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Forum article

Ozone pollution disrupts plant-pollinator systems

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Abstract

Ozone pollution disrupts floral visual and volatile signals, olfactory perception of volatile communication signals, and learning, memory, and behavior of pollinators. These changes could have implications for plant-pollinator systems.

Ozone pollution

In recent decades, **ozone** (see Glossary) levels in the lower **troposphere** have risen [1]. Ozone is a **secondary pollutant** formed by the reaction of **volatile organic compounds** (VOCs) and **nitrogen oxides** (NO_x) under sunlight, and this complex chemistry of ozone hinders its mitigation. As a result, ozone exposures are likely to widely exceed the **critical levels** of legislative standards for the protection of vegetation throughout the northern hemisphere by 2100 [1].

Ozone pollution causes widespread vegetation damage, including discoloration and other visible injuries. It also changes foliar chemical composition and the amounts and blend of plant-emitted VOCs [1]. These affect plant-insect interactions because (i) plant tissue color signals insects, (ii) nutrients and **secondary metabolites** are of dietary importance for insect herbivores or are toxins against them, and (iii) biogenic VOCs (BVOCs) are chemical communication signals [1]. These effects of ozone could alter the composition and structure of insect leaf herbivore communities [1]. More recent studies demonstrate that ozone also affects pollination [2–4]. Here, we discuss potential ecological, evolutionary, and agricultural implications of air pollution effects on plant-pollinator systems (Fig. 1).

Flowers and pollen

Ozone pollution affects pollen by oxidizing components of pollen wall or via production of hydroxyl radicals, inhibits pollen tube growth, and changes the amount of pollen and nectar and their chemical composition (reference in [3]). Ozone can accelerate flowering, extend flowering duration, or alter the number of open flowers [3,5]. This depends on the ontogenetic stage of the plant at exposure, due to different strategies for investment toward reproduction [3,5]. For example, ozone treatment increased the number of pollinators that visited younger *Sinapis arvensis* plants but generally caused negative effects on older plants, depending on the number of open flowers and pollinator guild [5]. Furthermore, high ozone can decrease petal size and changes pigmentation and color [6]. While BVOCs orient pollinators over long distances, visual acuity of pollinators is largely restricted to centimeters to few meters [7]. Such changes in flowers and pollen characteristics could disrupt short-range foraging behaviors and, thus, pollination in ozone-polluted atmospheres [7].

Semiochemicals emitted by plants

Pollinators utilize floral blends to orient in space, discriminate flowers, and select host plants [8,9]. Ozone differentially affects the emission of individual compounds, increasing some and decreasing others. It therefore changes the relative contribution of specific compounds to the scent blend and the ratios between compounds [7,10,11]. Ozone also produces new volatiles as a result of chemical reactions of already existing volatiles [7,12]. The ratio of specific compounds in a blend is important for information processing [9,13], and such qualitative changes in floral scents due to ozone affects learning and recognition of olfactive signals by pollinators [10]. Decreased concentration of pollinator-used volatiles and a reduction in the diffusion of volatiles in space suggests that pollinators will spend more time searching for scent trails to find flowers [11,12]. The length of the plant scent trails might decrease from kilometers in the pre-industrial period to less than 200 m today [10,12]. Such effects vary spatiotemporally, e.g. with greater relevance in areas with isolated flower patches and in relation with changes in ozone concentrations [12]. Ozone-induced chemical transformation of floral blends becomes stronger as the plume moves farther from the emitting flowers, which suggests a potentially greater threat to pollination in areas with distant plant patches [7,11]. Overall, the alteration of BVOCs emitted by flowering plants can modify the chemical-use efficacy of pollinators, decrease their success to locate floral scents plumes, and increase their foraging times [11].

Pollinator behavior

Ozone indirectly affects pollinator attraction by modifying BVOCs and decreasing the attractiveness of floral scent to pollinators, e.g. the generalist buff-tailed bumblebee *Bombus terrestris* to black mustard (*Brassica nigra*) [10]. It also affects pollinators directly by altering olfactory learning, decreasing the recall of learned scents, and enhancing the response to new scents, which also impairs discrimination of the antennae [14]. Ozone causes both direct and **carry-over effects** on the activity and sensitivity of antennae and insect motility of different pollinators, e.g. in the Western honey bee *Apis mellifera* [13,14] and fig wasp *Blastophaga psenes* [15]. The effect varies among volatile compounds, likely due to the distinct effects that ozone has on different proteins and chemoreceptors; however, we note a lack of evidence for ozone oxidation of olfactory receptors and odorant-binding proteins [13]. The sensitivity to ozone differs among pollinators, such as between the *B. psenes* and the *B. terrestris,* with the former being more affected by ozone [14]. Hence, ozone compromises the ability of ecologically-differing pollinators to trace and react to floral VOCs, but the effects depend on the type and concentration of BVOCs and the size and duration of ozone exposure [14].

Pollinators deal with olfactory cues through innate recognition of compounds together with behavioral plasticity [7]. Ozone also alters the color perception of pollinators, due to changes in flower optical properties, and this depends on both ozone exposure and pollinator guild [6]. Although it disrupts the innate attraction, e.g. of the tobacco hornworm *Manduca sexta* (nighttime pollinator) to sweet tobacco *Nicotiana alata*, visual navigation and learning to associate altered floral scents with rewards can counteract this effect in some cases [7]. The ability to learn new floral odors due to ozone-driven chemical transformation counteracts ozone impacts on plant-pollinator systems [7].

Ozone may further decrease the proportion of active pollinators, a distress behavior implying fewer potential foragers [15]. While ozone may not strongly affect overall pollinator preference in some cases, different pollinators have different responses [2,3]. For example, bumblebees (*Bombus terrestris*) visited more flowers on ozone-treated wild mustard (*S. arvensis*) plants, which might be due to increased number of open flowers [3]. Ozone-treatment also extended honeybee (*Apis mellifera*) flower visits, but hoverflies (*Eristalis tenax*) visits did not change with ozone treatment [3]. Likewise, diesel exhaust (containing NO_x) and ozone pollution individually and jointly decreased the number of wild and managed insect pollinators and their flower visits [2]. These effects decreased yields of black mustard (*Brassica nigra*), even at exposures considered safe by the existing air quality standards [2]. Changes in specific pollinator groups shaped these effects, as is the case of bees, butterflies, flies, and moths in this study [2]. Most of the evidence for the affected pollinator behavior come from laboratory assays or highly controlled experiments, but recent *in situ* evaluations confirm earlier findings [2,4].

Ecological implications

Ozone concentrations are usually lower during the nighttime. However, since nighttime ozone concentrations are increasing, ozone pollution may affect nocturnal pollinators more than previously thought. New studies are needed to test this assumption and to determine whether ozone pollution changes plant-pollinator systems due to altered interactions between daytime and nighttime pollinators.

Generalists learn floral scents and their value, whereas specialists inherently prefer the BVOC blends specific to their host plants [9,10], hinting at potential differences in the long-term responses to ozone between generalist and specialist pollinators. Expected responses also depend on the signals used by different pollinators and pollinator stability [2].

As ozone decreases with proximity to urban centers due to elimination by NO_x, potential shifts in pollinator communities and evolutionary changes in the plant-pollinator systems are expected among urbanization gradients. However, the prediction of such alterations due to the ozone specific effect is challenging because primary air pollutants (e.g. NO_x from diesel exhaust) also influence pollinator attraction toward flowers [2]. Nevertheless, preliminary evidence suggests that the effect of ozone on pollinator foraging behavior may not be modified by NO_x [2,4]. Moreover, data from North-West Europe suggest that high ozone exposures may also exacerbate the effect of pesticides on pollinators independent of NO_x [4].

Evolutionary implications

As pollinators rely on floral signals, ozone pollution can alter plant-pollinator mutualisms by affecting spatiotemporal patterns and characteristics of the floral scents. Hence, pollinator dispersal strategies may also be modified. The high spatiotemporal variation in floral scents over evolutionary time scales implies selection influence of floral scents [7–9]. But air pollution following the industrial revolution increases the variation in chemical signals [7], with unknown implications. Due to the long time scales, coupling new empirical data with models is needed to uncover potential effects at ecological or evolutionary time scales.

A new generation of inter-disciplinary research programs are needed to evaluate resilience of plant-pollinator interactions in areas exposed to ozone pollution. This will need to consider pollinator plasticity, responses of wild versus cultivated plants, and possible evolution of less ozone-reactive floral VOCs.

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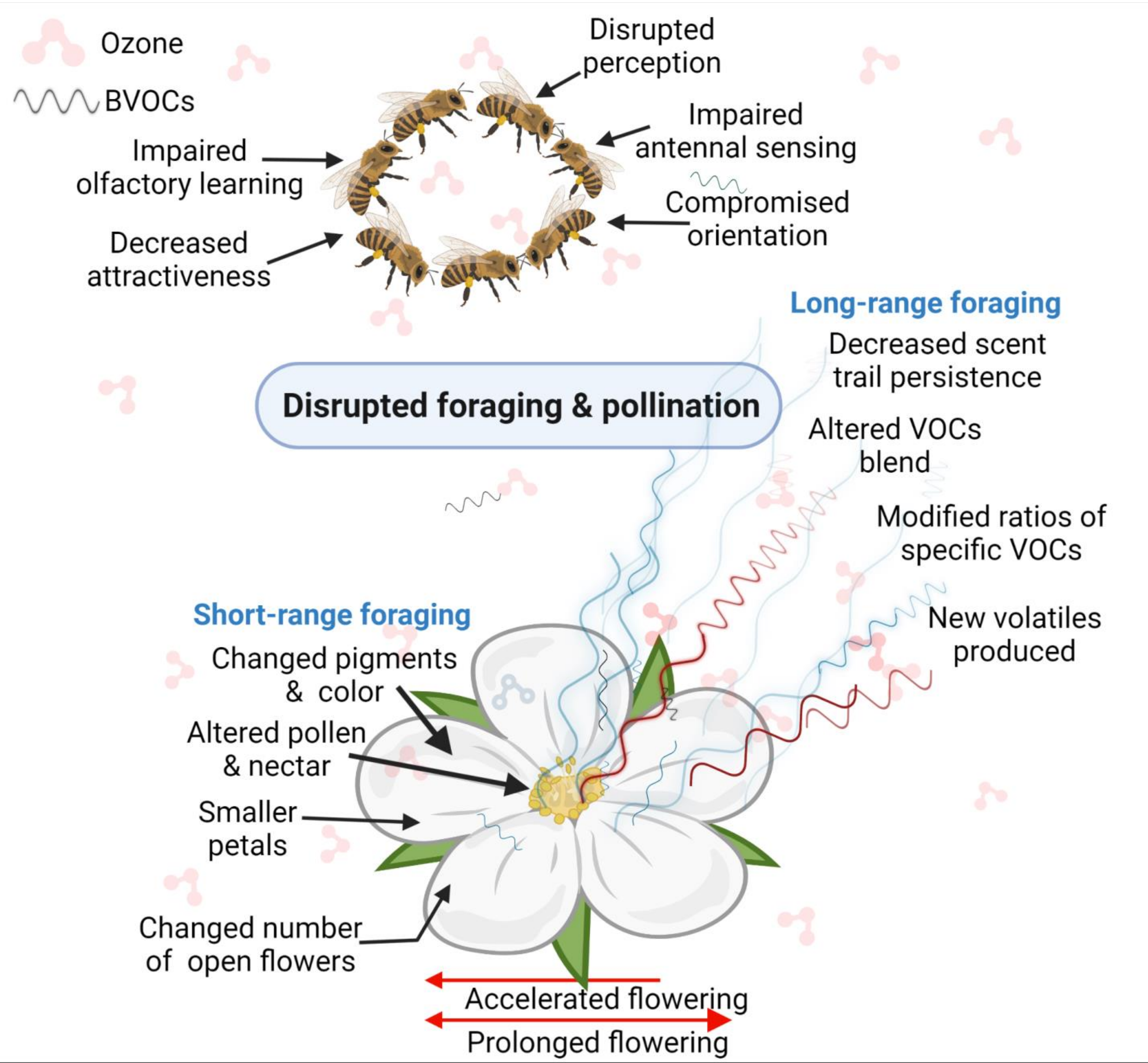
Figure

Fig 1<u>. Ozone pollution disrupts pollination, a key ecosystem service.</u> Ozone alters morphology and quality of flowers, and leads to chemical transformations of biogenic volatile organic compounds (BVOCs) in the air or to newly produced compounds. Ozone decreases pollinator olfaction, vision, and attraction to flowers and degrades and implicates long-distance signals. In ozone-polluted atmospheres, pollinators may have to shift their dependence toward BVOCs that are less or not reactive with ozone and/or learn identifying and utilizing new scent blends at or far from the emitting flowers. Considerable degradation of floral scents might require visual contact with the flowers by chance, since short-distance foraging is also compromised, thus decreasing pollination efficiency. Created with Biorender.



Glossary

Critical level: a level of exposure (concentration or dose) above which sensitive vegetation may be adversely affected.

Nitrogen oxides (NO_x): anthropogenic air pollutants that are formed by combustion of fuel at high temperatures and act as precursors to form ozone.

Ozone: a chemical with three molecules of oxygen (O_3), naturally occurring in the atmosphere. In the stratosphere (above the layer of the troposphere) it provides protection from radiation.

Secondary metabolites: organic chemicals produced as a result of plant metabolism.

Semiochemicals: chemicals produced and released by organisms in the environment and affect other recipient organisms.

Secondary pollutant: a pollutant formed by the reaction of other pollutants in the atmosphere, thus it is not emitted directly by a source.

Troposphere: the lowest part of the atmosphere toward the Earth's surface, contributing 75% of the planetary atmosphere's total mass.

Volatile organic compounds (VOCs): organic chemicals with low water solubility and high vapor pressure, emitted by both anthropogenic and natural sources and contribute to air pollution.