

## Review Article

# Environmental impacts of agricultural pest insects: five case studies reveal overlooked impact mechanisms and specify knowledge gaps

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## Abstract

Invasive species can cause environmental impacts through various mechanisms. Assessing their impact can inform management decisions and illuminate risks to non-invaded areas. Research on the environmental impacts of invasive insects is heavily focused on a few well-known examples, with agricultural pests in particular receiving little attention. We aimed to investigate whether evidence for environmental impacts of insect pests of agriculture may be overlooked. We conducted in-depth literature reviews of three globally relevant insect agricultural pests—*Halymorpha halys*, *Helicoverpa armigera*, and *Spodoptera frugiperda*. For comparison, we reviewed two forest pathogens known for their environmental impacts—*Bursaphelenchus xylophilus* and *Phytophthora ramorum*. We identified many published articles containing evidence of environmental impacts among the three insect agricultural pests that were not captured by existing reviews on invasive insects, with some demonstrating high levels of impact severity. Crucially, a preponderance of the identified articles did not directly address the findings in relation to environmental impacts. As expected, we recorded more conspicuous examples of environmental impacts among the case-study forest pathogens, though we also identified underappreciated impact mechanisms. We further provide evidence that supports the importance of considering management interventions as a key mechanism of non-target environmental impacts. This review raises awareness about the underreported environmental impacts of agricultural insect pests and specifies knowledge gaps that should guide future research.

**Key words:** Biodiversity, EICAT, environmental impacts, insects, pathogens, pesticides



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## Introduction

It is well established that invasive alien species can cause significant changes to biodiversity and the environment (Sandlund et al. 2001; Kenis et al. 2008; Pyšek et al. 2020), with adverse and complex consequences reported from all ecosystems across the world (Sheppard and Vandvik 2023). The frequency of species invasions continues to rise with the increasing globalization of human-mediated pathways such as international trade (Tobin et al. 2014; Seebens et al. 2017; Sheppard and Vandvik 2023). While it is very difficult to predict the impacts of species that have not yet been observed outside their native range, current impacts of species in already invaded areas often provide the best available indication of impacts in newly or more recently invaded regions, as impacts tend to grow over time after invasion (Blackburn et al. 2014; Cameron et al. 2016). A further challenge is to assign a common currency to environmental impacts that derive from a variety of impact

mechanisms (Kenis et al. 2008; Bacher et al. 2018). These mechanisms include, for instance, competition with native species, herbivory, and chemical, physical, or structural impacts on ecosystems (Kenis et al. 2008; Hawkins et al. 2015; IUCN 2020). Mechanisms of impact can be both direct, such as the consumption of native plants, and indirect, such as apparent competition through shared natural enemies with native species (Hawkins et al. 2015; IUCN 2020; Clarke and McGeoch 2023). The indirect and non-target impacts of management approaches are also an important aspect of the environmental consequences of invasive species (McGeoch et al. 2015).

While invasive insects are well known for their agricultural impacts (Diagne et al. 2020), they are underrepresented in the invasion biology literature addressing biodiversity impacts (McGeoch et al. 2015). This is despite crop environments being a known source of spillover for agricultural pests into neighboring natural habitats (Togni et al. 2021) and the fact that environmental impacts themselves can lead to additional economic or socioeconomic consequences (Bacher et al. 2018). A large proportion of the current literature focuses on a few well-known insect taxa. Attention is largely given to eusocial Hymenoptera, such as invasive ants (Hill et al. 2003), and herbivores of trees that impact the ecosystem processes of forests, such as emerald ash borer (*Agrilus planipennis* Fairmaire (Coleoptera, Buprestidae)) (Klooster et al. 2018), due to the impact mechanisms and outcomes associated with such species being direct and conspicuous (Kenis et al. 2008; McGeoch et al. 2015). Consistently reported reasons for knowledge gaps surrounding the environmental impacts of invasive insects include a lack of research interest, public awareness, or perceived magnitude of their environmental threat (Novoa et al. 2017; Evans et al. 2018; Clarke and McGeoch 2023). Additionally, insect pests of socioeconomic importance, like disease-transmitting mosquitoes, are studied in preference to those of potential environmental importance (Kumschick et al. 2015). However, it remains unclear whether the biases and underrepresentation of invasive insects in environmental impact literature represent the actual extent of their impacts or a lack of research effort (Kenis et al. 2008). Existing reviews published on the environmental impacts of invasive insects have collated these conspicuously studied examples and wide-ranging knowledge gaps (Kenis et al. 2008; McGeoch et al. 2015; Cameron et al. 2016; Clarke and McGeoch 2023). However, it is unclear to what extent inconspicuous or implicit examples were considered or whether literature search strategies captured such examples, which could expose overlooked evidence of how invasive insects may exert environmental impacts despite heavy focus on their economic impacts.

Targeting literature searches toward well-known case-study invasive insects may enable scrutiny of a manageable quantity of relevant articles to assess evidence among species that are not known for conspicuous environmental impacts, such as agricultural pests. We reviewed the literature for indications of environmental impacts exerted by three invasive insect agricultural pests: brown marmorated stink bug (*Halyomorpha halys* Stål (Hemiptera, Pentatomidae) (BMSB)), cotton bollworm (*Helicoverpa armigera* Hübner (Lepidoptera, Noctuidae) (CBW)), and fall armyworm (*Spodoptera frugiperda* Smith (Lepidoptera, Noctuidae) (FAW)); and two invasive forest pathogens: *Phytophthora ramorum* Werres (Peronosporales, Peronosporaceae) and pinewood nematode (*Bursaphelenchus xylophilus* Nickle (Aphelenchida, Parasitaphelenchidae) (PWN)). All of these organisms are of worldwide significance with invasion histories on different continents. The agricultural pests

are well known for their economic rather than environmental impacts, whereas the forest pathogens are known for both their environmental and economic impacts (ISSG 2015; Ries and Pagad 2020; Bacher et al. 2025). They are also considered major threats to Europe (Lammers and MacLeod 2007; EU 2009b; Kriticos et al. 2017; EU 2019) and, as such, are included in the European Horizon 2020 project “Plant pest prevention through technology-guided monitoring and site-specific control” (PurPest) as potential targets for the development of chemosensors for use during phytosanitary inspections and in-field detection. By focusing targeted reviews on this range of case-study species, we search for evidence of whether potential environmental impacts of economically important insect agricultural pests may be overlooked and compare the results to those of the well-known environmental impacts of forest pathogens to highlight biases in knowledge. However, any overlooked impact mechanisms uncovered for the forest pathogens will be additionally considered.

We structured our review using the Environmental Impact Classification for Alien Taxa (EICAT) scheme, as it provides a framework to target the assessment of impacts according to their mechanism and severity (Blackburn et al. 2014; Hawkins et al. 2015; IUCN 2020; Kumschick et al. 2020; Volery et al. 2020). EICAT considers environmental impacts as negative effects exerted upon native species, though it does not consider the impact of human interventions for management of invasive species, which we aim to examine as an additional impact mechanism in this review. The related frameworks EICAT+ and Socio-Economic Impact Classification of Alien Taxa (SEICAT) may be used to assess the positive environmental impacts and socioeconomic impacts of invasive species, respectively. However, our review strictly aims to investigate potentially overlooked mechanisms of environmental impact for invasive insects that are economic pests. In doing so, we hope to uncover evidence and specify knowledge gaps to stimulate future research that expands our understanding of the extent to which biological invasions impact biodiversity.

## Methods

### Literature searches on environmental impacts

To structure comprehensive literature searches (O’Dea et al. 2021) with the aim of finding all relevant published studies on the environmental impacts of the five case-study invasive organisms, we used the EICAT framework (Hawkins et al. 2015; IUCN 2020). We also considered published adaptations of this framework for invasive insects (McGeoch et al. 2015) and forest pathogens (Lapin et al. 2021). EICAT defines and categorizes the mechanisms through which invasive species can exert environmental impacts, and we selected and adapted the mechanisms that are relevant to either insect pests of agriculture or forest pathogens to target our literature searches (Table 1). We also considered the environmental impact of pest management interventions as an additional mechanism that was not included in EICAT. For each impact mechanism, and accounting for the ecological niche differences between agricultural insect pests and forest pathogens, a list of relevant search terms was developed. By clearly defining the mechanisms through which the case-study species could exert environmental impacts and designing search terms to find examples of each impact mechanism, we avoided restricting our searches to studies that directly aimed to investigate environmental impacts. This

**Table 1.** EICAT environmental impact mechanisms selected to target literature searches for the environmental impacts of invasive insect herbivores of agriculture and forest pathogens. The definition of each impact mechanism is that provided by IUCN (2020).

Impact mechanism	Definition
<b>Insects</b>	
Herbivory	Herbivory by the alien taxon leads to deleterious impacts on native plant species.
Competition	The alien taxon competes with native taxa for resources (e.g., food, water, space), leading to deleterious impacts on native taxa.
Hybridization	The alien taxon hybridizes with native taxa, leading to deleterious impacts on native taxa.
Interactions with other species	The alien taxon interacts with other taxa (e.g., through pollination, seed dispersal, or habitat modification), facilitating deleterious impacts on native species.
Management*	Management interventions used against the alien taxon lead to deleterious impacts on native taxa.
<b>Pathogens</b>	
Competition	The alien taxon competes with native taxa for resources (e.g., food, water, space), leading to deleterious impacts on native taxa.
Hybridization	The alien taxon hybridizes with native taxa, leading to deleterious impacts on native taxa.
Chemical, physical, or structural impact on ecosystem	The alien taxon causes changes to the chemical, physical, or structural biotope characteristics of the native environment, leading to deleterious impacts on native taxa.
Interactions with other species	The alien taxon interacts with other taxa (e.g., through pollination, seed dispersal, or habitat modification), facilitating deleterious impacts on native species.
Management*	Management interventions used against the alien taxon lead to deleterious impacts on native taxa.

\* Mechanism not included in EICAT.

was necessary considering the hypothesis that environmental impacts of invasive insects are overlooked. These terms were organized into a search string for each impact mechanism, which was used to conduct separate searches for each mechanism and repeated for all five case-study organisms—BMSB, CBW, FAW, *P. ramorum*, and PWN. For all organisms, the full species name and all common names that we were aware of were included in the searches. However, specific names are given to the diseases caused by *P. ramorum* and PWN, and these were additionally included in the searches for these species. Searches were conducted using the Web of Science (Core Collection) platform on 4 April, 18 April, 10 May, 4 June, and 25 June 2024 for CBW, BMSB, FAW, *P. ramorum*, and PWN, respectively. No time limit was applied to the searches, search terms were applied to all searchable fields, and no restrictions on document types or Web of Science indices were imposed. The full search strings can be found in Suppl. material 1: table S1.

To filter the relevant search results (out of a total of 619, 3,078, 3,047, 516, and 929 results for BMSB, CBW, FAW, *P. ramorum*, and PWN, respectively), we first applied broad eligibility criteria for including or excluding studies when screening the titles and abstracts to ensure that all potentially relevant examples received thorough consideration (O’Dea et al. 2021). This broad approach was particularly necessary given the hypothesis that environmental impacts of invasive insects are overlooked. All publications in which the title and abstract contained information potentially relevant to the species and impact mechanism being searched or contained any of the keywords used in the search were recorded. This included articles for which the title and abstract did not directly mention the case-study species but presented a disciplinary and taxonomic scope indicating that relevant information on the species may be provided in the full text. Studies were excluded if the title and abstract summarized taxonomies, methods, or results that clearly indicated irrelevance to the species and impact mechanism being searched; contained the correct search terms but applied them to an irrelevant disciplinary or taxonomic

context; applied the species' common name included in the search to a different species; or were clearly of an irrelevant discipline but appeared in the search results because the acronym of the species' common name used in searches is also used as an acronym for something unrelated.

The full text of each of these was then consulted to confirm whether the information within suggested the likelihood of environmental impacts relevant to the species and impact mechanism in question. Full texts that met one or more of the following criteria were included in the review: presented data indicating environmental impacts related to the species and impact mechanism searched; directly mentioned environmental impacts related to the species and impact mechanism searched; or mentioned the relevant impact mechanism in relation to the species searched without directly stipulating environmental impacts. If an article contained information relevant to more than one impact mechanism for a given organism, considering the inclusion criteria, it was listed individually under as many impact mechanisms as applicable. Review articles were also included, as they may address environmental impacts regardless of whether such impacts were addressed by the cited studies or without citing particular studies. Reviews may also address environmental impacts with reference to primary studies identified in our searches, though they were still considered as articles that independently present these impacts. The relevant publications were further categorized as either "direct," whereby the authors addressed their findings in relation to environmental impacts, or "implicit," whereby the findings suggested environmental impacts that were not explicitly addressed. However, for the management impact mechanism, we only selected publications that could be categorized as "direct," because virtually any human intervention could be considered "implicit" based on the above description, which rendered this designation arbitrary. The full list of publications deemed relevant, and their aforementioned categorizations, are provided in Suppl. material 1: table S2. Available non-peer-reviewed risk assessments for the case-study organisms (Suppl. material 1: table S3) were also consulted as a potential source of relevant publications on environmental impacts, though no articles were uncovered that were not already captured during literature searches. PRISMA flowcharts reporting the number of records for each impact mechanism at each stage of the literature screening process (O'Dea et al. 2021) are provided for each species in Suppl. material 2.

To assess geographic patterns of research effort, we recorded the country to which information on environmental impacts applied for each relevant study. For studies in which this information applied to multiple countries, each country was recorded. However, relevant studies in which information on environmental impacts could not be clearly assigned to a country were recorded as not applicable. This included laboratory-scale and theoretical studies that did not stipulate geographic relevance.

### Impact severity classification

Impacts were classified according to the severity reported in each publication as a result of the impact mechanism previously assigned. This method is also based on EICAT, which takes into account the highest level of biotic organization to be affected (Hawkins et al. 2015; IUCN 2020): Minimal Concern (unlikely to cause deleterious impacts); Minor (impacts do not reduce the population size of native species); Moderate (impacts reduce the population size of native species without



local extinction); Major (reversible local extinction of native species); and Massive (irreversible local extinction of native species). For studies that presented evidence of more than one impact severity, the highest severity was recorded. If insufficient information was available to assign any of these classifications, the example was categorized as Data Deficient. The designation of impact severity rankings strictly followed the criteria provided in EICAT, and Table 2 summarizes how these were applied to the key data sought.

## Environmental impacts of chemical control

To expand the assessment of the environmental impacts of pest management, we considered the potential non-target impacts of chemical pesticides used against the case-study organisms in Europe. For each organism, we selected the European countries where the European and Mediterranean Plant Protection Organization (EPPO) designates it as “present, widespread” (EPPO 2024a, b, c). Since nowhere in Europe has this designation for *P. ramorum* or PWN, we selected the countries where these pathogens are considered to have a “present, restricted distribution” status (EPPO 2024d). We referred to the plant protection product database for each selected country, provided by its respective National Plant Protection Organization, and recorded the active substances registered for use against each case-study organism. However, some countries could not be considered because their plant protection product databases did not exist, could not be accessed, or did not provide adequate taxonomic information regarding the targets of registered products. Because FAW was only recently detected in Europe, it has no pesticides registered for use against it. We therefore considered insecticides that are used effectively against FAW in Brazil or the USA and that are already approved for use in the EU, as listed by Babendreier et al. (2022), even though approval would, in some cases, require label extension for FAW. The final list of countries considered for each pest is provided in Table 3. We used the Pesticide Properties DataBase and Bio-Pesticides DataBase (Lewis et al. 2016) to record the overall ecotoxicity rating (low, moderate, or high) for each pesticide. This rating is based on ecotoxicological data for key indicator species and follows an established standard format that considers the maximum ranking given for birds, earthworms, bees, freshwater fish, and freshwater invertebrates. For further details regarding the methodology

**Table 2.** Description of how the EICAT impact severity ranking criteria were applied to each study included in this review.

Impact severity	Data sought
Data deficient	Methodology and results were assessed for data on the impact mechanism resulting in reductions in the performance of native individuals or the size of native populations, but the data do not allow conclusions to be drawn.
Minimal concern	Methodology and results of laboratory, semi-field, or field-scale studies provide data demonstrating that the impact mechanism is assessed but has no impact on the performance of native individuals or the size of native populations.
Minor	Methodology and results of laboratory, semi-field, or field-scale studies provide data demonstrating that the impact mechanism is assessed and reduces the performance of native individuals but not the size of native populations. This is the maximum impact severity for laboratory and semi-field studies, which do not demonstrate real-world population-level effects.
Moderate	Methodology and results of field-level studies provide data demonstrating that the impact mechanism is assessed and reduces the population size of at least one native species.
Major	Methodology and results of field-level studies provide data demonstrating that the impact mechanism is assessed and results in the local extinction of at least one native species within a wider community, which would be reversible in the absence of the invasive species.
Massive	Methodology and results of field-level studies provide data demonstrating that the impact mechanism is assessed and results in the local extinction of at least one native species within a wider community, which would be irreversible in the absence of the invasive species.

**Table 3.** Countries whose national plant protection product databases were searched for specific active substances approved for use against each case-study pest.

Pest species	Country	Database source
BMSB	Austria	Austrian Federal Office for Food Safety (2024)
	France	ANSES (2024)
	Germany	BVL (2024)
	Italy	Ministry of Health (2024)
	Switzerland	FSVO (2024)
CBW	Greece	Stavarakaki et al. (2024)*
	Portugal	SIFITO (2024)
	Romania	Ministry of Agriculture and Rural Development (2024)
	Spain	Ministry of Agriculture, Fisheries, and Food (2024)
FAW	European Union	Babendreier et al. (2022)
PWN	Portugal	SIFITO (2024)
<i>P. ramorum</i>	Belgium	FPS Public Health, Food Chain Safety and Environment (2024)
	Croatia	Ministry of Agriculture (2024)
	Netherlands	CTGB (2024)
	Slovenia	Ministry of Agriculture, Forestry and Food (2024)

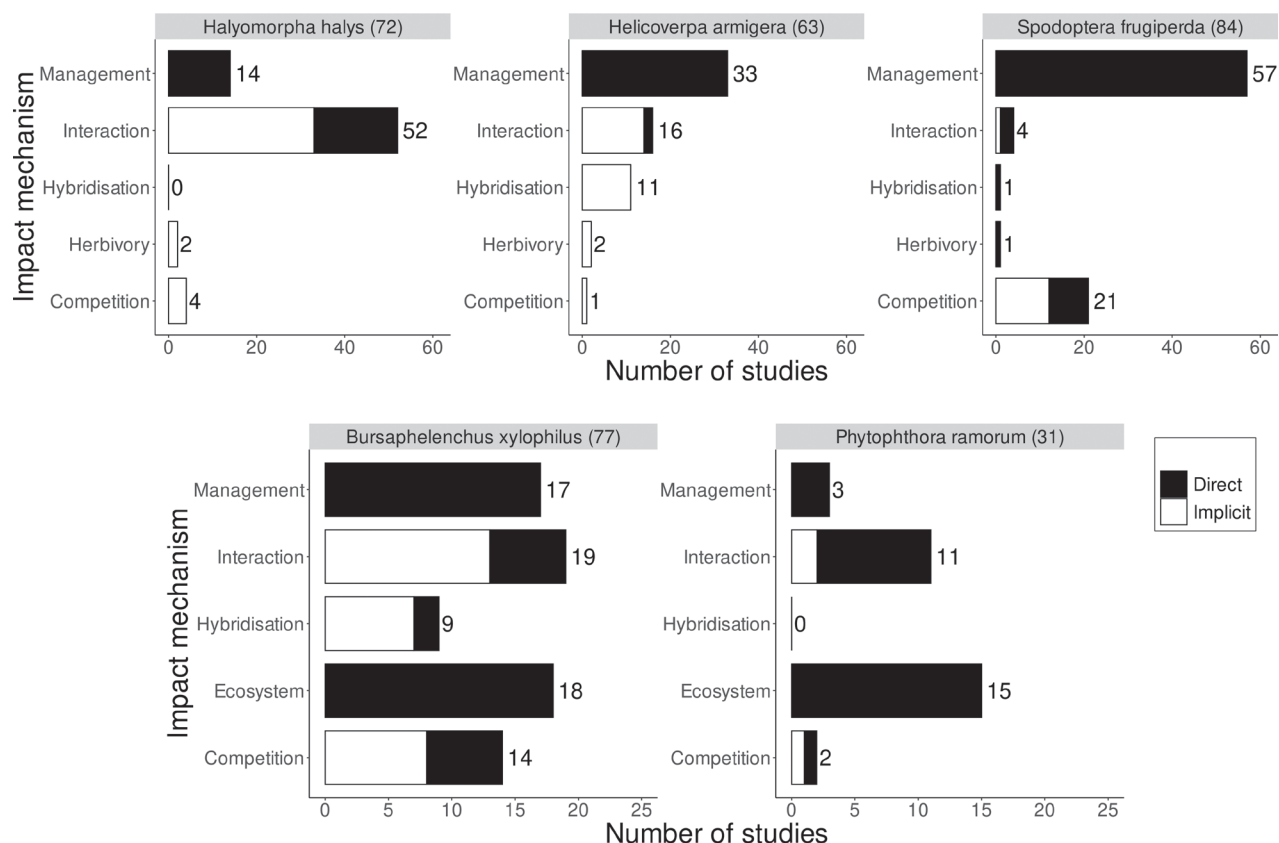
\* This recent publication was used, as it listed the pesticides used specifically against CBW in Greece, whereas the plant protection products database did not contain taxonomic information associated with registered products.

behind these databases, refer to the support documents available on the database website (Lewis et al. 2016). We did not provide an ecotoxicity rating for the single pesticide registered for use against PWN in Portugal (SIFITO 2024) because it is strictly used for trunk injection, and its application is therefore highly localized.

## Results

### Literature searches on environmental impacts

Among all impact mechanisms, we recorded a total of 327 studies in which the findings suggested environmental impacts of the five case-study organisms (Fig. 1). Excluding the management impact mechanism, which is not included in EICAT, 203 studies remained. Publications found for the insect agricultural pests exhibited a notably higher proportion of studies that implicitly indicated environmental impacts compared with those that directly addressed environmental impacts, particularly for CBW. However, significantly more studies were identified under the management impact mechanism for both CBW and FAW. The opposite trend was observed for the two forest pathogens, particularly for *P. ramorum*, for which most of the publications recorded directly addressed environmental impacts. For BMSB, the interaction with other species impact mechanism was well represented, and for FAW, the competition impact mechanism was the most reported. For CBW, both interaction with other species and hybridization yielded a notable number of studies. The ecosystem impacts and interaction with other species mechanisms were the best researched for *P. ramorum*. Relevant studies were captured for all impact mechanisms for PWN. Notably, for both pathogens, all studies found for the ecosystem impacts mechanism directly addressed environmental impacts. However, for PWN, most articles recorded for the impact mechanisms of competition, hybridization, and interaction with other species implicitly indicated environmental impacts.



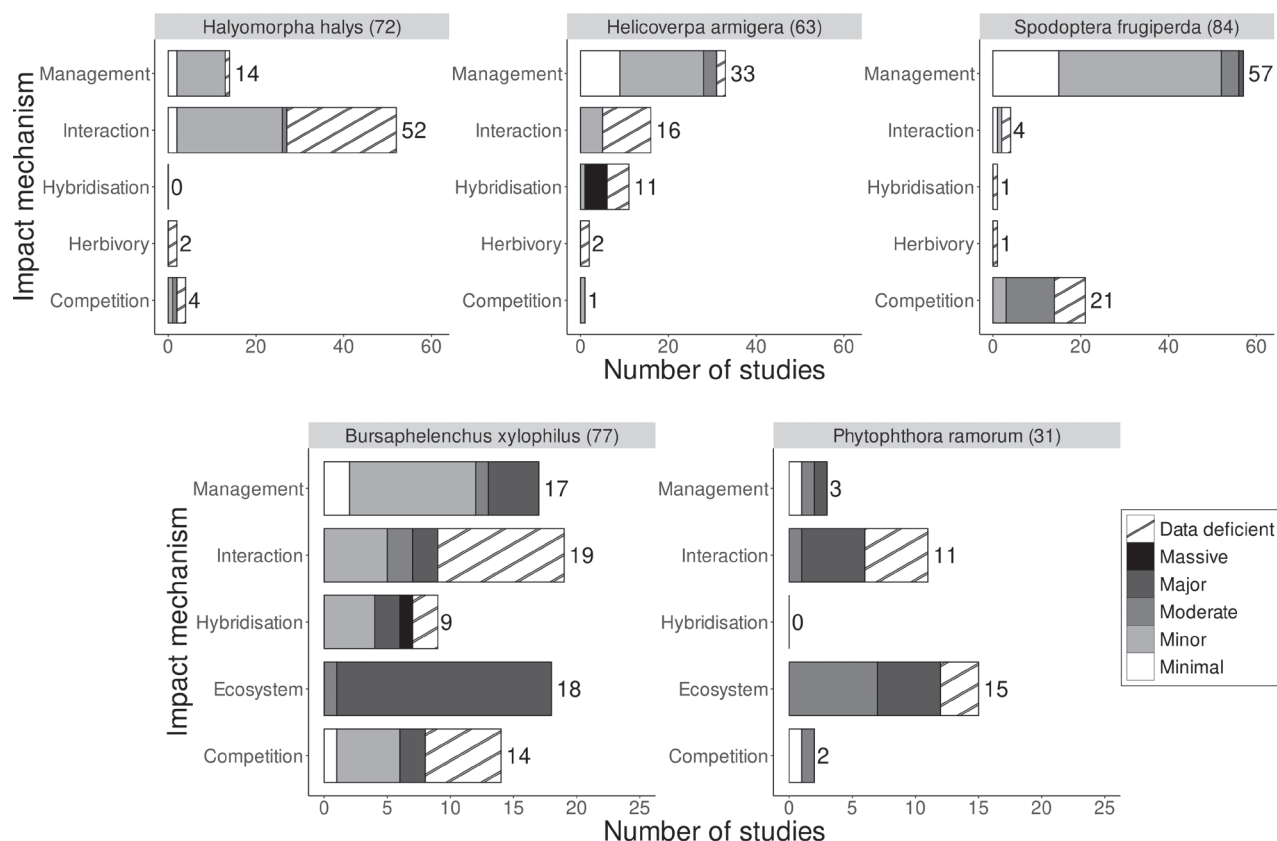
**Figure 1.** Number of studies from systematic searches for each impact mechanism for each case-study organism. The black portions of bars represent studies in which the findings directly suggest environmental impacts, and the white portions illustrate studies that implicitly address the environmental impacts. Numbers at the end of each bar signify the exact number of studies for each impact mechanism, and numbers next to species names display the total number of studies. On the y-axis, “ecosystem” refers to “chemical, physical, or structural impact on ecosystems,” and “interaction” refers to “interactions with other species.” For visualization, x-axis scales differ between the insect pests (top) and forest pathogens (bottom).

Research efforts relevant to environmental impacts differed geographically among the case-study organisms (Suppl. material 3: fig. S1). For BMSB, Italy and Switzerland were well represented compared with other European countries, with both Canada and the USA being similarly well represented in North America. Research efforts showed a wide geographic distribution for CBW but were best represented for India, Spain, the USA, Australia, Brazil, and Colombia. For FAW, Kenya, China, the USA, Brazil, and Mexico demonstrated notable research effort within their respective continents. The USA was well represented in research relevant to environmental impacts for *P. ramorum*, whereas the UK was the only European country represented by a few examples.

### Impact severity classification

Among all studies found for the case-study organisms, the vast majority contained data that enabled classification of impact severity, though this majority was much less pronounced when excluding studies under the management impact mechanism, particularly for the agricultural insect pests (Fig. 2). Most of the classifiable studies for BMSB were represented within the interaction with other species and management impact mechanisms, with the majority demonstrating minor impact. The maximum impact severity for BMSB was moderate under the competition and





**Figure 2.** Number of studies from systematic searches for each impact mechanism for each case-study organism. Increasingly dark shades illustrate increasing impact severity classifications, and the diagonal pattern represents relevant studies that did not contain sufficient data for such classification. Numbers at the end of each bar signify the exact number of studies for each impact mechanism, and numbers next to species names display the total number of studies. On the y-axis, “ecosystem” refers to “chemical, physical, or structural impact on ecosystems,” and “interaction” refers to “interactions with other species.” For visualization, x-axis scales differ between the insect pests (top) and forest pathogens (bottom).

interaction with other species mechanisms. The highest impact severity recorded for CBW was massive, as demonstrated by several studies under the hybridization impact mechanism, whereas minor impact was recorded for the competition and interaction with other species mechanisms. However, moderate impact was observed under the management impact mechanism. Classifiable studies were captured for the competition and interaction with other species impact mechanisms for FAW, with a maximum impact severity of moderate. Although the highest impact severity for management was major, most studies demonstrated minimal and minor impacts.

The forest pathogens tended to show a greater variety of impact severity classifications among the studies captured for the different impact mechanisms (Fig. 2). For PWN, impact severity could be classified among studies in all relevant impact mechanisms. The highest impact severity classified for PWN was massive, as demonstrated under the hybridization mechanism, and nearly all studies under the ecosystem impact mechanism demonstrated major impact. A maximum of major impact was also observed for each of the remaining impact mechanisms, though the majority of examples were of minor impact. Impact severity could be classified among studies under all impact mechanisms for *P. ramorum*, with the exception of hybridization, for which no examples were captured. The highest impact severity recorded was major, as demonstrated under the ecosystem impact, interaction with other species, and management mechanisms.

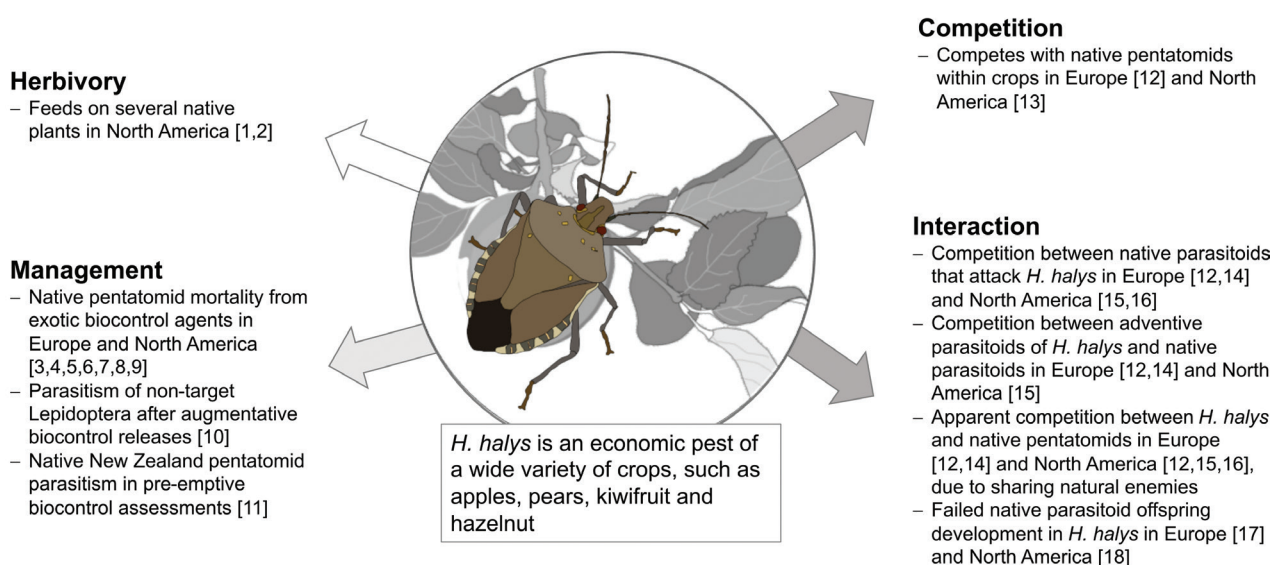
## Impact descriptions

Descriptions of key impacts and their associated severities for each pest and impact mechanism are illustrated in Figs 3–7. For BMSB, interaction with other species demonstrated key impacts resulting from indirect forms of competition. Impacts of management were all related to biological control (Fig. 3). The key impacts for CBW result from hybridization with the native *Helicoverpa zea* Boddie (Lepidoptera, Noctuidae) in Brazil and from the use of trapping, transgenic plants, and insecticides for management (Fig. 4). The same impacts were also important for FAW under the management impact mechanism, though direct competition with native species also caused impacts (Fig. 5). Changes to forest composition were the prominent ecosystem impact for *P. ramorum*, though it also caused numerous indirect impacts by interacting with other species (Fig. 6). Hybridization with the native *Bursaphelenchus mucronatus* Mamiya & Enda (Aphelenchida, Parasitaphelenchidae) in Asia caused the most important impacts from PWN. Ecosystem impacts were also prominent, including changes to community composition (Fig. 7).

## Environmental impacts of chemical control

We recorded a total of 46 active substances currently registered for use in European countries against four of the case-study organisms (BMSB, CBW, FAW, and *P. ramorum*) or for potential use against FAW in the future (Table 4). Of these, only one was ranked as exhibiting low ecotoxicity, whereas 14 were ranked as moderate and 31 as highly ecotoxic. Of the case-study organisms currently present in Europe, 16 active substances are registered for use against BMSB, 14 against CBW,

## *Halyomorpha halys*



**Figure 3.** Description of key impacts resulting from each impact mechanism for *Halyomorpha halys* (BMSB). The highest impact severity classification found among captured studies for each mechanism is represented by the arrows. White dashed arrows illustrate data deficiency, and increasing impact severity classifications correspond to increasingly darker arrow shades, with minimal impact being the lightest gray and massive impact being black. Numbers in rectangular brackets represent the corresponding references in Suppl. material 1: table S2. Further detail for these impact descriptions can be found in Suppl. material 3.

## *Helicoverpa armigera*

### Herbivory

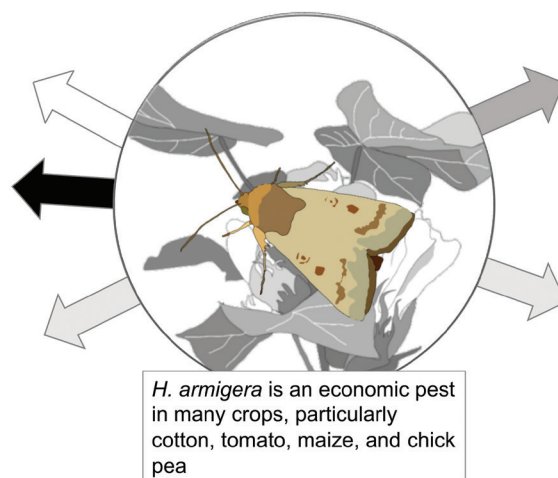
- *H. armigera* feeds on native plant in Brazil [19]

### Hybridization

- *H. armigera* hybridizes with native *H. zea* [20,21,22,23,24]

### Competition

- *H. armigera* competes with native *H. zea* in Brazil [25]



### Management

- Commercial traps capture non-target insects [26,27,28]
- Fitness impacts on natural enemies that target *H. armigera* feeding on Bt-expressing plants [29,30,31,32]
- Decrease in beneficial arthropod diversity after insecticide applications [33,34]

### Interaction

- *H. armigera* adults pollinate invasive weed in Asia [35]
- *H. armigera* parasite could spread to native Lepidoptera in the Americas [36]
- Competition between native predators of *H. armigera* in Spain [37] and Australia [38]
- Competition between native parasitoids of *H. armigera* in Asia [39]

**Figure 4.** Description of key impacts resulting from each impact mechanism for *Helicoverpa armigera* (CBW). The highest impact severity classification found among captured studies for each mechanism is represented by the arrows. White dashed arrows illustrate data deficiency, and increasing impact severity classifications correspond to increasingly darker arrow shades, with minimal impact being the lightest gray and massive impact being black. Numbers in rectangular brackets represent the corresponding references in Suppl. material 1: table S2. Further detail for these impact descriptions can be found in Suppl. material 3.

\*Although it meets the EICAT criteria for minor impact, negative effects on natural enemies due to reduced host/prey quality of pests targeted by Bt-expressing transgenic plants are an inevitable consequence of the intended effect and are not considered a risk.

## *Spodoptera frugiperda*

### Herbivory

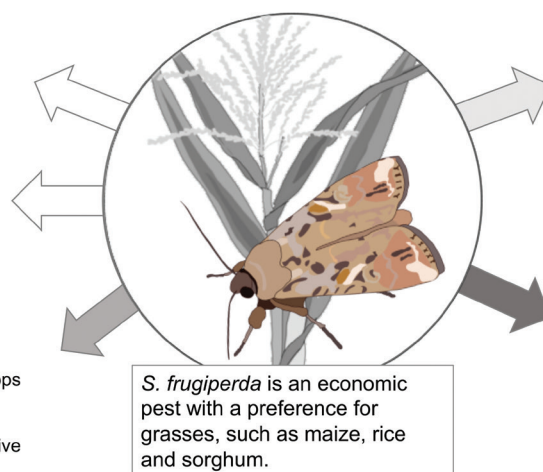
- Potential for *S. frugiperda* impact on native plants [40]

### Hybridization

- Hybridization between *S. frugiperda* and native *Spodoptera* spp. in invasive range considered, but no examples reported [40]

### Competition

- Displaces native pests within crops in Africa [41,42,43] and Asia [44,45,46,47,48,49,50,51]
- Competitive displacement of native noctuids impacts native natural enemy communities in Africa [43,52]



### Interaction

- Apparent competition with native pests due to sharing natural enemies in Africa [52]

### Management

- Impacts of insecticides on non-target arthropods in the Americas and Asia [53,54,55,56,57,58,59]
- Non-target Lepidoptera captured in monitoring traps [60,61,62,63,64,65]
- Fitness impacts on natural enemies that target *S. frugiperda* feeding on Bt-expressing plants [66,67,68]

**Figure 5.** Description of key impacts resulting from each impact mechanism for *Spodoptera frugiperda* (FAW). The highest impact severity classification found among captured studies for each mechanism is represented by the arrows. White dashed arrows illustrate data deficiency, and increasing impact severity classifications correspond to increasingly darker arrow shades, with minimal impact being the lightest gray and massive impact being black. Numbers in rectangular brackets represent the corresponding references in Suppl. material 1: table S2. Further detail for these impact descriptions can be found in Suppl. material 3.

\*Although it meets the EICAT criteria for minor impact, negative effects on natural enemies due to reduced host/prey quality of pests targeted by Bt-expressing transgenic plants are an inevitable consequence of the intended effect and are not considered a risk.

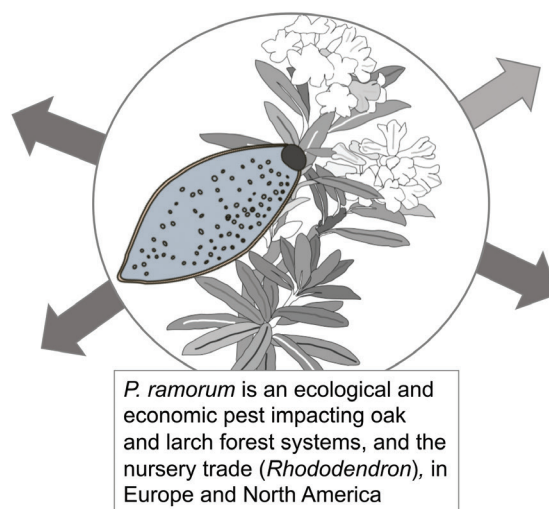
## Phytophthora ramorum

### Ecosystem impact

- Changes to forest composition in North America due to mortality and effects on soil chemical composition [69,70,71,72,73,74,75,76]
- Ecosystem changes from *P. ramorum* affect ant community composition in North America [77]
- Infected tanoak trees attract more bark beetles, accelerating tree mortality in North America [78]

### Management

- Removal of bay laurel (infective host) may impact forest biodiversity in North America [79]
- Tree removal alters species composition of ant communities in North America [80]



### Competition

- Displaces co-existing *Phytophthora* spp. in North America [81]

### Interaction

- Infected trees attract exotic bark beetles in North America [82,83]
- Weeds as foliar hosts of *P. ramorum* in North America [84,85]
- Apparent competition between host trees in North America [86,87]
- Disturbance in North American forests provide competitive advantage to deer mice over dusky-footed woodrat [88]
- Interaction of *P. ramorum* and fire changes competitiveness amongst resprouting trees North America [89]

**Figure 6.** Description of key impacts resulting from each impact mechanism for *Phytophthora ramorum*. The highest impact severity classification found among captured studies for each mechanism is represented by the arrows. White dashed arrows illustrate data deficiency, and increasing impact severity classifications correspond to increasingly darker arrow shades, with minimal impact being the lightest gray and massive impact being black. Numbers in rectangular brackets represent the corresponding references in Suppl. material 1: table S2. Further detail for these impact descriptions can be found in Suppl. material 3.

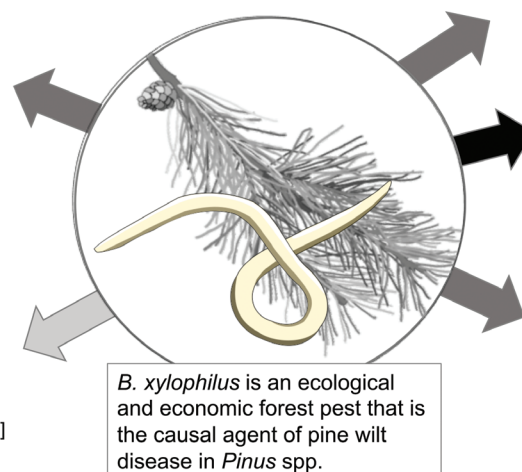
## Bursaphelenchus xylophilus

### Ecosystem impact

- Impacts on forest succession and soil properties alters the composition of microbial communities in Asia [90,91,92,93,94,95,96,97,98]
- Change in forest composition in Asia due to pine mortality and changes to soil properties [99,100,101, 102]
- Changes to forest functional types after regeneration following disease impact in Asia [103,104]

### Interaction

- Apparent competition between two host plants in Portugal [105]
- Effects the structure of host-associated fungal communities in Portugal and Asia [106,107], and bark beetle communities in Asia [108]
- Associated microbiota accelerates disease progression in host trees [109,110,111,112,113]



### Competition

- *B. xylophilus* displaces native *B. mucronatus* in Asia [114,115]

### Hybridization

- *B. xylophilus* hybridizes with the native *B. mucronatus* in Asia [116,117]

### Management

- Clear-cutting pine trees alters the soil microbial community structure in Asia [118]
- Tree removal reduces plant species diversity in Asia [119]
- Clearing diseased wood impacts ecosystem function in Asia [120]
- Insecticides to control *Monochamus* vector reduces species' abundance in Asia [121]
- Non-target species captured in *Monochamus* monitoring traps in Europe [122,123,124,125]

**Figure 7.** Description of key impacts resulting from each impact mechanism for *Bursaphelenchus xylophilus* (PWN). The highest impact severity classification found among captured studies for each mechanism is represented by the arrows. White dashed arrows illustrate data deficiency, and increasing impact severity classifications correspond to increasingly darker arrow shades, with minimal impact being the lightest gray and massive impact being black. Numbers in rectangular brackets represent the corresponding references in Suppl. material 1: table S2. Further detail for these impact descriptions can be found in Suppl. material 3.



**Table 4.** Active substances registered for use against BMSB, CBW, and *P. ramorum* in Europe, and their ecotoxicity rankings. Active substances likely to be used against FAW in the future are also presented. Ecotoxicity information was sourced from the Pesticide Properties DataBase and Bio-Pesticides DataBase (Lewis et al. 2016).

Pesticide	Overall ecotoxicity	Target organisms
Abamectin	High	BMSB, CBW
Acetamiprid	High	BMSB
Aluminium phosphide	High	BMSB
Ametoctradin	High	<i>P. ramorum</i>
Amisulbrom	High	<i>P. ramorum</i>
Azadirachtin	High	CBW
Azoxystrobin	Moderate	<i>P. ramorum</i>
Benzoic Acid	Moderate	<i>P. ramorum</i>
Chitosan hydrochloride	High	<i>P. ramorum</i>
Chlorantraniliprole	High	CBW, FAW
Copper Oxychloride	High	<i>P. ramorum</i>
Cyantraniliprole	High	CBW, FAW
Cyazofamid	Moderate	<i>P. ramorum</i>
Cymoxanil	Moderate	<i>P. ramorum</i>
Cypermethrin	High	BMSB, CBW, FAW
Dazomet	High	BMSB, <i>P. ramorum</i>
Deltamethrin	High	BMSB, CBW, FAW
Difenoconazole	High	<i>P. ramorum</i>
Dithianon	High	<i>P. ramorum</i>
Emamectin Benzoate	High	CBW, FAW
Esfenvalerate	High	CBW
Etofenprox	High	BMSB, CBW, FAW
Flonicamid	Moderate	BMSB
Fluazinam	High	<i>P. ramorum</i>
Flubendiamide	High	FAW
Fludioxonil	High	<i>P. ramorum</i>
Fluopicolide	Moderate	<i>P. ramorum</i>
Flupyradifurone	Moderate	BMSB
Fosetyl	Low	<i>P. ramorum</i>
Gamma cyhalothrin	High	BMSB
Lambda cyhalothrine	High	BMSB, CBW, FAW
Magnesium phosphide	High	BMSB
Mandipropamid	Moderate	<i>P. ramorum</i>
Metaflumizone	High	CBW
Metalaxyl-M	Moderate	<i>P. ramorum</i>
Methoxyfenozide	Moderate	CBW, FAW
Phosphane	High	BMSB
Potassium Phosphonates	Moderate	<i>P. ramorum</i>
Propamocarb	Moderate	<i>P. ramorum</i>
Propamocarb Hydrochloride	Moderate	<i>P. ramorum</i>
Pyraclostrobin	High	<i>P. ramorum</i>
Spinosad	High	BMSB
Tau-fluvalinate	High	BMSB, CBW
Tebufenozide	Moderate	BMSB, CBW, FAW
Trifloxystrobin	High	<i>P. ramorum</i>
Triflumuron	High	FAW

and 22 against *P. ramorum*. For FAW, 11 active substances were found that may potentially be used if the pest were to become widespread in Europe in the future. For full details regarding the ecotoxicity rankings of each pesticide for each key ecotoxicity indicator organism and the application methods used for each pesticide, refer to Suppl. material 1: table S4.

## Discussion

Capturing a surprisingly high number of publications for three insect pests of agriculture, particularly in comparison with previously published reviews (Kenis et al. 2008; McGeoch et al. 2015; Clarke and McGeoch 2023), provides examples of how economic insect pests may be overlooked with regard to their environmental impacts. The most recent and comprehensive review on the environmental impacts of invasive insects found evidence of impact for 125 species among 538 studies (Clarke and McGeoch 2023). However, the authors noted that a significant portion of these publications concentrated on a few well-studied species, none of which are considered agricultural pests, implying limited evidence for the majority of invasive insects captured by this study. We posit that targeting specific impact mechanism–related search terms to each pest enabled deeper scrutiny of a more manageable and relevant body of literature, beyond conspicuous examples that directly address environmental impacts. The wide geographic representation of the relevant literature (with the exception of *P. ramorum*) further supports case-study selection. Our approach revealed many more examples than had previously been accounted for among insect agricultural pests and provided a more refined outlook on knowledge gaps that complements broader review procedures. It was not surprising that our review recorded a large number of studies relating to environmental impacts for *P. ramorum* and PWN, considering that such impacts are well represented in the literature for these species and for forest pathogens in general (Grünwald et al. 2019; Kim et al. 2020). However, knowledge on the environmental impacts of forest pathogens largely focuses on conspicuous impacts on forest ecosystems, such as canopy gaps, successional and compositional changes, and changes to disturbance regimes (Tobin 2015; Lovett et al. 2016; Lapin et al. 2021). Applying this methodology to a greater diversity of taxonomies and life histories would further clarify whether environmental impacts among invasive insect agricultural pests are overlooked, as opposed to generally not exerting such impacts.

Studies addressing the environmental impact mechanisms for the three agricultural pests suggest that their impacts may result from interactions with native species in different ways. Certainly, for BMSB, interaction with other species is the most evidenced mechanism. For example, BMSB can act as an evolutionary trap for native parasitoids that recognize it as a suitable host, but their offspring fail to develop and emerge (Abram et al. 2013, 2016; Kaser et al. 2018), which could disrupt parasitoid communities and native pentatomid population dynamics due to apparent competition via shared natural enemies with BMSB (Herlihy et al. 2016; Konopka et al. 2018; Garipey et al. 2019). For FAW, competition is the most evidenced impact mechanism, with the population decline or competitive displacement of native herbivores that share the same host plants being the prominent impact (Mutua et al. 2022; Ayra-Pardo et al. 2024; Guo et al. 2024). Interaction with other species was the best-represented impact mechanism



for CBW, with competition between native parasitoids that attack it being reported (Tian et al. 2008). Hybridization resulting in introgression with the native pest and sister species *H. zea* in Brazil was also a prominent impact (Cordeiro et al. 2020; Valencia-Montoya et al. 2020). However, the negative impacts of FAW and CBW on native herbivores highlight the different contexts in which EICAT may be appropriately applied (Volery et al. 2020). For instance, *H. zea* is a native pest of maize in the Americas and is not considered threatened (Olmstead et al. 2016), though any impact on native species resulting from the invasion of CBW must be considered under EICAT (Hawkins et al. 2015; IUCN 2020). Realistically, such examples may be viewed differently by stakeholders with different values (Kumschick et al. 2020, 2024; Vimercati et al. 2022). Nevertheless, environmental impact mechanisms—and particularly indirect effects—should be explored for other globally important agricultural insect pests to assess how widespread these overlooked impacts may be.

Even for the two forest pathogens, the number of studies found for impact mechanisms other than the aforementioned ecosystem impacts is noteworthy. PWN exhibits hybridization and direct competition with a native congeneric nematode, *B. mucronatus*, in its invasive range in Asia (Cheng et al. 2008; Liao et al. 2014), and interacts with its associated microbiota to increase its virulence and exacerbate its impacts (Xue et al. 2020; Cai et al. 2022). However, the alien status of this nematode-associated microbiota is not entirely clear (Proença et al. 2014), which affirms the revised guidance to EICAT proposed by Volery et al. (2020) that interactions with other species—and not only with other alien species—should be considered under this impact mechanism. For *P. ramorum*, evidence of environmental impacts through competition includes direct competition with coexisting *Phytophthora* spp. (Kozanitas et al. 2017). Interaction with other species also causes apparent competition between tree species that share it as a pathogen (Cobb et al. 2010). Although effective in capturing such examples, we excluded studies demonstrating impacts on soil carbon and nutrients in forest ecosystems (Lamsal et al. 2011; Cobb et al. 2016), because EICAT explicitly limits environmental impacts to effects on native species (Blackburn et al. 2014; Hawkins et al. 2015; IUCN 2020). However, a new framework published after this review was conducted extends impact classification to the abiotic environment level and further clarifies the distinction between mechanisms and impacts (Carneiro et al. 2025).

Despite such results, most studies for the agricultural insect pests did not directly relate their findings to environmental impacts. There is a general pattern whereby many studies consider their results strictly in relation to economic relevance (e.g., Cordeiro et al. 2020; Valencia-Montoya et al. 2020; Rios et al. 2022). For BMSB and FAW, examples of competitive displacement of native herbivores and apparent competition were often only considered within the context of crop damage, pest management, and biological control efficacy (Pezzini et al. 2018; Formella et al. 2020; Cornelius et al. 2021; Nzouendja Kamtchou et al. 2022; Guo et al. 2024). However, a notable number of studies showing these impacts for BMSB and FAW did directly consider their findings in relation to environmental impacts, such as the potential for the former to impact native pentatomid–scelionid population dynamics in Canada (Konopka et al. 2018; Garipey et al. 2019; Sokame et al. 2021; Song et al. 2023). Our findings suggest that the environmental impacts of these (and likely other) pests are overlooked not only in the primary literature but also in broad reviews on the environmental impacts

of invasive insects (Kenis et al. 2008; McGeoch et al. 2015; Clarke and McGeoch 2023). Such linkages between environmental and economic or socioeconomic impacts should be further considered if sufficient data become available (Bacher et al. 2018; Dasgupta 2021). Because impacts on biodiversity can affect ecosystem services, recreation, conservation, and other human interests with socioeconomic implications (Pimentel et al. 2001; Hoffmann and Broadhurst 2016; Dasgupta 2021), this represents a potentially important avenue of inquiry in future studies of agricultural insect pest impacts.

Even for the two forest pathogens—but especially PWN—the relatively numerous publications categorized as implicit for impact mechanisms other than ecosystem impacts are intriguing. Many of the studies concerning PWN's competitive impact on the native *B. mucronatus* do not directly consider environmental impacts (Liao et al. 2014; Zhou et al. 2023), but rather, for instance, the ability of the native nematode to competitively resist PWN invasion (Vincent et al. 2008). This is also true for examples demonstrating hybridization between these two species, whereby studies may be concerned with the pathogenicity of hybrid offspring from a management perspective (Tomalak and Filipiak 2021) or with using this as a model system to understand the genetic traits of hybrid populations (Taga et al. 2011), without mention of environmental impacts. This pattern was less pronounced among the studies recorded for *P. ramorum* but nevertheless highlights that impact mechanisms other than conspicuous and well-studied ecosystem impacts may also be overlooked among invasive species that affect forests.

Ranking each publication based on the impact severity classification may further elucidate knowledge gaps with regard to both species and impact mechanisms (Hawkins et al. 2015; IUCN 2020; Clarke and McGeoch 2023). In particular, studies that are classified as data deficient can indicate potential environmental impacts where increased research effort could be valuable. For instance, all studies selected for herbivory among the insect pests were classified as data deficient because, although they demonstrated herbivory of native plants, they did not measure impact (Zalucki et al. 1994; Hoebeke and Carter 2003; Nielsen and Hamilton 2009; Tembrock et al. 2019; Ayra-Pardo et al. 2024). Although impacts on native flora caused by polyphagous agricultural pests may be overlooked, herbivory is a direct and conspicuous impact mechanism, and some invasive insects are well studied for severe and widespread impacts on native plants, such as *Aulacaspis yasumatsui* Takagi (Hemiptera, Diaspididae) and *Icerya purchasi* Maskell (Hemiptera, Monophlebidae) (Roque-Albelo 2003; Marler and Krishnapillai 2020). In other cases, study design may not allow for the classification of potentially higher impact severities. For BMSB, most of the studies recorded for the interaction with other species impact mechanism that were not data deficient were classified as minor impact because they demonstrated reduced fitness of native individuals but did not aim to measure population-level impacts (Hawkins et al. 2015; IUCN 2020). One study that did measure relative population sizes of native stink bugs compared with BMSB was classified as moderate impact (Formella et al. 2020). For FAW, the number of studies classified as moderate impact under the competition impact mechanism is notable because it suggests the potential for this pest to exert population-level effects on native species. However, this was the maximum impact classification possible based on the data presented, since it was not measured whether local extinction of native species had occurred, which would escalate the classification to major impact (Hawkins et al. 2015; IUCN 2020; Mutua et al.

2022; Nzouendja Kamtchou et al. 2022). It is important to consider whether the study design enables the detection of higher impact severities, because this highlights the potential for underestimation (Volery et al. 2020). The highest impact severity recorded among the insect agricultural pests was for CBW, as most of the publications on hybridization that were data sufficient met the EICAT criteria for massive impact (Hawkins et al. 2015; IUCN 2020) by demonstrating common and widespread hybridization with the native *H. zea* in Brazil (Anderson et al. 2018; Cordeiro et al. 2020; Valencia-Montoya et al. 2020). These patterns demonstrate that the degree of environmental impact warrants more comprehensive scrutiny in order to gain a conclusive understanding within the wider context of invasive species impacts, especially since the highest impact severity recorded for these species by previous reviews was minor concern (Clarke and McGeoch 2023).

Comparatively, very few studies under the ecosystem impact mechanism for PWN and *P. ramorum* were deemed data deficient, and the majority were ranked moderate or major. This reflects a more robust and well-recognized understanding of the environmental impacts of species that affect forest systems compared with polyphagous insect pests of agriculture (Kenis et al. 2008; Gandhi and Herms 2009; Økland et al. 2011; Grünwald et al. 2019; Kim et al. 2020; Clarke and McGeoch 2023). However, the other impact mechanisms relevant to forest pathogens are less clear with regard to impact classification, which may relate to the aforementioned abundance of studies that do not directly address environmental impacts. For both PWN and *P. ramorum*, studies demonstrating interaction with other species ranged in classification from minimal to major impact, which further affirms the importance of impact mechanisms other than conspicuous ecosystem changes. Despite this, most of the articles on interaction with other species were data deficient for PWN, which highlights that even for forest pathogens, certain impact mechanisms remain underappreciated.

Although it is also important to simultaneously consider impacts in the absence of management—given that effective control may reduce the maximum impact potential of invasive species—management itself can have impacts (Blackburn et al. 2014). Management was therefore treated as an impact mechanism in this review to ensure a holistic consideration of impacts. A relatively large number of studies were recorded on the environmental impacts of pest management. In general, the environmental impacts and risks of pest control tools such as synthetic chemical pesticides, biological control, and genetically modified crops are well studied (Bigler et al. 2006; Gill and Garg 2014; Suckling et al. 2014; Meissle et al. 2022) and typically required by regulatory entities (Craig et al. 2008; EU 2009a, 2022; Mason et al. 2017; Barratt et al. 2021). Nevertheless, the focus on types of pest management varied among the case-study pest species, largely reflecting research interest. For BMSB, for example, the studies concern the risk of non-target impacts of biological control agents, such as the exotic *Trissolcus japonicus* Ashmead and *Trissolcus mitsukurii* Ashmead (Hymenoptera, Scelionidae) for classical biological control (Rondoni et al. 2022; Haye et al. 2023) or native parasitoids for augmentative biological control (Stahl et al. 2018). Studies on the environmental impacts of CBW management generally cover the non-target impacts of transgenic Bt crop plants, pesticides, and biological control (Silva and Stouthamer 1999; Men et al. 2004; Sharma et al. 2007; Sun et al. 2009), and the same control tools have also been widely studied in relation to FAW management (Méndez et al. 2002; Gontijo et al. 2018; Hussain et al. 2021; de Souza et al. 2021). However, although meeting

the EICAT criteria for minor impact, negative effects on natural enemies due to reduced host/prey quality of pests targeted by Bt-expressing transgenic plants are an inevitable consequence of the intended effect and are not considered a risk (Romeis et al. 2006, 2019). For PWN, the preponderance of research effort regarding the environmental impacts of its management relates to the biodiversity impacts of clear-cutting affected forest areas and potential non-target impacts of trapping its vector, *Monochamus* spp. Dejean (Coleoptera, Cerambycidae) (Zhang et al. 2021; Sukovata et al. 2022). Our findings suggest that comparatively much less research has been conducted on the impacts of *P. ramorum* management, though all studies considered the biodiversity impacts of tree removal. We also found that, except for *P. ramorum*, the studies captured for the management impact mechanism were overwhelmingly represented by the less severe impact classifications of minimal and minor concern. However, few of these examples assessed the impacts of conventional chemical pesticide applications, as contemporary research on pest management tends to explore the efficacy and development of environmentally friendly and socially acceptable alternatives (Mankad et al. 2017; Suckling et al. 2017). Yet, the establishment and spread of invasive species are usually followed by a surge in pesticide use (Frisvold 2019).

We thus summarized the pesticides used against the case-study organisms (or, in the case of FAW, those likely to be used if it becomes established) based on the understanding that, despite extensive research on their environmental impacts, they remain commonly applied (Frisvold 2019). The large number of active substances, most exhibiting high ecotoxicity, registered for use against just four case-study organisms further emphasizes the importance of considering the impact of management interventions, despite their exclusion from EICAT. This is especially true considering that pesticide consumption continues to increase as the number of invasive pests requiring management escalates globally (Sharma et al. 2019). We therefore echo the advocacy of McGeoch et al. (2015) regarding the importance of this impact mechanism for a holistic understanding of environmental impacts associated with invasive species. Additionally, other risk assessment protocols require consideration of management impacts, such as priority pest ranking by the European Commission's Joint Research Centre (Sánchez et al. 2019). However, it should be noted that environmental impacts of management likely vary across recipient environments due to anthropogenic factors, such as the use of host-specific biological control agents that limit non-target impacts compared with broad-spectrum insecticides (Sharma et al. 2019; Andow et al. 2020).

## Conclusion

Our targeted literature reviews uncovered many previously overlooked examples of the environmental impacts of three case-study insect pests of agriculture—a type of pest rarely considered for their effects on native biodiversity. However, a large portion of examples did not directly address environmental impacts or contained uncertainties, such as data deficiency and study designs that did not enable detection of potentially higher impact severities. Although studies found for the two case-study pathogens, which are well known for their environmental impacts, more commonly addressed such impacts directly, the above-described uncertainties were also observed among studies that did not fall under the ecosystem impact mechanism. Our review therefore raises awareness of the potentially underappreciated

environmental impacts of invasive insect pests of agriculture and highlights impact mechanisms for which great uncertainty remains. We recommend that research on invasive insects and pathogens consider these patterns to improve our understanding of the impacts of invasive species.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

### Ethical statement

No ethical statement was reported.

### Use of AI

No use of AI was reported.

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## Author contributions

Kiran Horrocks: writing – original draft, conceptualization, data curation, investigation, methodology, visualization. Jörg Romeis: writing – review and editing, funding acquisition, methodology. Jana Collatz: writing – original draft, writing – review and editing, conceptualization, funding acquisition, investigation, methodology, visualization.

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## Data availability

All of the data that support the findings of this study are available in the main text or Supplementary Information.

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## Supplementary material 1

### Supplementary tables S1-S4: search strings, lists of studies, and ecotoxicity information.

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Data type: xlsx

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## Supplementary material 2

### PRISMA flowcharts.

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## Supplementary material 3

### Detailed impact descriptions and fig. S1.

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