RESEARCH ARTICLE

POLLINATION

Olfaction in the Anthropocene: NO_3 negatively affects floral scent and nocturnal pollination

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There is growing concern about sensory pollutants affecting ecological communities. Anthropogenically enhanced oxidants [ozone (O_3) and nitrate radicals (NO_3)] rapidly degrade floral scents, potentially reducing pollinator attraction to flowers. However, the physiological and behavioral impacts on pollinators and plant fitness are unknown. Using a nocturnal flower-moth system, we found that atmospherically relevant concentrations of NO_3 eliminate flower visitation by moths, and the reaction of NO_3 with a subset of monoterpenes is what reduces the scent's attractiveness. Global atmospheric models of floral scent oxidation reveal that pollinators in certain urban areas may have a reduced ability to perceive and navigate to flowers. These results illustrate the impact of anthropogenic pollutants on an animal's olfactory ability and indicate that such pollutants may be critical regulators of global pollination.

Human activities have drastically changed the environment, including introducing stimuli detected and processed by animals' sensory systems. Human introduction of noise, artificial lights, or anthropogenic chemicals—called sensory pollutants—can change animal behavior and fitness by providing new stimuli or modifying naturally occurring stimuli (*1*, *2*). Noise pollution has been found to negatively affect the fitness of birds, mammals, and insects (*1*, *3*–*5*), and light pollution in urban areas has been implicated in the mortality of migrating birds (*4*). By contrast, much less is known about the effects of airborne pollutants on animal olfactory systems and the corresponding ecological effects (*1*, *6*, *7*). Recent studies have shown that high concentrations of diesel exhaust, or tropospheric ozone, can affect insect odor recognition by potentially degrading the compounds in the scent (*7*–*13*). However, studies often do not reflect the natural spatial and temporal dynamics of atmospheric processing of the odors, and there is still a lack of understanding of how the degradation of natural scents by air pollution affects animal behavior and ecological interactions [however, (*14*, *15*)].

Plant-pollinator interactions are essential for ecological communities and may be especially susceptible to anthropogenic pollutants (*7*, *9*, *10*). Many pollinators navigate long distances by the scents released from flowers (*16*), and scent compounds can be quickly degraded in the atmosphere by reaction with hydroxyl radicals (OH), nitrate radicals (NO_3), and ozone (O_3) pollutants that are formed from natural sources and anthropogenic emissions, such as vehicle emissions (*7*, *11*). During the daytime, O_3 photolysis by sunlight in the presence of water vapor leads to OH, the primary oxidizing agent in the atmosphere (*17*). However, NO_3 is often the dominant oxidant at night in polluted regions (*18*). At night, NO_3 is formed from the reaction of O_3 with NO_2 and achieves high abundances because of the lack of NO_3 photolysis (*18*, *19*). Research has demonstrated that NO_3 is a dominant nighttime pollutant in the troposphere that reacts much faster than O_3 to volatiles, including monoterpenes (*20*, *21*). Despite the nocturnal predominance of NO_3 as a possible oxidant of floral scent in polluted regions, we know little about the relative effects of NO_3 and O_3 on pollinator olfactory behaviors and how these oxidants could affect local and global plant-pollinator interactions.

Oenothera pallida pollination

In the North American Deserts ecoregions, *Oenothera pallida* (Fig. 1) release a strong floral scent that attracts a rich diversity of pollinators, including crepuscular hawkmoths, which navigate many kilometers to locate patches of flowers (*22*, *23*). In these areas, hawkmoths and *O. pallida* will experience varying levels of anthropogenic and naturally produced O_3 and NO_3, with elevated levels of nocturnal NO_3 near or downwind from urban centers (*24*).

To understand the importance of various nocturnal and diurnal pollinators to *O. pallida*, in June and July of 2017 and 2018 we conducted pollinator observation and exclusion experiments at field sites located in eastern Washing[illegible] USA. We observed approximately 300 flow[illegible] over 200 total hours (110 hours at night and 90 hours in the day). This location provides an ideal site to examine plant-pollinator interactions and the impacts of anthropogenic pollutants (tables S1 and S2). During our observations, flowers were visited by diverse pollinators (Fig. 1, A to C, and table S2), particularly nocturnal hawkmoths and diurnal bees. Diurnal pollinators included species of bees, flies, and butterflies. Nocturnal and crepuscular pollinators include moths [mainly hawkmoths, including *Hyles lineata* (hereafter, *Hyles*) and *Manduca* spp. (hereafter, *Manduca*)] and *Lasioglossum* bees (Fig. 1D). To assess the contribution of the pollinator community to *O. pallida* pollination, we conducted a series of pollinator-exclusion treatments, including bagging (to prevent pollinator visits) and cross-pollinating individual flowers by hand, which were later assessed for fruit set. Plants in bagged treatments had significantly fewer fruit sets than those of unbagged plants (pairwise comparison of proportions with Holm correction, $P < 0.001$) (Fig. 1E and tables S3 and S4). The exclusion of nocturnal pollinators also resulted in fewer fruit sets than those of no-treatment controls ($P = 0.0082$), which is consistent with findings from Gregory (*22*) that night-blooming *Oenothera* species are pollinated by hawkmoths. These hawkmoths use their olfactory sense to navigate over kilometer distances and locate patches of *Oenothera* flowers (*25*). At our field site, *Hyles* and *Manduca* were observed to visit *O. pallida* flowers throughout the night (Fig. 1D and table S2).

Atmospheric oxidation of *O. pallida* floral scent

To understand how atmospheric pollution may affect floral scents, we first characterized the *O. pallida* floral scent and identified the principal bioactive compounds for attracting pollinators, especially the hawkmoths (*Hyles* and *Manduca*) (*22*). Floral scents were collected in the field by using headspace traps that allowed the collection of the floral scent compounds. The scent samples were then analyzed by use of gas chromatography (GC) with mass spectrometry (fig. S1 and tables S5 and S6), allowing identification of the compounds in the scent. To identify volatile compounds that pollinators might use to detect the flowers, we performed gas chromatography coupled with electroantennographic detection (GC-EAD) using *Megachile* bees and male *Hyles* and *Manduca* moths (Fig. 2A and fig. S2). All pollinators were sensitive to many of the same compounds in the scent, including monoterpenes such as *cis*-β-ocimene and β-pinene. In particular, the hawkmoths had similar antennal responses and were especially sensitive to monoterpenes (*cis*-β-ocimene and β-pinene) (Fig. 2A). We created a floral odor composed of moth antennal-active

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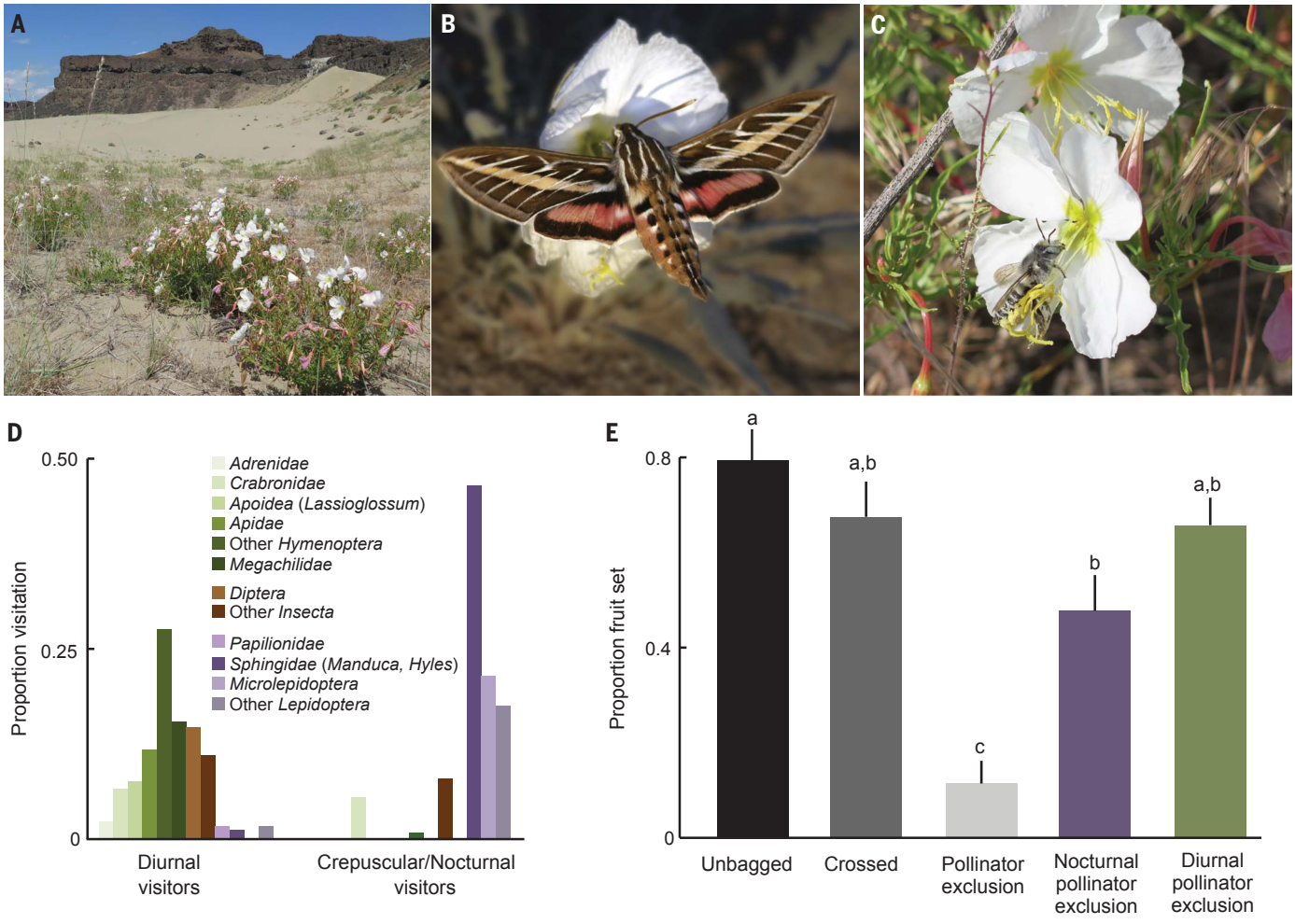

Fig. 1. *O. pallida* pollinator assemblage at near-pristine sites in eastern Washington, USA. (**A**) Example of *O. pallida* habitat in sandy areas in sagebrush steppe of the Columbia Plateau (Echo basin, Washington, USA). (**B** and **C**) Major pollinators of *O. pallida*, including (B) *Hyles* moths and (C) *Megachile* bee species. (**D**) Diurnal and nocturnal pollinators visiting and pollinating *O. pallida*. There was a significant difference in pollinator assemblages ($Z = 17.67$, $P < 0.0001$). (**E**) Pollinator exclusion treatments. Treatments included unbagged (no-treatment control flowers), crossed (bagged flowers, total exclusion of pollinators with manual cross-pollination between individual plants), pollinator exclusion (bagged flowers, total pollinator exclusion treatment), nocturnal pollinator exclusion (nocturnal and crepuscular pollinators excluded), and diurnal pollinator exclusion (diurnal pollinators excluded). Bars are the mean ± SEM. Letters denote groups whose members are not statistically different from each other.

compounds (table S6), and with an emission rate similar to that of the *O. pallida* flower, for use in subsequent laboratory experiments (tables S6 to S8).

To examine the relative atmospheric degradation of floral volatile organic compounds (VOCs) by NO_3 and O_3 (Fig. 2B), we used an atmospheric pressure flow reactor coupled to a time-of-flight mass spectrometer (LToF; TOFWERK AG, Thun, Switzerland) with chemical ionization by benzene cations (*26*) and proton-transfer reactions (Vocus PTR; TOFWERK AG, Thun, Switzerland) (*27*) to measure the concentrations of floral volatiles in real time (Fig. 2C) (*28*). This system allowed us to measure the degradation of the floral volatiles under realistic atmospheric conditions and timescales and to scale our measurements to a variety of different conditions and environments (fig. S3). Exposure of the floral scent to both O_3 and NO_2 [120 parts per billion (ppb) and 60 ppb, respectively]—corresponding to urban environments and downwind from urban areas (*29*, *30*), and leading to the presence of NO_3 and N_2O_5 (fig. S4)—decreased concentrations of certain constituents in the scent, particularly certain monoterpenes. By contrast, other scent compounds, such as 2-methyl butanal oxime, showed little change in concentration (fig. S5). These effects were dose-dependent: Increasing or decreasing the NO_3 exposure time or concentration caused corresponding changes in the processing of the monoterpenes. Reaction products of the monoterpenes with O_3 and NO_3 were also identified in the scent (fig. S6). Experiments that tested the relative oxidation by NO_3 and O_3 on the individual compounds alone showed similar results: Monoterpenes (such as β-pinene and *cis*-β-ocimene) were sensitive to the pollutants. However, whereas the monoterpenes were partially oxidized by O_3 (decreased by ~30%), these compounds were severely degraded in the presence of NO_3 (decreased by 84 and 67%, respectively; $P < 0.001$, Welch's *t* test/Mann-Whitney *U*-test) (Fig. 2D and table S9), confirming previous work (*20*, *21*) and emphasizing the role of NO_3 in the atmospheric oxidation of floral scents.

NO_3 suppresses plant-pollinator visitations

We next conducted laboratory and field experiments to determine how atmospheric oxidation affects hawkmoths' ability to locate *O. pallida* scent sources and flower visitation. We performed laboratory wind tunnel experiments, which enabled reproducible simulation of the physicochemical conditions present in the field and determination of the impacts of

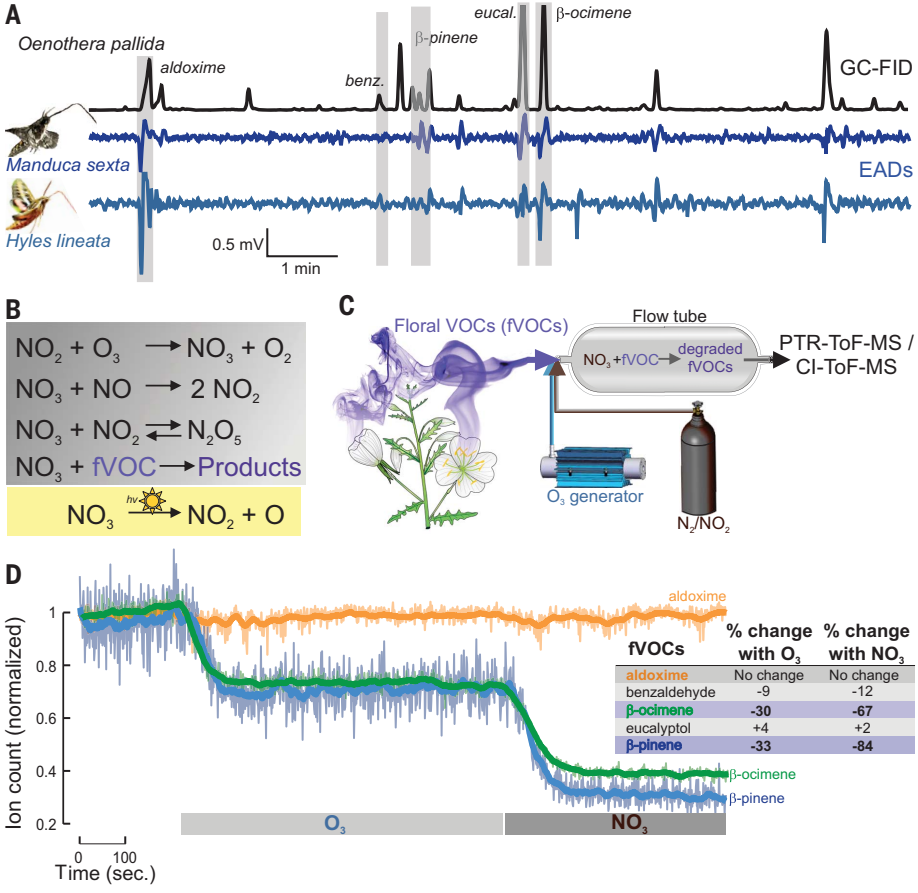

Fig. 2. Sensitivity of floral odor to degradation by free radicals. (**A**) GC-EAD traces of male (top) *Hyles lineata* and (bottom) *Manduca sexta* antennal response to *O. pallida* night scent sample from the field. Responses to the monoterpenes β-pinene and *cis*-β-ocimene, 2-methylbutanal oxime (aldoxime), benzaldehyde (benz.), and eucalyptol (euca.) are highlighted in gray. (**B**) Chemical equations for the formation of the nitrate radical (NO_3) from nitrogen dioxide (NO_2) and ozone (O_3). Dinitrogen pentoxide (N_2O_5) forms reversibly from NO_3 and NO_2 and acts as a reservoir of NO_3. During the day, ultraviolet light causes the dissociation of NO_3 to NO_2 and O, preventing the buildup of NO_3. NO_3 reaction with floral volatile organic compounds (fVOCs) rapidly yields reaction products that are not detected by the moths. (**C**) Schematic of the setup for generating NO_3 from NO_2 and O_3 and oxidizing the fVOCs in a flowtube. (**D**) Example traces of O_3 followed by NO_x oxidation of 2-methylbutanal oxime (orange line), β-pinene (blue line), and *cis*-β-ocimene (green line), measured with a Vocus-PTR-TOF mass spectrometer. (Inset) Table of measured volatiles and their degradation rates under NO_x and O_3 oxidation (all differences $P < 0.001$, Welch's *t* test/Mann-Whitney *U* test) (table S9). The O_3 and NO_2 concentrations in the flowtube were 120 and 60 ppb, respectively, which correspond to the upper range of highly polluted urban environments (*29*, *30*). The reaction time in the flowtube was 73 s, which simulates the impacts on odor transmission within 50 to 100 m from the odor source.

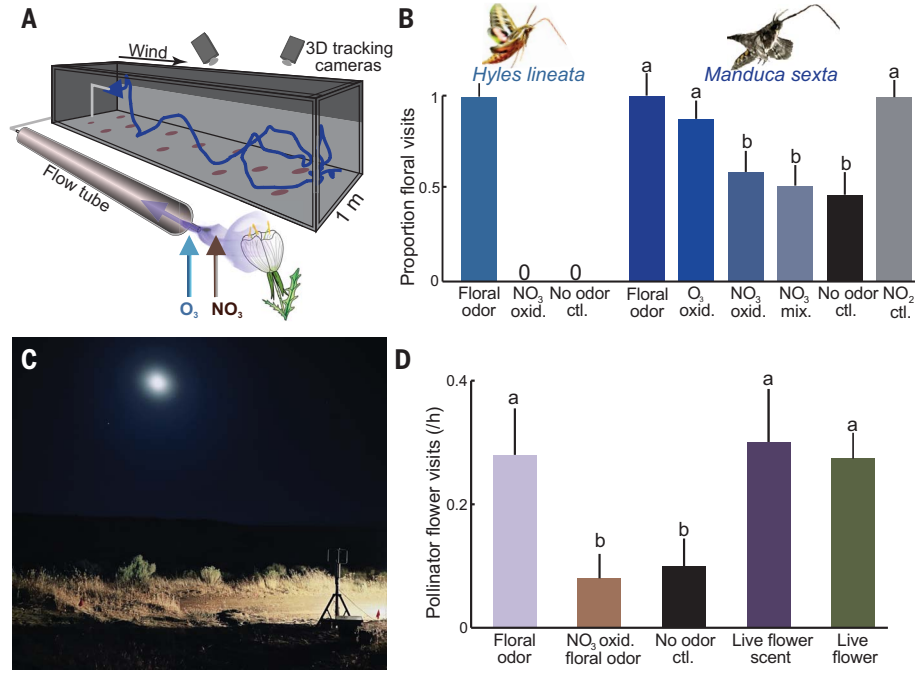

Fig. 3. The impacts of NO_3 on moth visitation to flowers. (**A**) Diagram of experimental setup and hawkmoth flight path in the wind tunnel upwind toward the odor source. (**B**) Wind tunnel behavioral results for *Hyles* and *Manduca* at 0.5 m/s laminar airflow. Individual male hawkmoths were released 2 m directly downwind of the odor source, and the proportion of moths that attempted feeding from the source was recorded. NO_3 oxidation conditions are equilibrium N_2O_5 from 120 ppb O_3 and 60 ppb NO_2 at room temperature with 73 s reaction time in a glass flowtube. O_3 and NO_2 oxidation conditions include just the O_3 or NO_2 component of the NO_3 treatment. Controls were done with dry, filtered air. Another odor treatment of NO_3-proxy mixture (NO_3 mix.) was performed with a synthetic floral odor containing 84% less β-pinene and 67% less β-ocimene than the original floral odor to simulate oxidation by NO_3. Bars are the mean ± SEM (n = 15 to 35 moths per treatment). (**C**) Photograph of the field site. (**D**) Field behavioral results showing the hourly nocturnal visits to a single scent source of each treatment. Five treatments were performed simultaneously, including a real flower treatment, real floral scent treatment, floral odor treatment, NO_3 oxidized floral odor treatment, and clean air control. All treatments except the real flower involved air from the scent treatment delivered through a humidified filter paper cone. We performed 43 to 152.5 observation hours for each treatment (total of approximately 344 hours). Bars are the mean ± SEM.

NO_3 and O_3 levels found in either the polluted urban or near-pristine environments (Fig. 3A). For *Hyles*, NO_3 oxidation of the floral odor eliminated their behavioral attraction (Fig. 3B). For *Manduca*, which was more sensitive to the floral odor (fig. S7), NO_3 oxidation resulted in a 50% decrease in *Manduca* visitation rate (P = 0.047, comparison of population proportions) and to a level that was not significantly different from that of the solvent (no flower odor) control. By contrast, O_3 oxidation of the floral odor—at O_3 concentrations typical of highly polluted environments (120 ppb)—had no impact on hawkmoth visitation (Fig. 3B).

Our scent oxidation experiments showed that a subset of monoterpenes in the floral odor were degraded with NO_3 exposure. However, the decline of hawkmoth attraction could be due to the decreased monoterpene concentrations or the moth's perception of the oxidation products from the odor reacting with NO_3. Examination of the oxidation products from our flowtube experiments showed the production of organic nitrates associated with the odor compounds (fig. S6). We created a synthetic mixture of *O. pallida* scent compounds to simulate the selective depletion of monoterpenes by NO_3 (called the NO_3-proxy mixture). The NO_3-proxy mixture (with 84% less β-pinene and 67% less β-ocimene, but lacking the oxidation products) elicited significantly fewer responses than did the untreated flower odor and the same amount of responses as those with the clean air (no odor) control and the NO_3-degraded scent that contained the oxidation products. Controls of the floral odor exposed to nitrogen dioxide (NO_2; the nonreactive precursor to NO_3) or O_3 alone (to control for any physiological effects on the moth) were not significantly different from responses to the untreated floral odor (Fig. 3B). Taken together, our results show that the moth's inability to navigate and recognize the flower is from NO_3 selectively degrading a subset of compounds in the scent and not because of the moth perception of the oxidation products.

To determine how oxidation of floral scents may affect plant-pollinator interactions in the field, we conducted experiments to test various scent oxidation treatments in our Grants Pass, Washington, site (Fig. 3C). Treatments included real flowers, artificial flowers emitting the floral untreated or NO_3-degraded scent, or artificial flowers not emitting a scent (visual control) (*28*). Visitation rates to the floral odor—both real floral odor (one flower) and our synthetic floral odor—and to real flowers were not significantly different (Fig. 3D). By contrast, the visitation rate to floral odor exposed to NO_3 was significantly less than to the untreated odor (P = 0.027, generalized linear model, Poisson, logistic link) (tables S10 and S11) and not significantly different from the clean air control (Fig. 3D). To establish the effects of scent oxidation on fruit set, we determined the relationship between hawkmoth visitation and the resulting fruit set. From our experiments, an untreated *O. pallida* flower was visited by a hawkmoth approximately twice per night (1.9 ± 0.9), whereas flower visitation in the oxidized scent treatment fell to 0.57 (±0.28) visits per night, or a 70% (±20%) drop in visitation. In our experiments, hawkmoths and crepuscular bees account for 40% (±10%) of all fruits (table S3); thus, a 70% drop in visitation will cause a 28% (±11%) reduction in the total fruit set. Although these results do not consider the effects of diurnal pollinators—such as bees, some of which are affected by the degradation of flower compounds by high-concentration pollutants such as diesel exhaust or O_3 (*7*, *9*, *10*, *14*, *31*)—they do illustrate the potential impact of field-relevant concentrations of NO_3 and O_3 on plant-pollinator interactions.

Global modeling of pollutant impacts

Our research and work with other pollinators such as bees (*7*, *11*) show that oxidation of specific monoterpenes in the floral odors causes declines in attraction. NO_3 dominates the nighttime oxidation of biogenic VOCs, particularly near and downwind of urban areas where nitrogen dioxide and O_3 are elevated. To estimate the potential impacts of anthropogenic enhancements to O_3 and NO_3 concentrations on pollinator olfactory navigation, we used global distributions of O_3 and NO_3 concentrations simulated by the GEOS-Chem global chemical transport model (*25*, *32*). The GEOS-Chem model—which couples meteorology (for example, temperature, three-dimensional wind fields, precipitation, and boundary layer heights) (*33*) with chemical emissions and mechanisms—allows simulation of atmospheric composition at local to global scales

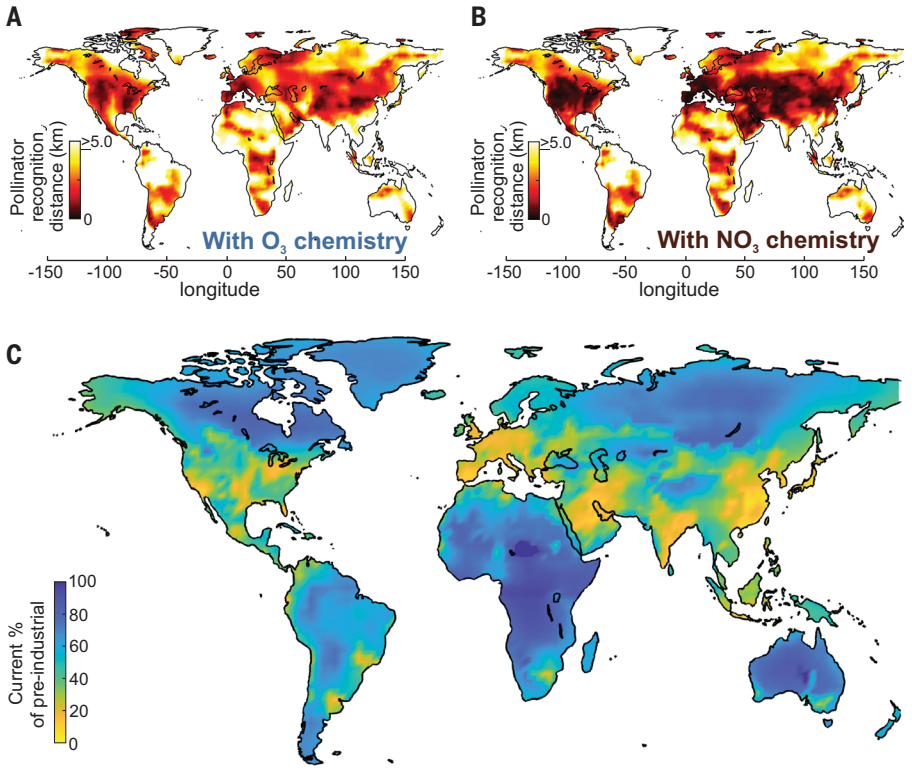

Fig. 4. Global impacts of O_3 and NO_3 on pollinator recognition. (**A**) Map of floral scent recognition distance by using O_3 degradation of the volatiles β-pinene and *cis*-β-ocimene, with degradation thresholds of 84 and 67%, respectively, and horizontal wind speed from the bottom grid of the GEOS-Chem model. The NO_3 and O_3 distributions were generated by using GEOS-Chem standard 12.1.0 with the 2013 emissions inventory and 2013 meteorology with a 2°-by-2.5° grid and 72 vertical levels to 0.01 hPa for the monthly average of January 2013 to February 2014. The bottom vertical level and the average concentrations for July 2013 (northern latitudes) and January 2013 (southern latitudes)—summer periods when the pollinators were present—were used. (**B**) Map of floral scent–recognition distance by using NO_3 degradation of the volatiles β-pinene and *cis*-β-ocimene with the same conditions as in (A), and with data from the same GEOS-Chem model run. (**C**) Map of 2013 floral scent–recognition distance from (B) divided by preindustrial floral scent–recognition distance as a percentage. The preindustrial NO_3 and O_3 distributions were generated by using GEOS-Chem 13.2.1 classic with the 2013 nonanthropogenic emissions inventory and 2013 meteorology with a 4°-by-5° grid and 72 vertical levels to 0.01 hPa for January 2013 to December 2013. The bottom vertical level and the average concentrations for July 2013 (northern latitudes) and January 2013 (southern latitudes) were used. The outputs for the plots in (A) to (C) were masked by using a land-ocean mask to remove the values over bodies of water.

and has been evaluated against observations in several studies (*28*). Using known rate constants for reactions of monoterpenes with O_3 and NO_3, we calculated the distance for floral scents to be oxidized to a level unrecognizable by hawkmoths, given the simulated concentrations of O_3 and NO_3 and wind velocities within the lowest grid level in the GEOS-Chem model (*34*). A scent-recognition distance was computed for each location and for the respective summer months (July for the Northern Hemisphere and January for the Southern Hemisphere) and plotted as a series of global maps that illustrate the differing impacts of NO_3 and O_3 on pollinator perception of the floral scents (Fig. 4).

Results from the model show that NO_3 degradation of monoterpenes in the floral scent has a more severe impact on recognition distance than that by O_3 alone (Fig. 4, A and B) and that scent-recognition distances are reduced to below 400 m in many populated areas. Regions with the most severe impacts from NO_3 include North America, Europe, Central Asia, the Middle East, and southern Africa. In addition, we performed a simulation of the preindustrial atmosphere using GEOS-Chem to assess the percent change in scent-recognition distance that has occurred since the preindustrial era (Fig. 4C). The comparison map shows that in most populated regions of the world, there has been a 75% or more decrease in scent-recognition distances since preindustrial times (Fig. 4C). In certain sparsely populated areas (such as Greenland), NO_3-related changes are relatively small and do not affect the scent-recognition distances. In other areas (parts of Southern Africa), scent-recognition distances may be unchanged relative to preindustrial times because of both natural O_3 and NO_x emissions and chemical feedbacks that stem from their couplings with arboreal VOC emissions (fig. S9 and table S13) (*19*). Geographic areas may thus differ widely in the impact of NO_3 on pollinator recognition of floral scents. Over the past 10 years, annual variation in NO_3 may occur, especially in regions with biomass burning or other meteorological effects. However, when comparing across years (2013, 2019, and 2021), the model showed similar global trends in O_3 and NO_3 concentrations and distributions, with level impacts orders of magnitude greater when compared with preindustrial conditions (table S13) (*30*), which is consistent with anthropogenic inputs of NO_3 around urban areas.

Our results demonstrate that atmospheric O_3 and NO_3 oxidation affects nocturnal pollinator visitations in the field by changing floral scent chemical composition, reducing scent-recognition distances. As a further example of the impacts of NO_3 on many common floral volatiles, we compared the oxidation rates of diverse compounds with NO_3 and O_3 under mean environmental conditions of the northern latitudes (fig. S8B and table S12). Building on past atmospheric chemistry work on the effects of NO_3 (*20*, *21*), our results show that most floral compounds had significantly greater reactivity toward typical NO_3 concentrations than O_3, except for the sesquiterpenes α-humulene and β-caryophyllene (fig. S8B and table S12). The monoterpenes were the most susceptible to O_3 and NO_3 degradation of the floral scent compounds analyzed, with certain monoterpenes being more reactive than others. Many studies (*7*, *11*, *35*–*37*) have established that monoterpenes are ubiquitous floral volatiles important for scent recognition by pollinators; our results demonstrate that certain subsets of compounds in the scent are more sensitive to anthropogenic pollutants and generalize to other systems that use NO_3-reactive monoterpenes as key volatiles for scent recognition. Although other classes of volatiles such as sesquiterpenes, green leaf volatiles, and aromatics have different reactivity profiles, our analytical framework can be used to estimate the impacts of O_3 and NO_3 on scent-recognition distances in other systems if the relevant volatiles and rate constants can be determined.

Olfaction and chemical signaling mediate diverse ecological and evolutionary processes, including predator-prey interactions, host selection, and mate selection (*38*, *39*). At the population level, our results indicate that nitrate radicals, stemming from nitrogen oxide pollution, negatively affect both plants (by decreasing fitness) and insect pollinators (by decreasing their ability to locate nectar resources) and in a region-specific manner. Future work is needed to determine the community-level response to anthropogenic pollutants and to identify how different ecological processes are affected. Anthropogenic pollutants are temporally and regionally variable, and it will be necessary to characterize these impacts in different geographic locations to understand and ultimately mitigate these effects.

REFERENCES AND NOTES

1. D. M. Dominoni *et al*., *Nat. Ecol. Evol.* **4**, 502–511 (2020).
2. W. Halfwerk, H. Slabbekoorn, *Biol. Lett.* **11**, 20141051 (2015).
3. B. M. Siemers, A. Schaub, *Proc. Biol. Sci.* **278**, 1646–1652 (2011).
4. B. M. Van Doren *et al*., *Proc. Natl. Acad. Sci. U.S.A.* **114**, 11175–11180 (2017).
5. A. C. Owens *et al*., *Biol. Conserv.* **241**, 108259 (2020).
6. E. Agathokleous, Z. Feng, J. Peñuelas, *Trends Ecol. Evol.* **37**, 939–941 (2022).
7. R. D. Girling, I. Lusebrink, E. Farthing, T. A. Newman, G. M. Poppy, *Sci. Rep.* **3**, 2779 (2013).
8. B. Cook *et al*., *J. Chem. Ecol.* **46**, 987–996 (2020).
9. F. Démares, L. Gibert, P. Creusot, B. Lapeyre, M. Proffit, *Sci. Total Environ.* **827**, 154342 (2022).
10. S. Dötterl, M. Vater, T. Rupp, A. Held, *J. Chem. Ecol.* **42**, 486–489 (2016).
11. G. Farré-Armengol *et al*., *New Phytol.* **209**, 152–160 (2016).
12. J. D. Fuentes, M. Chamecki, T. Roulston, B. Chen, K. R. Pratt, *Atmos. Environ.* **141**, 361–374 (2016).
13. Q. S. McFrederick, J. C. Kathilankal, J. D. Fuentes, *Atmos. Environ.* **42**, 2336–2348 (2008).
14. J. M. W. Ryalls *et al*., *Environ. Pollut.* **297**, 118847 (2022).
15. J. M. W. Ryalls *et al*., *Proc. Biol. Sci.* **289**, 20221692 (2022).
16. J. A. Riffell, L. Abrell, J. G. Hildebrand, *J. Chem. Ecol.* **34**, 837–853 (2008).
17. D. H. Ehhalt, *Phys. Chem. Chem. Phys.* **1**, 5401–5408 (1999).
18. N. L. Ng *et al*., *Atmos. Chem. Phys.* **17**, 2103–2162 (2017).
19. R. A. Graham, H. S. Johnston, *J. Phys. Chem.* **82**, 254–268 (1978).
20. R. Atkinson, S. M. Aschmann, A. M. Winer, J. N. Pitts, *Environ. Sci. Technol.* **18**, 370–375 (1984).
21. R. Atkinson, S. M. Aschmann, A. M. Winer, J. N. Pitts, *Environ. Sci. Technol.* **19**, 159–163 (1985).
22. D. P. Gregory, *Aliso* **5**, 385–419 (1964).
23. R. E. Stockhouse, *Am. Midl. Nat.* **96**, 241–245 (1976).
24. H. Simon, A. Reff, B. Wells, J. Xing, N. Frank, *Environ. Sci. Technol.* **49**, 186–195 (2015).
25. W. A. Haber, G. W. Frankie, *Biotropica* **21**, 155–172 (1989).
26. A. Lavi, M. P. Vermeuel, G. A. Novak, T. H. Bertram, *Atmos. Meas. Tech.* **11**, 3251–3262 (2018).
27. J. Krechmer *et al*., *Anal. Chem.* **90**, 12011–12018 (2018).
28. Materials and methods are available as supplementary materials.
29. M. Huang *et al*., *Atmos. Chem. Phys.* **17**, 5721–5750 (2017).
30. M. Khan *et al*., *Atmos. Res.* **164-165**, 347–357 (2015).
31. M. Vanderplanck *et al*., *Antioxidants* **10**, 636 (2021).
32. D. A. Satterfield, T. S. Sillett, J. W. Chapman, S. Altizer, P. P. Marra, *Front. Ecol. Environ.* **18**, 335–344 (2020).
33. R. Gelaro *et al*., *J. Clim.* **30**, 5419–5454 (2017).
34. K. R. Mylne, *Boundary-Layer Meteorol.* **60**, 15–48 (1992).
35. J. T. Knudsen, R. Eriksson, J. Gershenzon, B. Ståhl, *Bot. Rev.* **72**, 1–120 (2006).
36. G. Farré-Armengol, M. Fernández-Martínez, I. Filella, R. R. Junker, J. Peñuelas, *Front. Plant Sci.* **11**, 1154 (2020).
37. J. A. Riffell, H. Lei, L. Abrell, J. G. Hildebrand, *Science* **339**, 200–204 (2013).
38. T. Eisner, J. Meinwald, *Proc. Natl. Acad. Sci. U.S.A.* **92**, 1 (1995).
39. B. S. Hansson, M. C. Stensmyr, *Neuron* **72**, 698–711 (2011).
40. J. A. Riffell, Olfaction in the Anthropocene: NO3 negatively impacts floral scent and nocturnal pollination [Dataset]. Dryad (2024); https://doi.org/10.5061/dryad.vt4b8gtzk.
41. J. A. Riffell, riffelllab/Chan-et-al: Chan *et al* - Olfaction in the Anthropocene (version v1). Zenodo (2024); https://doi.org/10.5281/zenodo.8411927.
42. The International GEOS-Chem User Community, geoschem/geos-chem: GEOS-Chem 12.1.0 (12.1.0). Zenodo (2018); https://doi.org/10.5281/zenodo.1553349.
43. The International GEOS-Chem User Community, geoschem/GCClassic: GEOS-Chem 13.2.1 (13.2.1). Zenodo (2021); https://doi.org/10.5281/zenodo.5500717.

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SUPPLEMENTARY MATERIALS

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Materials and Methods
Equation S1
Figs. S1 to S9
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MDAR Reproducibility Checklist

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