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Impact of invasive insects on native insect communities

Taiadjana M Fortuna¹, Philippe Le Gall¹, Samir Mezdoor² and Paul-André Calatayud^{1,3}

Several biophysical factors are leading to the loss of biodiversity, among them the dominance of exotic invasive species on native communities is important. Their dominance can lead to changes in the structure of insect communities, by competing and displacing native species to other crops or habitats. These changes can impact the herbivore's natural enemies in invaded areas by diverging them from suitable herbivores and altering their biological control process. The development of edible insects and derived products at an industrial scale can also have an impact on the local fauna by the risks of spillover and accidental release in nature. Several area-wide integrated pest management programs are also using the sterile insect technique to control insect pests and disease vectors. This technique is becoming largely used; however, its application as 'non-intrusive to the environment' is controversial particularly when eradication is concerning species that are at the basis of food webs.

Addresses

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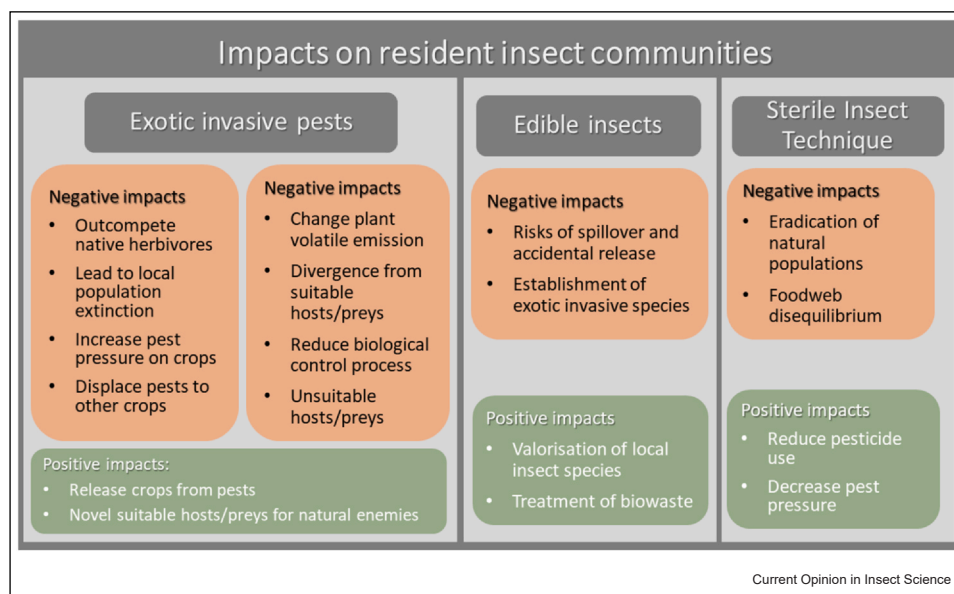
Introduction

Globalization and climate change have promoted the spread of non-native or exotic species all over the globe. Some species become established, spread and a subset of these species, called invasive, cause serious environmental, economic, and human health impacts [1]. Once an invasive species integrates into an ecosystem, its

control becomes complex because of interactions with both the resident species and other invaders. One important factor is the lag time between when an exotic species becomes established and when it truly becomes invasive. This lag time is short in some cases and established exotic species spread rapidly in the new environment; however, it can also be long, which complicates the detection of species with the potential invasive ability [2]. In this sense, invasive species can also be native species, like some introduced species after a lag time, that undergo a rapid demographic growth as a result of a change in their environment related in most cases to human activities (e.g. land use and climate change) [3].

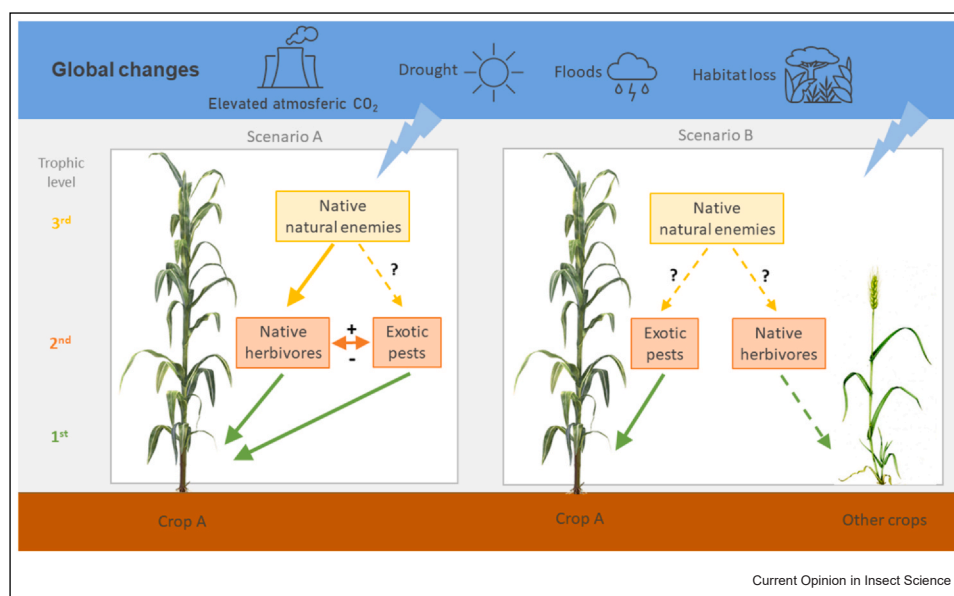
Exotic insects can impact native biodiversity through direct interactions, for example, herbivory, predation, and hybridization with resident species. They can also affect ecosystems indirectly, through cascading effects, for example, disease transmission, competition for space, food, and hosts. To date, most studies on exotic invasive insects have focused on their impact on native plants [4–6] and on the direct and indirect impacts of exotic natural enemies of insect herbivores in novel environments [7–9]. However, studies focusing on the impact of exotic insect pests on native natural enemy–host trophic interactions are scarce [10], and even absent on the impact that intensive farming of exotic or native insect's species and the massive introduction of sterile insects in invaded areas and consequences thereof on resident insect communities. The insects-as-food industry is promoted as a sustainable alternative to conventional livestock systems; however, there is still a tremendous lack of knowledge in many aspects of insect mass rearing. One important issue that should be addressed by scientists is the environmental risk of accidental release, for example, the risk that commercialized species, which are commonly exotic become locally invasive under a climate change scenario [11•]. In this context, this paper focused on the impacts of exotic invasive insect pests (Sections *Interactions between exotic invasive insect pests and native insect herbivores* and *Interactions between exotic invasive insect pests and native natural enemies*), the risks of intensive farming of exotic and native insect species for food or feed (Section *Risks of intensive farming of exotic invasive species for food or feed on native insect's communities*), and the risk of using a sterile insect technique (SIT) (Section *Risks of the use of the insect's sterile technology on native insect's communities*) on native insect's

Figure 1



Negative and positive impacts of exotic invasive insect pests, of edible insects for food and feed and of SIT on native insect communities.

Figure 2



Scheme of possible tritrophic interactions between exotic insect pests and native insect communities in the invaded areas and how anthropogenic global changes can influence the different interaction scenarios. Scenario A shows how exotic pests can use a common resource, crop A, that is already used by native herbivores for their survival, predisposing them to interact in a competitive (-) or facilitative (+) manner. These interactions impact not only native herbivores, but also their associated native natural enemies, which may or may not switch to novel potential hosts or preys (question mark over dash yellow arrow). The main challenge is to predict the predominance of an exotic species which may cause the displacement or extinction of the native species, leading to changes in species distribution and host range in the long term. Scenario B illustrates a multi-pest system sharing the same resource, where exotic pests dominate the native herbivores leading to the displacement of native species into other crops or habitats but without extinction evidence. The main question is whether natural enemies associated with native species follow their original hosts or preys or, on the contrary, adapt to new hosts in the invaded habitat (question mark over dash yellow arrow).

communities (Figure 1). We mainly considered exotic insect species (but also natives see Sections *Risks of intensive farming of exotic invasive species for food or feed on native insect's communities* and *Risks of the use of the insect's sterile technology on native insect's communities*) with invasive trends and negative impacts in agrosystems, namely invasive insect pests.

Interactions between exotic invasive insect pests and native insect herbivores

The capacity of an invasive species to occupy a wide range of environments and to significantly impact the biology of native species is a major cause of biodiversity loss [12]. In agriculture, exotic insect pests can impact native species by using a common resource, which is already used by natives for their survival, predisposing them to interact in a competitive (e.g. [13]) or facilitative manner (e.g. [14]; Figure 2). Among these interactions, despite the frequent indication for competition in the literature [15], there is limited evidence for the dominance of competition in phytophagous insect communities leading into a new paradigm on how interspecific competitions will contribute to changes in the phytophagous insect community structures [16] by, for example, changes in insect host ranges [17]. Several examples of exotic invasive insect pests corroborate such paradigm. This is the case of the exotic lepidopteran stemborers in tropical habitats worldwide. In East Africa, *Chilo partellus* (Lepidoptera: Crambidae) caused the displacement of native species, as *Busseola fusca* (Lepidoptera: Noctuidae) from sorghum [18], and as *Chilo orichalcolciliellus* (Lepidoptera: Crambidae) from maize to alternative grasses, not commonly hosts of *C. partellus* [19]; and more recently of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), after its recent invasion in Africa in 2017, is pushing the native *B. fusca* from maize to other crops (e.g. [20•]). *Spodoptera frugiperda* is also currently reducing the attack intensity of native lepidopteran pests and the diversity of associated natural enemies in Indonesia [21•], and it is out-competing other insect pests such as *Helicoverpa zea* in South America [22].

The main challenge is to predict the predominance and the lag time of an exotic species which may cause the displacement or extinction of the native species. This will depend on the population stability of an insect species competing for the same resources [23]. For example, it was shown that when a species feeds on a resource, it will be able to establish and sustain a stable population that fluctuates based on the resource availability [23]. However, in a competing context with different species feeding on the same resource, it is generally observed a combination of the three parameters, half-saturation, growth rate and mortality rate, and that determine which species will dominate for the

resource use (e.g. [24••]). In this context, under a multi-pest system sharing the same resource, it was reported that the exotic invasive species dominate the native species resulting of a likelihood displacement of these native species to other crops or habitats but without extinction evidence [24••] (Figure 2). In addition, it has long been recognized that human activity is responsible for the vast majority of biological invasions, and it is highly related to the openness of global trade [25]. Understanding how and when invasive insect pests were transported is important to explain current invasions and predict future ones to minimize impact on local biodiversity [25]. However, the anthropogenic climate change will probably alter the distribution, abundance, and phenology of, not only the native insect pests, but also the exotic ones [26**,27].

Interactions between exotic invasive insect pests and native natural enemies

It is reported that exotic invasive insect herbivores interfere significantly with native herbivore–natural enemy interactions in invaded areas [10,28,29]. Different processes of interference are described. Herbivore natural enemies use the volatiles emitted by plants infested by their prey or host to orient themselves towards host in nature [30]. Interferences can occur if these volatiles attract the natural enemies towards suitable or unsuitable exotic insect herbivores or if the plants coinfested by both exotic and native herbivores emit volatiles that become less attractive to natural enemies [10]. In case the natural enemies are attracted and then attack unsuitable exotic pests (i.e. unable to feed or to develop in them), they spend time and energy which can negatively affect their fitness [10,31]. In case the natural enemies are attracted and attack suitable exotic pests, they may be diverted from their initial resident targets (Figure 2). In all cases, native natural enemies can use exotic invasive insect herbivores as prey or host and these novel interactions may have detrimental consequences at the community level [32] and on a pre-existing biological control process [31].

An important process that is reported to be detrimental on a pre-existing biological control program is the non-reproductive mortality of native natural enemies induced by the exotic insect pests. In hymenopteran parasitoids, for example, a model on the biological control effects of nonreproductive host mortality predicts that native parasitoids may have a large biological control impact on the population dynamics of the invasive pests in areas where suitable native hosts coexist [32]. In this case, parasitoids may have higher metabolic costs of unproductive foraging behaviors, for example, when they do not complete development in the invasive host but respond to volatile cues from the plant–herbivore complex and oviposit in this unsuitable host [33•]. This

may directly affect the reproductive output of the parasitoids in the field [30], resulting in reduced parasitism rates of its native hosts.

In addition, anthropogenic climate change will alter the distribution, abundance, and phenology of the natural enemies of insects' herbivores as well as their herbivore hosts (Figure 1). Even though several studies are predicting changes in the future distribution of pest species under climate change [34], few models have included the effect of climate change on natural enemies. Thus, little is known about the impact of climate change on the distribution of biological control agents used to control insect pests worldwide (but see Ref. [35]). Although it was predicted that herbivore species will be able to establish and sustain by cyclical relationship between populations of the pest and the associated natural enemies [24••], the climate change may, for example, increase pest problems by increased herbivore performance and reduced top-down control by natural enemies [36]. Climate change may then influence in diverse ways the multitrophic interactions between herbivores and natural enemies, among which, changes in species distribution might be crucial [37].

Risks of intensive farming of exotic invasive species for food or feed on native insect's communities

Since 2010, the potential of insects as food and feed in order to ensure food security has gained momentum. Insects have been identified as suitable candidates to supplement other animal-protein sources based on their nutritional value [38,39].

In many parts of the world, edible insects are already well-known local insects, which are collected from the wild and directly sold to the consumers. It is estimated that more than 2000 edible species are part of traditional meals eaten by at least 2.5 billion people living in tropical countries [40]. The new idea now is to rear insects to limit the ecological impacts of gathering them in the wild [41] and to have alternatives in case of edible insects' population decline following global changes [42]. In addition, the need to find alternative sources of proteins and set up circular economies for the treatment of biowaste has led to the development of this new industry in western countries. The use of insects as a significant source of edible raw materials is based on the possibility to rear and process them on an industrial scale, but the change from small-scale rearing units to those on an industrial scale is a challenge that is not only ethical [43], scientific [44], and economic [38], but also concerns health issues [45,46]. One of the unsolved questions is whether, in the context of global warming, can production of tons of insect pests as an alternative food resource take place without the risks of their

accidental release and dispersion in the natural environment?

In Europe, the 'Novel Foods' legislation (Regulation (EU) 2015/2283) regulates edible insects and derived products [47]. In 2021, the European Food Safety Authority (EFSA) released an opinion on the safety of dried yellow mealworm, *Tenebrio molitor* (Coleoptera: Tenebrionidae) as novel food [48]. This is the first species that reached the authorization level amongst the 10 species of insects (Table 1), which were considered available for human consumption in some European countries. We can see that most species on this list were classified as 'pests' during the 20th Century before they have been considered potential resources of food or feed. Similarly, insect pests are also now proposed as novel food [49].

The industrial development of insect production for food and feed is ideally considered as a promising sector [50••], though the proposed target is to rear edible insects that are in most cases exotic species, as, for example, the tropical locusts, the crickets *Gryllobates* and the beetles *Zophobas*. Considering those development prospects, one has to take into account the impact of insect rearing on the local fauna, and the possibility of proliferation and problems for nearby residents. Although European authorities have provided a regulatory framework for insect rearing facilities, the risks of accidental release of these exotic insects in nature have rarely been considered by the industrial sector, or by scientists. The species from the European list are also taken into consideration for importation in Tropical countries where the environmental risks are much greater. Documenting this question is an increasingly urgent matter. In addition, depending on the location of the rearing facilities and to minimize the risk of accidental release, research should be conducted to find native insect species, rather than exotic species, that can be efficiently used for insect production for food in feed.

Risks of the use of the insect's sterile technology on native insect's communities

Together with genetically modified organisms, the SIT is the most discussed approach on the way to the eradication of insect pest species. Historically, it has been tested for controlling the Tsetse flies in the 1930s and 1940s and developed against the New World screw-worm fly in the 1950s [51]. After its utilization against important agricultural insect pests, including invasive species as Tephritid fruit flies (e.g. *Ceratitis capitata*, *Bactrocera* spp., *Anastrepha fraterculus*), *Drosophila suzukii*, and moths (*Cydia pomonella*, *Lobesia botrana*, *Ectomyelois ceratoniae*) [52••], the SIT is now largely evoked not only to control but also to eradicate mosquitoes [53] or tsetse flies' species that are important vectors of diseases worldwide. Several area-wide integrated pest

Table 1**Insects species considered available for human consumption in Europe and their previous status in agriculture [60,61].**

Species	Latin name	Diet	Agricultural status
House cricket	<i>Acheta domesticus</i>	Polyphagous	Commensal species of man
African locust	<i>Locusta migratoria migratorioides</i>	Herbivorous	Declared migratory pest
Giant mealworm	<i>Zophobas atratus morio</i>	Granivorous	Indifferent species
Mealworm	<i>Tenebrio molitor</i>	Cereal flour eater	Considered as a storage pest
Buffalon worm	<i>Alphitobius diaperinus</i>	Cereal flour eater	Pest of stored food grain products
Greater wax moth	<i>Galleria mellonella</i>	Honeybee wax eater	Ubiquitous pest of the honeybee
American bird grasshopper	<i>Schistocerca americana</i>	Herbivorous	Declared migratory pest
Tropical house cricket	<i>Grylodes sigillatus</i>	Polyphagous	Commensal species of man
Lesser wax moth	<i>Achroia grisella</i>	Honeybee wax eater	Ubiquitous pest of the honeybee
Silkworm	<i>Bombyx mori</i>	Herbivorous	Domestic

management programs with an SIT component have been deployed [54].

The idea that the SIT is ‘non-intrusive to the environment’ must be discussed. This idea came from the fact that SIT is a genetic-based method that is only affecting the target populations. But one lesson we must retained from the last passed years of observation of insects’ [55••] and bird’s population decline is that in such modified landscapes the drastic modification of the size of pest’s population will also affect the entire ecosystem. The question is not to decide if we must control or not the species in the system. It is more to clearly identify how we will modify the equilibrium between the diverse components. If the limitation of chemical pesticides-based methods is an honorable target, we do not have to act as if we will not have any impact. Thus, any method used in the agrosystems for pest control or for mosquitoes control in natural ecosystems should have to be clearly documented for their impact not only in the scope of the cultivated fields but also at a large landscape scale. The ethics of eradicating natural populations is rarely discussed. Today, we are facing two different cases. The first is targeting local species, like tsetse flies, which are part of the local biodiversity [56]. In this case, eradication is not the right measure and natural populations, for example, in protected areas, should be conserved [57]. The second is the attempted eradication of invasive insect pests, where SIT could represent a real alternative to the use of great quantities of chemical pesticides. This is well illustrated by the fruit flies, which became major pests of numerous fruits and vegetables around the World. The SIT has been successfully tested to control these species and it allows the reduction of insecticide treatment [58,59]. Nevertheless, the advantages of SIT against classical chemical pesticides should not allow its use without estimating the potential impacts on non-target fauna.

Conclusions

This paper discusses first how interferences of exotic invasive insect pests may impact not only other

phytophagous insects into the invaded area but also their associated natural enemies, particularly under a multi-pest system sharing the same resource, where displacement of native species to other crops or habitats may occur. The main challenge under the current global change scenario is, therefore, to predict the predominance of an exotic pest species which may cause the displacement or extinction of the native species. Special concern should be given, as well, to the production of edible insects for food and feed, which is now facing great development in industrial countries. However, although a regulatory framework is now applicable in the EU, important risks such as those of spillover or accidental release of edible insect species are still rarely taken into account by either the industrial sector or the scientific community. This question is of an urgent matter, especially because most species reared at industrial level are exotic pest species. In the same way, risks underlying the use of SIT to control and eradicate insect pest populations should be discussed. Can one consider this technique totally ‘non-intrusive to the environment’ without clearly identifying how we will modify the equilibrium between the diverse components of agroecosystems? In the end, the decision should depend on the society as a whole and to policymakers. But are they clearly informed and does their education help them in taking such decisions? And how will the scientific community be of a good help for them? The last months of debates and emotional-based decisions about our health and social life showed us that we need a strong corpus of scientific data clearly explained to all citizens.

Conflict of interest statement

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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