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Will climate change affect insect pheromonal communication?

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Understanding how climate change will affect species interactions is a challenge for all branches of ecology. We have only limited understanding of how increasing temperature and atmospheric CO_2 and O_3 levels will affect pheromone-mediated communication among insects. Based on the existing literature, we suggest that the entire process of pheromonal communication, from production to behavioural response, is likely to be impacted by increases in temperature and modifications to atmospheric CO_2 and O_3 levels. We argue that insect species relying on long-range chemical signals will be most impacted, because these signals will likely suffer from longer exposure to oxidative gases during dispersal. We provide future directions for research programmes investigating the consequences of climate change on insect pheromonal communication.

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Introduction

Since the 19th century, the atmospheric concentration of greenhouse gases, particularly carbon dioxide (CO_2), have drastically increased causing changes to environmental parameters at a global scale, including temperature [1]. Recent studies now highlight the impact of such modifications on the whole dynamics of life [2]. Through cascade effects, entire ecosystems are being disturbed, impacting the population dynamics of inhabiting species and altering the ways that they interact with one another. This phenomenon has been well documented for insect–plant interactions mediated by plant secondary metabolites [3,4•].

Communication between insects relies mainly on semiochemicals, which are organic molecules involved in the chemical interactions between organisms [5]. They include pheromones (intraspecific communication) and allelochemicals (interspecific communication). Pheromones have a variety of important roles, especially related to foraging, aggregation or sexual behaviour [6]. Using behaviour-changing pheromones (named releaser pheromones) is central to integrated pest management (IPM) [7], so predicting the impact of climate change on IPM programmes depends on understanding the impact of changes in related abiotic parameters on insect pheromonal communication. However, few studies have focused on how changes in climate will disturb each stage in the pheromone pathway from emitters to receivers (Figure 1).

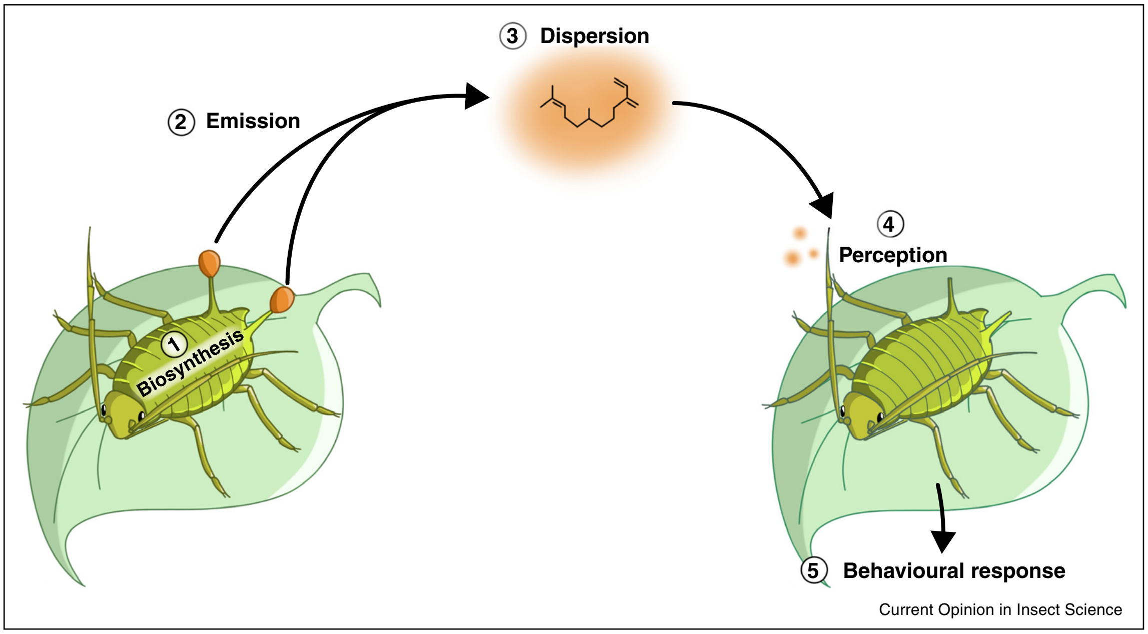
A pheromone's long journey

Biosynthesis

Most insect pheromones are synthesised *de novo* and secreted in specialised glandular tissues, regulated by various enzymatic activities [8,9]. Others are sequestered and/or derived from dietary precursors and depend on the nutritive quality of the diet. Elevated temperatures will likely have pronounced effects on pheromone biosynthesis. Because insects are ectothermic and poikilothermic, changing their body temperature will influence enzymatic activities [10], and impact pheromone biosynthesis both quantitatively and qualitatively. For example, temperature modifies the ratio of compounds in the sex pheromone of the potato tuber worm moth *Phthorimaea operculella* [11]. Moths (Lepidoptera: Heterocera) differentially use the same precursors to synthesise different pheromone components, thanks to a wide variety of enzymes (*i.e.* oxidase, desaturases, reductase), allowing specific recognition [12]. Although these insects can perceive a wide range of pheromone components, the activation of neurons in their macroglomerular complexes, and the elicitation of relevant behavioural responses, is combinatorial: it will happen only when the right combination and ratio of components is perceived at the same time [6].

Developmental temperature has a strong influence on adult life history, morphology, and physiology. Furthermore, in some species, pheromone production and availability is

Figure 1



Intraspecific chemical communication in insects may be subdivided into five steps that are probably impacted by modifications to atmospheric gas composition and associated raise in ambient temperature. Graphic art by Carolina Levicek.

dependent on larval, pupation, and/or adult developmental conditions [8,13,14], hence the effect of abiotic parameters on all the insect life stages is important. In the male beewolf, *Philanthus triangulum*, an increase of 5 °C in the larval rearing temperature led adult males to produce more pheromonal secretions [13]. Moreover, warmer rearing conditions led to higher relative amounts of compounds with high molecular weight. As a consequence, a shift in temperature could weaken intraspecific relationships of these insect species by reducing the efficiency (*i.e.* specificity, activity, timing of production, *etc.*) of their chemical communication.

Increasing atmospheric CO_2 concentrations [1] could also affect the biosynthesis of insect pheromones. Changes in CO_2 concentrations affect plant biochemistry, including the synthesis of secondary metabolites [4•]. Since some phytophagous insect species produce their pheromone components based on precursors taken from their host plant, we hypothesise that phytophagous insects could be among the most vulnerable to changes in atmospheric CO_2 concentrations, through cascade effects of CO_2 on plant chemistry [15,16•]. In *Holomelina* spp. moths, leucine is the starting material for sex pheromone production [17]. In bark beetles, while pheromones are produced primarily *de novo* mainly through the mevalonate pathway, some aggregation pheromone components arise from the hydroxylation of host tree-derived secondary metabolites [18].

Emission

Few studies have specifically investigated how changes in temperature and atmospheric gas composition act on pheromone release. In the moth *Striacosta ablicosta*, increase in average temperature does not affect the calling behaviour of females, while an increasing variation between photophase and scotophase temperatures alter significantly this behaviour, as also observed in *Phyllonorycter junoniella* [19]. Ladybird larvae deposit more long-chained hydrocarbons — used as oviposition deterring pheromone — when exposed to rising temperature [20••]. An increase in atmospheric CO_2 concentration reduces the emission rate of the alarm pheromone in pea aphids (*Acyrthosiphon pisum*) (Boullis *et al.*, unpublished).

Signal dispersal

After pheromone release by the emitter, volatile pheromones may be altered by oxidative gases such as ozone on their way to the receiver. Most pheromones are simple, lipophilic and of low molecular weight, which facilitate their long-distance dispersal in the air. Other pheromones are heavier molecules, including semi-volatile pheromones and cuticular hydrocarbons (CHC), which are used in short-range or contact communication [6]. Like phytogenic volatile organic compounds (VOCs), insect pheromones made of unsaturated terpenes may be decomposed by ozone [21–23]. Similar terpenes are constitutive of sexual, aggregation or alarm pheromones in several insect taxa, such as ladybirds [24,25], aphids

[26,27], bark beetles [28] and fruit flies [29]. As highlighted for *Drosophila melanogaster*, terpenes could lose their biological activity after short-term ozone fumigation at environmentally-realistic concentrations (ranging from 40 to 120 ppb) [30]. The lifespan of trail-pheromones and alarm-pheromones, which act in a short time window and small spatial scale [31,32], may thus be further reduced in an ozone-rich atmosphere. In addition to the effect of ozone on pheromones, temperature acts on the volatility of semiochemicals. In the case of pheromones dispersed over long distances such as sex or aggregation pheromones, temperature changes may modify the shape of scent plumes and disturb the efficiency of insects to reach their target [33].

Increased temperature may also alter heavy molecules, such as cuticular pheromones involved in contact recognition. Because of their low volatility, temperature will likely more affect the chemical composition of pheromonal blends (ratios of components). Insects' cuticular lipids exist in a solid state at ambient temperatures, but they can partially melt upon contact with the animal's surface (with higher than ambient temperature), which, in turn, induces modifications in the ratios of cuticular composition [34]. As observed in *D. melanogaster*, a 4 °C increase of ambient temperature changes cuticular hydrocarbon composition, which lead to sexual isolation and affect the stability of ecological communities [35].

Perception

Pheromone perception occurs through a complex series of events, starting when pheromones enter the sensilla lymph and ending at brain processing [36–38]. Very few data are available on how environmental changes will impact pheromone perception, but one recent study showed that the sex pheromone perception was altered in male moth *Caloptilia fraxinella* under elevated temperature [39].

Because insects are poikilotherms, changes in their body temperature may alter the affinity between a pheromone and its binding protein (PBP) that transports this molecule through the sensillum lymph to olfactory receptor neurons. In *Apis mellifera* and *A. cerana*, ASP1 acts as PBP that has a good affinity to the queen mandibular pheromone [40]. However, increasing temperature weakens the van der Waals and hydrogen bonds established between the queen mandibular pheromone and PBP, which implies that binding affinity between these molecules can be lessened, inducing a reduced efficiency of the signal transportation trough the hydrophilic lymph [41].

Behavioural response

Although insect responses to pheromones are innate, they may be conditional and influenced by direct (age, sex, hormonal status, experience) and indirect (cascade effect) factors [6]. Temperature is a major abiotic factor together with photoperiod that determines the intensity and timing of various insects' activities [42,43]. Field studies related to IPM approaches on several lepidopterans have shown that the diel periodicity of their sexual attraction is modified by both photoperiod and ambient temperature [44–46]. Moreover, the seasonal rate of capture by trap catching is generally related to the associated temperature, depending on specific seasonal degree-days that insects are subjected to [47,48]. By this logic, an increase in global surface temperature may shift the seasonal periodicity of sex-related flights in insects, requiring an adaptation of monitoring and treatment periods against these pest insects. Another example is the impact of changing temperatures on ant foraging activity. Ants that use chemical recruitment tend to forage at lower temperatures compared to those that do not [49]. Therefore, accelerated pheromone decay caused by increased temperatures is expected to alter trail-following behaviour and to be more detrimental to foraging by mass-recruiting ant species [50].

In addition to a general increase in insect mobility, some specific behavioural responses to pheromones can be altered by elevated temperature. For instance, male moths *C. fraxinella* reared under increased temperature during their reproductive diapause and subsequently exposed to female sex pheromones in a wind tunnel show more pronounced sexual responses [39]. At higher temperatures, male moths also show a lower level of specificity towards their sex pheromones, due to shifts in behavioural thresholds related to plume orientation and to the elicitation of upwind flight [51].

With regards to the impact of atmospheric CO_2 concentration, the escape behaviour of aphids reared under elevated CO_2 concentrations (*i.e.* 2100 predicted levels) is lower compared to those reared under ambient CO_2 conditions [52,53,54••]. The increase in CO_2 concentration could affect the escape behaviour of aphids by reducing the enzymatic activity of acetylcholinesterase, which is involved in neuronal transmission related to alarm signal perception [55]. This altered ability of aphids to produce and/or respond to the alarm pheromone may alter their defensive behaviours under changing climatic scenarios.

Conclusions, wider context and future directions

Based on the existing literature, we suggest that pheromonal communication in insects will be disturbed by increases in temperature and atmospheric gas concentrations. Insects relying on long-range chemical signalling, involving complex blends of molecules, are likely to be more impacted, due to the possible perturbation of enzymatic properties (leading to modification in compound ratio) or signal degradation by oxidative gases during dispersal (disrupting pheromone plumes). Behavioural aspects of chemical communication (emission of the signal and induced behaviours) could also be affected as a consequence of shifts in optimal conditions affecting phenology and/or physiology. However, because climate change effects on pheromonal communication may be masked by the daily and seasonal rhythms of behaviour and physiology, our knowledge of the specific effects of climate change on pheromone signalling is sparse.

In this review we only focused on intraspecific (pheromonal) chemical communication, although allelochemical-mediated communication in the broader sense will likely also be affected by climate change. Indeed, as already suggested in plant–insect relationships, the changes of several abiotic parameters could affect interactions between organisms from different trophic levels, and thus affect the dynamics of ecological systems. However, it is difficult to predict how climate change will impact chemical communication between insects for several reasons. Abiotic factors could affect the different stages of insect pheromone communication (Figure 1), and the response of insects to particular environmental conditions could be species-specific. Moreover, the interactive effects of elevated atmospheric ozone and CO_2 concentrations, as well as temperature increase, on chemical-mediated interactions have received limited attention, despite that all of these factors are affecting ecosystems' stability. A key solution lies in the use of mesocosms and other facilities where multiple components of climate change can be manipulated in a multispecies context [56]. This approach could be used to assess how all climatic changes associated with a predicted scenario in the coming century might interact to impact the production of plant secondary metabolites, and the associated cascade effects on the pheromone production in phytophagous insects.

In an IPM context, the efficiency of pheromone slow-release devices could be reduced following climatic modifications, since their release kinetics are sensitive to various climatic parameters including temperature [57]. Moreover, because the behavioural response of insects to pheromones and allelochemicals could also be modified as a consequence of climate change, we suggest that all semiochemical-based IPM strategies will be impacted, including mass trapping, mating disruption, monitoring, push-pull strategies and other intercropping systems.

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