Map for Integrated Pest Management (IPM) places a special emphasis on invasive species (OPMP, 2018).

Previous experiences with insect invasions helped to shape modern awareness of the challenges posed by invasive species. For example, invasion by the North American grape phylloxera, *Viteus vitifoliae*, devastated European vineyards and inspired European nations to enact some of the first quarantine regulations globally to prevent the introduction of insect pests. Further, invasions

http://dx.doi.org/10.19103/AS.2019.0047.06
Published by Burleigh Dodds Science Publishing, 2020.

Chapter taken from: Kogan, M. and Heinrichs, E. A. (ed.), *Integrated management of insect pests: Current and future developments*, Burleigh Dodds Science Publishing, Cambridge, UK, 2020, (ISBN: 978 1 78676 260 3; www.bdspublishing.com)

of North America in the late nineteenth century by cottony cushion scale, *Icerya purchasi*, and red scale, *Aonidiella aurantii*, from Australia; the San Jose scale, *Quadraspidiotus perniciosus*, from China; and the gypsy moth, *Lymantria dispar*, and brown tail moth, *Euproctis chrysorrhoea*, from Europe illustrated the striking effects invasive insects can have on trees in forests and orchards. These events helped to prompt some of the first quarantine regulations in the United States, in particular the Plant Quarantine Act of 1912. During this time, the United States was transitioning from a permissive, arguably enthusiastic, perspective towards plant introductions to one that was more cautious, to exclude unwanted pests.

The rationale for greater vigilance to prevent the movement of invasive species around the globe is clear. As world trade and human transport continue to grow and diversify, new species will continue to be transported to new habitats. For example, if previous trends hold, approximately five new insect species can be expected in North American forests every 2 years with a 'high impact' species arriving approximately every 3 years (Aukema et al., 2010). High impact species in agriculture and forestry disrupt traditional production practices and typically dictate substantially greater inputs and associated costs to maintain productivity. Global economic losses from invasive insects vastly exceed $70 billion annually (Bradshaw et al., 2016). Relatively recent invasions by spotted wing drosophila, *Drosophila suzukii*, and brown marmorated stink bug, *Halyomorpha halys*, in many parts of the world exemplify the severe economic consequences that invasive species inflict (Asplen et al., 2015; Mazzi et al., 2017; Leskey and Nielsen, 2018). Fortunately, such outcomes are the exception, not the norm. Only about 1 of every 1000 accidentally introduced species becomes a severe pest (Schwarzländer et al., 2018). Thus, biological invasions are characterized as a low-probability, high-consequence event.

The uncertainties associated with biological invasions create numerous challenges for IPM practitioners. Effective IPM demands extensive information, such as the ecology and impact of the pest complex, costs and effectiveness of various management alternatives and response of the valued resource to management. With each arrival of new, potential pest species, managers frequently confront a dearth of knowledge about such factors and are forced to adapt and apply general understanding of taxonomically or functionally similar pests and their responses to management alternatives. Researchers regularly respond with a trove of studies to address these information gaps and support decision-making, often at the scale of an individual farm or forest stand.

The purpose of this chapter is to highlight common elements of invasive species ecology and review how broad management options change as invasions progress. As the number of invasive species increase, some scientists and decision-makers question if species-by-species research and farm-by-farm management are the optimum ways to address the problem. Here, the authors address two more fundamental questions: can the various approaches to invasive species management still be considered IPM, and why does it matter if they can or cannot? Lastly, the authors acknowledge that the management of invasive species presents as a 'wicked problem', a type of problem that sociologists recognize as being particularly difficult to solve because appropriate solutions are sensitive to context. The effectiveness of future invasive species management will depend on cooperative, transdisciplinary efforts to tame the problem.

2 Ecology of invasive species

Populations of successful invasive species progress through four overlapping stages: entry (arrival), establishment, spread and impact (Fig. 1). Entry occurs when individuals of a species are transported beyond historical biogeographic constraints to their distribution and arrive in an area where conspecifics do not occur. These translocations are typically associated with intentional or accidental movement by humans, often as a consequence of international trade. Commercial importation of live plants, for example, is a significant pathway for the inadvertent movement of sap-feeding and foliage-feeding forest pests (Liebhold et al., 2012; Smith et al., 2007). In the case of accidental introductions, the idiosyncrasies of the pathways by which new species might arrive affect the likelihood of establishment by changing propagule pressure, that is the number, condition and location of individuals that ultimately escape

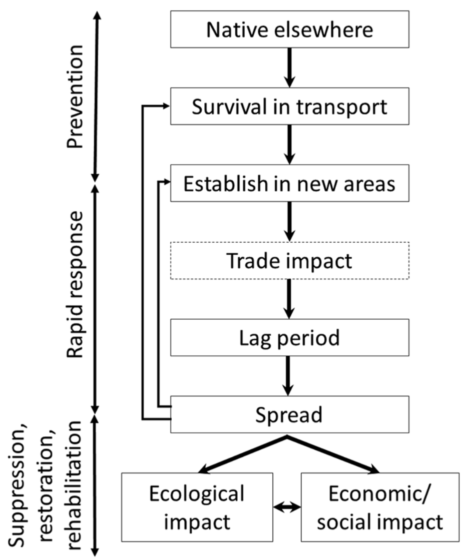

Figure 1 Conceptualized stages of the invasion process and their impact on management alternatives for invasive species. Source: modified from Sakai et al. (2001).

into the environment (Simberloff, 2009a). Leung et al. (2012) conceptualize the problem as having three parts: uptake at the origin, population growth during transport and release into the environment. These components may vary widely by source, destination, vector, volume and timing, thereby highlighting the complexity of forecasting the precise time, location and identity of a new pest incursion.

For establishment to occur, the newly arrived individuals must initially survive and ultimately maintain a new population through local reproduction. While a single gravid female could theoretically found a population, it is unlikely. Small populations are particularly vulnerable to extinction events through environmental stochasticity (variation in mortality and reproduction from unpredictable environmental fluctuations), demographic stochasticity (random variation in birth and death rates from 'sampling'), Allee effects and genetic bottlenecks (Sakai et al., 2001; Liebhold and Tobin, 2008). Allee effects describe unique processes, such as challenges in mate finding, overcoming host plant resistance or succumbing to inbreeding depression. These processes disproportionately affect births or deaths of small populations (Blackburn et al., 2015). As a consequence, an unstable equilibrium density exists below which populations go extinct and above which populations will increase to the carrying capacity of the site (Liebhold and Tobin, 2008).

As propagule pressure increases, so does the probability of establishment (Leung et al., 2012). By definition, the intrinsic rate of population increase, r (a measure of the difference in per capita birth and death rates), must be greater than or equal to zero for establishment to occur. The number of individuals in the invading population initially changes through time, t, according to $N_t = N_0e^{rt}$, if reproduction occurs continuously, or $N_t = N_0\lambda^t$, if reproduction occurs in discrete events. A balance of endogenous and exogenous factors affect the intrinsic rate of population increase and abundance of the population across space and time (Turchin, 1999). Endogenous factors, such as host-resource availability or parasitism rates, are affected by population densities of the invading species. Exogenous factors, such as temperature and moisture, are unaffected by population densities. Climate suitability plays a particularly important role in the establishment of alien plants, pathogens and arthropods. Climate suitability for an invading species is often inferred from conditions where the species has been reported or knowledge of the effects of temperature or moisture on the invaders' demography (e.g. Peterson, 2003; Venette, 2017). Phenotypic plasticity to environmental conditions can complicate the reliability of such forecasts (e.g. Sultan, 2001).

As the population of an invasive species grows, individuals require physical space, so spread inherently follows establishment. Spread is a well-studied stage of the invasion process. Numerous texts and reviews exist to describe biological processes and mathematical models of spread (Shigesada and

Kawasaki, 1997; Lockwood et al., 2013; Lei et al., 2014; Fahrner and Aukema, 2018). In general, spread rate is affected by population growth rate and the dispersal kernel, the probability that individuals will move a particular distance from a source. When the distance and direction of movement are random, the dispersal kernel can be represented by a normal (Gaussian) statistical distribution. The asymptotic rate of spread is mathematically represented by $2\sqrt{rD}$, where D is the squared mean displacement of individuals per unit of time and r is as defined previously. This model provides good approximations of the spread rates during the invasions of the United States by cereal leaf beetle, *Oulema melanopus*, and European gypsy moth, *Lymantria dispar dispar* (Andow et al., 1990).

The simplifying assumptions of certain spread models frequently do not apply, especially when dispersal is directional, when long-distance movement occurs more often than predicted by a normal distribution or when a species is subject to anthropocentric movement (Lockwood et al., 2013). Stratified dispersal models characterize the joint effects of long-distance movement by people and short-distance movement through natural process collectively resulting in an accelerating rate of spread. Identifying genetic factors that govern establishment and spread of invasive species remains an active area of research (Dybdahl and Kane, 2005; Chown et al., 2007; Lee and Gelembiuk, 2008; Hoffmann and Sgrò, 2011).

A lag phase, also called a latent phase, frequently occurs after a new population establishes but before it begins to spread. During this time, the area occupied by the invading species remains relatively constant. Whether this dynamic reflects limits to awareness and detection of a population, or is a reflection of the inherent ecology of invasions remains controversial, even after more than 20 years of study. Lags could reflect the number and positioning of sub-populations, a period of selection for locally adapted genotypes, a period of accumulation of additional genetic diversity (through multiple entry events) or transitions from suboptimal to optimal weather conditions (Wagner et al., 2017). For example, the elongate hemlock scale, *Fiorinia externa*, remained localized near New York City for more than 60 years before it began a northward range expansion after local adaptation to winter temperatures (Preisser et al., 2008). Despite recognition that lags exist, forecasting the duration of the lag period may be unfeasible (Coutts et al., 2018).

Invasive species impact is measured as adverse changes to the economy, environment, society or human health and transcends several stages of the invasion process. It conceptually follows spread as a reflection of the additional time that may be required for populations to build to damaging levels (Sofaer et al., 2018). In this context, impact reflects the geographic range occupied by the invading species, the density of the species within the range and an estimate of damage per individual (Parker et al., 1999), akin to crop loss models. However, impact does not always have a simple relationship to density (Sofaer et al., 2018), and the invasion of certain 'high risk' pests may trigger phytosanitary restrictions on trade, such that the detection of a single individual would have significant economic consequences. For example, detection of an individual of several key fruit fly species (Tephritidae) could trigger trade restrictions in an effort to prevent future spread to other countries. As such, impact may occur concurrently with entry and establishment. Ultimately, impact is a social construct, a reflection of perceived and realized value loss (or gain) from invasion (Tassin et al., 2017).

Studies of impacts from invasive species have been criticized for their brevity and lack of a temporal context (Strayer et al., 2006). Impacts are often measured shortly after the species arrives, before the new species and invaded community have had much opportunity to evolve and respond. Indeed, changes in the behaviour of the invading species, changes to the genetics of the invader and genetic and non-genetic changes to members of the affected community might be expected, all potentially contributing to boom-bust dynamics (Strayer et al., 2017). For instance, invasions of aphids frequently progress through periods of outbreak, attenuation and endemism, with the transition away from outbreak being driven by responses of resident aphidophagous guilds (Colares et al., 2015). In some instances where the sugarcane aphid, *Melanaphis sacchari*, invaded, resistant sorghum varieties and responses of natural enemies interacted to lessen the impact of the pest (Brewer et al., 2017).

Amidst the transition from establishment to impact lies integration, wherein an invasive species and the residents of invaded communities experience selection and adapt to each other (Mooney and Cleland, 2001). This process is ongoing, so its 'position' in the course of invasion is debatable. Genetic adaptation is increasingly shown among invading populations, including instances of rapid evolutionary change (Reznick and Ghalambor, 2001; Dlogosch and Parker, 2008; Urbanski et al., 2012). The ability to rapidly adapt to extreme biotic stressors has been suggested as particularly prevalent among invasive species that successfully spread (Lee, 2002; Butin et al., 2005; Whitney and Gabler, 2008). Evidence varies about the relative importance of phenotypic plasticity or genetic adaptation for biological invasions. However, given that phenotypic plasticity can produce conditions that result in an adaptive genetic response and that phenotypic plasticity is itself under genetic control, a mix of mechanisms is possible (Via et al., 1995; Sexton et al., 2002; Ghalambor et al., 2007; Richards et al., 2006).

3 Invasive species management strategies

Broad strategies for invasive species management, that is the intentional manipulation of pest densities or distributions, generally correspond to the phases of invasion (Fig. 1) and typically fall into one of four categories: prevention; rapid response, especially eradication; suppression; or restoration and rehabilitation (Table 1). Flint and van den Bosch (1981) recognized several elements of an effective pest management programme including a clear statement of management goals, recognition of who is responsible for action and means to determine the effectiveness of management activities. Below, we discuss these three elements within the context of each broad invasive species management strategy. In addition, we briefly discuss examples of current research to improve each strategy.

3.1 Prevention

Prevention strategies are appropriate when species of concern do not occur within an endangered area and the goal is to maintain that absence (Table 1). Prevention describes the series of pest/pathway risk assessments, biosecurity regulations, pre-border treatments, import inspections and disinfestation technologies to exclude threatening pests. Pest/pathway risk assessments are useful to identify which species are most likely to invade, where they are most likely to occur and the potential magnitude of impact should they invade. These assessments help to focus prevention efforts on the highest-risk species. A number of classification schemes have been proposed to distinguish high-risk species or pathways from those that are low risk or need more information (Leung et al., 2012). Such schemes often are based on life history traits and/or a species invasion history elsewhere (Stohlgren and Schnase, 2006; Hayes and Barry, 2008), while pathway models typically are flow- or agent-based with or without stochasticity (Douma et al., 2016). Of the management options for invasive species, prevention is the most cost-effective (Lodge et al., 2006; Lovett et al., 2016).

Because prevention efforts frequently affect the movement of goods or people across geopolitical borders, national governments typically have primary responsibility for implementation (Hulme, 2009). Those efforts can be supported through transnational cooperation, particularly in the development of systems approaches to mitigate the risk of pest introduction through commodity imports (Follett and Neven, 2006). This form of risk management can require foreign producers to use stringent practices to lower densities of threatening pests, foreign packagers or processors to remove infested fruits or apply disinfestation treatments and foreign inspectors to certify all pest management activities are meeting standards. Nations can only act unilaterally to reduce risks from invasive species when such actions are well supported by scientific evidence.

The effectiveness of prevention is difficult to measure. The increasing number of species invasions provides evidence that prevention efforts are not

Table 1 Relationship between management strategies for invasive species and broad elements of an effective integrated pest management programme

Management strategy	Definition	Goal	Responsible party(ies)	Assessment method(s)
Prevention	*The series of pest/pathway risk assessments, biosecurity regulations, pre-border treatments, import inspections and disinfestation technologies to prevent pest incursion*	Exclude unwanted organisms from a given geopolitical area	• National and transnational agencies • Foreign producers, processors and inspectors	Commodity inspection; statistically based infestation and approach rates (e.g. AQIM[a])
Rapid response	*Approaches that can be implemented quickly, often without much background information. Damage from future spread may outweigh risk of treatment non-target effects*	Return the density of a high-threat species to zero (*eradication*) or limit the spatial extent of damages (*containment*)	• National, state and tribal governments • Universities • NGOs[b] • Diverse stakeholders from general public	Sampling methods (e.g. pheromone traps) that detect population levels equal to, or lower than, those vulnerable to Allee effects
Suppression	*Activities, typically occurring in a localized area, that decrease a pest population to protect a valued entity. Based on cost/benefit analysis of treatment*	Reduce the density of unwanted species to, or below, a desired threshold level (e.g. ET, EIL[c])	• Landowner or manager of area of interest (private, public, tribal, NGO) • Universities	Post-treatment monitoring of pest densities, concomitant with measuring desired attribute (e.g. yield)
Restoration and rehabilitation	*Long-term activities that return an ecosystem to pre-invasion conditions. Typically begin at small spatial scales*	Return system to pre-invasion conditions via restoring valued species or ecological processes	• Landowner or manager of area of interest (private, public, tribal, NGO) • Universities • Natural resource agencies	Variable; often divided among measures assessing specific, intermediate goals

[a] Agricultural Quarantine Inspection Monitoring.
[b] Non-governmental organization.
[c] Economic threshold, economic injury level.

completely effective. However, the number of new invasions has not increased as quickly as the volume of foreign trade over time, indirect evidence that prevention efforts are providing benefits. Disagreements over the effectiveness of prevention are fuelled primarily by inferences that can be drawn from commodity inspections (Caley et al., 2015). Most commodity inspections are intended simply to detect threatening species. The inspections do not conform to any particular statistical design and often stop when the first actionable pest is detected. Without a statistical design, it is impossible to estimate approach rates effectively.

Approach rates quantify the number of live insects that enter an area of concern per unit of trade. In the United States, a small number of shipments are subjected to Agricultural Quarantine Inspection Monitoring (AQIM), a statistically based sampling protocol (Venette et al., 2002). Data from AQIM were instrumental to demonstrate that infestation rates of wood packaging materials coming to the United States declined by 36–52% after the implementation of International Standard for Phytosanitary Management No 15 (ISPM15), an improvement that fell short of expectations (Haack et al., 2014).

Efforts to improve the effectiveness of prevention are generally species- or pathway-centric, reflecting a subtle tension in strategic goals. Species-centric research presupposes significant differences in the biology and manageability of possible invaders. From this perspective, differences need to be understood and addressed before prevention approaches are developed; identification of pathways is important, but only insofar as to manage avenues for the entry of high-risk pests (Saccaggi et al., 2016). For example, trait-based screening approaches have been proposed to distinguish invasive from non-invasive insects (Emiljanowicz et al., 2017). Similarly, a number of analytical approaches have been developed to assess whether the climate in a threatened area might be suitable for the invasive species (Venette, 2017). Requisite doses of heat, cold, fumigants or radiation as quarantine treatments to disinfest commodities of high-risk pests remain under investigation (Follett and Neven, 2006). In contrast, the pathway-centric approach assumes that the number and diversity of invasive species associated with a conveyance or commodity at any point in time remains difficult to know and a separate prevention plan for each species is impractical (Kenis et al., 2007). The identification of recalcitrant species provides confidence that other, sensitive species will succumb during a treatment schedule.

3.2 Rapid response

Should an incursion of a high-risk species occur, rapid response is appropriate, either through eradication or containment. In this case, the goal is to return the density of a high-threat species to zero or to limit the spatial extent of damages

(Table 1). The concentrated application of labour-intensive, broad-spectrum methods (so-called scorched-earth methods) may be appropriate to eradicate a nascent population (Simberloff, 2009b). Such approaches do not require significant background information, so they can be implemented quickly. The argument follows that while non-target effects from the treatments may be severe, they will be spatially limited and substantially less than the future damages caused by the invasive species if it were allowed to spread.

Eradication may be achieved through various methods, such as area-wide applications of insecticides, pheromone disruption, sterile insect technique or other methods of genetic control. Eradication has been attempted more often for Diptera, Coleoptera and Lepidoptera compared to Hymenoptera and Hemiptera, and ~59% of reported eradication attempts were considered successful (Tobin et al., 2014). The goal of containment is to restrict the distribution of an invading species to a particular area, both to protect resources in uninvaded areas and to preserve options for future eradication. For example, bait stations with insecticides at colony margins slowed the spread of Argentine ants, *Linepithema humile*, in Hawaii (Krushelnycky et al., 2004).

For the eradication to be successful, every individual need not be killed directly. Recent evidence suggests that if the population densities can be reduced to below an Allee threshold, then density-dependent processes will drive a population to extinction (Liebhold and Tobin, 2008). For example, the likelihood that gypsy moth females will find a mate increases with population density, so reducing the density of reproductively successful males can have an exaggerated effect on future population growth. The likelihood of successful eradication increases if response occurs shortly after entry, if sensitive detection tools (e.g. pheromone baited traps) exist and if target-specific control tools are available (Pluess et al., 2012; Tobin et al., 2014).

Eradication or containment typically falls to national governmental bodies with authorities to work across political borders, often in cooperation with tribal, subnational or foreign governments. For example, the US Department of Agriculture (USDA) appropriated $17.5 million in 2018 to contain, ostensibly eradicate, spotted lanternfly, *Lycorma delicatula*, in the northeastern United States (Merlin, 2018). This effort involves particularly close collaboration with the Pennsylvania Department of Agriculture, though consultation and collaboration with neighbouring state agencies is ongoing. Pennsylvania State University and other academic institutions in the region provide information to support management decisions. The management campaign includes regulations, surveys, egg mass removals, host plant eliminations, herbicide treatments and insecticide applications. Quarantine regulations prohibit the movement of potentially infested materials to limit the potential for spread to uninfested areas.

Determining whether an attempted eradication has been successful can be challenging. The Food and Agricultural Organization indicates that the eradication process follows three primary steps: surveillance to determine the spatial distribution of a pest, containment procedures to prevent spread and treatment to reduce population densities of the pest (FAO, 2017a). Similarly, an area can be declared pest free when general surveillance or targeted surveys suggest a pest is not present, when phytosanitary measures are taken to exclude a pest and verification systems are put into place to ensure the pest remains absent (FAO, 2017b). No international agreement exists about when a pest population can be considered 'eradicated', but criteria for success need to be specified before an eradication attempt (FAO, 2017a).

Small populations can be difficult to detect without a significant survey effort, and zero trap capture does not equate to the absence of a pest. Therefore, a number of operational definitions exist to determine when a pest might be considered eradicated, such as negative trap data for a time equivalent to three or more generations of the insect. For example, eradication of Queensland fruit fly, *Bactrocera tryoni*, in southeastern Australia can be declared following treatment if no more flies are caught after three generations plus 28 days from the last capture (Clift and Meats, 2002).

Successful eradication or containment of invasive pests often requires more than technical solutions. Efforts to engage people (e.g. high-level managers, the populous within a treatment area or other stakeholder groups) can be critical to programmatic success (Moon et al., 2015). Invasions frequently start in populated areas (Paap et al., 2017), so treatments may occur in or near areas where people live, work or recreate (Crowley et al., 2017). In some cases, perceptions of high costs, undesirable impacts and limited benefits undermine eradication efforts (Crowley et al., 2017; Liebhold and Kean, 2019).

In general, non-scientists accept uncertainty less than scientists when weighing policy options for invasive species management. In fact, Garcia-Llorente et al. (2011) found that a heterogeneous stakeholder group was willing to pay nearly 1.5 times more for eradication than prevention, while the scientific community generally concludes that prevention is a better investment (e.g. Leung et al., 2002). Perceived difficulties in forecasting/preventing invasions and a desire to respond to active invasions drove the stakeholders' preference. Sense of place, interest in nature and knowledge of invasive species engender support for action in general. Public engagement requires more than unidirectional communication (e.g. from technical experts to lay public) and could benefit from co-productive efforts in which non-experts play a substantive role in achieving programmatic goals, though not all members of the public should be expected to participate equally (Moon et al., 2015).

Technical research in support of eradication largely involves new methods of detection and treatment. Careful inspection of plants in foreign arboreta for pests and diseases might provide a natural screening tool to identify future invasive species threats (Britton et al., 2010; Kenis et al., 2018). Significant research continues with the identification and development of semiochemicals and other attractants to improve the sensitivity and specificity of trapping efforts (Seybold et al., 2018; Hayes et al., 2016; Leskey et al., 2015; Sarles et al., 2018) and to deploy these compounds for eradication (El-Sayed et al., 2009; Lance et al., 2016). Major advances are being made with genetic technologies, such as the sterile insect technique, gene drives, sex-ratio biasing and artificial speciation to eradicate invasive insects (Harvey-Samuel et al., 2017; Maselko et al., 2017). For example, the use of the sterile insect technique, mating disruption and transgenic cotton producing an endotoxin from soil bacterium *Bacillus thuringiensis* in the United States led to the successful eradication of pink bollworm, *Pectinophora gossypiella*, officially declared on 19 October 2018 (Hearden, 2018). These genetic approaches offer prospects for efficient area-wide control, but some approaches raise significant concerns over ecological impacts, particularly if modified individuals are released into the pest's native range (Dhole et al., 2018).

3.3 Suppression

The goal of suppression is to protect the value of a resource by reducing the density of an invading insect, not necessarily eliminating it (Table 1). Within a traditional IPM context, the target suppression level reflects the balance between the costs and benefits of a treatment. Calculation of an economic injury level (EIL) identifies the pest density at which economic benefits from a treatment match its costs, and an economic threshold (ET) provides a benchmark density at which action should be taken to stop a growing pest population from reaching the EIL (Higley and Peterson, 2009). EIL and ET concepts are reviewed extensively elsewhere in this volume. However, estimation of both EILs and ETs requires extensive knowledge of pest population dynamics, per capita pest impacts, treatment efficacy, treatment costs and commodity pricing as well as the effects of weather, natural enemies, crop phenology and crop variety among other factors. Such information is commonly unavailable at the time a new pest arrives. In fact, the ET for soybean aphid, *Aphis glycines,* (~250 aphids per plant) was not published until 7 years after the aphid was first confirmed in North America (Ragsdale et al., 2007).

Action thresholds (ATs) also indicate a pest density or range of densities when treatment is appropriate, but ATs have no formal relationship to the EIL (Nault and Shelton, 2010). ATs are determined through expert judgement and are influenced by knowledge of insect-host interactions (Hines and Hutchison, 2001). For example, ATs for invasive crane flies, *Tipula oleracea* and *T. paludosa*, differ in vigorous turf (160–270 larvae/m^2), less-vigorous turf (100–140 larvae/m^2) or native rangeland (100 larvae/m^2) (Petersen et al., 2011).

Suppression activities typically operate on a single farm or forest-stand scale with infrequent consideration given to the impact on neighbouring farms/stands (note: the opposite is true for eradication or containment). As such, management decisions typically fall to the land owner or manager (private, public or non-governmental organization). Notable exceptions do occur, as with the area-wide suppression of highly mobile pests such as the non-native codling moth *Cydia pomonella* (Witzgall et al., 2008). Suppression of invasive insects relies on physical, chemical, cultural and biological approaches. Physical methods can be particularly useful when populations are small or spatially confined. For example, removal and destruction (i.e. chipping) of infested trees has been a common, moderately effective approach for the early management of emerald ash borer, *Agrilus planipennis* (Fahrner et al., 2017). Crop destruction was also used to control small populations of melon thrips, *Thrips palmi*, in the Netherlands (Cannon et al., 2007)

When physical removals are no longer practical, particularly during outbreak conditions, managers may choose to pursue insecticides or other chemical control methods. In some cases, the arrival of a new pest into a production system may disrupt IPM programmes for other pests of the same system (OPMP, 2018). For example, the invasion of Europe by the tomato leafminer, *Tuta absoluta*, necessitated intensive insecticide use in tomatoes, a preferred host for this species, and interfered with IPM programmes for other tomato pests (Biondi et al., 2018). Frequently, attention also turns to the impact of resident, generalist natural enemies on an invading pest population. For severe pests, the pursuit of classical biological control, initially driven by federal and university scientists working in close collaboration with scientists in areas where the invasive species is native, may follow (Liebhold et al., 2017). Stringent screening protocols and regulatory reviews exist to ensure that any candidate biological control agent poses little threat to non-target species before the agent is released (Heimpel and Mills, 2017). Breeding and deployment of host plants with resistance to an invasive pest are complementary, long-term solutions (Showalter et al., 2018).

The effectiveness of suppression depends on the proper timing and application of treatments but ultimately must be demonstrated through post-treatment monitoring. However, the focus of monitoring to document changes is not always intuitive. Comparisons of pest densities before and after treatment or in treated and untreated areas are common, but such comparisons are not especially useful if the relationship between pest density and the environmental value of interest is complex or not understood (Prior et al., 2018). More meaningful assessments of effectiveness are obtained if changes in desired attribute (e.g. damage or yields) are measured concomitantly. For example, while it was possible to measure parasitism rates of emerald ash borer from released parasitoids (Duan et al., 2012, 2013, 2015; Abell et al., 2014), associated benefits to mature trees were inconclusive, though benefits were observed for seedlings and saplings (Abell et al., 2014).

Numerous, diverse lines of research, often directed at specific pests, are ongoing to improve suppression efforts. Universities and industry play critical roles in conceptualizing and evaluating new technologies and tactics for IPM. The National Roadmap for IPM recognizes the significance of research for IPM, particularly understanding the basic biology of new pests and their hosts and developing new technologies and techniques for pest management; these advancements need to be fully integrated into decision-support frameworks (OPMP, 2018). For example, after the invasion of Europe by spotted wing drosophila, a community of researchers proposed several studies that would be useful for the development of an IPM programme (Cini et al., 2012). Studies were broadly classified into monitoring (e.g. new semiochemicals, traps and trapping designs), modelling (e.g. high-resolution spatial and temporal models, degree-day/phenological models and insect-host interactions) and management (e.g. prevention, insecticides, mating disruption and biological control). Lists of such information needs are common following pest invasions (Dix and Britton, 2010). More effort is needed generally to prioritize research needs systematically and demonstrate how research findings have improved management.

3.4 Restoration and rehabilitation

The goal of restoration and rehabilitation with respect to invasive species is to return valued species or ecological processes to a system, typically a forest, grassland or wetland (Table 1). In some cases, the ultimate goal might be to return elements of an ecosystem to a pre-invasion condition. In other cases, the restoration of a few iconic individuals of highly valued species might suffice. Management to suppress the density of a particular invasive species may be a component, but is not required. For example, invasive plants may play several constructive roles in the restoration of native plant species (D'Antonio and Meyerson, 2002).

Restoration typically begins at relatively small spatial scales with a goal of restoration over broader areas in mind. Much like suppression, decisions to undertake restoration and rehabilitation typically come from a landowner or manager, often in close consultation with relevant researchers, natural resource management agencies or non-profit governmental organizations. Typically, when managing to minimize the effects of invading insects, the choices involve planting non-host species to preserve ecological functions provided by hosts of an invading species or to deploy resistant or tolerant host genotypes (Liebhold et al., 2017; Muzika, 2017). For example, to preserve some ecological functions provided by eastern hemlock in the eastern United States lost from the activity of hemlock woolly adelgid, *Adelges tsugae*, Vose et al. (2013) proposed planting of non-native Chinese hemlock or native eastern white pine to replace lost tree cover.

Evaluating the effectiveness of rehabilitation and restoration can be challenging. For the breeding and deployment of resistant trees in support of restoration efforts, Sniezko and Koch (2017) recognize four elements – research, tree improvement, planting and sustained commitment – each having a unique measure of success. While the ultimate goal might be a return of a valued species to previous densities, intermediate goals must often suffice (e.g. survival of trees under insect/disease pressure for multiple years in multiple locations). Beech trees with resistance to beech bark scale, *Cryptococcus fagisuga*, provide an example of successful selection and breeding for resistance to a non-native insect (Sniezko and Koch, 2017). However, more work remains to deploy resistant trees in stands affected by beech bark disease. Such breeding efforts are important but relatively rare for forest species.

Research to improve rehabilitation is far reaching (Dumroese et al., 2015). Efforts have explored the feasibility of developing transgenic trees that could produce toxins from other species. Transgenic trees might be useful to control gypsy moth (Ding et al., 2017; Robison et al., 1994) or emerald ash borer; however, concern with escape of transgenes into the wild have slowed development (Meilan, 2006). Other research has focussed on identifying natural sources of resistance to other insect pests, such as emerald ash borer (Koch et al., 2015). Alternative research is prioritizing sites for restoration efforts to begin, particularly in or near areas where remnant populations of the native species might exist (Morin et al., 2018). Similarly, studies are evaluating silvicultural treatments, such as selective thinning, to create conditions that might be more suitable for restoration (Looney et al., 2015; Brantley et al., 2017).

Significant thought has also gone into management for resistance and resilience. Resistance describes the capacity of an ecosystem to preclude change, whereas resilience describes the potential of a system to return to initial conditions after a perturbation, such as the arrival of a new species. Ideally, general management approaches, not efforts to manage a single species, could create resistant and resilient systems. For example, increasing plant diversity, encouraging natural enemies, connecting patches of native vegetation and emphasizing ecological function (not just species identity) could be essential for building resistance and resilience (Fisher et al., 2006; Larson et al., 2011).

Management for high-level ecosystem properties faces some fundamental challenges. While factors that contribute to resistance and resilience are known, currently no approach exists to objectively measure resistance or resilience before perturbation (Donohue et al., 2016). While systems may seem resistant or resilient to one invasive species, it is unclear if these properties apply to other invasive pests. Further, management to improve resistance or resilience to one group of invasive species might compromise resilience to another.

4 Relationship of invasive species management to IPM

Invasive species management strategies vary considerably with the stage of invasion. Can each strategy still be considered a form of IPM? The answer depends on the definition of IPM that one applies. The semantic and conceptual origins of IPM have been reviewed elsewhere (Bajwa and Kogan, 2002; Ehler, 2006; Kogan, 1998; Smith et al., 1976), and these reviews highlight the variability and myriad foci associated with the term. Some contend that IPM must involve two or more methods of control; anything less does not qualify as 'integrated' (Stenberg, 2017), but see also Kogan (1998). Some IPM management programmes rely on the discriminate use of one or more chemical controls when field scouting and threshold recommendations dictate. From this perspective, most strategies for invasive species management would qualify as IPM and would not be fundamentally different from IPM for native pests (Venette and Koch, 2009).

A common tenet during the formalization of IPM concepts has been the need to reduce or eliminate chemical controls. The earliest concerns with an overreliance on insecticides revolved around the development of insecticide resistance. Concomitant concerns with the abundance and activity of natural enemies, to both regulate pest densities and delay resistance development, reaffirmed the need for forms of pest management that did not depend on insecticides. So management plans that only rely on chemical tactics to affect pest densities, even plans that require scouting and thresholds for decision-making, have been considered to be antithetical to IPM (Ehler and Bottrell, 2000).

The current definition posed by the USDA encapsulates many of the values frequently associated with IPM: '... a sustainable, science-based, decision-making process that combines biological, cultural, physical and chemical tools to identify, manage and reduce risk from pests and pest management tools and strategies in a way that minimizes overall economic, health and environmental risks' (OPMP, 2018). This definition sets lofty goals for pest management practitioners, but remains ambiguous about key terms such as 'sustainable' (what is it?), 'science-based' (who decides?), 'reduce' (by how much?) and 'minimize' (when is it achieved?). This aspirational definition highlights the numerous factors that (should) affect pest management decisions, but the lingering linguistic uncertainty will fuel debates over whether particular pest management programmes for invasive species qualify as IPM.

With this broader definition, we can argue for or against prevention and rapid response being forms of IPM. Both strategies are consistent with the broadest goals of reducing risks from invasive pests and management activities. Further, these approaches rely on the integration of available science and tools to achieve this outcome. What is available, though, may be insufficient. Significant uncertainties stemming from a lack of knowledge about an invasive species and chance events during the course of an invasion limit response options and can interfere with IPM development, particularly for prevention and rapid responses. A significant obstacle to IPM during these early stages of invasion is that little or no allowance is made for the presence of moderate- or high-risk pests. A basic philosophy of IPM recognizes that some pest occurrences are acceptable under appropriate circumstances (Flint and van den Bosch, 1981). Once an invasive species has integrated with its invaded environment and demonstrated predictable dynamics, the elements of managing invasive species with IPM during suppression and restoration are nearly identical for established species (Venette and Koch, 2009).

Clear communication and evaluation of when and how IPM may be applied to invasive species extend beyond a call for semantic integrity. The founding principles of IPM remain valued and sought as a model for sustainable and effective management (OPMP, 2018). Even with resident/established species, cementing a uniform definition of IPM is an important challenge for the field (e.g. Ehler, 2006). It allows for accurate assessments of success and implementation. With invasive species, this can be particularly critical. First, invasive species may be amenable to IPM standards only at certain stages of invasion. If IPM is unrealistically applied to and declared for a given species, it may not only result in inappropriate implementation of the control measure, but also ineffective control of the target species. Secondly, invasive species management requires the involvement of numerous agencies and organizations, often coordination across large spatial scales (relative to the more typical field- or regional-level scale of an established species). If a given strategy (e.g. IPM) is stated as the method of choice to mitigate the effects of a new invasive, but that strategy is unable to be evaluated for success, this can severely erode accountability and coordination efforts. Ultimately, this could inhibit effective management.

5 Future trends

Sociologists formally recognize 'wicked problems' as defying simple definition because of their multiple causes and competing solutions (Conklin, 2006; Head, 2008). Such problems include security, poverty and wellness. Management of invasive species may be another case (Woodford et al., 2016). For example, the problem with invasive species, broadly speaking, has been attributed to economic globalization, climate change, phytosanitary failures and public unawareness, among other factors. Wicked problems have a number of common features. They emerge from the interaction of uncertainty, complexity and value divergence (Head, 2008). Each problem is perceived as unique; consequently, perspectives on the nature of the problem are likely to differ among stakeholders, and a common understanding of the problem may not be evident until solutions are proposed (Rittel and Webber, 1973). The number of alternative solutions may be seemingly limitless (Head, 2008). Furthermore, no *a priori*, objective methods exist to determine if a proposed solution is right; rather, solutions can only be considered better or worse than other alternatives (Rittel and Webber, 1973). If a solution is found, it is likely to be considered unique to that case; unfortunately, a stopping rule, a point at which there will be general agreement that the problem has been solved, does not exist (Rittel and Webber, 1973; Head, 2008). Wicked problems can be especially challenging for researchers and managers because stakeholders make no allowances for wrong decisions (Rittel and Webber, 1973).

Research on wicked problems frequently does not progress in an orderly manner from problem to solution. The classic research model maintains that with a thorough understanding of the problem and careful analyses of new or existing information, a solution will become evident and be readily adopted (Fig. 2). In contrast, for wicked problems, certain solutions may seem readily apparent, only to be dismissed as new elements of the problem become apparent (Conklin, 2006). As perceptions of the problem change, previous analyses may seem incomplete or inappropriate (Head, 2008). These complex dynamics make it difficult to know when solutions have been reached and should be implemented with confidence.

A number of approaches exist to 'tame' wicked problems (Conklin, 2006; Head, 2008). We dismiss the options of simply giving up or asserting that the problem has been solved (Conklin, 2006). Problem definition, reflecting

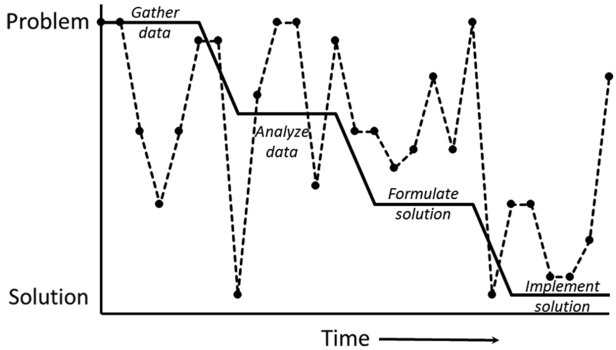

Figure 2 Conceptual diagram of the train of thought from problem to solution for a technical problem (solid line) or a wicked problem (dashed line). Source: modified from Conklin (2006).

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multiple stakeholder perspectives and priorities, is critical. It may be useful to describe the similarities of the problem to other issues that have been solved; the problem definition should include measurable elements, so that progress towards the agreed-upon goals can be measured unambiguously (Conklin, 2006). Any recommendation (e.g. new insecticide, sampling scheme or management plan) would be stronger if it were evaluated relative to the constraints managers and decision-makers face and relative to the likely course of action without the research result. A project manager might be able to reduce the 'relative wickedness' of the problem by arbitrarily focussing on a few possible solutions and forcing discussion about those options; however, the criteria by which the action might be judged should be specified in advance (Conklin, 2006).

Failure to recognize the wickedness of the invasive species problem will create challenges for managers and researchers. Under increasing pressure for accountability on the use of public funds, managers and researchers are likely to face growing cynicism about the effectiveness of recommended plans or the utility of proposed research. Outbreaks of new pests and subsequent public outcry will drive specific, short-term funding increases, but perhaps at the expense of other invasive species work. In a highly competitive fiscal environment, our impression is that some researchers and managers have adopted a 'something-is-better-than-nothing' philosophy about budgets. The philosophy could be true, but without an unambiguous definition of 'better', meaningful measurement of the gain from the investment is impossible. In our opinion, an inability to clearly demonstrate the impact of research or the benefits of IPM for invasive species will adversely affect future funding prospects. Conversely, demonstrating synergisms among managers, researchers and other stakeholders to affect measurable improvements might spark a renaissance in invasive species management.

6 Acknowledgements

A portion of this project was supported by the Minnesota Invasive Terrestrial Plants and Pest Center at the University of Minnesota.

7 Where to look for further information

Three texts are particularly useful for a better understanding of the ecology of invasions:

- Elton, C. S. 1958. *The Ecology of Invasions by Animals and Plants*. Springer, Boston, is often credited as the first academic effort to explain biological invasions as a process common to many species.

- Williamson, M. D. 1996. *Biological Invasions*. Chapman & Hall, New York, presents common rules that govern the course of biological invasions. The text is one of several products from the work of Scientific Committee on Problems of the Environment, a major international effort in the 1980s and early 1990s to understand the factors that make species invasive, where invasions are most likely to occur and how to utilize that information to improve invasive species management.
- Lockwood, J. L., Hoopes, M. F. and Marchetti, M. P. 2013. *Invasion Ecology* (2nd edn.). Wiley-Blackwell, Oxford provides a comprehensive review of advances in ecological theory and their application to invasive species with particularly useful discussions on the spatial ecology of invasions, evolutionary consequences of biological invasions and ecological complexities arising from the interaction of invasive species with climate change.

Centres of expertise on invasive alien insects include:

- Minnesota Invasive Terrestrial Plants and Pests Center, University of Minnesota (https://mitppc.umn.edu/)
- Center for Invasive Species and Ecosystem Health, University of Georgia (https://www.bugwood.org/)
- European Food Safety Authority (https://www.efsa.europa.eu/en/topics/topic/invasive-alien-species)
- CSIRO Australia (https://www.csiro.au/en/Research/BF)
- Centre of Excellence for Biosecurity Risk Analysis, The University of Melbourne (https://cebra.unimelb.edu.au/home)
- Centre of Excellence for Invasion Biology, Stellenbosch University (http://academic.sun.ac.za/cib/team_research.asp)
- Forestry and Agricultural Biotechnology Institute, University of Pretoria (https://www.fabinet.up.ac.za/)

Relevant resources for breaking issues on invasive alien species:

- International Standards for Phytosanitary Measures from the International Plant Protection Convention administered by the Food and Agriculture Organization of the United Nations (https://www.ippc.int/en/core-activities/standards-setting/ispms/) describe accepted guidelines and procedures for the management of invasive alien species that may affect international trade.
- The European and Mediterranean Plant Protection Organization (https://www.eppo.int), the US Department of Agriculture Animal and Plant Health Inspection Service Plant Protection and Quarantine (https://www.aphis.u

sda.gov/aphis/ourfocus/planthealth/plant-pest-and-disease-programs) and the CABI Invasive Species Compendium (https://www.cabi.org/isc/) provide useful summaries of the bionomics and management of invasive species.

The US Department of Agriculture, Forest Service makes all research publications, including those on invasive alien insects, publicly available through TreeSearch (https://www.fs.usda.gov/treesearch/).

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