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Jordanna D. H. Sprayberry, Robbie D. Girling, James M. W. Ryalls, James D. Blande & Ben Langford

A perceptual model indicates air pollution-induced shifts in honeybee floral-scent recognition

Jordanna D.H. Sprayberry[1,2], Robbie D. Girling[3,4], James M.W. Ryalls[3], James D. Blande[5], Ben Langford[6]

[1]Muhlenberg College, Allentown PA, United States of America
[2]Stony Brook University, Stony Brook NY, United States of America
[3]University of Reading, Reading, United Kingdom
[4]University of Southern Queensland, Toowoomba, Australia
[5]University of Eastern Finland, Kuopio, Finland
[6]UK Centre for Ecology and Hydrology, Penicuik, United Kingdom

Abstract

Air pollution threatens pollination by degrading floral odors essential for attracting pollinators. This study explores the utility of the Compounds Without Borders method, which quantifies odor changes using molecular features, as a tool for understanding how pollutants like ozone affect scent perception. We identified a pollution-degradation threshold as quantified by Compounds Without Borders by analyzing published datasets on honeybee proboscis extension responses to pollution-modified *Brassica* odors: odors degraded beyond 10 degrees show decreased response rates. Application of Compounds Without Borders analysis to different plant scent profiles indicates the scents of some species (canola) are vulnerable to air pollution, while others (apple) are resilient. Our results support the utility of Compounds Without Borders to assess the effects of air pollution on honeybee olfaction, offering a predictive tool and establishing a foundation to build a model that could be used to safeguard pollination services against the growing threat of air pollution and other environmental stressors.

Introduction

Insect pollination supports ecosystem stability and agricultural productivity [1], with insect pollinators contributing to the yield, quality and stability of 70% of crop species [2]. Insect pollinators use a combination of visual, olfactory and to a lesser extent tactile cues to make foraging decisions about flowers [3–6]. Odor cues are particularly crucial as they can be detected over longer distances and provide specific information about the flower's identity and reward status [7,8]. Floral odors, composed of volatile organic compounds (VOCs), are vital for attracting many species of pollinating insects, and these odor-mediated interactions underpin the reproduction of numerous plant species [9].

Air pollution increasingly threatens this interaction by degrading VOCs as they travel through the air away from a flower, reducing the distance these cues travel and the integrity of the information they convey. Many floral VOCs react with naturally occurring atmospheric oxidants such as the hydroxyl radical (OH) and ozone (O_3), along with atmospheric oxidants elevated by air pollution like nitrogen oxides (NO_X) and additional ground-level O_3, altering their chemical composition, which can disrupt pollinator attraction and reduce foraging efficiency [10,11]. Understanding these impacts is limited by several factors. The reactivity between pollutants and VOCs varies depending on their chemical properties, with O_3 reacting rapidly with alkenes, but more slowly with aromatic compounds[12]. Each plant species emits a unique VOC floral profile [13], leading to species-specific impacts. Pollinator species differ in their reliance on odor cues; honeybees, for example, have a highly developed olfactory system and can learn odor-reward associations [14]. Pollution levels and types fluctuate spatially and temporally due to industrial activity, traffic and weather, and interactions between pollutants like O_3 and NO_X add complexity [15,16]. Empirical studies addressing these variables are time-consuming and costly, making it impractical to test all combinations of plants, pollinators, and pollution scenarios. As such, there is a critical need for a predictive model to inform policy and practice in understanding and managing the potential effects of air pollution on pollination. Additionally, an effective predictive model will help narrow the scope for future empirical studies, potentially increasing the time and resource efficiency of such investigations.

Gaining greater insight into the effect of pollution on insect pollinators' ability to locate flowers, requires information on the floral VOC blend a plant releases, the reactivity of its components with key air pollutants, and how these changes alter pollinator-perception. Many floral VOC blends have already been documented in the ecological literature (e.g. [13]; likewise, the reaction kinetics of many common floral VOCs with oxidative pollutants, such as O_3, have been documented in the atmospheric chemistry literature [17–19]. Pioneering work modelled how interactions between oxidative pollutants and the VOC components of floral odor blends changed the relative ratios of those VOCs within the odor[10,20]. However, until recently the effects of these pollutant-induced changes in VOC blends on insect pollinator perception and behaviour have been limited to empirical studies [15,21–23], which have shown that not all VOC changes have an equal impact on behaviour. For example, honeybees trained to *Brassica napus* scent show a drastic decrease in response when terpinene is removed but no significant change when farnesene is removed[21]. One study has begun the important work of bridging the body of empirical pollinator behaviour literature with landscape models of floral scent degradation in the context of nocturnal pollination, grounded in the assumption that loss of beta-pinene and cis-beta-ocimene would be equally impactful in all floral odor blends[24].

The odor signals provided by flowers are detectable at greater distances than visual cues[1] , and are likely to be more heavily utilized by insect pollinators during foraging flights to locate novel resource patches. Flowers produce complex blends of scent, rather than monomolecular odors [9,13]. The perceptual identity of odor blends is established by insect olfactory systems using a 'combinatorial code', meaning that the neural response to a complex blend of VOCs is not a simple linear sum of responses to each individual VOC[25]. Therefore, as pollution interacts differentially with individual components of a blend, it is challenging to predict the perceptual impacts on a foraging pollinator.

Traditional methods of describing the relative similarity (or dissimilarity) of complex odor blends have relied on statistical analyses such as principal components analysis (PCA) or nondimensional metric scaling (NMDS) [26–29]. While these methods have excellent descriptive power, the dimensions of the odor spaces they create are based upon the identity of the odors' component molecules rather than their structures. However, studies on insect olfactory receptor neurons (ORNs) indicate that many ORNs respond to multiple molecules sharing functional group characteristics [30,31]. Likewise, seminal work on olfactory processing in the honeybee antennal lobe demonstrated that carbon chain length and functional group are reliably encoded [28]. Thus for complex odors, insect olfactory systems maintain information about molecular characteristics, rather than molecular identity. Statistical approaches based on molecular identity do not provide independent quantitative axes capable of calculating differences between intact and pollution degraded odor plumes.

This study utilizes a recently established method for geometric representation of odors, 'Compounds Without Borders' (CWB), which defines an odor-space whose dimensions are derived from physiologically-relevant attributes of molecules based on the current understanding of how odorants are encoded by insect-olfactory systems [25,26,28,30–34]. Specifically, the organization of insect olfactory systems preserves information about molecular features of VOCs such as functional groups (e.g. such as alcohol, ester, etc.) and carbon characteristics (carbon chain length and number of carbons in cyclic structures). The CWB odor space utilizes these features as the dimensions in a Euclidean space [35]. Any odor (either single VOCs or VOC blends) can be represented within this space as a vector of consistent length, and the angular distance between the resulting vectors of two odors can serve as a measurement of their similarity (or lack thereof). This odor-space is thus a mathematical representation of an odor's stimulus characteristics, much as a spectrogram describes the distribution of wavelengths within color stimuli available to a visual system. The efficacy of CWB in describing and predicting odor-behaviour has been tested in bumblebees [35], but its effectiveness in describing honeybee (*A. mellifera*) behaviour is unknown.

The objectives of this study are to: 1) explore CWB's ability to predict honeybee behavioural responses to pollution-degraded odors using published datasets; and 2) evaluate how air pollution could impact the ability of honeybees to recognise the known floral VOCs from a range of honeybee-pollinated plants from different plant families and with different lifecycles. Therefore, four major crops known to be pollinated by honeybees (canola, white mustard, apple and strawberry) were selected to model this new approach.

Understanding how air pollution disrupts pollinator sensory ecology and how this might vary between plant species is crucial for developing strategies to safeguard pollination services in both natural and agricultural ecosystems. Our results show that with modification CWB quantification of changes in odor blends due to air pollution correlates with a consistent 10 degree disruption threshold in honeybee responses across studies. Applying this to four plant species predicted varying susceptibilities, with canola/oilseed rape being the most affected. This highlights CWB's potential to predict how air pollution might influence odor-driven interactions between pollinators and a wide range of agriculturally and horticulturally important insect-pollinated crops. This in turn could help develop mitigation strategies for the adverse effects of VOC degradation on pollination services in agricultural and natural ecosystems. Additionally this establishes a foundation for future empirical work on the relationship between odor-structure, odor-degradation susceptibility, and pollination services.

Results

Development of CWB model for honeybees and air pollution

CWB vectorization and original angular calculation were applied to three published datasets: Girling et al 2013, Lusebrink et al 2015, and Langford et al 2023[21,36,37]; three studies that investigated how honeybee odor responses were impacted by the altered odor structure that reactions between floral odorants and anthropogenic air pollutants (e.g. diesel, O_3) incur. CWB vectorization and original angular calculation of the three published datasets demonstrated that CWB-angle was internally predictive for all three studies, but Girling et al (2013) data showed a lower angular threshold of disruption (Fig 1A). Girling et al (2013) and Lusebrink et al (2015) took a more rudimentary approach to blend manipulation by entirely removing those floral VOCs from the original odor that were highly reactive with the pollutant, while Langford et al (2023) took a more nuanced approach by recreating the ratio changes in the VOCs driven by pollution exposure. Given the extensive lateral processing within the antennal lobe (Martin 2011, Clifford and Riffell 2012), it is likely that removal of an odorant could have larger impacts on olfactory perception than reducing its ratio. Thus angular calculations were modified by preprocessing vectors. Vectors were compared prior to running angle calculations and any dimensions that were gained or lost between the two vectors were amplified by an order of magnitude (CWB_{GLA}, Fig 1, Supplementary Video 1). With modified angular calculations there is a consistent disruption threshold, with average PER response rates dropping to 50% in the 10-15 degree range (Fig 1B, C).

Predicting honeybee responses to floral odors altered by air pollution

Modeling the impact of ozone on floral odor profiles

Representations of how air pollution impacts floral scent profiles necessarily focus upon changes in VOC ratios, because it is the chemistry of those profiles that change as a result of oxidative pollution. Four different crop odors were analyzed: white mustard (*Sinapis alba*), *Fragaria × ananassa* (Strawberry. Malwina cultivar), *Malus domestica* (Apple, Golden Delicious cultivar), and canola / oilseed rape (*Brassica napus*) (Table 1). These crops encompass both annual and perennial systems; with two seed-crop representatives (canola and mustard) and two fruit-crop representatives (strawberry, a berry-fruit, and apple, a tree-fruit). Modelling the changes to floral VOCs over time in response to exposure to O_3 demonstrates that increasing concentrations of O_3 increase the rate of degradation of some VOCs, but that not all are susceptible and the rate of change of those reactive VOCs vary from one species to another (Fig 2). The floral VOCs that make up the profile of apple scents are less reactive to O_3 than those of canola, and the floral scent profiles of strawberry and mustard demonstrate an intermediate level of reactivity. Visualising these profile changes using a cosine similarity analysis allows a representation of the holistic impact of air pollution on the blend structure (Fig 3) and demonstrates that changes to the canola profile are clearly the most pronounced and rapid, followed by changes to the strawberry profile.

3.2.2 *Predicting changes in honeybee recognition of altered floral odors*
Insect brains utilize a combinatorial code for neural encoding of floral scent; therefore, neurophysiological and behavioural responses can be more strongly influenced by the attributes of molecules within a blend, rather than simply the VOC identity. While strawberry floral VOCs show slightly greater susceptibility than mustard floral VOCs to O_3-induced chemical degradation when assessed through traditional VOC ratio analysis (Fig 3), a different picture emerges when the CWB perceptual model is applied (Fig 4). Although the ratios of VOCs from strawberry change more dramatically over time (Fig 3), the perceptual impact, as estimated by changes in CWB_{GLA} angles, is greater for mustard (Fig 4). Specifically, mustard VOCs cross the 15° angular threshold (a value proposed to mark the onset of major perceptual change in honeybee scent recognition) more rapidly than those of strawberry. Mustard floral VOCs resulted in changes in CWB_{GLA} angles over 15° within 8 to 10 minutes depending upon the O_3 concentration. After these initial shifts, further angular change occurred more slowly compared to both canola and strawberry floral VOCs. In contrast, angular changes in response to strawberry floral VOCs O_3 degradation were initially slower, but then underwent faster angular changes than those of white mustard. This difference arises because the CWB model represents structural similarity between molecules, rather than simply changes in VOC identity. Strawberry loses three molecules in a similar time frame as mustard losing 2 molecules. A cosine similarity analysis based on odorant identity shows a larger change for strawberry than mustard because of the higher component loss. However, the structural overlap *between* molecules is higher for strawberry than mustard: the loss of three molecules from strawberry drops 2 CWB-dimensions to zero, while the loss of two molecules from mustard drops 6 CWB-dimensions to zero (Table 2). This indicates that despite the VOC profile change in mustard occurring at a slower rate than strawberry, perceptual reduction in recognition by honeybees occurred quicker in mustard than strawberry.

Overall, changes in CWB_{GLA} angles over time varied considerably between the four different crop floral VOC profiles (Fig 4). The most pronounced effects were observed for canola, where CWB angles shifted by 15° or more, within 3 minutes of exposure to high levels of O_3 (>140 ppb), which is a 9-fold decrease in longevity from the 27-minute lifetime at ambient O_3. Apple VOCs were the most stable, with negligible changes in CWB_{GLA} angles at all concentrations within 60 minutes.

Discussion

Over the past two decades, research has increasingly focused on how human activities, particularly air pollution, indirectly disrupt chemical communication in pollination systems. Modeling studies have shown that air pollutants like O_3 differentially degrade VOCs within floral odors, altering their relative ratios and, therefore, the odor's structure [15,20,21,36]. This degradation does not simply reduce signal intensity or range; it transforms VOC profiles, potentially impairing pollinator perception and recognition [10,38]. Understanding the relationship between changing blend-ratios and pollinator perception currently relies on empirical studies that recreate modelled change in scent structure [15,21,36,37]. This is an effective way of understanding how a pollinator species responds to changes in an individual plant species' floral bouquet. However, previous studies have demonstrated an ambiguity in response to the removal of single VOCs, indicating that a threshold of pollution-disruption cannot be determined by the number of susceptible molecules in the blend. For example, honeybees trained to associate *Brassica napus* scent with a sucrose reward show recognition dropping to <35% when a key VOC (α-terpinene) is removed, yet retain 75% recognition when an alternative VOC (α-farnesene) is absent [21]. This variability indicates that disruption cannot be predicted solely by the number of degraded VOCs, highlighting the need for either experimental testing of behavioural responses to large numbers of floral odor blends, or a computational representation of odor perception grounded in olfactory neurophysiology.

Taking the latter approach by utilising CWB odor vectors offers two advantages. First, they can represent any odor blend, and its subsequent degradation, in the same geometry. This allows calculation of the angular change between unpolluted and polluted scent, giving a single variable (theta) for determination of behavioural disruption. Second, the CWB-geometry is constructed from functionalized dimensions that are neurophysiologically relevant; in other words angular shifts in CWB space correlate with changes in the neural representations of odor stimuli. Therefore, CWB should be computationally capable of describing and predicting changes in pollinator perception. This approach to odor quantification was developed in bumblebees (Sprayberry 2020); this study describes a modification to CWB-vector processing that facilitates its use for honeybees. With modification, analysis of published datasets indicate that pollution shifts of 10-15° substantially reduce response rates, dropping odor recognition to below 50% for all angles over 15°.

Applying CWB to floral VOC profiles of crop plants demonstrated large variation in the potential of air pollution to disrupt flower recognition between crop plant species. *Brassica napus* (canola/oilseed rape) was the most susceptible, with its scent degrading beyond recognition within five minutes at 110 ppb O_3 exposure. *Sinapis alba* (white mustard) was also susceptible, reaching this threshold of disruption within approximately fifteen minutes. At a wind speed of 1 m/s this would correspond to functional loss of recognizability at distances of 300m and 1200 respectively, while a wind speed of 4 m/s (environmental condition that alters honeybee flight behaviour [39]) would result in viable scent-recognition at >1000m for both. These two most susceptible species in terms of degradation are both members of the

Brassicaceae, which accounted for 44 million hectares of agricultural cultivation and a value of 92 billion USD in 2022 [40]. Field tests found that increasing O_3 concentrations surrounding *Brassica nigra* plants resulted in a 62% reduction in insect visitation and significant reduction in seed metrics.

Contrasting the results for strawberry and white mustard shows the change in their volatile profiles did not reflect the change in their CWB-dimensional structure. The change in relative-ratios of VOCs from strawberry changed more rapidly over time than those of mustard (Fig 3); however, changes in CWB-angles estimated dimensional structure, which corresponds to perceptual impact, occur more rapidly for mustard (Fig 4). This demonstrates the importance of considering the receiver and not just the chemical signal in understanding the impact of signal degradation as predictions based on chemical change alone are likely to prove inaccurate. This demonstrates the potential of CWB to pinpoint vulnerable plants, informing targeted agricultural and conservation strategies.

A recent multi-disciplinary working group identified the importance of an 'organismally-informed systems approach' to investigating pollination biology, in order to better understand how human-activity might disrupt and threaten pollination networks [41]. Specifically this group called for modelling studies that elucidate which variables derived from the underlying organismal-biology of pollination-network constituents have a meaningful impact on emergent properties of that network; i.e. pollination services, species distributions, etc. Those variables should then be empirically investigated, so that subsequent models can better capture the complexity of interspecies interactions and their effects. In line with these recommendations, the analyses presented here set the foundation for this iterative, systems approach to investigating the effects of air pollution on food-security.

In conclusion, this study successfully supports the utility of the CWB method for predicting how air pollution alters floral odors and disrupts honeybee foraging behaviour. By quantifying odor changes through molecular features relevant to insect perception, a consistent perceptual disruption threshold of 15° in odor structure was identified, which correlated with a 50% decrease in honeybee response to learned odors across multiple datasets. Applying this method to economically important crops revealed substantial variation in their vulnerability to air pollution-induced odor degradation, with canola proving particularly susceptible compared with more resilient crops like apple. These findings provide a framework supporting CWB's potential to predict, and inform mitigation of, the impacts of air pollution on pollination services. Future studies that utilize this framework in combination with additional empirical data could build robust landscape-scale models to predict dynamic changes in pollination services in variable air pollution and environmental scenarios.

2. Methods

2.1 Development of CWB model for honeybees and air pollution

Odor Vectorization

The sensory attributes of stimulus odors were characterized using the CWB vectorization method [35]. This approach to odor characterization calculates the amount of sensory energy (power) present in odor. The dimensional signature of each odor-blend was calculated from the molecular structure of odorant molecules based upon their respective carbon chain length (CCL), cyclic carbon count (CCC), and functional group (FG) characteristics (Supplemental Video 1). Each odorant's relative headspace ratio was assigned to multiple dimensions; with a minimum of three (CCL,CCC, and at least one FG) and no maximum. From a dimensional perspective, the power for each dimension was calculated as the summed relative headspace ratio (measured using Gas Chromatography Mass Spectrometry) from molecules with that attribute (CCL, CCC, or FG). If no molecules within a given odor-blend have that attribute, that dimension has a power of zero. This dimensional representation aligns with known odorant-attributes that are coded for in insect olfactory systems [42–44]. For full details on this method see Sprayberry (2020).

Odor Comparisons using CWB

The CWB method was developed utilizing bumblebee behaviour experiments, with the goal of being able to represent the sensory-distance between two odors with a single variable (analogous to plotting how far apart two flower colors are in a bee color-space), because CWB vectors allow the difference between odors to be calculated as the angular distance between their vectors with the following equation:

$$\theta = cos^{-1}\left(\frac{a \cdot b}{|a| \times |b|}\right) \quad (1)$$

These original vectors are representations of physical odors, not perceptual odors that have been filtered by a sensory system. Additionally, the original approach to angle calculations uses unmodified vectors; a mathematical assumption that differences between vectors are not amplified or attenuated by neural processing. In the first proof of concept study (Sprayberry 2020), this approach effectively described bumblebee behaviour. However, in this study we explore the utility of modified vector calculations to better describe honeybee behaviour. Due to the extensive lateral inhibition networks between glomeruli in the honeybees' antennal lobe [45], the loss or gain of a dimensional attribute from a learned odor could have substantial impacts on emergent glomerular activation patterns. To account for this, before angular calculations, odor vectors were compared and any dimension gained or lost was amplified by an order of magnitude (Fig 1, Supplemental Video 1).

Honeybee Datasets

CWB vectorization and original angular calculation were applied to three published datasets: Girling et al 2013, Lusebrink et al 2015, and Langford et al 2023[21,36,37]. All three studies investigated how reactions between floral odorants and anthropogenic air pollutants (e.g. diesel, O_3) alter odor structure and influence honeybee behaviour. Despite differences in the specific odor stimuli used, the behaviour assays were consistent across studies: honeybees were trained via Pavlovian conditioning to associate a sucrose reward with an unpolluted odor blend, then tested with (recreated) polluted blends. Generalization responses were measured using the proboscis extension reflex (% PER, see Girling et al 2013 for details). The odor stimuli utilized in these three studies covered a range of ethologically relevant floral odor components; with Girling et al utilizing a recreated floral odor from the commercial crop plant *Brassica napus*[2] , Lusebrink using an 8 component blend of the most ubiquitous floral odorant compounds (as reported in Knudsen 2006, as cited by Lusebrink et al[3] , and Langford et al[4] using a 4-component blend of common floral odorants that introduced a novel odorant (Table 3). Across these stimuli a panel of 18 odorants are present with 12 functional group dimensions and 14 carbon dimensions, representing scent characteristics common in floral odors.

2.2 Predicting honeybee responses to pollution-altered floral odors

2.2.1 Predicting Ozone Degradation of Floral Odors

The atmospheric lifetime of a VOC with respect to the hydroxyl radicals (OH) and O_3 depends on their reaction rate constants and the concentrations of these oxidants in the atmosphere. The lifetime (τ) with respect to a specific oxidant is calculated as:

$$\tau = \frac{1}{k \cdot [oxidant]}, \qquad (2)$$

where k is the rate constant for the reaction of the VOC with the oxidant (units: cm^3 $molecule^{-1}$ s^{-1}), and [oxidant] is the atmospheric concentration of the oxidant (units: molecule cm^{-3}). In the daytime, the primary oxidants are OH and O_3, with nitrate radicals becoming the dominant sink for VOC oxidation at night [46]. Here, our analysis is limited to daytime oxidation, using a typical OH concentration of 1×10^{-6} molecules cm^3 and varying O_3 concentrations from background levels (10 ppb) to those experienced during episodes of ground-level O_3 pollution (200 ppb).

To calculate the total gas-phase oxidation lifetime of the VOC, contributions from each individual oxidant need to be combined. Since each reaction pathway acts independently of the others, their respective rate constants are additive. The total loss rate (k_{total}) is the sum of the individual loss rates:

$$k_{total} = k_{OH}[OH] + k_{O_3}[O_3]. \qquad (3)$$

The total atmospheric lifetime (s^{-1}) is then derived as the inverse of the total loss rate:

$$\tau_{total} = \frac{1}{k_{total}}. \qquad (4)$$

Rate constants for the reactions of VOCs with OH and O_3 are often available in the scientific literature. These values are typically measured experimentally under controlled conditions or calculated using detailed chemical models. Table 1 lists the VOCs that have been recorded from the floral odor of four plant species, white mustard (*Sinapis alba*), *Fragaria × ananassa* (Strawberry. Malwina cultivar), *Malus domestica* (Apple, Golden Delicious cultivar), and canola / oilseed rape (*Brassica napus*). These crops encompass both annual and perennial systems; with two seed-crop representatives (canola and mustard) and two fruit-crop representatives (strawberry, a berry-fruit, and apple, a tree-fruit). The rate constants for each floral VOC with respect to OH and O_3 are included with references to the literature sources. Where published data on atmospheric lifetimes or rate constants are unavailable, rate constants were obtained from estimates provided by the Environmental Protection Agency's EPI Suite software.

EPI Suite estimates atmospheric lifetimes using the structural properties of the molecule. Specifically, it uses the Atmospheric Oxidation Program for Windows (AOPWIN) module, which applies structure-activity relationships (SARs) to predict the rate constants for the reactions of VOCs with OH and O_3. The SAR methodology involves identifying structural features of the molecule, such as the presence of functional groups or unsaturated bonds and assigns reactivity values based on these features. These reactivity values are then used to calculate the second-order rate constants for oxidation. This combination of measured data and model predictions enabled the atmospheric lifetimes of all floral VOCs to be estimated, even for compounds that have not been extensively studied.

The reaction of each individual VOC within the four floral odors was modelled over a 60-minute time period, with calculations performed at 10-second intervals. The percentage of the VOC reacted at each step was determined using its atmospheric lifetime, accounting for reactions with OH radicals and across a range of O_3 concentrations. The cumulative reaction losses are shown over a timescale relevant to odor-mediated insect activity.

Our analysis considers only the effects of chemical degradation, and for simplicity, assumes that a VOC is effectively removed once its atmospheric lifetime has been exceeded. In reality, atmospheric lifetime represents the time required for the concentration to fall to 1/e of its initial value, meaning approximately ~36% of the compound would still remain. However, the effects of physical dilution are not incorporated into our model. Dilution—driven by wind speed, turbulence, and atmospheric stability—can be highly variable but is likely to reduce concentrations dramatically over the same timeframe. As such, while our model may slightly underestimate the chemical persistence of VOCs, this is offset by the absence of dilution effects, which would similarly act to lower all VOC concentrations at short distances from the source.

2.2.2 Estimating Change in Response by Honeybees to Degraded Floral Odors

The CWB analyses of the published honeybee datasets, in which angular thresholds of odor-response disruption were determined, were combined with the outputs of the modelled scent decay of four selected crop-species.

To quantify the extent of chemical degradation in floral odour blends under O_3 pollution, we calculated angular distances between each crop's VOC profile and its original, undegraded state. These comparisons were made under a fixed background OH radical concentration (1×10^6 molecules cm^{-3})[8], while O_3 levels were varied to simulate different pollution scenarios.

Simulations were run over a 60-minute period to capture the full trajectory of chemical transformation. The timescale over which odour signals remain ecologically relevant is uncertain, but insects generally respond to odour cues within seconds to minutes under field conditions[9]. Beyond approximately 15 minutes, under most atmospheric conditions, turbulent mixing and dispersion are expected to fragment the plume and increase intermittency to levels that preclude effective insect navigation[10]. For this reason, we consider the first 15 minutes to represent the biologically active window for signal recognition, while the full simulation duration provides an upper bound on potential degradation under sustained atmospheric exposure.

Data Availability: all data used in this manuscript are previously published and publicly available as part of those publications

Code Availability: Code for CWB functions is available as a .py file in the supplementary materials

Author Contributions

Jordanna D.H. Sprayberry contributed project conceptualization, analysis, manuscript drafting and editing. Robbie D. Girling contributed project conceptualization, manuscript drafting and editing. James M.W. Ryalls contributed project conceptualization, manuscript drafting and editing. James D. Blande contributed project conceptualization, manuscript drafting and editing. Ben Langford contributed project conceptualization, analysis, manuscript drafting and editing.

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Competing Interests

The authors declare no competing interests.

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Figure 1. CWB analysis of honeybee odor pollution studies. This figure demonstrates application of the original CWB-analysis (Sprayberry 2020) to three published datasets, and our proposed modification of that odor representation system for subtractive odor pollution in honeybees. The three studies (Girling et al 2013, Lusebrink et al 2015, and Langford et al 2023) all measured changes in proboscis extension reflex (PER) of honeybees trained to an unpolluted source odor when the individuals were tested with 'polluted' version. The source odors varied across the three studies, and the pollution ranged from diesel exhaust to ozone. (A) PER data from each of the three studies analyzed with the original CWB odor-geometry show a decrease in PER response as the CWB-angle between the learned source odor and polluted test odor increases. However, the rate of decline is variable across the three studies. (B) Plotting PER responses in 5 degree bins demonstrates the improved predictive potential of the proposed CWB-modification (CWB_{GLA}). In contrast with the original method, responses plotted against CWB_{GLA}-angles do not drop below 50% until the 10-15 degree bin, and once they drop below 50% they do not cross back over. (C) Similarly, PER responses plotted against angle for data ranging from 0 degrees to the angle at which all subsequent responses stay below 50% (14° for both original and G/L amplified) and fit a linear regression to those we see a substantial increase in the R^2 for CWB_{GLA} data (R^2 of 0.74 versus 0.31).

Figure 2. **Stacked area plots of relative VOC changes driven by ozone and hydroxyl radical degradation.** The relative ratios of VOCs for four different crop scents over 1 hour of reaction with ozone and hydroxyl radical (1×10^{-6} molecules cm^3) are plotted at two different ozone concentrations (50ppb and 190 ppb). The odor-molecule represented by color within each species is shown in the legend next to each row of plots. This time frame represents the upper bound on potential degradation under sustained atmospheric exposure.

Figure 3. Cosine similarity analysis of VOC changes in odor-blends across ozone concentrations. The cosine-similarity of relative VOC changes for four crop scents are plotted in a matrix of changing ozone concentration over 1 hour of reaction time. Cosine similarity values range from 1 (identical structure (VOC ratios)) to 0 (perfectly dissimilar structure). Insets for apple and canola show a range that better

represents their changes: a smaller range showing the high stability of apple and a larger range showing the high reactivity of canola.

Figure 4. Changes in gain/loss amplified Compounds Without Borders (CWB_{GLA}) angles over time in response to the degradation by ozone and hydroxyl radicals (1 x 10^{-6} molecules cm^3) of floral scent profiles. Changes in CWB_{GLA} angles indicate predicted changes in honeybee recognition of the floral Volatile Organic Compound profiles of four crop plants in response to modelled degradation of floral VOCs at different concentrations of ozone. Black lines indicate CWB_{GLA} angular changes of 10° (solid line) and 15° (dotted line), representing the range in which the recognition of odor profiles by honeybees in proboscis extension response studies drops to less than 50%. The dotted grey lines mark 15 minutes, the time point at which odor plumes are likely degraded beyond ethological viability in many environmental conditions.

Table 1 Reaction rates of hydroxyl radicals and ozone with each floral Volatile Organic Compound (VOC) identified from the floral odors of four crop plants, white mustard[2], strawberry[5], apple[6] , and canola[7].

Crop species	Floral VOC	VOC relative ratio	k_{O_3}	Rate constant source	k_{OH}	Rate constant source
Sinapis alba (White mustard)	cis-3-hexen-1-ol	0.02	6.4 E-17	Atkinson et al (1995)[47]	1.08 E-10	Atkinson et al (1995)[47]
	benzaldehyde	0.5	1 E-25	EPISuite	1.79 E-11	EPISuite
	cis-3-hexen-1-ol acetate	0.08	5.4 E-17	Atkinson et al (1995)[47]	7.84 E-11	Atkinson et al (1995)[47]
	benzyl alcohol	0.01	6 E-19	Harrison & Wells (2009)[48]	2.8 E-11	Harrison & Wells (2009)[48]
	benzeneacetaldehyde	0.002	1 E-25	EPISuite	2.63 E-11	EPISuite
	(E)-β-ocimene	0.03	3.85 E-16	Kim et al (2010)[49]	3.04 E-10	Kim et al (2010)[49]
	acetophenone	0.01	1 E-25	EPISuite	1.87 E-12	EPISuite
	methyl salicylate	0.03	4 E-21	Canosa-Mas et al (2002)[50]	1.11 E-11	EPISuite
	anisaldehyde	0.3	1 E-25	EPISuite	1E-25	EPISuite
	β-caryophyllene	0.01	1.16E-14	Shu & Atkinson	2E-10	Shu & Atkinson

				(1994)[51]		(1995)[52]
Fragaria × ananassa (Strawberry)	(Z)-3-hexenol	0.004	6.40E-17	Atkinson et al (1995)[47]	1.08E-10	Atkinson et al (1995)[47]
	(E)-2-nonenal	0.005	1.82E-18	EPISuite	4.27581E-11	EPISuite
	heptanal	0.007	1.00E-25	EPISuite	3.02442E-11	EPISuite
	n-decane	0.013	1.00E-25	EPISuite	1.11105E-11	EPISuite
	(Z)-3-hexenyl acetate	0.001	5.40E-17	Atkinson et al (1995)[47]	7.84E-11	Atkinson et al (1995)[47]
	butyl acetate	0.281	1.00E-25	EPISuite	4.6E-12	EPISuite
	benzyl benzoate	0.536	1.00E-25	EPISuite	6.9698E-12	EPISuite
	2-butenoic acid, 3-methyl-, 2-phenylethyl ester	0.034	7.39E-17	EPISuite	3.8519E-11	EPISuite
	b-pinene	0.005	1.50E-17	Bonn & Moorgat (2002)[53]	7.89E-11	Bonn & Moorgat (2002)[53]
	limonene	0.06	2.10E-16	Atkinson et al (1990)[17]	1.63793E-10	Gill & Hites (2002)[54]
	g-terpinene	0.042	1.40E-16	Atkinson et al (1990)[17]	1.76E-10	Atkinson et al (1990)[17]
	a-ionone	0.003	4.27E-17	EPISuite	1.15798E-10	EPISuite
	myrcene	0.009	3.78396E-16	Kim et al (2010)[49]	2.1E-10	Atkinson et al (1986)
Apple (*Malus domestica*)	benzaldehyde	0.18	1E-25	EPISuite	1.7867E-11	EPISuite
	benzyl alcohol	0.77	6E-19	Harrison & Wells (2009)[48]	2.8E-11	Harrison & Wells (2009)[48]
	benzyl formate	0.01	1E-25	EPISuite	6.3395E-12	EPISuite
	benzyl acetate	0.02	1E-25	EPISuite	6.3816E-12	EPISuite
	(E)-cinnamaldehyde	0.01	2.2E-18	Smith et al (1996)[55]	4.8E-11	Smith et al (1996)[55]
	methyleugenol	0.01	1.2E-17	EPISuite	7.51143E-11	EPISuite
Canola /	alpha pinene	0.27	2.83E-17	Liu & Hu (2001)[56]	5.40493E-11	Montenegro et al (2012)[57]
	phenylacetaldehyde	0.01	1.00E-25	EPISuite	2.63E-11	EPISuite
	p Cymene	0.3	5.00E-20	Atkinson et	8.536E-12	EPISuite

Oilseed rape (*Brassica napus*)				al (1990)[17]		
	alpha Terpinene	0.09	8.70E-15	Atkinson et al (1990)[17]	3.6E-10	Atkinson et al (1986)[58]
	Linalool	0.11	4.30E-16	Aazaad & Lakshmipathi (2018)[59]	5.3E-11	Aazaad & Lakshmipathi (2018)[59]
	2-phenylethanol	0.05	1.00E-25	EPISuite	1.01548E-11	EPISuite
	(E,E) alphat Farnesene	0.01	1.00E-15	Bouvier-Brown et al (2009)[60]	2.19E-10	Kim et al (2010)[49]
	3-Carene	0.16	3.80E-17	Atkinson et al (1990)[17]	8.8E-11	Pratt et al (2012)[61]

Table 2. The change in non-zero CWB dimensions resulting from early pollution-changes in odor-blend structure for mustard and strawberry. Despite the fact that ozone and OH degradation results in rapid loss of 3 molecules quickly from the strawberry blend compared to 2 for mustard, mustard loses 6 dimensions while strawberry only loses 2.

Mustard			Strawberry		
	Number of molecules containing dimension			Number of molecules containing dimension	
non-zero dimensions	unpolluted	two molecules lost	non-zero dimensions	unpolluted	three molecules lost
methyl	3	3	alcohol	1	1
aldehyde	3	3	aldehyde	2	2
alkene	4	2	alkane	1	1
allylic methyl	2	**0**	alkene	8	6
aromatic	6	6	allylic methyl	5	2
bicyclic	1	**0**	aromatic	2	2
cyclic alkene	1	**0**	bicyclic	1	1
ester	2	2	cyclic	3	1
ether	1	1	cyclic alkene	3	1
ketone	1	1	ester	4	4
methyl	1	**0**	ketone	1	1
CCL2	5	4	methyl	3	2
CCL3	2	2	CCL2	2	2
CCL6	2	2	CCL3	2	**0**
CCL8	1	**0**	CCL4	2	2
CCC6	5	5	CCL5	1	1

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CCC11	1	**0**	CCL6	2	2
n/a	n/a	n/a	CCL7	1	1
n/a	n/a	n/a	CCL8	1	**0**
n/a	n/a	n/a	CCL9	1	1
n/a	n/a	n/a	CCL10	1	1
n/a	n/a	n/a	CCC6	4	2
n/a	n/a	n/a	CCC7	1	1
n/a	n/a	n/a	CCC12	1	1

Table 3. Volatile Organic Compound (VOC) composition of scents (relative proportions of each VOC) from published honeybee proboscis extension response datasets that were reanalyzed in this study.

Compound	**Girling et al 2013**	**Langford et al 2022**	**Lusebrink et al 2015**
2-phenylethanol	0.05	-	-
3-carene	0.16	-	-
Benzaldehyde	-	-	0.21
Benzyl alcohol	-	-	0.04
ß-caryophyllene	-	0.25	0.02
p-cymene	0.30	-	-
α-farnesene	0.01	-	-
Limonene	-	-	0.20
linalool	0.11	0.25	-
Methyl salicylate	-	-	0.09
MHO (6-Methyl-5-hepten-2-one)	-	0.25	-
Myrcene	-	-	0.16

E-ß-Ocimene	-	-	0.11
Z-ß-Ocimene	-	-	0.05
phenylacetaldehyde	0.01	-	-
α-pinene	0.27	-	-
ß-pinene	-	-	0.11
α-terpinene	0.09	0.25	-

Editorial summary:

The Compounds Without Borders method can be used to provide insights into air pollution impacts on pollination, according to examination of a perceptual modelling tool for understanding how pollutants like ozone affect honeybee scent perception.

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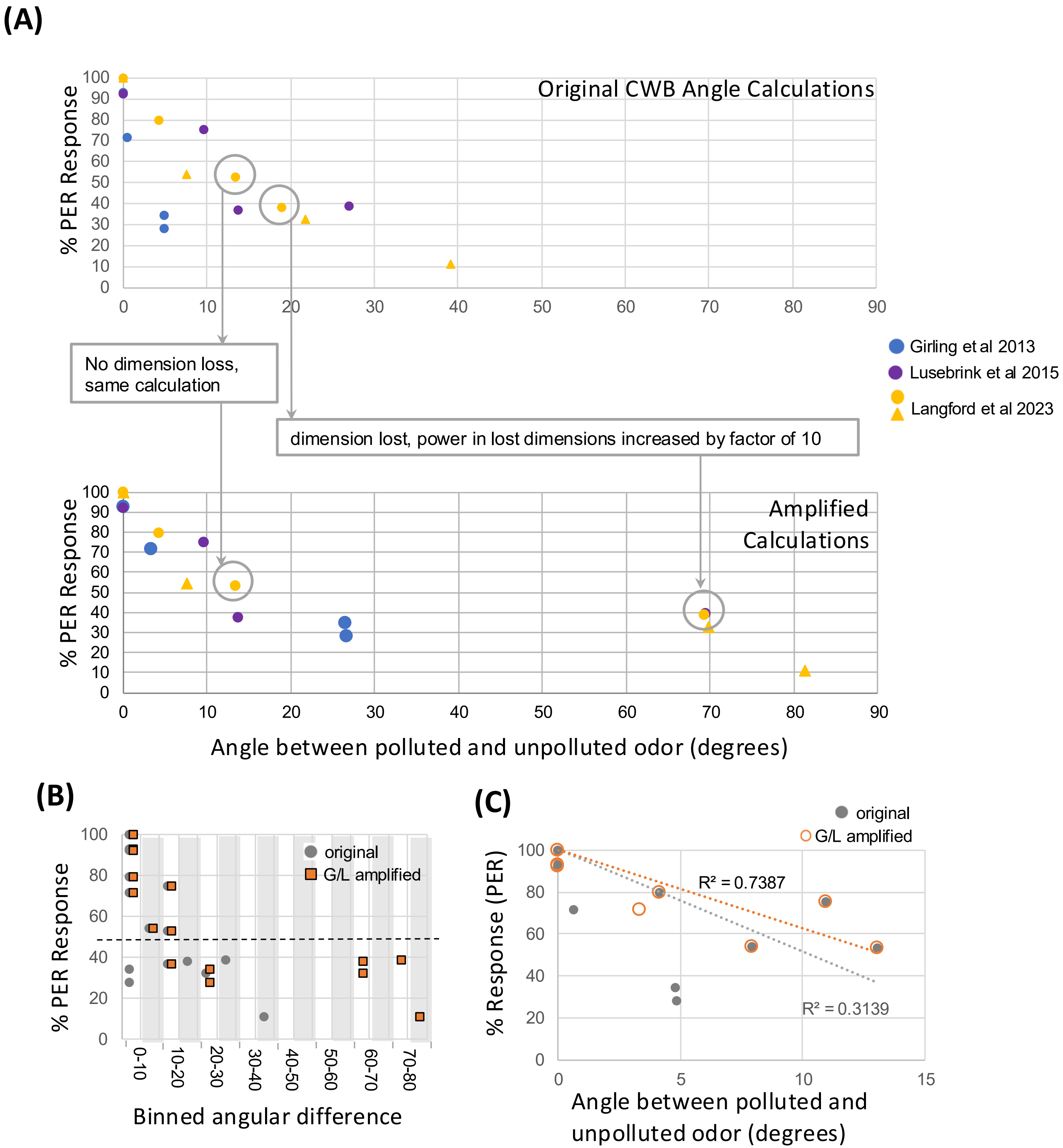
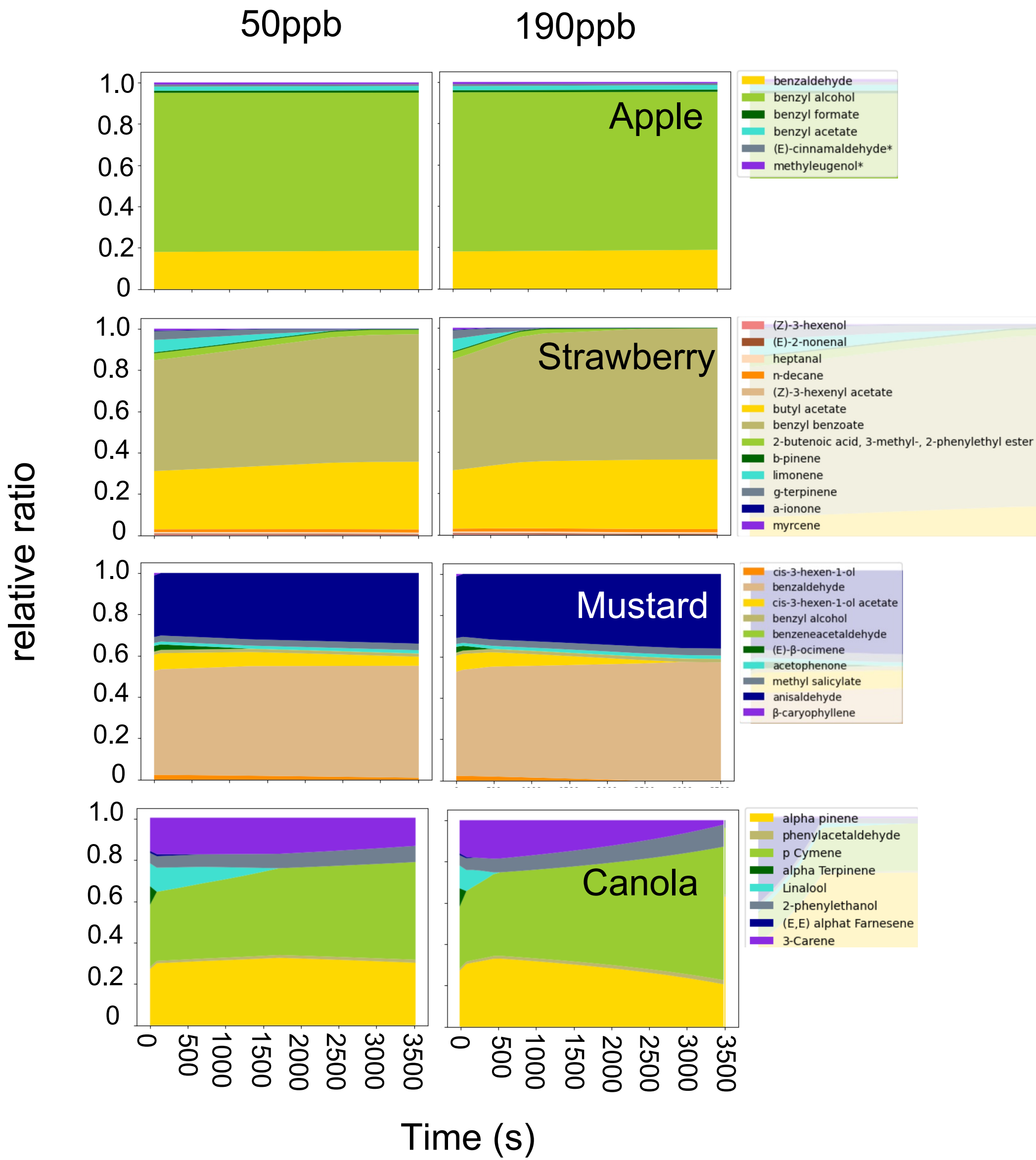
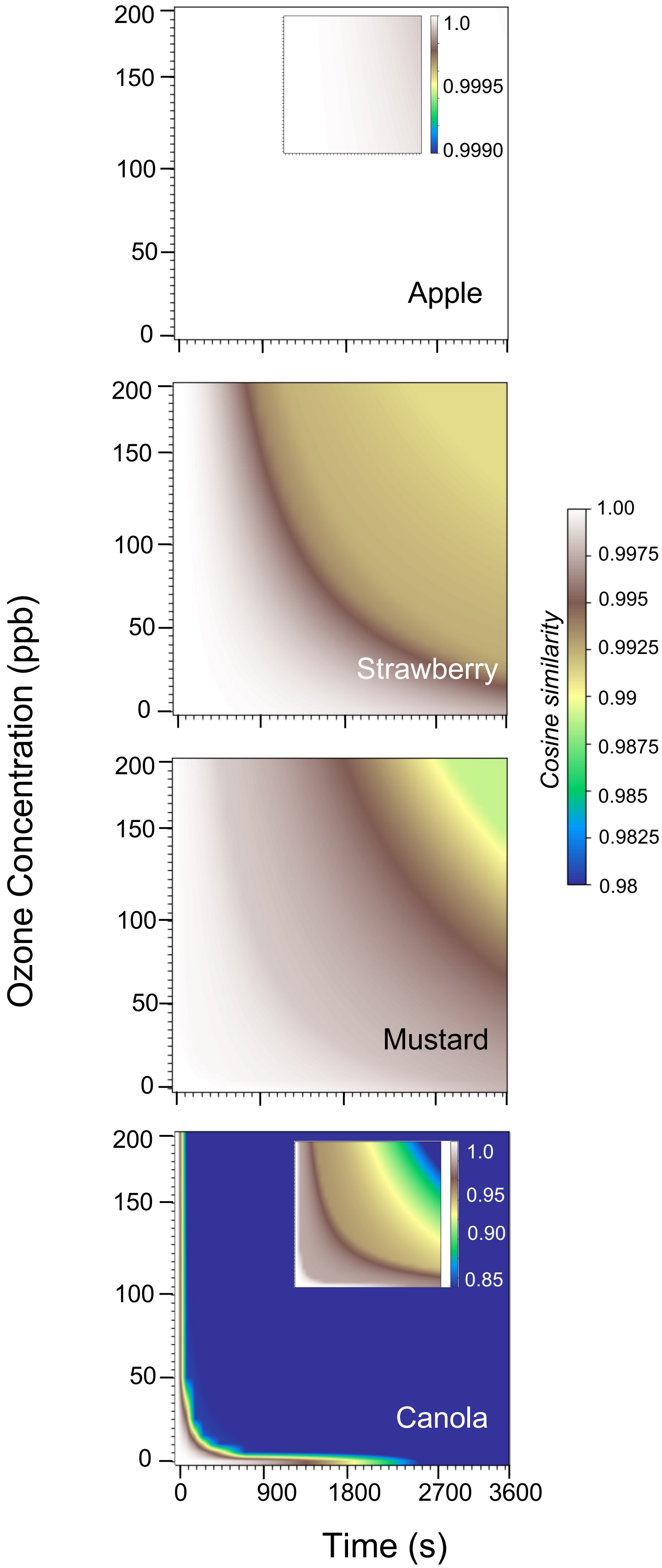
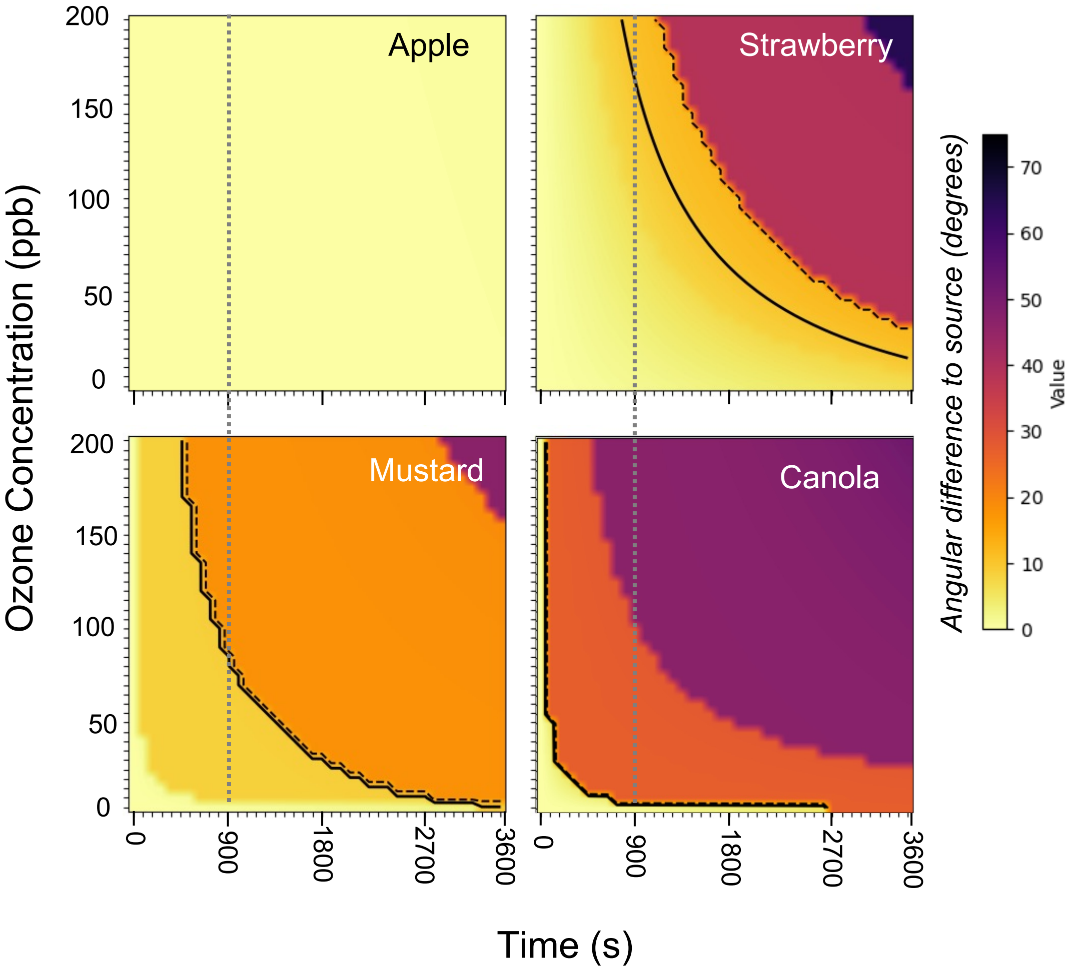


(A)
Original CWB Angle Calculations
% PER Response
Angle between polluted and unpolluted odor (degrees)
Girling et al 2013
Lusebrink et al 2015
Langford et al 2023
No dimension loss, same calculation
dimension lost, power in lost dimensions increased by factor of 10
Amplified Calculations
(B)
original
G/L amplified
% PER Response
0-10
10-20
20-30
30-40
40-50
50-60
60-70
70-80
Binned angular difference
(C)
original
G/L amplified
R² = 0.7387
R² = 0.3139
% Response (PER)
Angle between polluted and unpolluted odor (degrees)


50ppb
190ppb
Apple
benzaldehyde
benzyl alcohol
benzyl formate
benzyl acetate
(E)-cinnamaldehyde*
methyleugenol*
Strawberry
(Z)-3-hexenol
(E)-2-nonenal
heptanal
n-decane
(Z)-3-hexenyl acetate
butyl acetate
benzyl benzoate
2-butenoic acid, 3-methyl-, 2-phenylethyl ester
b-pinene
limonene
g-terpinene
a-ionone
myrcene
Mustard
cis-3-hexen-1-ol
benzaldehyde
cis-3-hexen-1-ol acetate
benzyl alcohol
benzeneacetaldehyde
(E)-β-ocimene
acetophenone
methyl salicylate
anisaldehyde
β-caryophyllene
Canola
alpha pinene
phenylacetaldehyde
p Cymene
alpha Terpinene
Linalool
2-phenylethanol
(E,E) alphat Farnesene
3-Carene
relative ratio
Time (s)


Ozone Concentration (ppb)
Time (s)
0
900
1800
2700
3600
200
150
100
50
0
Apple
1.0
0.9995
0.9990
Strawberry
Mustard
Canola
0.95
0.90
0.85
Cosine similarity
1.00
0.9975
0.995
0.9925
0.99
0.9875
0.985
0.9825
0.98



Apple
Strawberry
Mustard
Canola
Ozone Concentration (ppb)
200
150
100
50
0
0
900
1800
2700
3600
Time (s)
Angular difference to source (degrees)
Value
0
10
20
30
40
50
60
70