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Is the evolution of insect odorscapes under anthropic pressures a risk for herbivorous insect invasions?

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Highlights

- Olfaction is crucial to insect mobility and exploitation of their milieu.
- Olfactory cues contribute to the establishment and spread of invasive species.
- Global change, through changes in odorscapes and insect`s sensory environments, may increase insect invasion risk.
- Adapting semiochemicals uses in biocontrol is crucial under global change.

Abstract

Olfaction is directly involved in the insect capacity to exploit new habitats by guiding foraging behaviors. We searched in the literature whether some traits of olfactory systems and behaviors are associated to invasiveness and the impact of anthropogenic activities thereof. Human activities dramatically modify habitats and alter insect odorscapes. Air pollution, for instance, decreases lifetime and active range of semiochemicals. Plasticity and behavioral adaptability of invasive species are decisive by allowing host shifts and adaptative responses to new habitats. Changes in biophysical environments also impact on the use of semiochemicals in biocontrol. Although no evidence for a unique ensemble of olfactory traits associated to invasiveness was found, a growing number of case studies reveal characteristics with risk predicting value, opening the paths to better invasion control strategies.

Conflict of interest

The author declares to have no conflict of interest

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Introduction

Pheromones, host odors, habitat cues but also many other volatile organic compounds (VOCs) that interfere with their olfaction constitute the odorscapes on which insect depend for communication, reproduction and feeding [1]. A growing number of studies documents the alteration of insect's odorscapes during the Anthropocene alerting conservationists to the risks for the entomological biodiversity [2] and the ecosystem services [3]. Olfaction is directly involved in the insect capacity to exploit new habitats by guiding their foraging behaviors [4]. It is thus surprising that we know so little about its role in the establishment and spread of invasive insects. Olfaction probably does not contribute to introduction, during which displacements are most often passive. However, olfaction is decisive in finding favorable sites and sparse resources, which should enhance establishment and dispersal. The present review thus focuses on the olfaction role on mobility and what human activities change to insect olfactory communication. Specifically, I address three questions: (1) might some traits in olfactory system and olfactory-driven behaviors explain invasiveness? (2) Do new odorscapes increase risks of biological invasions? And (3) how do changes in odorscape impact biocontrol of invasive species? This information is critical in unraveling factors contributing to invasiveness and may explain the role of anthropogenic activities in aiding insect pest invasions.

The role of olfaction in invasive insect species spread

The course of a biological invasion process is influenced by the attributes of invading species, their modes of displacement and the characteristics of the invaded ecosystems [5]. I will thus examine how invasive species use olfaction and the olfactory characteristics of invaded habitats.

Olfaction guides active insects' movements

Once released in the atmosphere, the VOC molecules constituting the odors to which insects are sensitive disperse at the speed and direction of air flows to travel in filaments interspersed with odor-free air [6]. Concentrations inside filaments stay well above the mean concentration, which decreases as the square of the distance. When detected by insects, filaments induce most often a locomotion change. It can be a mere increase in amount of movement as the insect performs an unfocused local search. Active flyers fly upwind to follow odor plumes but navigate crosswind while losing the plume. In aphids, and other small insects with poor control of their flight direction, olfactory cues nevertheless play their role in targeting the landing on hosts [7]. In fragmented landscapes the capacity to detect from a distance and navigate toward a remote favorable habitat offers a big advantage. Evaluating odorant active ranges remain difficult because of the complexity of natural odorscapes and insect behaviors. Transport models built by physicists predict filament detectability from several hundred of meters downwind [8]. Experimental data are rare, but maxima for moths and beetles are probably in the range 200-500 m [9]. Odor intensity depends not only on emission rates, but also on source size and numbers of emitting organisms [10]. Monocultures create enormous sources of attractive cues. In social insects, which comprise several invasive species, information regarding a food source is quickly transmitted from one individual to the next by chemical trail. Trails are maintained by the workers that follow it, which enables information transit over large distances independently from source strength. Interestingly, the largest insect societies rely more on chemical cues for foraging [11] showing a remarkable high capacity for mass recruitment through the deposit of chemical trails.

A high olfactory sensibility, allowing detection from a greater distance, should be an appreciable advantage for invasive species. Ecologically adaptative differences in the olfactory organs within insect groups have been looked for with mixed results. The number of sensilla may be larger either in polyphagous, or in specialist herbivores, according to the taxa considered [12]. The antennal length of the invasive moth *Uraba lugens* is correlated to the male's ability to detect female pheromone, probably because longer antennae carry more sensilla [13]. However, many other parameters like olfactory receptor number, or degree of convergence on antennal lobe neurons also contribute to sensitivity and whether the dispersal rate of insects is correlated to responsiveness to odor cues warrants experimental evidence.

Importance of odorscape quality and habitat cues

The quality of a milieu depends not only on the abundance of resources it contains, but also on their accessibility and absence of dangers. Similarly, in addition to host cues, odorscapes contain VOCs released by unsuitable plants and anthropogenic volatile organic compounds (AVOCs) that may disrupt communication [3,14,15]. On the other hand, hosts are often associated with specific habitats which makes habitat cues (HCs) good predictors of their presence [16]. It is thus important to consider the odorscape global "quality" defined by the congruence of information carried by the different VOC categories. I believe this concept is particularly important in the case of invasive herbivores which must find their usual hosts in different environment. For instance, I expect them to be less responsive to HCs, which has been verified in some cases [17,18], while maintaining high responses to host cues [19]. However, HC importance varies between insect species [16] and the limited empirical data available does not permit to generalize to any invasive species.

Adaptability and behavioral plasticity of insect olfaction

Invasive insects are necessarily confronted with new environments and their capacity to extract relevant information from the new odorscapes determines their survival. Within newly invaded assemblages they may be naïve to cues from resident predators or toxic plants, unsensitive to VOCs released by attacked indigenous plants, confronted to local plants that may not respond to attacks by exotic pests… An example of such "olfactory mismatch" is provided by the numerous bark beetle species shifting from saprotrophy to attack live trees in their introduction area [20]. Thus, invasive insects need behavioral plasticity, genetic adaptability, and related traits to thrive [21].

Behavioral plasticity through individual experience is suggested to be favored when environment is predictable within the lifespan of an individual but unpredictable between generations [22], which is the case in invasions. Innate behaviors may be changed through associative and non- associative forms of learning after experiencing new odorants [22]. Generalization is the capacity to respond to newly encountered odorants the same way as stimuli already experienced. Resulting lower discrimination could increase adaptability to new resources. Whether invasive phytophagous pests show larger behavioral variability and learning capacities remains to be demonstrated. Some evidence comes, however, from social insects. The newly invasive Asian needle ant, *Pachycondyla chinensi,* can settle in areas dominated by an established invader, the Argentine ant, *Linepithema humile.* Its submissive behavior and decreased responsiveness to further encounter with *L. humile,* facilitate the colonization of territories occupied by more aggressive ant species [23].

A striking example of response to a new niche are host shifts that may occur in herbivorous insects when encountering a novel plant species, where either the insect or the plant is exotic. The gracillariid moth *Marmara gulosa,* for instance, expanded its host range from native willows to various introduced crops [24]. Host shifts result from coordinated genetic changes and are often mediated through evolution within sensory system, including changes in chemoreceptor genes. A novel phenotype has given *Drosophila suzukii* the opportunity to occupy a new niche, ripe fruits, and within the past decade it has spread throughout Europe and North America causing substantial damages in orchards [25]. The implication of rapid sensory receptor evolution in the adaptation to new niches is pervasive in Drosophilidae. For example, modifications to receptor genes are linked to the transition to herbivory in *Scaptomyza flava* [26] or the oviposition preference for morinda fruits in *Drosophila sechellia* [27,28].

Anthropogenic stresses to insect chemical communication

Consequences of insect odorscape artificialization

Most agrosystems are artificialized habitats of recent origin in which agricultural practices favor the growth of a single crop plant or cultivar and eliminate weeds or edge plants and their associated fauna. Although it needs experimental confirmation, I postulate that the resulting odorscapes show three main characteristics: (1) dominance of one plant volatilome, (2) low emission variability due to the low genetic variability of the cultivated plant, (3) crop volatiles are not masked by the odors of other plants. The consequences are intense, reliable, and salient host cues associated to a high resource density, which probably favor the spreading of mobile phytophagous species with high multiplication capacities, a characteristic of invasive species. The crop plant being the only available resource agrosystems offer no alternative but starving, resulting in strong habituation and adaptation to defense signals and finally increasing damages to crop. Odorscapes themselves may have direct physiological effects. For example, exposure of *Helicoverpa* caterpillars to plant volatiles enhances their P450 system, which in turn increases resistance to pesticides or natural toxins [29].

Air pollution

Semiochemicals half-life in the atmosphere has considerably decreased in the Anthropocene due to increased production of reactive oxygen species (ROS) [30]. The most studied ROS, ozone, can theoretically interfere with host plant localization by (1) altering olfaction (however, direct effects of ozone on olfactory organs of insects have been found relatively modest [31]); (2) altering the emitting plant metabolism and (3) modifying the plant odor by reaction in the atmosphere [32–34]. Even moderate levels of air pollutants (e.g. 60 ppb O_3) substantially degrade floral volatiles reducing pollinator ability to locate flowers [33]. Reduction of host plant attractivity by ozone has been observed [35,36]. However, what has been identified as a major problem for pollinators, that are very mobile when foraging, may not be so critical for crop pests because of food abundance. Pollution impacts also depend on insect behavioral plasticity. Foraging *Manduca sexta* that initially find an ozone altered floral scent unattractive can target an artificial flower using visual cues and associate the ozone-altered floral blend with a nectar reward [37]. Besides ROS, we know virtually nothing on the impacts of anthropogenic VOCs (AVOCs) on herbivory. Although significant efforts are paid to limit the effects of organic pollution in rivers or the atmosphere, its effects on communication probably start at very low concentration. AVOC effects on ecosystems are all the more difficult to assess as they could indirectly favor opportunist species by giving them an advantage over less resilient native competitors or antagonists.

Global change effects on host-plant volatilomes and odorscape

Global change affects plant emissions of VOCs in intensity and quality so we can fear it alters information flows between trophic levels. Plants producing more stress signals, become either attractive for beetles feeding on weakened trees or repellent to many herbivorous insects. Global change will probably increase the variability in plant volatile emissions, because different metabolisms are affected, the effects of the different factors combine not linearly, and plant reactions show inter-individual variability [14]. This will make plant volatiles less reliable to insects. Moreover, pheromone communication is affected by physical change in the environment like temperature elevations [38], so we can expect direct effects of global change on insect reproduction. The spectrum of phenotypic traits that make a species vulnerable to global change (specialized habitat or microhabitat requirements, narrow environmental tolerances, poor ability or limited opportunity to disperse to, or colonize, a new or more suitable range [39]) differ from traits shared by invasive species. For instance, opportunistic herbivores are probably more tolerant to plant emission variability, which should globally advantage invasive species over specialized herbivorous insects.

Invasive species as sources of odorscape changes

Invasive species themselves disrupt the functioning of native communities with effects rippling through the food chain [40]. An example of how chemically mediated interferences act in a multitrophic context is provided by two lepidopteran species, *Plutella xylostella* and *Pieris rapae*, which coexist on crucifers. The same crucifer host emit a different odor blend in response to damages by each herbivore. The wasp *Cotesia vestalis* is attracted to the odors of plants attacked by its host *P. xylostella*, but not by plants attacked by *P. rapae*, an unsuitable host. Female *P. xylostella* take advantage of that fact by preferring to oviposit on plants attacked by *P. rapae* [41]. Exotic and native species may also compete for communication channels, which could disturb the sexual communication of native species. Possessing a pheromone very different from that of the native potential competitors confers an advantage [42]. Unfortunately, there are too few studies at community-level of olfaction-mediated interactions involving invasive species [40,43].

Global change and challenges for biocontrol using semiochemicals

Invasive species monitoring and attractant technologies

Pheromone traps are effective tools for tracking invaders at low densities in their establishment phase. However, they may locally create an infestation if individuals attracted are not trapped [44]. Care must be taken to design trapping devices adapted to specific pests and working under variable environments. Evaporation or permeation, mechanisms by which semiochemicals are released from passive dispensers, are temperature dependent and volatility is also affected by hygrometry. It this makes semiochemicals emission rates very sensitive to climate. Increased air pollution may necessitate adding more antioxidants and UV-protectants but additives can significantly influence release rates. Despite progress in dispenser technology, ratio control remains a technological issue when attractant blends include VOCs whose emission rates have different temperature optima, which can result in sub-optimal attractivity. Over their large distribution area invasive insects may present different pherotypes, either because they adapt their pheromone to local conditions, or because they stem from different genetic pools. To achieve optimal attractivity it will be increasingly necessary to adjust lure composition according to local populations and to develop dispensers maintaining emission rates and ratios independently from climatic conditions.

Managing odorscapes to mitigate invasions

Mating disruption is a good example of a successful odorscape manipulation. To get around the technological challenges already mentioned, using companion plants that naturally emit repellents, masking host cues, or attract insects away from fields, has been a success [45]. Plants used as natural emitters offer other "ecoservices", providing for instance olfactory cues for beneficial arthropods. Agroecological practices maintaining diversity might simultaneously preserve the odorscape functionality. Invasive insects can be controlled by introducing natural enemies and attention should be paid to the odorscape when introducing beneficial arthropods either to enhance their activity, or avoid side effects [46]. The generalization of these strategies to the growing number of invasive species demands better knowledge of the odorscapes.

Conclusions

While global change effects on olfaction and impact on insect populations seems sufficiently documented, their consequences on insect invasiveness are less explored. This review fails to delineate an universal "olfaction invasiveness syndrome" but case studies revealed traits with risk predicting value. Capacity to rapidly adapt to perturbated environments and anthropogenic disturbances favors species with high sensory flexibility. Many more sensory traits of invasive species should emerge from meta-analyses. To better evaluate risks and anticipate solutions, we plead for the development of a sensory ecology investigating production, transmission and perception of chemical signals, at landscape level. Landscape level is critical to understand invasion dynamics, but we know virtually nothing on the spatiality of odors among habitat patches, corridors, and matrices. A landscape ecology integrating semiochemicals within spatial patterns will open the path for invasion mitigation in agrosystems.

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Recommended references

*[3] A paper reviewing the effects of air pollution on the olfactory interactions between flowering plants and their pollinators and suggesting future research topics.

*[16] A detailed recent review paper emphasizing the importance of habitat cues in diverse insect groups.

*[20] This paper explains the emergence of virulence in invasive bark beetles by a combination of factors coming from host-plant, fungi and insects, resulting in “sensory mismatch” between innate behaviors and new ecological context.

*[45] The authors show how air pollution disrupts communication between plants and pollinators. However, because of multimodality and learning capacities, foraging moths can shift to other cues to locate flowers.

*[14] This review paper offers a perspective on the complexity of olfactory interactions in ecosystems and stimulates reflection by showing the increasing complexity of olfactory communication as a function of the trophic level.

*[40] This paper shows how invasive species can modifies the olfactory interactions at different trophic levels.

*[25] One of the most recent among the different papers dissecting the mechanisms underlying host shift in the invasive fruit fly, *Drosophila suzukii*, a case example of genomic and behavioral adaptation in an invasive insect species.

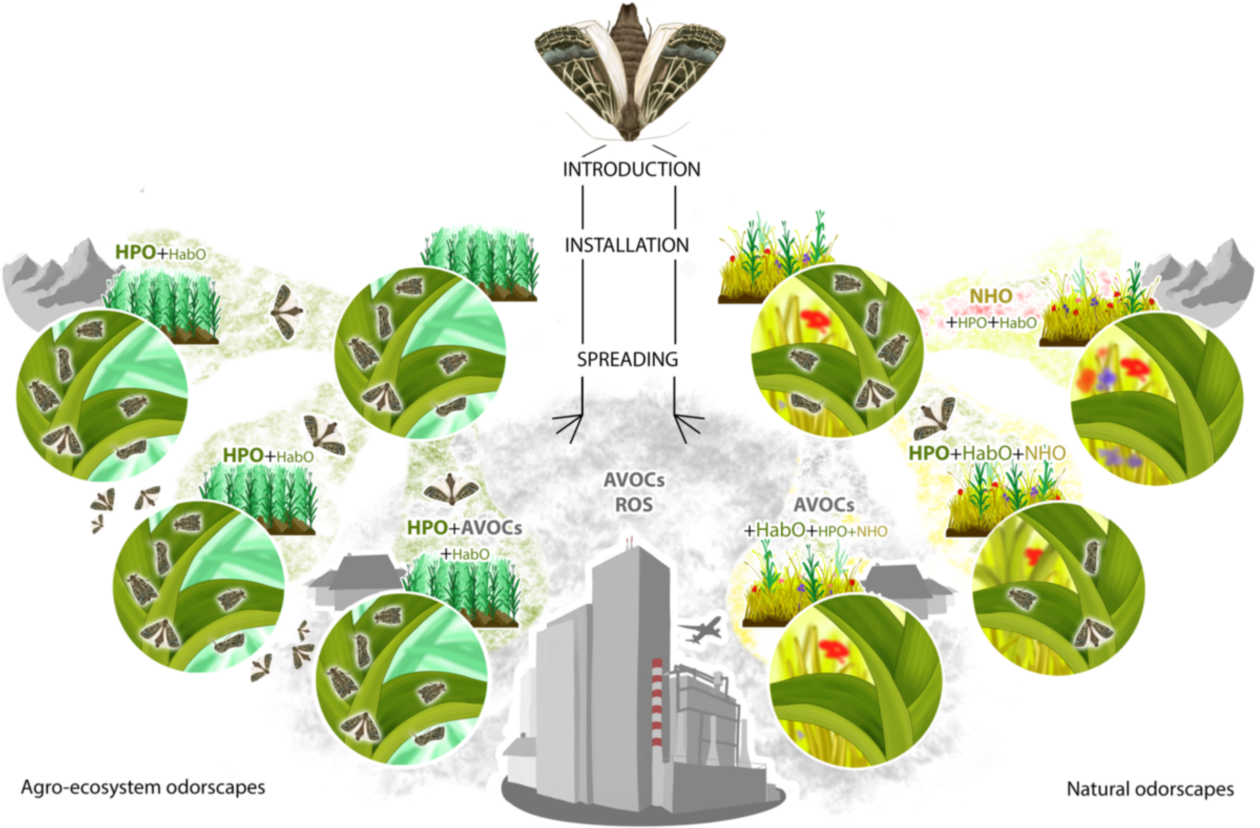
Figure

An interpretative scheme of the role of olfaction in insect invasion under the pressure of global change.

The figure illustrates how different odorscapes could facilitate invasions by herbivorous insect in agro-ecosystems (*left side*) *versus* natural ecosystems (*right side*) under different degrees of global change and anthropic pressure (from top to bottom). Three hypothetical odorscape evolutions are evoked for both ecosystems. *Bottom line*: in close proximity to urban or industrial areas odorscapes are strongly affected by air pollution and emissions of anthropogenic volatile compounds (**AVOCs**); *middle line*: odorscapes of rural or wild areas are made of host plant odors (**HPO**), associated to the typical habitat odors (**HabO**) and mixed with some non-host plant odors (**NHO**); *upper line*: in the odorscapes of semi-rural less intensive systems or fragmented populations in less favorable natural areas, HPO salience decreases due to masking by NHO and untypical HabO.

The first step of biological invasions, introduction, is most often passive, depending for instance of transportation along international trading roads. By contrast, installation and spreading rely on the capacity of invaders to identify HPO in spite of eventual differences in volatile emissions, because of geographical genetic variability, and in different odorscapes. Industries, transports, animal husbandry, or agro-food industries result in the production of atmospheric pollution by reactive oxygen species (**ROS**) and sensory pollution by **AVOCs**. Mainly produced in urbanized and industrialized areas, both types of pollution spread over peri-urban agro-ecosystems, and even remote natural ecosystems, with strong impacts on the olfactory interactions. However, pollution impacts are probably less critical for crop pests because they rely on larger amounts of HPO. By contrast, specialized local herbivorous, pollinators, natural enemies and potential competitors are affected by diminution of active range, alteration of odor blends of host signals, which could indirectly favor invasive species.

Following differences in floristic diversity, HPO salience greatly varies in the odorscapes of cultivated and wild areas. In intensive culture areas (*left side*), the crop plants cultivated over large surfaces form huge HPO sources. The available land is mainly occupied by a single variety of the crop plant and most companion plants are eliminated. Low genetic and species diversities result in simplified odorscapes that contain a low diversity of HabO and NHO. Host plants are thus easy to find and installation is made easier by the resource abundance over large areas. Attractivity over longer distance facilitates spreading from field to field. In natural landscapes (*right side*), host-plants often grow in a much more complex biological matrix where HPO mix to a great diversity of HabO and NHO. Botanical biodiversity reflects in the VOC diversity which reduces HPO salience. However, in the habitat typical of the host-plant HabO provide reliable information on the habitat quality. HPO salience is even lower for host plants growing in less favorable natural habitats in which they are in competition with more NHO that may mask them, or even repel invasive phytophagous insects from less suitable habitats.


INTRODUCTION
INSTALLATION
SPREADING
HPO+HabO
HPO+HabO
HPO+AVOCs
+HabO
AVOCs
ROS
NHO
+HPO+HabO
HPO+HabO+NHO
AVOCs
+HabO+HPO+NHO
Agro-ecosystem odorscapes
Natural odorscapes