Potential effects of ozone pollution on crop pollinators and pollination

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Abstract

Human activities induce strong environmental changes that affect the quality of air, water and soil and increase the concentrations of polluting reactive compounds in the troposphere, such as ozone and nitrogen oxides. These changes can lead to a loss of biodiversity and alter plant physiology and plant-pollinator interactions, essential for pollination services, with potential consequences for agricultural production. Taking into account possible interactive effects with landscape quality and pesticide input, we investigated how air pollution (ozone and nitrogen oxides) and other sources of nitrogen is related to pollinator visitation rate and their contribution to agricultural production. We showed that ozone modulates the effect of pesticide exposure on crop pollinators, increasing the probability of negative impacts on crop pollination. Our results suggest that air pollution may have unexpected consequences for food safety and highlight the need for more sustainable transport and manufacturing policies to help safeguard biodiversity and related food production

Introduction

Human activity is changing environmental conditions worldwide (Rockstrom et al. 2009), affecting global biogeochemical flows (e.g. nitrogen, ozone; Fowler et al. 2013; Mills et al. 2013; Lefohn et al. 2018; Smil 2000) and, consequently, air, water and soil quality. In addition to habitat loss and climate change (with increased greenhouse-gas contributors), environmental pollution, including nitrogen deposition, is considered a major driver of biodiversity loss (Sala et al. 2000; Mazor et al. 2018) and can negatively impact ecosystem functioning and associated ecosystem services such as crop pollination (Gonzalez-Varo et al. 2013).

Nitrogen deposition (estimated to be 413 Tg N yr^{-1} in 2010) has more than doubled over the last century (Fowler et al.2013) due to emissions of ammonia (NH_3, from pecuary and agriculture) and nitrogen oxides (NOx produced in the combustion of fossil fuels). Such increases have affected plant communities (Tilman et al. 2002; Carvalheiro et al. 2020), with associated bottom-up impacts on higher trophic levels including pollinators (Poyry et al. 2017; Ramos et al. 2018; David et al. 2019; Wang & Tang 2019; Carvalheiro et al. 2020; Johnson et al.2020). While scarcity of nitrogen can constrain the positive effect of pollinators on crop production (e.g. sunflower; Tamburini et al., 2016; oilseed rape; Garratt et al. 2018), negative effects of excess nitrogen on pollination have also been reported (Marini et al.2015; Tamburini et al. 2017; Ramos et al. 2018).

Such responses are likely mediated by changes in oral resources quality and quantity, which in turn can be moderated by changes in climatic conditions (Flores-Morenoet al. 2016).

Another important air pollutant is tropospheric ozone, a major greenhouse-gas which is also phytotoxic (Mills et al. 2013; Lefohnet al. 2018; Ilic & Maksimovic 2021). Ozone levels have increased since the beginning of the industrial period (estimated to up of 35%; Mills et al., 2013; Guerreiro et al., 2014; IPCC, 2014). While there are other sources of ozone (e.g. volatile organic compounds, carbon monoxide and methane), oxidized nitrogen (NO_x) is one of the two major ozone precursors (Millset al. 2013; Lefohnet al. 2018). Increased concentrations of ozone can reduce photosynthesis and plant growth (Tjoelker & Luxmoore 1991; Blacket al. 2007) and negatively a ect the timing of owering and number of owers (Feder & Sullivan 1969; Hayes et al. 2012; Leisner & Ainsworth 2012) (Fig. 1). Increased ozone concentration in the air (e.g. 80-120 ppb, frequently found near urban areas; Paoletti et al., 2014) can also change the concentration and emission distance of oral volatile organic compounds (Heidenet al. 1999; McFrederickeet al. 2008; Farre-Armengol et al. 2016; Fuenteset al. 2016; Jurgens & Bischo 2017) and, consequently, a ect pollinator olfaction and foraging behaviour (Farre-Armengolet al. 2016; Fuenteset al. 2016; Vanderplancket al. 2021) (see Fig. 1). These e ects on plant pollinator interactions may partly explain the reported negative e ects of ozone on seed and fruit production detected in previous studies (Millset al. 2013; Farre-Armengolet al. 2016; Fuhrer et al. 2016). Yet, few studies have explored the e ects of air pollution (e.g., nitrogen oxides and ozone) on pollinator foraging patterns and e ciency, and if the strength and direction of such e ects depends on other important environment drivers, such as pesticide use (Walker & Wu 2017) or land use (Mazor et al., 2018; Sala et al., 2000).

Taking into account potential interactive e ects with landscape quality for pollinators (i.e., natural and semi-natural vegetation composition) and pesticide exposure, we investigated how air pollution by ozone and di erent sources of nitrogen compromise pollinator visitation rates and their contribution to crop production (apple, blueberry, fava bean, oilseed rape). Given the negative e ects on ower abundance and odours described above, and the fact that previous studies detected greater bene t from pollination under lower N availability (Marini et al. 2015; Ramoset al. 2018), we expect that increased ozone and nitrogen will lead to declines in crop pollinator visitation rates and pollination service delivery. However, availability of non-crop habitats is an important determinant of pollinator abundance, richness and pollination services (Kennedy et al. 2013; Daineseet al.2019). We also expect that the e ect of ozone and nitrogen on pollinators and pollination will be weaker in structurally more simple landscapes (less semi-natural habitat and greater risk of exposure to pesticides), where the only potential pollinators would be species with greater resilience to land use intensi cation (Williams et al.2010; Bartomeuset al. 2013; Kremen & M'Gonigle 2015; Kleijnet al. 2015).

The results of this study contribute to our understanding of interactive e ects among atmospheric pollution, land-use management and eutrophication on crop pollinators and pollination and as such help inform the development of new practices and policies to safeguard pollinators and crop pollination.

Material and Methods

Pollinator and crop production data

A total of 133 unique data points with information on pollinator visitation rate and pollinator contribution to crop production were obtained from databases of previous studies, sampled in various crops in the UK (Garratt et al. 2014b, a, c, 2016) and the Netherlands (De Groot et al.unpublished data). A unique dataset is de ned by their sampling year, crop species and spatial location (see dataset details in Table 1, Fig. 2). Pollinator data was collected using transects surveys over a de ned distance and time, recording visitors to crop owers as *Apis* or non-*Apis* species (including bees and hover ies). At each site, pollinator contributions to crop production were measured using pollinator exclusion treatments and compared with open controls to establish a proportional contribution of insect pollinators to production (for further methodological details see Garratt et al., 2014a, 2014b, 2016, and De Groot unpublished data in supplementary material).

Whenever studies provided more than one crop production metric, we selected the most pertinent variable to define crop production: seed set for oilseed rape, pod set for fava bean (Garratt et al. 2014b) and fruit set for blueberry. For apple, studies conducted in the Netherlands gave information on fruit quality, i.e., fruit weight. For studies in apple orchards in the UK, data available concerned final fruit set at harvest. For each experimental branch, the number of apples which had developed on experimental inflorescences was recorded (see Garratt et al., 2014a, 2014b, 2016).

As data from different studies applied different methodologies to extract information on pollinators and pollination, we calculated z-scores within each study for crop pollination (i.e., contribution of pollinators to crop production) and pollinator abundances (*Apis* and non-*Apis* pollinators separately). This measure allows for the standardisation of scores with respect to the other scores into the same group (site/crop/year) (Garibaldi et al. 2011, 2015).

Ozone and NO_x data

Information on atmospheric nitrogen (NO_x) and ozone (O_3) were obtained from the Tropospheric Monitoring Instrument (TROPOMI), hosted by the European Space Agency's (ESA) Sentinel-5P satellite under the Copernicus programme (https://sentinel.esa.int/web/sentinel/missions/sentinel-5p). The Sentinel-5 Precursor mission is the first Copernicus mission dedicated to monitoring our atmosphere and provides information and services on air quality, climate, ozone (O_3) and Nitrogen dioxide (NO_2) between the surface and the top of the troposphere and the ozone layer. The spatial resolution of the Sentinel-5P is 7x3.5 km. Data of O_3 and NO_2 were extracted using the NASA Panoply 4.11.1 software (NASA 2020) (Fig. 2).

To generate mean NO_2 and O_3 values over our specific sites, we extract daily values from TROPOMI layers between may 2019 (first of the TROPOMI-Sentinal5P products was released at the end of April 2019) and September 2019. We did not include data from 2020 in our mean calculation, due to the unusual change in human activity caused by covid-19 health crises. While nitrogen oxides are one of the several precursor of ozone (Mills et al. 2013), O_3 and NO_2 are not correlated (*cor* = 0.070; p-value = 0.421).

Agricultural nitrogen input data

Estimated average total annual application of manufactured nitrogen (1km resolution, $kg/km^2/year$) was extracted for England from the raster CEH Land Cover(r) plus Fertilisers (CEH, Wallingford, UK; https://www.ceh.ac.uk). CEH dataset used data from Defra British Survey of Fertiliser practice (2010-2015) to derive average annual application of manufactured fertilisers for each crop type and then derived total application at 1km resolution using crop areas from CEH Land Cover(r) plus: Crops (averaged 2015-2017) (Osorio et al.2019). As changes in land use intensity in the UK were limited, with trends stable overall since 1994 (Martay et al. 2018), we assume that values based on these maps are representative for the sampling years (2011 and 2012).

For the Netherlands, mean values of nitrogen fertilizer application rate by crop were extracted from the database of the Netherlands Enterprise Agency (RVO) for 2016 (*Gewascodelijst Stikstofgebruiksnormen*, https://english.rvo.nl). To estimate the mean value of nitrogen applied as fertilizer at 1km resolution (in $kg/km^2/year$), we calculated a weighted average, taking into account the proportion of each crop in the landscape. Crop coverage per site were extracted for each $1km^2$ cell as an average of the BRP (*Basisregistratie gewaspercelen*) shapefiles 2015 and 2016 obtained from the RVO (https://english.rvo.nl/).

$$N\_Fer = \sum (\text{Proportion of each crop category} \times \text{mean annual application rate for the category})$$

These years (2015-2016) correspond to the median of study years in the Netherlands included in the analyses, that are 2013, 2014, 2017 and 2018.

Pesticide input data

To estimate average level of pesticide applied per crop at each field site (1km buffer), we calculated a pesticide risk assessment (RI), including herbicides, insecticides, molluscicides and fungicides, using the methodology described by Yasrebi-de-Kom et al. (2019) as:

$$RI = \sum HQ = \frac{\text{Application rate } (g.ha^{-1})}{\text{Toxicity } (LD_{50} \text{ in mg per bee})} > 50$$

with HQ the hazard quotient (HQ) of each active molecule and the median lethal dose per bee (LD_{50}). The median lethal dose is one way to measure the short-term poisoning potential (acute toxicity) of a substance. The LD_{50} is the amount of a substance, given all at once, which causes the death of 50% of a group of test animals. The hazard quotient ratio gives an approximation of how close the likely exposure of bees is to a toxicologically significant level. The pesticide risk index (RI) was defined as the number of high risk active ingredients (HQ>50; see EPPO, 2010) that were applied. If HQ<50, the active ingredient was categorized as low risk to bees.

The LD_{50} of 390 active ingredients used in the UK and the Netherlands were extracted from the Pesticides Properties DataBase (PPDB) from the University of Hertfordshire, UK (https://sitem.herts.ac.uk/aeru/ppdb/en/index.htm; Lewis et al., 2016; Lewis and Tzilivakis, 2019) (see list of active ingredients in Appendix S1 in Supporting Information). As proposed by EPPO (2010), the risk assessment was carried out selecting the lowest of the oral and contact LD_{50} values available across the different bee species (honey bees, bumble bees and other wild bees), to take the most conservative approach for the entire bee community (see Table S2). However, LD_{50} values were mainly available for honey bees, sometimes for bumble bees, and much less frequently for other pollinators (Lewis et al., 2016; Lewis and Tzilivakis, 2019; Yasrebi-de Kom et al., 2019).

For the UK, the average annual application rate at 1km resolution (in kg/km^2/year) was obtained for 130 pesticide active ingredients from the CEH Land Coverfi plus: Pesticides 2012-2016 (Jarvis et al. 2019) of the Centre for Ecology and Hydrology (CEH, Wallingford, UK; https://www.ceh.ac.uk), across a four-year period (from 2012, 2013, 2014 and 2016). For the Netherlands, we created the average annual allowed application rate at 1km^2 (in kg/km^2/year) across a two-year period (2015 and 2016) for 179 pesticide active ingredients, combining allowed application rates produced by Yasrebi-de-Kom et al. (2019) and the BRP shapefiles for crops in 2015 and 2016 obtained from the RVO (https://english.rvo.nl).

Land cover composition data

The availability of crop pollinators strongly depends on landscape quality (Kennedy et al. 2013; Dainese et al. 2019). We therefore calculated the proportion of forest and (semi-)natural habitats combined in a 1km radius buffer zone for each sampling site. For the UK, data were extracted from the Land Cover Map for 2015 (LCM2015; 25m resolution raster) (CEH Data Licence Agreement 1338). For the Netherlands, we merged data from the BRP shapefiles 2015 and 2016 (https://www.pdok.nl/introductie/-/article/basisregistratie-gewaspercelen-brp-) and the BBG (Bestand Bodemgebruik) shapefile 2015 (https://www.pdok.nl/introductie/-/article/cbs-bestand-bodemgebruik) obtained from the RVO (https://english.rvo.nl) and Statistics Netherlands (CBS, https://www.cbs.nl/en-gb) respectively for an optimal coverage (especially for not improved grasslands). These habitats included the proportion of forest areas and natural areas (including natural grasslands), but excluded agricultural improved grasslands and pastures due to their generally intensive management strategy and low habitat quality for pollinators (Ekroos et al. 2020).

Statistical analyses

We used linear mixed models to analyse effects of ozone, nitrogen enrichment (i.e., including both the mean values of N fertilizer application on the agricultural fields and the NOx concentration in the air from satellite data), the risk of pesticide exposure and the proportion of (semi-) natural habitats and their two-way interactions on the abundance of pollinators and their contribution to crop production (see correlation matrix in Appendix S2).

The local abundance of honey bees is primarily determine by beekeeper behaviour rather than local e ects of habitats (Buchler et al. 2014; Wood et al. 2020). As managed species they are in uenced di erently by environmental pressures compared to wild pollinators, and we therefore analysed *Apis mellifera* separately from non-*Apis* pollinators (i.e., other bees and hover ies).

To account for variation associated with the crop system on pollinators and pollination, crop identity was included as random e ect in all models. Moreover, to remove potential confounding e ects with study region or country, all explanatory variables included in each model were centered within study-year combinations (Van de Pol & Wright 2009).

As previous studies have also shown that densities of non-*Apis* pollinators can in some circumstances be negatively a ected by honey bee densities (e.g. Lindstrom et al., 2016; Geslin et al., 2017; Mallinger et al., 2017), honey bee abundance was included as explanatory variable in non-*Apis* pollinator models. For the analysis of the contribution of pollinators to crop production, in addition to sources of eutrophication, ozone pollution, pesticide risk and proportion of (semi-)natural habitats, we included abundance of honey bees (*Apis mellifera*) and non-*Apis* pollinators as covariates.

First, to test for spatial autocorrelation, we compared models with di erent spatial correlation structure (exponential, Gaussian, Linear, rational quadratics and spherical spatial autocorrelation) and without spatial correlation structure, and de ned the best random structure of the model based on their AICc scores (Akaike Information Criterion for small samples). Then, we applied model selection to the xed terms of the model ([?]AICc < 2 with the best model; Anderson et al., 2001). To not over t the global model in relation to our sample size, the number of parameters in each tested model was restricted to 5 (including potential interaction e ects). Selection of the best candidate models are presented in Supplementary material (see Appendix S3, S4 and S5 in Supporting Information). All analyses were computed using the ape (Paradis et al. 2019), nlme (Pinheiro et al. 2020) and MuMIn (Barton 2011) packages in R software, version 3.4.2 (R Development Core Team 2018). All spatial extraction or landscape index calculation from shape le and raster maps were made using QGIS software version 3.10 A Coruna (QGIS Development Team 2020).

Results

The observed abundances of pollinators at each sampling transect varied from 0 to 367 for honey bees (*Apis*) and from 0 to 154 non-*Apis* pollinators (i.e., wild bees and hover ies).

Mean ozone value per study site varied from 0.140 to 0.144 mol.m^{-2} in the Netherlands and from 0.142 to 0.147 mol.m^{-2} in UK (for reference, worldwide it varies from 0.079 to 0.222 mol.m^{-2}). The mean tropospheric NO_2 per study site ranged from 27.8 to 76.5 mmol.m^{-2} (from 0 to 2.14 mmol.m^{-2} worldwide) and the gradient of fertilizer N input varied from 2.28 to 21.09 t.km^{-2} (2.28 to 12.32 in UK and 3.89 to 21.09 in the Netherlands). The risk index of pesticide exposure varied between 2 to 8 in the Netherlands and between 2 to 10 in UK, (i.e., between 2 and 10 high risk active molecules were applied in the 1km bu er around study sites). The proportion of natural and semi-natural habitats in the 1km^2 surrounding bu er varied from 0.1 to 37% in UK (with a mean=8.9 and median=4.4) and from 0 to 47% in the Netherlands (with mean=7.0 and median=1.8).

We observed e ects of pesticide risk exposure and ozone on crop pollinator abundance as well as interacting e ects between these two environmental factors, but such e ects di ered between *Apis* and non-*Apis*. We found that abundance of honey bees (*Apis mellifera*) in crops was negatively related to concentration of ozone but positively related to the risk of pesticide exposure (see Appendix S3). However, the positive relationship observed between the abundance of honey bee and the risk of pesticide exposure becames less strong with increasing ozone levels (Fig. 3A; see Appendix S3). In other words, the negative e ect of ozone on *Apis* pollinators is more accentuated when this risk of exposure increases (see Appendix S6). As for non-*Apis*, the negative e ect of pesticides on abundance was more accentuated at higher ozone exposition

(Fig. 3B; see Appendix S4).

As hypothesized, we found a negative correlation between ozone and the contribution of pollinators to crop production (i.e., crop pollination assessed by the difference of production between open and close treatments; see Appendix S5 and S6), but also an interacting effect between ozone and the risk of pesticide exposure on crop production. While at low concentration of ozone the risk index (RI) of pesticide exposure was positively related to the contribution of pollinators to crop production, the relationship became negative when ozone levels were high (Fig. 3C; see Appendix S5).

Contrary to our expectations, we found no evidence of a relationship of any Nitrogen sources studied here (i.e., atmospheric nitrogen dioxide deposition and mean application rate of nitrogen fertilisers at 1km resolution) on the abundance of *Apis* and non-*Apis* pollinators nor on the contribution of pollinators to crop production (see Appendix S3, S4 and S5). We also did not observe evidence of a correlation between the proportion of semi-natural habitats and the abundance of crop pollinators or on their contribution to crop production.

Discussion

Despite the recognised influence that ongoing human driven changes on nitrogen and ozone availability have on plant communities (Fowler et al. 2013; Mills et al. 2013; Guerreiro et al. 2014), little is known about how such changes impact pollinators and the services they provide to crop pollination, or how this interacts or is moderated by other drivers of pollinator decline. Recent studies showed that ozone pollution can impact directly and indirectly many fundamental ecological processes with consequences on biodiversity and sustainability of ecosystem services, such as pollination (Tai et al. 2014; Fuhrer et al. 2016; Duque et al. 2020; Emberson 2020). Here, we highlighted that ozone is part of a complex interacting system, mediating the strength of the effects pesticide exposure has on crop pollinators and the contribution of these pollinators to crop production. Below, we discuss in detail the potential mechanisms behind the patterns detected and the implications of our findings for conservation and management of crop pollination.

Interacting effect of ozone with pesticide exposure

As expected (Hayes et al. 2012; Leisner & Ainsworth 2012; Mills et al. 2013), ozone levels were negatively correlated to crop pollination. Recent studies have estimated that global agricultural losses due to high ozone levels totalled 79–121 million metric tons in 2000 with global economic losses ranging from $11 to $26 billion (Van Dingenen et al. 2009; Avnery et al. 2011a) and predicted increases of between $17 and $35 billion annually by 2030 (Van Dingenen et al. 2009; Avnery et al. 2011a). Such effects may be partly related to a reduction in pollen germination (Leisner & Ainsworth 2012; Taia et al. 2013; Gillespie et al. 2015). Our results suggest that changes in pollination by insects (due to changes in flower visitation patterns) may also play an important role.

The fact that increasing ozone levels modified the response of crop pollination to pesticide exposure (which turns from positive to negative) may be related with pest control. Farmers widely use pesticides to minimize infestations by pests and protect crops from potential reduction of crop production, both in quality and quantity (Damalas 2009), and hence positive effects of pesticide use on production are expected if pests are more limiting than pollinators to production.

It is however possible, that in more degraded environments, i.e., with a higher level of ozone pollution, the cost/benefit ratio of pesticides on crop production changes. In less intensive landscapes with higher pollinator pool, the negative impact of pesticides on pollinators and these consequences on crop pollination can be compensate by the benefit of pest regulation by pesticide use. However, in highly intensive landscapes, due to scarcity of pollinators which limits pollination and crop production, the negative effects of pesticides on crop pollinators (which are more accentuated under high ozone levels, Fig 3) may outweigh the positive effects on pest reduction on crop production.

The negative relationship between ozone pollution and flower visitor abundance could be due to changes in plant-pollinator communication and flower attractiveness that may affect crop pollinator foraging behaviour. Previous studies have showed that ozone induces changes in availability of floral resources by modifying owering timing and number of owers, some plant species being particularly sensitive (Hayes et al. 2012; Leisner & Ainsworth 2012; Mills et al. 2013). Ozone also alters pollinator decision-making, modifying and reducing the volatile oral scents (Farré-Armengol et al. 2016; Fuentes et al. 2016; Saunier & Blande 2019; Vanderplanck et al. 2021) and damaging pollinators olfactory organs (Dotterl et al. 2016; Vanderplanck et al. 2021).

The fact that the negative e ect of pesticide exposure on non-Apis pollinators (Mancini et al. 2019; Walker & Wu 2017; Woodcock et al. 2017) was more accentuated under high ozone concentration (Table S1) could be due to communities being less diverse and/or abundant in regions with high ozone, but also to changes in pollinator assemblages. In more degraded areas (high pesticide exposure, high ozone concentration), crop pollinator communities are dominated by a handful of very dominant widespread species that are more resilient to intensive land use (Kleijn et al. 2015), which often have a more generalist diet and may be more mobile (Biesmeijer et al. 2006; Goulson et al. 2008; Connop et al. 2010). Consequently, in such regions the negative e ect of ozone on non-Apis crop pollinators might be less detectable, only under more degraded environment, i.e., under high level of pesticide exposure.

Although the negative impact of pesticides on honey bees is well known (e.g. Mancini et al., 2019; Walker and Wu, 2017; Woodcock et al., 2017; Park et al., 2015; Tosi et al., 2017), we found that pesticide exposure was positively related to honey bee density in crops. This result is probably due to beekeeping management strategies that are likely more frequent in intensive agricultural areas where the demand for colony supply to ensure e cient pollination is high (Garibaldi et al.2017; Rollin & Garibaldi 2019), masking (and even compensating) the negative e ects of pesticides. However, the positive relationship between abundance of honey bees in crops and pesticide exposure was lower when ozone concentration increased. This can re ect the negative e ect of pesticides on honey bees, decreasing the pollination e ciency and survival of honey bees (Prado et al. 2019), despite the local increase of individuals due to the import of colonies by beekeepers in intensive farming systems.

E ect of nitrogen enrichment

Contrary to our expectations, we did not observe e ects of nitrogen enrichment sources on crop pollinators and pollination. It is possible that the proxies used in our study do not adequately represent the real nitrogen exposure levels in our study elds. Indeed, while pollinators can be a ected by local (i.e. within eld) changes in nutrient availability (David et al. 2019), our proxies for nitrogen levels are taken at much broader scales. The amount of nitrogen that is in reality deposited in a speci c location of the biosphere may not be well represented by the NO2 levels measured in the troposphere at much larger spatial resolution of the available data from the Sentinel-5 satellite (i.e., 7x3.5 km). Similarly, the estimated mean application rate of fertilizers at each study region (which is based on average application levels for each crop at country level, and do not consider personal decisions of landowners) may not be of a su cient resolution to detect changes in fertilization rate and its e ects at the local scale. For example, the presence of (semi-)natural habitats in the landscape will inevitably decrease the estimated average fertilizer application rate at 1km^2 resolution, while a high proportion of highly enriched crops, such as cereals, maize or fertilised grasslands (e.g., ray grass) will tend to increase the estimated average application rate. Future works involving farmer interviews asking for the actual amount of fertilizer applied to better characterize nutrient availability would be important. Moreover, although we had a clear gradient of N fertilizer input across sites, all study sites were located in landscapes with a critical positive surplus of nitrogen inputs (that goes up to 20 t.km^2 for the year 2010) (European Environment Agency, 2020). Consequently, it is possible that throughout the study region pollinator communities are dominated by nitrophilous species (Carvalheiro et al. 2020) well adapted to high nitrogen conditions and the negative e ects of nitrogen on pollinators and their contribution to crop production are no longer detectable in our speci c study sites.

Finally, it is possible that functional composition of pollinators has changed along the nitrogen availability gradient but with no net change in pollinator abundance, or their contribution to crop production. Indeed, N enrichment can have contrasting e ects on pollinator species. Pollinators with more diversi ed diets might be less a ected by landscape eutrophication potentially due to their ability to forage on a higher diversity of owers in a diverse set of habitats (Poyry et al. 2017; Carvalheiro et al. 2020). N deposition that changes soil nutrient availability is an important driver of plant species composition change and result in the decline of oligotrophic plant species, such as nitrogen xing Fabaceae species (Roth et al. 2013, 2019). Fabaceae are the main food resource of most bumble bee species and many other solitary bees (Goulson et al. 2008; Kleijn & Raemakers 2008; Connop et al. 2010). Thus, species specialised on Fabaceae (and other N sensitive plants), can have more di culty in nding adequate resources be more susceptible to the e ects of N enrichment than other pollinator species (Stevens et al. 2018). But if, for the crops studied here, species that prefer nitrophilous environments (see Carvalheiro et al. 2020) are equally e cient for crop pollination than species which are negatively a ected, pollinator community compositional changes would not a ect the net crop pollination outcome.

Conclusions and implications for conservation of crop pollinators and pollination.

Increased air pollution can a ect plant and animal physiology in multiple ways (Van Dingenen et al. 2009; Mills et al. 2013; Emberson 2020). In Europe, the biggest problem today is the increased concentrations of tropospheric ozone due to its harmful e ects on health and ecosystems (Ilic & Maksimovic 2021). Air pollution does not constitute a single problem, but presents an array of threats and opportunities to plants and animals (Dudley & Stolton 2021). Plants are more sensitive to ozone than animals, but air pollution, by modifying the physiology and biochemistry of plants, has a decisive in uence on the interactions of plants and insects (Ilic & Maksimovic 2021). Thereby, changes in plant communities can propagate throughout the food webs to a ect other organisms (Lovett et al. 2009; Dudley & Stolton 2021; Ilic & Maksimovic 2021).

While we were not able to detect e ects of oxide nitrates, our results highlight potential negative e ects of ozone on crop pollinators and changes in the contribution of pollinators to crop production, while also a ecting the sensitivity of pollinators to pesticide exposure. Indeed, di erent air pollutants (such as ozone and NOx) can act at di erent spatio-temporal scales and interact with other natural and anthropogenic factors that also alter ecosystem functioning (Dudley & Stolton 2021).

Even if more detailed studies are required and further evidence from other regions and crops is needed, our ndings suggest management plans involving changes in pesticide use, should take into account the ongoing increase in air pollution, and speci cally of the predicted increased concentration of tropospheric ozone in the near future (Van Dingenen et al. 2009; Avnery et al. 2011b; Archibald et al. 2020). Our results also highlight that negative impacts of ozone pollution on pollinators and pollination exist, and should be considered when developing transport, manufacturing and renewable energy policies in favor of the protection of air quality and the conservation of biodiversity and associated ecosystem services.

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Table 1. Sources of data for crop production and pollinator abundance included in the analyses. UK: United Kingdom; NL: Netherlands.

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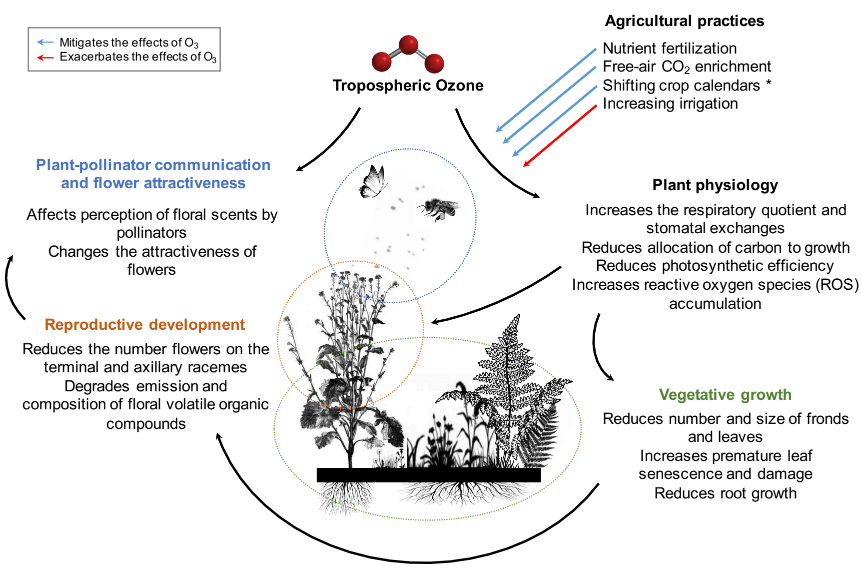
image1.emf available at https://authorea.com/users/733032/articles/711001-potential-effects-of-ozone-pollution-on-crop-pollinators-and-pollination

Figure and Table captions

Figure 1. Review of known effects of tropospheric ozone on plants and plant-pollinator interactions. Blue and red arrows indicate agricultural practices that can respectively, mitigate or exacerbate effects of ozone on plant physiology (*Shifting crop calendars consists of a change in the sowing period to dissociate the peak of flowering and production of sensitive crops from the peak of atmospheric ozone concentration).

Figure 2. Sampling sites (red dots) included in the study and gradient of ozone (O_3) and dioxide nitrogen (NO_2) in the United Kingdom (UK) and the Netherlands (NL). O_3 and NO_2 gradients were mapped using the software NASA Panoply v.4.11.1 (e.g. Sentinel-5 satellite data extraction for August 2019) (NASA 2020) and QGIS v.3.6 (QGIS Development Team 2020).

Figure 3. The increase in ozone concentration modifies the relationship between the risk of pesticide exposure and (A) the abundance of honey bees, (B) the abundance of non-*Apis* pollinators and (C) the contribution of pollinators on crop production. The dashed lines show a null difference of the response variable with the mean of the study (combination crop/year/country.


Mitigates the effects of O_3
Exacerbates the effects of O_3
Tropospheric Ozone
Agricultural practices
Nutrient fertilization
Free-air CO_2 enrichment
Shifting crop calendars *
Increasing irrigation
Plant-pollinator communication and flower attractiveness
Affects perception of floral scents by pollinators
Changes the attractiveness of flowers
Plant physiology
Increases the respiratory quotient and stomatal exchanges
Reduces allocation of carbon to growth
Reduces photosynthetic efficiency
Increases reactive oxygen species (ROS) accumulation
Reproductive development
Reduces the number flowers on the terminal and axillary racemes
Degrades emission and composition of floral volatile organic compounds
Vegetative growth
Reduces number and size of fronds and leaves
Increases premature leaf senescence and damage
Reduces root growth