TITLE:

Out of sight, Out of mind – but not Out of scope. The need to consider ozone in restoration science, policy and practice

RUNNING HEAD:

Ozone in restoration discourse

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ABSTRACT

Restoration ecologists have local- to global-scale ambitions in a policy framework of sustainable development goals and reversing biodiversity loss. Emphasis is given to environmental alteration, typically considering land degradation and climate change. Other environmental drivers, such as pollution, receive less attention. Here we emphasize that terrestrial restoration discourse needs to consider tropospheric ozone (O_3) pollution. O_3's pervasive influence on plants and other ecosystem components provides for the possibility of consequences at community and ecosystem levels. The precursor chemicals which lead to O_3 formation are increasing, precipitously so in rapidly-industrialising regions of the world. Yet, a review of critical restoration guidance and journals suggests that because O_3 is out of sight, it remains out of mind. Based on a narrative cross-discipline literature review, we examine: (i) how O_3 could affect the achievement of restoration goals; and, (ii) how restoration interventions could feedback on tropospheric O_3. Evidence, currently limited, suggests that O_3 could impair the achievement of restoration goals to as great an extent as other drivers, but, in general, we lack direct quantification. Restoration interventions (e.g. tree planting) that may be considered successful can actually exacerbate O_3 pollution with negative consequences for food security and human health. These wide-ranging effects, across multiple goals, mean that O_3 is not out of scope for restoration science, policy and practice. In detailing a strategic ozone-aware restoration agenda, we suggest how restoration science and policy can quantify O_3's influence, while outlining steps practitioners can take to adapt to/mitigate the impacts of O_3 pollution.

KEYWORDS

air pollution, biodiversity, climate change, nitrogen deposition, restoration targets, tropospheric ozone, UN Decade on Ecosystem Restoration

CONCEPTUAL IMPLICATIONS

Restoration science, policy and practice need to account for impacts of tropospheric ozone (O_3) pollution on the attainment of restoration goals.

Restoration science needs to examine how O_3 interacts with multiple drivers to affect restoration success at community and ecosystem levels.

Restoration science needs to examine how restoration interventions feedback on O_3 generation, with implications for food security, human health and wealth.

Restoration policy documents need to consider the risk posed by O_3, including in relation to scaling-up e.g. continued high-quality seed supply.

Restoration practice needs to consider the ozone-tolerance and/or susceptibility of plant species, and other ecosystem components, in different environmental contexts.

INTRODUCTION

National and international restoration targets are designed to tackle integrated socio-ecological issues, encompassed by the sustainable development goal (SDG) agenda. Issues restoration can address include climate change, biodiversity loss, dwindling water supplies, and land degradation (Gann et al. 2019). In trying to reach targets of resilient and sustainable systems, restoration ecologists, policy makers and practitioners often focus on threats such as climate change, but are also aware of air pollution issues, especially nitrogen deposition (e.g. Bobbink et al. 2010; McPhee et al. 2015). In this review article, we emphasize that threat awareness does not yet extend to one key aspect of air pollution: tropospheric (ground-level) ozone (O_3). There appears to be a void in the science, policy and practice of ecological restoration in relation to O_3.

Here, we explore this void from the perspective of terrestrial ecosystem restoration. We explain the relevance of O_3 for the current terrestrial restoration agenda, and we detail how the void can be filled. Filling the void will enable restoration scientists, practitioners and policy makers to appropriately place O_3 among other drivers and threats affecting, and affected by, restoration interventions. It will also allow them to assess how actions to address O_3 may trade-off or synergise with approaches to other drivers.

We first present useful background on O_3 in the context of ecological restoration. We particularly note O_3's cascade of consequences for individual plants, and plant-plant, plant-soil and plant-animal interactions. We demonstrate that key guidance documents and publications for restoration apparently overlook O_3. We then use a narrative review, from agricultural, forestry and conservation literature, to describe and exemplify how O_3 may compromise selected key goals for ecological restoration at community and ecosystem levels. Based on contemporary foci across the restoration continuum, we cover biodiversity restoration, contaminated land remediation, carbon storage and climate change mitigation, and the provision of multiple ecosystem functions and services (ES). We then examine how restoration interventions may directly, or indirectly, affect tropospheric O_3 itself, at regional to global-scales, with consequent feedbacks on wider society through O_3's effects on climate change, food security and human health. Finally, we provide a strategic agenda to show how restoration science, policy and practice can act in the face of tropospheric O_3 pollution.

TROPOSPHERIC OZONE: A PRIMER IN RELATION TO ECOLOGICAL RESTORATION

Some of the processes behind atmospheric ozone formation, transport, and destruction, and its effects on plants and other organisms, can be complex and/or nuanced. Here, we provide an overview of important elements, relevant to the terrestrial restoration agenda. However, we do not aim to present a detailed discussion of the complex nature of these processes.

Tropospheric O_3 forms when emissions of precursor chemicals, such as nitrogen oxides and volatile organic compounds (VOCs), associated with soil, vegetation and fires, coincide with sunlight (Jaffe & Wigder 2012).

This 'natural' formation has implications for how restoration interventions themselves could feedback on tropospheric O_3 dynamics. Species selection will influence which biogenic VOCs (bVOCs) are emitted, and the balance between those bVOCs that tend to increase O_3 formation (e.g. isoprenes), and those (e.g. sesquiterpenes) that tend to depress O_3 concentrations through ozonolysis (as explored in more detail later: see *Feedbacks* subsection).

Rapid industrialisation has led to large increases in precursor chemicals, meaning the formation of O_3 has been bolstered beyond 'natural' rates; from atmospheric amounts of 10 to 20 parts per billion (ppb) in pre-industrial times to a global-average 40 ppb (Mills et al. 2018a). These current ambient O_3 concentrations damage human health and materials, have deleterious consequences for plants and other ecosystem components (Emberson et al. 2018; Agathokleous et al. 2020a) and exacerbate climate change (Lee et al. 1996; Ainsworth et al. 2012; Malley et al. 2017; Zhang et al. 2019). Even in the absence of future changes in industrial precursors, high O_3 concentrations will remain due to its continued generation under the influence of climate change, and dynamics of the VOC methane (CH_4) (Fu & Tian 2019).

Plants have defence mechanisms that can deal with possible deleterious consequences of low concentrations of O_3 (Wieser & Matyssek 2007; Grulke & Heath 2020). However, under high O_3 concentrations and conditions favouring O_3 uptake, plant defences can be overwhelmed, leading to cell death and visible leaf injury. Even at lower concentrations, chronic exposure and uptake leads to a "phytotoxic ozone dose" (POD) with plant leaf responses including altered metabolism (e.g. reduced photosynthesis) and stomatal sluggishness. The latter means there is a slower response from the stomata in response to external stimuli, such as light, temperature and soil moisture. For instance, stomata can take longer to open when atmospheric conditions are suitable for photosynthesis or can take longer to close under adverse conditions, such as limited soil moisture, leading to excessive water loss. Consequences at the individual plant level include changed allocation of assimilates, accelerated senescence, reduced whole-plant leaf area, lowered productivity, fewer flowers, and poor seed yield and quality (Leisner & Ainsworth 2012; Emberson et al. 2018). Poorer seed yield is especially problematic when trying to ensure adequate seed supply for scaling up restoration. Furthermore, plant volatile emission profiles are changed, with impacts on pollinators, herbivores and predators (e.g. Papazian & Blande 2020). Greater shoot-to-root ratios, although not a universal response (Grantz et al. 2006), can increase the susceptibility of plants to other threats such as drought and insect pests (Grulke & Heath 2020). Changed nutrient contents can also affect below-ground organisms through altered litter quantity and chemistry (Agathokleous et al. 2020a) (Figure 1).

O_3 concentrations are spatially and temporally variable, due to the reactive nature and relatively complex atmospheric chemistry of O_3. This variability has implications for the achievement of restoration goals at global, regional and local levels, given not all interventions and goals will be equally exposed to O_3. Typically, O_3 increases with elevation (e.g. Chevalier et al. 2007), meaning that restoration projects in higher altitude areas will likely have higher O_3 exposures. Geographically, O_3 is likely to affect restoration targets in areas where restoration will increase in scale and ambition in the coming decades (e.g. sub-Saharan Africa, Ethiopia, and Asia particularly the Himalaya, Indian coastline, the south of Asia and Japan), while it is unlikely to affect restoration goal achievement in Australasia (Thompson et al. 2014; Agathokleous et al. 2020a). Some authors have limited expectations for high O_3 exposure in South America (Agathokleous et al. 2020a). However, there are 'hotspots' of concern (Figure 2) and recent evidence suggests fire activity in certain South American systems (e.g. the cerrado) has increased O_3 concentrations by 10 ppb per decade (Pope et al. 2020). In the Mediterranean Basin, elsewhere in Europe, and in North America, the likelihood of high O_3 exposures in rural systems will remain as peak episodes decline but background concentrations continue to increase (Paoletti et al. 2014). Background O_3 concentrations are also increasing in cities North America and Europe, ironically because of lower levels of other pollutants such as NO that previously broke down O_3 (Sicard et al. 2018); urban restoration projects also need to consider O_3 pollution.

THE OZONE VOID IN RESTORATION ECOLOGY DISCOURSE

Given the widespread evidence for impacts of O_3 on terrestrial plant growth and O_3's wider implications for society, you might expect restoration ecology discourse to consider it. However, despite comprehensive searching (Supplement S1), the discipline apparently overlooks O_3. For instance, "ozone" was only mentioned twice, and with reference to stratospheric O_3 depletion, in a selection of 22 key restoration ecology guidance documents, position papers and/or reviews, and it doesn't appear in the recently released Standards (Gann et al. 2019). In contrast, "degraded / degradation" was found 417 times, "climate change" 213 times and "nitrogen" 83 times in the 22 documents (Supplement S1). Web of Science (WoS) searches in 5 restoration ecology / conservation biology disciplinary journals only found 49 articles considering "ozone" (out of a total of 29335); none of these articles had a clear focus on tropospheric O_3 and its implications for restoration science, policy or practice (Supplement S1). A more general search on WoS with topic "restoration ecology" OR "ecological restoration" found 22571 results (August 2021) only ten of which remained when these were searched for "ozone" (or O_3). Of these ten articles, one considered feedbacks between removal of invasive species, VOC emissions and O_3 generation for urban air quality (Mistry et al. 2021), one examined O_3 effects on tree growth in nature reserves in the Czech Republic (Vacek et al. 2019), and the remainder tended to refer to O_3 only in passing (Supplement S1). Further searches suggested this overlooking of O_3 may relate to air pollutants more generally, with only 82 journal articles or book chapters out of the 22571 results (compared to e.g. nearly 3000 articles with "climate change") (Supplement S1).

We contend that the demonstrated void suggests policy makers, restoration ecologists and practitioners are unaware of O_3's cascade of consequences for plants and other ecosystem components, and any implications this has for the achievement of restoration goals (Figure 1).

POTENTIAL EFFECTS OF OZONE ON RESTORATION GOALS AND FEEDBACKS FROM RESTORATION INTERVENTIONS

People do restoration for many reasons and use a variety of interventions (Hobbs et al. 2011; Gann et al. 2019), but generally aim to place systems on a trajectory of change that will improve (socio-) ecological conditions locally, and potentially over larger scales. Since O_3 is missing from restoration discourse, it is difficult to quantify how restoration trajectories may be deflected, or how restoration interventions feedback on tropospheric O_3. To gain an overview of the range of possible effects and feedbacks, we carried out a cross-disciplinary narrative review. Our review aimed to assess a representative selection of classic papers and recent advances in the field through capturing a breadth of evidence from agriculture, forestry and ecological enquiries in semi-natural vegetation. To capture recent advances across disciplines, and in May 2021, we considered papers published since 2010 in any journal retrieved from a Web of Science search with the topic ‘ozone’ refined by ‘tropospher*’ or ‘ground level’. To capture classic papers from a range of relevant journals that consistently publish on the ecological effects of O_3, we searched for highly-cited (> 100 citations as of 13th May 2021) papers from any year with ‘ozone’ in the title from *Global Change Biology*, *Science of the Total Environment*, *Environmental Pollution* and *Water, Air, & Soil Pollution*. From these same journals, and to avoid any date penalty associated with citation number, we searched for papers from any year and any number of citations with topics ‘ozone’ and ‘ground level’ or ‘tropospher*’ (see Supplement S2 for search statistics). Our review included any relevant manuscripts not otherwise incorporated that we encountered when addressing the void in restoration discourse (Supplement S1).

We considered how paper findings applied to a selection of pertinent restoration goals, from biodiversity restoration to multiple ecosystem functions. Our choice of goals was necessarily subjective, but reflects contemporary foci (some of which have a long history in restoration discourse), the local to global-scale ambitions of restoration ecologists, and accounts for restoration occupying a continuum of approaches (Gann et al., 2019). The body of evidence for each considered restoration goal varies, partially reflecting the fact that the strength of evidence declines from individual-level plant effects to community and ecosystem level impacts (Figure 1), the latter organisational levels being the foci of restoration. In a separate section, we considered how restoration interventions themselves feedback on tropospheric O_3 dynamics. We use the main text to communicate general messages from the literature, while illustrative specific case study findings are presented in Tables, along with their source references.

TROPOSPHERIC OZONE AND RESTORATION GOALS

Goal 1: Biodiversity restoration with a focus on (plant) community composition

Ecological restoration was historically focused on plant compositional goals (Young 2000), and such biodiversity goals remain pertinent. Given differential sensitivities of species to O_3 it has been suggested that communities across trophic levels and functional roles (e.g. microbial decomposers) will be modified by sustained chronic O_3 exposure (Agathokleous et al. 2020a). However, we only have knowledge of O_3's effects on a limited selection of the world's flora, and even less knowledge on other organisms (Weigel et al. 2011; Agathokleous et al. 2020a) (Table 1) (but note Bosch et al. 2021). There are suggestions that generally herbs / deciduous trees are more susceptible than grasses / conifers to O_3 (Bergmann et al. 2017), and legumes more deleteriously affected than non-legumes (Hewitt et al. 2016). Different metrics can indicate different susceptibilities to O_3 – for instance, declines in flower number in grassland perennials occur at lower O_3 fluxes than declines in biomass (Hayes et al. 2021). These results imply that in locations where O_3 could be influential, and change in a restored community is greater than desired, there may need to be flexibility in choice of target communities, and/or a need for careful species selection.

Interactions among individuals of different species in plant communities means that simple expectations based on individual responses may not occur (Table 1). The impact of O_3 on communities may also depend on other environmental changes, and legacies from previous events. For instance, O_3 is suspected to have more of an impact in subalpine grassland communities under increased temperature (Bassin et al. 2013). In dune systems with a history of high nitrogen deposition, ozone-sensitive species have been lost, leaving the remaining community resistant to O_3 exposure (Hayes et al. 2019). Legacies of old fields are particularly problematic in a restoration context (Standish et al. 2008) and O_3 has been shown to alter maternal seed traits that will make undesired weed communities more difficult to remove (Landesmann et al. 2013), as well as altering communities at other trophic levels e.g. carnivorous arthropods (Martinez-Ghersa et al. 2017). The legacy of elevated O_3 itself may affect restoration trajectories: changed bacterial and fungal composition, and the nematodes that feed upon these microbes, can have knock-on effects on plant growth even after O_3 levels have decreased (Li et al. 2015). The extent to which such initial responses matter for longer-term restoration trajectories is unknown.

Indeed, restoration is focused on the assembly of communities, rather than impacts on extant communities. We are not aware of restoration projects that have specifically considered the impact of O_3 on biodiversity / community composition restoration trajectories. However, seeded plots in semi-natural vegetation demonstrated more ozone-resistant individuals persisting through high seedling mortality events. Competitive dynamics in the understorey were then affected by ozone-induced premature senescence of taller species which allowed more light to this layer (Pfleeger et al. 2010). Whether assembled communities are then at risk from further O_3 exposure is hard to estimate.

Goal 2: Contaminated land remediation

Remediation of contaminated land was historically a core focus of restoration projects (Bradshaw 1983) and remains in some restoration goals (Gann et al. 2019). Given the importance of industrial processes for generating O_3 precursors, it may be that there is spatial overlap between areas of contaminated land, especially due to deposition of airborne pollutants, and O_3 exposure. Regardless of overlap, plants on contaminated landscapes often need to be metal hyperaccumulators and able to tolerate extremely stressful conditions (Kramer 2010; Drzewiecka et al. 2012), the latter aided by pre-formed and inducible defence mechanisms to deal with oxidative stress. These defence mechanisms are key in plant responses to O_3 (Wieser & Matyssek 2007; Emberson et al. 2018), suggesting that contaminated land remediation will be resilient to O_3 exposure. This contention requires testing.

Goal 3: Carbon storage and climate change mitigation

Restoration is suggested as a key approach to increasing terrestrial carbon (C) storage, and thus mitigating climate change (Griscom et al. 2017). The O_3 effects on individual plants, in terms of their structure and function, have consequences for the ability of entire systems to sequester C. Across modelling, longitudinal observational studies, and experiments, O_3 has been shown to compromise gross and/or net primary productivity (by up to 43%), with subsequent deleterious effects on soil C storage (Table 1). These negative effects can be offset by species compositional change, at least in mature forests (Wang et al. 2016). Of particular concern for achieving climate mitigation goals through forest restoration is that impacts of O_3 on productivity are expected to be far greater for young trees. With immature trees, and in successional phases of renewal, plants tend to have traits of low leaf density, high photosynthetic capacity per dry weight, low water use efficiency and low leaf longevity (Bussotti 2008). Such traits can make plants more susceptible to the oxidative pressures induced by O_3 (see also Landry et al. 2013) in a way that adult trees in late successional stands are not, especially those that have acclimated to higher O_3 conditions (Bussotti 2008). Currently, it is difficult to assess the likely impact of O_3 on carbon drawdown in immature restoration tree plantings, especially at landscape scales. This is compounded by the fact that there is a need to incorporate within-plant feedbacks (e.g. sluggish stomatal responses) (Huntingford et al. 2018) (see also *Feedbacks: Restoration interventions as a solution to tropospheric ozone pollution?*). O_3 can however increase stability of soil C, with this effect depending on plant community composition (Hofmockel et al. 2011), reinforcing the message that species choice in restoration interventions could modify the expected impact of enhanced O_3 on climate mitigation potential.

In peatlands, the evidence of O_3's effects is mixed (Table 1), perhaps because temperature, photosynthetically active radiation and water level more strongly regulate carbon dioxide (CO_2) and CH_4 exchange (Rinnan et al. 2013). Some grasslands also appear to be relatively resistant to the impacts of elevated O_3 (Table 1), at least in terms of their carbon dynamics (note the responses presented in Goal 1 subsection). Like peatland, this may be because other factors more strongly regulate their carbon exchange dynamics. On the other hand, recent evidence from subtropical grasslands, and the Mediterranean, suggest that O_3 will deleteriously impact C drawdown and soil C (e.g. Dolker et al. 2020).

The degree to which restoration can contribute to carbon drawdown and climate mitigation also likely depends on co-occurring stressors, such as nitrogen (N) deposition, temperature increases, pests and diseases, and drought. Other stressors may even mask the influence of O_3; for instance, mortality seemingly associated with insect outbreaks in forests may be indicative of underlying stress due to O_3 (Grulke & Heath 2020). A recent meta-analysis concluded that O_3 will remain an ecological issue across systems regardless of N deposition (Feng et al. 2019). O_3 generally, but not universally, leads to decreases in individuals' root to shoot ratios (Figure 1) suggesting restoration interventions may be less resilient to future drought, heat stress or nutrient shortage, further compromising their ability to store carbon. Indeed, recent model analyses suggest O_3 and drought stress may both damage GPP in to the future (Otu-Larbi et al. 2020).

Goal 4: Multiple ecosystem functions and services

Practitioners can attempt to restore multiple functions, including ecosystem services (ES) such as regulated water supply and replenishment of freshwater aquifers (van Wilgen & Wannenburgh 2016), efficient nutrient cycling, pollination, aesthetics (e.g. for recreational users), and pest control (Dudley et al. 2018; Manning et al. 2018) (Figure 1). More recently, forest (and) landscape restoration consider the use of agroforestry and the delivery of livestock feed and browse from restored landscapes (FAO 2020). Air pollution amelioration, including of O_3, is another ES provided by restoration interventions. Given the potential for feedbacks between restoration interventions and atmospheric O_3 dynamics we devote a separate subsection to this aspect (see *Feedbacks: …*).

In general, trajectories towards multiple functional / ES goals can be altered by O_3 effects on individuals that then cascade to stand / landscape levels. For instance, and in a non-restoration context, late-season stream flow was reduced in six forested watersheds across the south-eastern United States due to impaired stomatal control of transpiration under elevated O_3, with potential effects on aquatic biota (Sun et al. 2012). However, in contrast to carbon drawdown, the evidence for O_3 effects on hydrology, and nutrient cycling, remains quite mixed (Table 1).

Clearer evidence exists for the impact of O_3 in relation to pollination and aesthetics. When provided by fauna, pollination depends on the presence of flowers / nectar rewards, and the presence of the pollinator. O_3 can reduce flower number and size, and thus lower the amount of reward available for pollinators. O_3 also changes the volatile emission profiles from flowers making them harder for pollinators to discover (Table 1) (e.g. Papazian & Blande 2020). If such changes lead to declines in pollinator populations, achieving a restoration goal of a sustainably pollinated system can become more difficult, while potentially compromising pollinators' abilities to sustain pollination in agricultural areas. In O_3 episodes, plant appearance can be affected, due to visible leaf injury i.e. areas of cell death. Under chronic O_3 exposure reddening, early senescence and mottling can occur, with superficial resemblance to drought effects. Such responses, and those of reduced flower number in certain systems, compromise aesthetic goals, potentially affecting recreationists' enjoyment and giving a sense of failure to restoration activities.

Recently, agroforestry / degraded rangeland restoration schemes can aim to provide food and medicinal plants for humans, or shelter and fodder for livestock (Table 1) while returning native biodiversity. Again, evidence suggests that O_3 could affect trajectories towards these goals, sometimes in positive ways (e.g. Ansari et al. 2021) but more likely negatively through compromising fodder value and food security (e.g. Tai et al. 2014).

FEEDBACKS: RESTORATION INTERVENTIONS AS A SOLUTION TO TROPOSPHERIC OZONE POLLUTION?

In attempting to reach different targets, restoration practices may depress ambient O_3 concentrations. This occurs through (i) plants taking up O_3 through their stomata, with the potential consequences for restoration goals explored above; (ii) non-stomatal deposition pathways; and, (iii) reactions with bVOCs. Any decrease in O_3 through restoration interventions suggests they could reduce tropospheric O_3 pollution. However, complicated feedbacks among plant species selection, plant volatile emissions, climate change and atmospheric O_3 dynamics mean restoration may not be the first-glance solution to O_3 pollution it appears to be (Table 2). We elucidate this complexity below, emphasizing that further investigations are needed to quantify the O_3 (dis)benefit from restoration interventions relative to other goals, and with comparisons of O_3 dynamics between restoration trajectories and the unrestored state.

Firstly, the determinants of the magnitude and spatio-temporal variability of non-stomatal deposition remain poorly understood (Clifton et al. 2020). For instance, in a restoration context, how does species composition and associated canopy roughness affect deposition velocities of ozone? Secondly, climate warming and associated changes, such as the rise in CH_4, will likely increase O_3 concentrations in the future. The expected magnitude of this 'climate change penalty' depends on feedbacks. Some key feedbacks are not yet characterised, including dynamic changes in plant species composition (Fu & Tian 2019), a key role of restoration interventions, especially as they are rolled out at scale.

Indeed, species selection would play a key role in the evolution of atmospheric O_3 dynamics even in the absence of climate change, through biogeochemical and biogeophysical pathways. Plant species emit varying bVOC profiles, with younger plants making a greater contribution to bVOC emissions, and with dependence on environmental conditions and on the O_3 concentration in the surrounding air (Table 2). In some cases, bVOCs react with the O_3 in the atmosphere outside of the plant and change it into other products (e.g. secondary organic aerosols) through ozonolysis (Yáñez-Serrano et al. 2020). Again, this pathway is not insignificant: in Amazonia, the net O_3 flux can be reduced by nearly 30% through sesquiterpenes reacting with O_3 in the canopy (Jardine et al. 2011). However, in other cases, biogeochemical activity from plant-emitted isoprenes, aromatics and monoterpenes can raise summer maximum O_3 levels by 14 ppb (Porter et al. 2017). Emitted bVOCs can contribute to ozone formation, so that trees and other plants can indirectly generate O_3, but how this compares to canopy deposition (stomatal and non-stomatal) which would ‘protect’ lower strata from harmful O_3 effects, remains unclear. At global scales, were the terrestrial surface to be covered by ‘potential natural vegetation’, isoprene would be expected to increase by 55 % (Unger et al. 2013). The implications of such a rise for O_3 generation may depend on the relative saturation state of the atmosphere i.e. NO_x or VOC-saturated (Table 2). Any estimation of a restoration intervention’s benefit also needs to consider how the target trajectory compares to the unrestored state: for instance, restoration could increase bVOC emissions but decrease contributions from NO_x, relative to inaction. Equally, if forested areas depress fire intensity and frequency compared to other land uses, it may be that other indirect pathways to O_3 generation are altered, for example, as ozone precursor molecules are formed during fires and biomass burning.

Biogeophysical effects from land use land cover change (LULCC) include modification of albedo and evapotranspiration, leading to changes in surface temperature, hydrometeorology and atmospheric circulation with subsequent impacts on O_3 pollution (Table 2). Even subtle changes in species composition can have biogeophysical (as well as biogeochemical) effects with subsequent impacts on O_3. Admixing of silver fir (*Abies alba*) into a beech (*Fagus sylvatica*) forest landscape in Europe decreased albedo, increased evapotranspiration and thus led to a warmer and drier forest. Together with changes in bVOCs, Bonn et al. (2020) estimated these effects would increase O_3 concentrations regionally.

Better quantification of biogeochemical and biogeophysical feedbacks in the light of restoration interventions likely needs to consider other aspects. For instance, agricultural research has shown that the release of stress volatiles in response to O_3 is highly dependent on priming from low-level O_3 exposure (Li et al. 2017). Likewise, interactions with other abiotic and biotic stressors, such as drought (Saunier et al. 2017) and insects (Ghimire et al. 2017), can influence the release of bVOCs with subsequent impacts on O_3 pollution.

A STRATEGIC OZONE AGENDA FOR RESTORATION ECOLOGY

We have presented evidence that tropospheric O_3 pollution can potentially undermine restoration goals and provided arguments as to how it may deflect restoration trajectories. Exactly where O_3 lies in the ‘league table’ of drivers and threats affecting restoration interventions is unclear, since the evidence base from specific restoration projects is lacking. However, in agricultural systems, O_3 has been shown to have effects of similar, or even greater, magnitude compared to other stressors that restoration ecologists do consider, such as aridity, nutrient stress, and heat stress (Mills et al. 2018b). At the same time, restoration interventions could play a role in reducing O_3 pollution, from local to global scales, and mitigate O_3’s broader contributions to climate change, food security and human health. Yet such mitigation depends on species selection, and biogeochemical and biogeophysical feedbacks that remain to be fully elucidated.

For these reasons, and given the current gap in the subject-specific literature, we argue that restoration ecology needs a strategic agenda for O_3. This agenda needs to account for O_3 in the context of other socioenvironmental factors that will affect the success of restoration goals, thus ensuring restoration for resilience to global environmental change (Timpane-Padgham et al. 2017). The agenda also needs to consider how actions to address other threats may complement, or impinge, addressing O_3. For instance, tree planting for climate change mitigation may exacerbate O_3 pollution if the 'wrong' species are used, and furthermore compromise climate mitigation efforts due to O_3's warming potential. We suggest shaping the strategic agenda in three strands: restoration science, practice and policy (Table 3) but emphasize that integration across these strands is key. Collaborative actions will increase the awareness around the phenomenon of O_3 pollution, and help restoration achieve an overall goal of sustainable, resilient ecosystems for the benefit of nature and people.

Actions suggested in Table 3 can be undertaken at different scales, and opportunities exist to integrate O_3 into restoration discourse at relatively low cost. For instance, stakeholders can be made more aware of O_3 injury symptoms and register possible instances through the Ozone Injury App (https://icpvegetation.ceh.ac.uk/get-involved/ozone-injury/record). This will help scientists build up a more accurate picture of where O_3 risks are. Restoration scientists can actively collaborate with practitioners, and other citizens, to deploy sensor networks (e.g. Ripoll et al. 2019), including through the use of 'phytometers'; i.e. planting a small area up with a known ozone-sensitive species (e.g. Pina et al. 2017) or through the use of other biomonitoring methods (Agathokleous et al. 2020b). These assessments are particularly important in Africa, South America and to some extent Asia, regions where it is rare to directly estimate tropospheric O_3 concentrations.

A more involved collaboration could be through screening for ozone-sensitive and ozone-tolerant species, especially species commonly planted in restoration interventions. This will avoid restoration failure through planting sensitive species. For interventions that irrigate to aid establishment, avoiding O_3 episodes will further prevent failure (Table 3). Screening would arguably be most useful if conducted in the frame of plant functional traits, as understanding in the form of trait frameworks allows knowledge transfer in a way that a purely taxonomic focus does not (McGill et al. 2006). Indeed, traits can provide unifying explanations as to when species are expected to be ozone-sensitive or ozone-tolerant (Zhang et al. 2012; Feng et al. 2018). Screening can also use techniques 'borrowed' from agriculture, such as ethylenediurea (EDU) application, as soil drench or on leaves, to quickly assess O_3 tolerance (Manning et al. 2011; Agathokleous et al. 2015) or to protect trees from O_3 damage (Paoletti et al. 2011) (noting the potential for unanticipated side effects (Agathokleous et al. 2018)).

Restoration scientists themselves need to collaborate with other disciplines (e.g. atmospheric physicists and chemists) to help quantify the feedbacks from restoration interventions, both locally (e.g. through urban greening (Manes et al. 2012)) and at regional to global levels as restoration interventions scale up. Quantifying feedbacks will lessen the likelihood of restoration interventions having unintended consequences e.g. for biodiversity, for atmospheric pollutants.

A primary scientific focus must be understanding how and why background and episodic O_3 concentrations affect the achievement of restoration goals. Embedding experiments in a networked manner (Gellie et al. 2018) will help reveal the relative importance of O_3 as a driving force of system change while improving restoration practice. Such investigations need to explore interactions amongst co-occurring phenomena such as drought and nitrogen deposition (Mills et al. 2016; Ainsworth et al. 2020) as well as legacies, which can be crucial for dictating the trajectories of change that systems follow under contemporary change (Brudvig et al. 2021). Scientific understanding will likely be bolstered by understanding what constitutes a POD for different species and/or communities i.e. the amount of O_3 taken into the plant that subsequently leads to damage. Policy makers can encourage rapid progress in this area given their need to accurately map areas, and vegetation types, most at risk from O_3 pollution (e.g. Anav et al. 2016; De Marco et al. 2020) to help avoid restoration failure.

CLOSING REMARKS

The growth in acute and/or chronic O_3 exposure is one of a number of environmental changes facing ecosystems, but suffers from the lack of attention given to it in the restoration literature. This is a large knowledge gap which needs to be filled, especially given some evidence for the potential of important effects on restoration goals, and feedbacks on tropospheric O_3 dynamics from restoration interventions themselves. Next steps for restoration ecology are:

- quantify the relative and absolute importance of O_3 pollution in relation to other environmental changes affecting restoration goals;
- identify when and where different restoration goals may be affected by variable O_3 exposures;
- estimate feedbacks from restoration interventions on O_3 dynamics; and,
- elucidate where restoration actions to address O_3 pollution complement or trade-off with actions to address other threats and drivers.

Progress needs the adoption of a strategic agenda that will encompass integrated action by restoration scientists, practitioners and policy makers. Ozone may be out of sight, and apparently out of mind at the beginning of the UN Decade on Ecosystem Restoration. Yet, it is not out of scope as ecological restoration aims to achieve targets associated with sustainable development goals.

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LITERATURE CITED

Agathokleous E, Feng Z, Oksanen E, Sicard P, Wang Q, Saitanis CJ, Araminiene V, Blande JD, Hayes F, Calatayud V, Domingos M, Veresoglou SD, Peñuelas J, Wardle DA, De Marco A, Li Z, Harmens H, Yuan X, Vitale M, and Paoletti E (2020a) Ozone affects plant, insect, and soil microbial communities: A threat to terrestrial ecosystems and biodiversity. Science Advances **6**:eabc1176

Agathokleous E, Koike T, Watanabe M, Hoshika Y, and Saitanis CJ (2015) Ethylene-di-urea (EDU), an effective phytoproctectant against O-3 deleterious effects and a Valuable research tool. Journal of Agricultural Meteorology **71**:185-195

Agathokleous E, Paoletti E, Manning WJ, Kitao M, Saitanis CJ, and Koike T (2018) High doses of ethylenediurea (EDU) as soil drenches did not increase leaf N content or cause phytotoxicity in willow grown in fertile soil. Ecotoxicology and Environmental Safety **147**:574-584

Agathokleous E, Saitanis CJ, Feng Z, De Marco A, Araminiene V, Domingos M, Sicard P, and Paoletti E (2020b) Ozone biomonitoring: A versatile tool for science, education and regulation. Current Opinion in Environmental Science & Health **18**:7-13

Ainsworth EA, Lemonnier P, and Wedow JM (2020) The influence of rising tropospheric carbon dioxide and ozone on plant productivity. Plant Biology **22**:5-11

Ainsworth EA, Yendrek CR, Sitch S, Collins WJ, and Emberson LD (2012) The Effects of Tropospheric Ozone on Net Primary Productivity and Implications for Climate Change. Annual Review of Plant Biology **63**:637-661

Anav A, De Marco A, Proietti C, Alessandri A, Dell'aquila A, Cionni I, Friedlingstein P, Khvorostyanov D, Menut L, Paoletti E, Sicard P, Sitch S, and Vitale M (2016) Comparing concentration-based (AOT40) and stomatal uptake (PODY) metrics for ozone risk assessment to European forests. Global Change Biology **22**:1608-1627

Ansari N, Agrawal M, and Agrawal SB (2021) An assessment of growth, floral morphology, and metabolites of a medicinal plantSida cordifoliaL. under the influence of elevated ozone. Environmental Science and Pollution Research

Bassin S, Volk M, and Fuhrer J (2013) Species Composition of Subalpine Grassland is Sensitive to Nitrogen Deposition, but Not to Ozone, After Seven Years of Treatment. Ecosystems **16**:1105-1117

Bastin J-F, Finegold Y, Garcia C, Mollicone D, Rezende M, Routh D, Zohner CM, and Crowther TW (2019) The global tree restoration potential. Science **365**:76-79

Bergmann E, Bender J, and Weigel HJ (2017) Impact of tropospheric ozone on terrestrial biodiversity: A literature analysis to identify ozone sensitive taxa. Journal of Applied Botany and Food Quality **90**

Bobbink R, Hicks K, Galloway J, Spranger T, Alkemade R, Ashmore M, Bustamante M, Cinderby S, Davidson E, Dentener F, Emmett B, Erisman J-W, Fenn M, Gilliam F, Nordin A, Pardo L, and De Vries W (2010) Global assessment of nitrogen deposition effects on terrestrial plant diversity: a synthesis. Ecological Applications **20**:30-59

Bonn B, Kreuzwieser J, Magh RK, Rennenberg H, Schindler D, Sperlich D, Trautmann R, Yousefpour R, and Grote R (2020) Expected Impacts of Mixing European Beech with Silver Fir on Regional Air Quality and Radiation Balance. Climate **8**

Bosch J, Elvira S, Sausor C, Bielby J, González-Fernández I, Alonso R, and Bermejo-Bermejo V (2021) Increased tropospheric ozone levels enhance pathogen infection levels of amphibians. Science of The Total Environment **759**:143461

Bradshaw AD (1983) The reconstruction of ecosystems: Presidential address to the British Ecological Society, December 1982. Journal of Applied Ecology **20**:1-17

Brudvig LA, Turley NE, Bartel SL, Bell-Dereske L, Breland S, Damschen EI, Evans SE, Gibbs J, Hahn PG, Isaacs R, Ledvina JA, Orrock JL, Sorenson QM, and Stuhler JD (2021) Large ecosystem-scale effects of restoration fail to mitigate impacts of land-use legacies in longleaf pine savannas. Proceedings of the National Academy of Sciences **118**:e2020935118

Bussotti F (2008) Functional leaf traits, plant communities and acclimation processes in relation to oxidative stress in trees: a critical overview. Global Change Biology **14**:2727-2739

Chevalier A, Gheusi F, Delmas R, Ordóñez C, Sarrat C, Zbinden R, Thouret V, Athier G, and Cousin JM (2007) Influence of altitude on ozone levels and variability in the lower troposphere: a ground-based study for stern Europe over the period 2001-2004. Atmospheric Chemistry and Physics **7**:4311-4326

Clifton OE, Fiore AM, Massman WJ, Baublitz CB, Coyle M, Emberson L, Fares S, Farmer DK, Gentine P, Gerosa G, Guenther AB, Helmig D, Lombardozzi DL, Munger JW, Patton EG, Pusede SE, Schwede DB, Silva SJ, Sorgel M, Steiner AL, and Tai APK (2020) Dry Deposition of Ozone Over Land: Processes, Measurement, and Modeling. Reviews of Geophysics **58**

De Marco A, Anav A, Sicard P, Feng ZZ, and Paoletti E (2020) High spatial resolution ozone risk-assessment for Asian forests. Environmental Research Letters **15**

De Marco A, Sicard P, Fares S, Tuovinen JP, Anav A, and Paoletti E (2016) Assessing the role of soil water limitation in determining the Phytotoxic Ozone Dose (PODY) thresholds. Atmospheric Environment **147**:88-97

Dolker T, Mukherjee A, Agrawal SB, and Agrawal M (2020) Responses of a semi-natural grassland community of tropical region to elevated ozone: An assessment of soil dynamics and biomass accumulation. Science of The Total Environment **718**

Drzewiecka K, Mleczek M, Waskiewicz A, and Golinski P. (2012) Oxidative Stress and Phytoremediation.

Dudley N, Bhagwat SA, Harris J, Maginnis S, Moreno JG, Mueller GM, Oldfield S, and Walters G (2018) Measuring progress in status of land under forest landscape restoration using abiotic and biotic indicators. Restoration Ecology **26**:5-12

Emberson LD, Pleijel H, Ainsworth EA, Van Den Berg M, Ren W, Osborne S, Mills G, Pandey D, Dentener F, Büker P, Ewert F, Koeble R, and Van Dingenen R (2018) Ozone effects on crops and consideration in crop models. European Journal of Agronomy **100**:19-34

Fao (2020) Restoring the Earth - The next decade. Unasylva **71**

Feng Z, Büker P, Pleijel H, Emberson L, Karlsson PE, and Uddling J (2018) A unifying explanation for variation in ozone sensitivity among woody plants. Global Change Biology **24**:78-84

Feng Z, Shang B, Li Z, Calatayud V, and Agathokleous E (2019) Ozone will remain a threat for plants independently of nitrogen load. Functional Ecology **33**:1854-1870

Fu T-M, and Tian H (2019) Climate Change Penalty to Ozone Air Quality: Review of Current Understandings and Knowledge Gaps. Current Pollution Reports **5**:159-171

Gann GD, Mcdonald T, Walder B, Aronson J, Nelson CR, Jonson J, Hallett JG, Eisenberg C, Guariguata MR, Liu J, Hua F, Echeverria C, Gonzales E, Shaw N, Decleer K, and Dixon KW (2019) International principles and standards for the practice of ecological restoration. Second edition. Restoration Ecology

Gellie NJC, Breed MF, Mortimer PE, Harrison RD, Xu J, and Lowe AJ (2018) Networked and embedded scientific experiments will improve restoration outcomes. Frontiers in Ecology and Environment **16**:288-294

Ghimire RP, Kivimaenpaa M, Kasurinen A, Haikio E, Holopainen T, and Holopainen JK (2017) Herbivore-induced BVOC emissions of Scots pine under warming, elevated ozone and increased nitrogen availability in an open-field exposure. Agricultural and Forest Meteorology **242**:21-32

Grantz DA, Gunn S, and Vu H-B (2006) O3 impacts on plant development: a meta-analysis of root/shoot allocation and growth. Plant, Cell & Environment **29**:1193-1209

Griscom BW, Adams J, Ellis PW, Houghton RA, Lomax G, Miteva DA, Schlesinger WH, Shoch D, Siikamäki JV, Smith P, Woodbury P, Zganjar C, Blackman A, Campari J, Conant RT, Delgado C, Elias P, Gopalakrishna T, Hamsik MR, Herrero M, Kiesecker J, Landis E, Laestadius L, Leavitt SM, Minnemeyer S, Polasky S, Potapov P, Putz FE, Sanderman J, Silvius M, Wollenberg E, and Fargione J (2017) Natural climate solutions. Proceedings of the National Academy of Sciences **114**:11645-11650

Grulke NE, and Heath RL (2020) Ozone effects on plants in natural ecosystems. Plant Biology **22**:12-37

Hayes F, Harmens H, Mills G, Bender J, and Grunhage L (2021) Ozone critical levels for (semi-)natural vegetation dominated by perennial grassland species. Environmental Science and Pollution Research

Hayes F, Lloyd B, Mills G, Jones L, Dore AJ, Carnell E, Vieno M, Dise N, and Fenner N (2019) Impact of long-term nitrogen deposition on the response of dune grassland ecosystems to elevated summer ozone. Environmental Pollution **253**:821-830

Hewitt DKL, Mills G, Hayes F, Norris D, Coyle M, Wilkinson S, and Davies W (2016) N-fixation in legumes - An assessment of the potential threat posed by ozone pollution. Environmental Pollution **208**:909-918

Hobbs RJ, Hallett LM, Ehrlich PR, and Mooney HA (2011) Intervention Ecology: Applying ecological science in the 21st Century. BioScience **61**:442-450

Hofmockel KS, Zak DR, Moran KK, and Jastrow JD (2011) Changes in forest soil organic matter pools after a decade of elevated CO2 and O-3. Soil Biology & Biochemistry **43**:1518-1527

Huntingford C, Oliver RJ, Mercado LM, and Sitch S (2018) Technical note: A simple theoretical model framework to describe plant stomatal "sluggishness" in response to elevated ozone concentrations. Biogeosciences **15**:5415-5422

Jaffe DA, and Wigder NL (2012) Ozone production from wildfires: A critical review. Atmospheric Environment **51**:1-10

Jardine K, Serrano AY, Arneth A, Abrell L, Jardine A, Van Haren J, Artaxo P, Rizzo LV, Ishida FY, Karl T, Kesselmeier J, Saleska S, and Huxman T (2011) Within-canopy sesquiterpene ozonolysis in Amazonia. Journal of Geophysical Research-Atmospheres **116**

Kramer U (2010) Metal hyperaccumulation in plants. Annual Review of Plant Biology **61**:517-534

Landesmann JB, Gundel PE, Martinez-Ghersa MA, and Ghersa CM (2013) Ozone Exposure of a Weed Community Produces Adaptive Changes in Seed Populations of Spergula arvensis. PLOS ONE **8**

Landry JS, Neilson ET, Kurz WA, and Percy KE (2013) The impact of tropospheric ozone on landscape-level merchantable biomass and ecosystem carbon in Canadian forests. European Journal of Forest Research **132**:71-81

Lee DS, Holland MR, and Falla N (1996) The potential impact of ozone on materials in the U.K. Atmospheric Environment **30**:1053-1065

Leisner CP, and Ainsworth EA (2012) Quantifying the effects of ozone on plant reproductive growth and development. Global Change Biology **18**:606-616

Li Q, Yang Y, Bao XL, Liu F, Liang WJ, Zhu JG, Bezemer TM, and Van Der Putten WH (2015) Legacy effects of elevated ozone on soil biota and plant growth. Soil Biology & Biochemistry **91**:50-57

Li S, Harley PC, and Niinemets U (2017) Ozone-induced foliar damage and release of stress volatiles is highly dependent on stomatal openness and priming by low-level ozone exposure in Phaseolus vulgaris. Plant Cell and Environment **40**:1984-2003

Malley CS, Henze DK, Kuylenstierna JCI, Vallack HW, Davila Y, Anenberg SC, Turner MC, and Ashmore MR (2017) Updated Global Estimates of Respiratory Mortality in Adults >= 30 Years of Age Attributable to Long-Term Ozone Exposure. Environmental Health Perspectives **125**

Manes F, Incerti G, Salvatori E, Vitale M, Ricotta C, and Costanza R (2012) Urban ecosystem services: tree diversity and stability of tropospheric ozone removal. Ecological Applications **22**:349-360

Manning P, Van Der Plas F, Soliveres S, Allan E, Maestre FT, Mace G, Whittingham MJ, and Fischer M (2018) Redefining ecosystem multifunctionality. Nature Ecology & Evolution **2**:427-436

Manning WJ, Paoletti E, Sandermann H, and Ernst D (2011) Ethylenediurea (EDU): A research tool for assessment and verification of the effects of ground level ozone on plants under natural conditions. Environmental Pollution **159**:3283-3293

Martinez-Ghersa MA, Menendez AI, Gundel PE, Folcia AM, Romero AM, Landesmann JB, Ventura L, and Ghersa CM (2017) Legacy of historic ozone exposure on plant community and food web structure. PLOS ONE **12**

McGill BJ, Enquist BJ, Weiher E, and Westoby M (2006) Rebuilding community ecology from functional traits. Trends in Ecology and Evolution **21**:178-185

McPhee J, Borden L, Bowles J, and Henry HaL (2015) Tallgrass prairie restoration: implications of increased atmospheric nitrogen deposition when site preparation minimizes adventive grasses. Restoration Ecology **23**:34-42

Mills G, Harmens H, Wagg S, Sharps K, Hayes F, Fowler D, Sutton M, and Davies B (2016) Ozone impacts on vegetation in a nitrogen enriched and changing climate. Environmental Pollution **208**:898-908

Mills G, Pleijel H, Malley CS, Sinha B, Cooper OR, Schultz MG, Neufeld HS, Simpson D, Sharps K, Feng ZZ, Gerosa G, Harmens H, Kobayashi K, Saxena P, Paoletti E, Sinha V, and Xu XB (2018a) Tropospheric Ozone Assessment Report: Present-day tropospheric ozone distribution and trends relevant to vegetation. Elementa-Science of the Anthropocene **6**

Mills G, Sharps K, Simpson D, Pleijel H, Frei M, Burkey K, Emberson L, Uddling J, Broberg M, Feng Z, Kobayashi K, and Agrawal M (2018b) Closing the global ozone yield gap: Quantification and cobenefits for multistress tolerance. Global Change Biology **24**:4869-4893

Mistry AP, Steffeck AWT, and Potosnak MJ (2021) Edge Growth Form of European Buckthorn Increases Isoprene Emissions From Urban Forests. Frontiers in Forests and Global Change **3**

Otu-Larbi F, Conte A, Fares S, Wild O, and Ashworth K (2020) Current and future impacts of drought and ozone stress on Northern Hemisphere forests. Global Change Biology **26**:6218-6234

Paoletti E, De Marco A, Beddows DCS, Harrison RM, and Manning WJ (2014) Ozone levels in European and USA cities are increasing more than at rural sites, while peak values are decreasing. Environmental Pollution **192**:295-299

Paoletti E, Manning WJ, Ferrara AM, and Tagliaferro F (2011) Soil drench of ethylenediurea (EDU) protects sensitive trees from ozone injury. Iforest-Biogeosciences and Forestry **4**:66-68

Papazian S, and Blande JD (2020) Dynamics of plant responses to combinations of air pollutants. Plant Biology **22**:68-83

Pfleeger TG, Plocher M, and Bichel P (2010) Response of pioneer plant communities to elevated ozone exposure. Agriculture Ecosystems & Environment **138**:116-126

Pina JM, Souza SR, Meirelles ST, and Moraes RM (2017) Psidium guajava Paluma responses to environmental conditions and ozone concentrations in the urban forest of Sao Paulo, SE-Brazil. Ecological Indicators **77**:1-7

Pope RJ, Arnold SR, Chipperfield MP, Reddington CLS, Butt EW, Keslake TD, Feng WH, Latter BG, Kerridge BJ, Siddans R, Rizzo L, Artaxo P, Sadiq M, and Tai APK (2020) Substantial Increases in Eastern Amazon and Cerrado Biomass Burning-Sourced Tropospheric Ozone. Geophysical Research Letters **47**

Porter WC, Safieddine SA, and Heald CL (2017) Impact of aromatics and monoterpenes on simulated tropospheric ozone and total OH reactivity. Atmospheric Environment **169**:250-257

Rinnan R, Saarnio S, Haapala JK, Morsky SK, Martikainen PJ, Silvola J, and Holopainen T (2013) Boreal peatland ecosystems under enhanced UV-B radiation and elevated tropospheric ozone concentration. Environmental and Experimental Botany **90**:43-52

Ripoll A, Viana M, Padrosa M, Querol X, Minutolo A, Hou KM, Barcelo-Ordinas JM, and Garcia-Vidal J (2019) Testing the performance of sensors for ozone pollution monitoring in a citizen science approach. Science of The Total Environment **651**:1166-1179

Ronan AC, Ducker JA, Schnell JL, and Holmes CD (2020) Have improvements in ozone air quality reduced ozone uptake into plants? Elementa-Science of the Anthropocene **8**

Saunier A, Ormeno E, Boissard C, Wortham H, Temime-Roussel B, Lecareux C, Armengaud A, and Fernandez C (2017) Effect of mid-term drought on Quercus pubescens BVOCs' emission seasonality and their dependency on light and/or temperature. Atmospheric Chemistry and Physics **17**:7555-7566

Sicard P, Agathokleous E, Araminiene V, Carrari E, Hoshika Y, De Marco A, and Paoletti E (2018) Should we see urban trees as effective solutions to reduce increasing ozone levels in cities? Environmental Pollution **243**:163-176

Standish RJ, Cramer VA, and Hobbs RJ (2008) Land-use legacy and the persistence of invasive *Avena barbata* on abandoned farmland. Journal of Applied Ecology **45**:1576-1583

Sun G, Mclaughlin SB, Porter JH, Uddling J, Mulholland PJ, Adams MB, and Pederson N (2012) Interactive influences of ozone and climate on streamflow of forested watersheds. Global Change Biology **18**:3395-3409

Tai APK, Martin MV, and Heald CL (2014) Threat to future global food security from climate change and ozone air pollution. Nature Climate Change **4**:817-821

Thompson AM, Balashov NV, Witte JC, Coetzee JGR, Thouret V, and Posny F (2014) Tropospheric ozone increases over the southern Africa region: bellwether for rapid growth in Southern Hemisphere pollution? Atmospheric Chemistry and Physics **14**:9855-9869

Timpane-Padgham BL, Beechie T, and Klinger T (2017) A systematic review of ecological attributes that confer resilience to climate change in environmental restoration. PLOS ONE **12**:e0173812

Unger N, Harper K, Zheng Y, Kiang NY, Aleinov I, Arneth A, Schurgers G, Amelynck C, Goldstein A, Guenther A, Heinesch B, Hewitt CN, Karl T, Laffineur Q, Langford B, Mckinney KA, Misztal P, Potosnak M, Rinne J, Pressley S, Schoon N, and Seraca D (2013) Photosynthesis-dependent isoprene emission from leaf to planet in a global carbon-chemistry-climate model. Atmospheric Chemistry and Physics **13**:10243-10269

Vacek S, Vacek Z, Bilek L, Remes J, Hunova I, Bulusek D, Kral J, and Brichta J (2019) Stand dynamics in natural Scots pine forests as a model for adaptation management? Dendrobiology **82**:24-42

Van Wilgen BW, and Wannenburgh A (2016) Co-facilitating invasive species control, water conservation and poverty relief: achievements and challenges in South Africa's Working for Water programme. Current Opinion in Environmental Sustainability **19**:7-17

Wang B, Shugart HH, Shuman JK, and Lerdau MT (2016) Forests and ozone: productivity, carbon storage, and feedbacks. Scientific Reports **6**

Weigel HJ, Dauber J, and Bender J (2011) Ground-level ozone - a threat for biodiversity? Gefahrstoffe Reinhaltung Der Luft **71**:98-102

Wieser G, and Matyssek R (2007) Linking ozone uptake and defense towards a mechanistic risk assessment for forest trees. New Phytologist **174**:7-9

Yáñez-Serrano AM, Bourtsoukidis E, Alves EG, Bauwens M, Stavrakou T, Llusià J, Filella I, Guenther A, Williams J, Artaxo P, Sindelarova K, Doubalova J, Kesselmeier J, and Peñuelas J (2020) Amazonian biogenic volatile organic compounds under global change. Global Change Biology **26**:4722-4751

Young TP (2000) Restoration ecology and conservation biology. Biological Conservation **92**:73 - 83

Zhang JF, Wei YJ, and Fang ZF (2019) Ozone Pollution: A Major Health Hazard Worldwide. Frontiers in Immunology **10**

Zhang WW, Feng ZZ, Wang XK, and Niu JF (2012) Responses of native broadleaved woody species to elevated ozone in subtropical China. Environmental Pollution **163**:149-157

FIGURE LEGENDS

Figure 1: Evidence for the impacts of tropospheric ozone (O_3) on individuals, and community and ecosystem processes. Elevated levels of O_3 (compare right hand side of each subpanel with the left hand side) have a number of impacts on plant individuals, including fewer leaves, reduced growth, accelerated senescence, altered biomass allocation, and changed volatile emission profiles. These effects have a cascade of consequences (solid arrows) for above- and below-ground communities (e.g. altered microbial community, changed plant communities), and ecosystem processes (e.g. changed nutrient quantities and quality, altered water relations, and impaired pollination), as explained in the main text and Table 1. The changes in communities and ecosystems can feedback on each other and the plant individual (dotted arrows) although these effects are not described herein. Based on a narrative review across disciplines, and as explained in the main text, O_3 effects on individuals, but particularly on communities and ecosystems, could have consequences for numerous restoration goals (top of figure), while restoration interventions themselves can feedback on tropospheric O_3 concentrations. However, evidence is scarce for specific O_3 effects on restoration trajectories because the discipline has its own 'ozone hole'. The main text provides a strategic agenda for how this void can be filled.

Figure 2: Potential exposure of restoration projects to ozone (O_3) risk. The risk to (some) restoration projects from O_3 could be calculated based on a "phytotoxic ozone dose" (POD). POD expresses the exposure to O_3 taking into account the rate of uptake into the plant based on environmental conditions, and accounting for the innate ability of the plant to detoxify O_3. POD varies by species, and is difficult to calculate at the community level but is preferred to exposure-based metrics which may not reflect what is taken in by vegetation (De Marco et al. 2016; Ronan et al. 2020). Here, we overlay areas (red hatching) on or above a single POD value (3 nmol $m^{-2}s^{-1}$) based on unirrigated vegetation, against a smoothed (aggregated to same resolution as POD values) map of global tree restoration potential (Bastin et al. 2019) (per pixel = (potential) tree cover percentage). This figure demonstrates certain regions of the globe are expected to have forest restoration projects that will be more affected by O_3 pollution than others. Readers should note the preliminary nature of this analysis: as noted in Table 3, O_3 risk assessment for communities and ecosystems needs advancement.

FIGURES

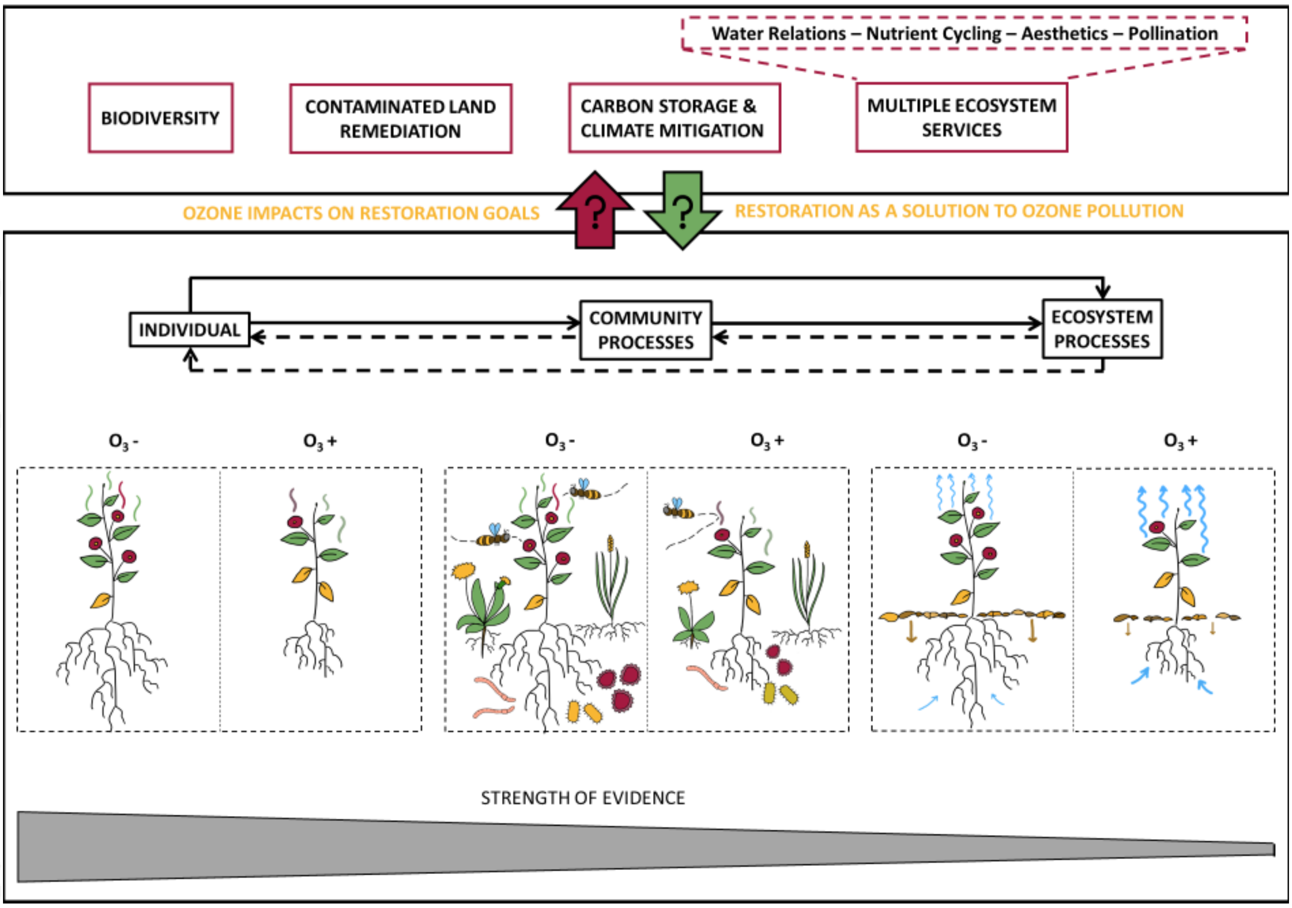

Figure 1: Evidence for the impacts of tropospheric ozone (O_3) on individuals, and community and ecosystem processes. Elevated levels of O_3 (compare right hand side of each subpanel with the left hand side) have a number of impacts on plant individuals, including fewer leaves, reduced growth, accelerated senescence, altered biomass allocation, and changed volatile emission profiles. These effects have a cascade of consequences (solid arrows) for above- and below-ground communities (e.g. altered microbial community, changed plant communities), and ecosystem processes (e.g. changed nutrient quantities and quality, altered water relations, and impaired pollination), as explained in the main text and Table 1. The changes in communities and ecosystems can feedback on each other and the plant individual (dotted arrows) although these effects are not described herein. Based on a narrative review across disciplines, and as explained in the main text, O_3 effects on individuals, but particularly on communities and ecosystems, could have consequences for numerous restoration goals (top of figure), while restoration interventions themselves can feedback on tropospheric O_3 concentrations. However, evidence is scarce for specific O_3 effects on restoration trajectories because the discipline has its own 'ozone hole'. The main text provides a strategic agenda for how this void can be filled.

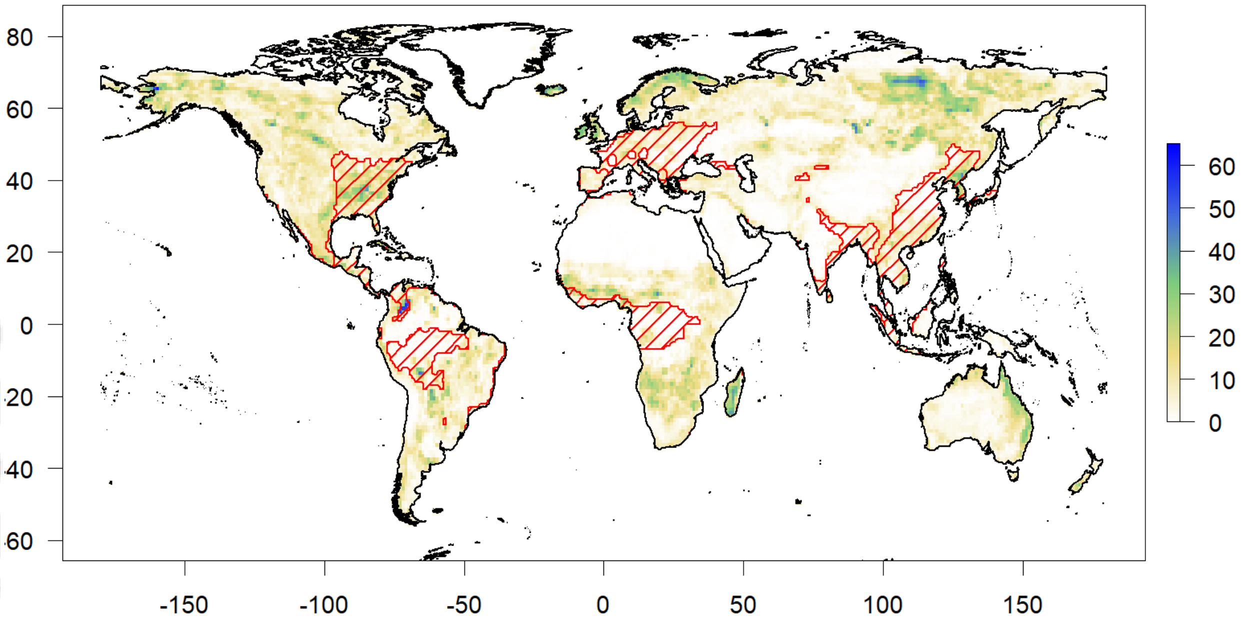

Figure 2: The risk to (some) restoration projects from O_3 could be calculated based on a "phytotoxic ozone dose" (POD). POD expresses the exposure to O_3 taking into account the rate of uptake into the plant based on environmental conditions, and accounting for the innate ability of the plant to detoxify O_3. POD varies by species, and is difficult to calculate at the community level but is preferred to exposure-based metrics which may not reflect what is taken in by vegetation (De Marco et al. 2016; Ronan et al. 2020). Here, we overlay areas (red hatching) on or above a single POD value (3 nmol $m^{-2}s^{-1}$) based on unirrigated vegetation, against a smoothed (aggregated to same resolution as POD values) map of global tree restoration potential (Bastin et al. 2019) (per pixel = (potential) tree cover percentage). This figure demonstrates certain regions of the globe are expected to have forest restoration projects that will be more affected by O_3 pollution than others. Readers should note the preliminary nature of this analysis: as noted in Table 3, O_3 risk assessment for communities and ecosystems needs advancement.

TABLES

Table 1: The potential impact of tropospheric ozone (O_3) on restoration targets. Note that literature cited within tables is provided in Supplement S3.

Restoration Target	**Example ozone effects with a bearing on restoration trajectories**	**Example future directions**	**Key literature**
Biodiversity restoration (with an historic focus on plant community composition)	Expectation that forbs more susceptible than grasses (Bergmann, Bender, & Weigel 2017), yet in a plant community the effect is dependent on the relative sensitivity of the component species. Decline in key grass species (*Anthoxanthum odoratum*) under O_3 means forb: grass ratio increased in grassland community[1]. Expectation that legumes more susceptible than non-legumes (Hewitt et al. 2016a), but interactions among species in Mediterranean annual pastures means one legume profits (*Ornithopus compressus*) at expense of others (*Trifolium sp.*)[2]. Limited impacts in subalpine grassland but juveniles more strongly affected, regardless of mycorrhizal colonization[3] Other trophic levels: soil Collembola strongly decreased under O_3 exposure but this can be buffered depending on the plant species present[4]. In peatlands, testate amoebae (important microbial consumer) declined in diversity with elevated O_3 exposure, while undifferentiated microalgae, nematodes and rotifers were unchanged. One particular consumer genus (Phyrganella spp) markedly increased, likely related to fungal species[5].	Consider interactions with other variables (e.g. drought, climate change, N deposition). Interactions with other trophic levels and mutualists e.g. pollinators and mycorrhizae. Importance of legacy effects What are the mechanisms that drive the structure and function of plant, insect and soil communities in O_3 polluted atmospheres[6]?	1: (Hayes et al. 2010) 2: (Calvete-Sogo et al. 2016) 3: (Bassin et al. 2017; Bassin, Volk, & Fuhrer 2013; Bassin et al. 2009) 4: (Chang, Liu, & Ge 2011) 5: (Payne et al. 2017) 6: (Agathokleous et al. 2020)
Contaminated land remediation	No evidence	Physiological mechanisms for e.g. heavy metal tolerance[7] should confer O_3 resistance – needs to be tested	7: (Drzewiecka et al. 2012)

Restoration Target	Example ozone effects with a bearing on restoration trajectories	Example future directions	Key literature
Climate change mitigation through carbon storage	Generally negative consequences for GPP, NPP (ranging from 0.4 to 43 %) and soil C storage. Direction and range can depend on consideration of other driving factors, forest / vegetation type and composition, and location[8], but some evidence for increased soil C stability[9]. Peatland methane emissions can reduce by 25 % under high O_3[11], but have also been shown to increase and then decline across a gradient[12], or be little affected[13]. CO_2 emissions have shown minor impacts of O_3 exposure[14]. Limited evidence of an effect of O_3 on carbon dynamics in subalpine grassland, likely because management and drought dominated a signature of C loss, exacerbated by nitrogen deposition[15]. Above and below-ground biomass reduced by 26 and 30 % respectively in subtropical grassland of Indo-Gangetic plain, with a 24 % decrease in total organic carbon[16]. Green and total aboveground biomass reduced, by up to 25 %, in annual Mediterranean pastures. Could be offset by N deposition, at least at moderate O_3 levels[17] but cumulative N_2O emissions (another greenhouse gas) doubled due to peaks in soil microbe activity[18].	Understand what happens with peak O_3 decreases: observations include limited mature forested ecosystem responsiveness due to photosynthesis happening in shade leaves[10]. Understand what happens with peak O_3 increases: in peatland, methane emissions reduced under elevated O_3 peaks in summer[12]. Interactions with other air pollution variables e.g. N deposition. For instance, a decline in carbon increment was observed at moderate O_3 levels (20 to 30 ppb) and moderate N deposition (15 to 25 kgN ha^{-1} yr^{-1}) in Californian ponderosa pine; this disappears at highest pollution levels[19]. Conversely, Japanese *Fagus crenata* forests are more at risk of O_3-induced relative growth reduction at higher levels of N deposition[20]. Interactions with other stressors e.g. drought, pests and diseases	8: (Banger et al. 2015; Braun, Schindler, & Rihm 2014; de Vries et al. 2017; Fenn et al. 2020; Kou et al. 2014; Oliver et al. 2018; Ollinger et al. 2002; Proietti et al. 2016; Ren et al. 2011; Talhelm et al. 2014; Wang et al. 2016; Wang et al. 2019; Yue & Unger 2014) 9: (Hofmockel et al. 2011) 10: (Yue et al. 2016) 11: (Toet et al. 2011) 12: (Williamson et al. 2016) 13: (Toet et al. 2017) 14: (Haapala et al. 2011) 15: (Volk et al. 2011) 16: (Dolker et al. 2020) 17: (Calvete-Sogo et al. 2014) 18: (Sanchez-Martin et al. 2017) 19: (Fenn et al. 2020) 20: (Watanabe et al. 2012)
Multiple ecosystem services	Water supply – reduction in stream flow from lower forest water use efficiency due to stomatal sluggishness, and changed root and branch structure[21]. Note that some mature beech forests can show resistance to elevated O_3[22].	What species and communities can show resistance to elevated O_3 such that the delivery of multiple ecosystem services is not compromised? To what extent do other trophic levels (e.g. herbivores) mediate litter	21: (Rhea et al. 2010; Rhea & King 2012; Sun et al. 2012) 22: (Paoletti, Grulke, & Matyssek 2020) 23: (Baldantoni et al. 2013; Baldantoni, Fagnano, & Alfani

Restoration Target	Example ozone effects with a bearing on restoration trajectories	Example future directions	Key literature
	Nutrient cycling – mineralization and decomposition rates slowed across systems with potential impacts on soil health[23] but can be a weak effect[24]. Pollination – O_3 effects on flowers and pollinators. For the flowers: reproductive period sensitive to O_3, sometimes with lagged effects to subsequent seasons, and becoming earlier and/or with fewer flowers (number and biomass), depending on species[25]. For the pollinator, disruption of volatile signalling from plant prevents efficient search, at cost to plant and pollinator[26]. Agroforestry – limited evidence for O_3's effects on medicinal plants[28]. More evidence for deleterious impacts on sugar content and total consumable value in improved grassland, deleterious impacts on leguminous components, increases in acid detergent fibre, crude fibre and lignin content thus reducing metabolizable energy across pasture types, and a loss of feed quality for mammalian herbivores[30]. Note that this loss of quality may not persist, with regrowth grasses in pasture showing increased relative feed value and percentage crude protein in doubled O_3 exposure as compared to ambient O_3 regrowth grasses[31].	decomposition dynamics and sustainability of nutrient cycling? To what extent can adaptation to O_3 exposure occur in plant and pollinator populations[27]? To what extent will O_3 contribute to perception of restoration failure due to acute and chronic leaf injuries? Wider screening of O_3 effects on medicinal plants e.g. recent evidence for increase in steroid metabolites[29]. To what extent will food security in multiple use restoration schemes be compromised? Given O_3 is deposited on upper surfaces, plants at lower heights within a multi-layered system may be less exposed to the damaging effects of O_3, potentially alleviating 'open-field' effects.	2011; Dolker et al. 2020; He et al. 2014; Holmes et al. 2003) 24: (Chen et al. 2015; Kasurinen et al. 2017) 25: (Hayes et al. 2021; Hayes et al. 2011; Hayes, Williamson, & Mills 2012) 26: (Papazian & Blande 2020) 27: (Cook et al. 2020) 28: (Agathokleous, Saitanis, & Koike 2015) 29: (Ansari, Agrawal, & Agrawal 2021) 30: (Hayes et al. 2016 Gilliland et al. 2012; Hewitt et al. 2016a,b; Volk et al. 2006) 31: (Gilliland et al. 2016)

Table 2: The pathways to impact of restoration interventions on ozone (O_3) pollution. The balance between vegetation's O_3-generating and O_3-depleting activity is unclear and the extent to which restoration interventions will help provide a solution to O_3 pollution, locally and at scale, depends on species selection, comparison to the unrestored state, and saturation state (NO_x *vs* VOC) of the atmosphere. Note that literature cited within herein is provided in Supplement S3.

Impact pathway	**Description**	**Key references**
Non-stomatal and stomatal deposition	These processes lead to deposition of O_3 on the plant and soil surface, or to the absorption of O_3 by vegetation, thus lowering the remaining amount of O_3 in the atmosphere. To our knowledge, we lack direct quantification of how restoration plantings can affect deposition velocities.	(Clifton et al. 2020)
bVOC emissions	The emission of bVOCs, which will depend on plant species composition, can react with O_3, removing it from the atmosphere[1]. O_3 itself can change the bVOCs emitted by plants[2].	1: (Yáñez-Serrano et al. 2020) 2: (Calfapietra et al. 2013)
Biogeochemical feedbacks	bVOCs emitted by plants, especially isoprene, can act as O_3 precursors (rather than solely being reaction sinks for O_3 (see above)). Impact of planting decisions can be negligible[1] to a net increase[2] at regional level, while vegetation change can depress O_3 concentrations e.g. shift from oak to red maple in north eastern forests of the United States[3]. At the global level, a shift to 'potential natural vegetation' would increase isoprene emissions by 55 %[4] although models are sensitive to vegetation variability and climate[5] Evidence that younger individuals emit more bVOCs[6] (with implications for restoration plantings) and that increased O_3 concentrations from bVOC emissions are most likely in NO_x-saturated regions[7].	1: (Zenone et al. 2016) 2: (Zhang et al. 2020) 3: (Drewniak et al. 2014) 4: (Unger et al. 2013) 5: (Arneth et al. 2011) 6: (Lim et al. 2011) 7: (Porter, Safieddine, & Heald 2017; Rasmussen et al. 2013)
Biogeophysical feedbacks	Biogeophysical impacts can be more important than any biogeochemical impacts at the global scale on O_3 pollution. Models suggest that intensive reforestation in boreal and temperate mixed forest regions will lead to higher O_3 pollution. Even in regions remote from substantial land use – land cover change (LULCC), O_3 pollution will increase due to the evolution of warmer and drier conditions. Reforestation in broadleaf forests of the subtropics has minimal impacts on O_3 levels due to limited boundary layer meteorology effects.	(Wang et al. 2020)

Table 3: A strategic ozone agenda in restoration ecology. Restoration ecology can address the phenomenon of tropospheric O_3 pollution through initiatives in restoration science, practice and policy.

Restoration Science	Restoration Practice	Restoration Policy
• Answer how and why background and episodic O_3 concentrations affect restoration trajectories and the achievement of restoration goals. • Answer this primary focus in different environmental contexts, especially considering co-occurring threats e.g. drought and nitrogen deposition and different legacy conditions, preferably using networked, embedded experiments. • Help atmospheric O_3 science by including field-based estimations of atmospheric O_3 concentrations in restoration projects, and by quantifying feedbacks of restoration interventions on atmospheric pollutants. • When, where and what restoration interventions will exacerbate / ameliorate O_3 levels? Can restoration reduce the effects of O_3?	• Cost-effectively assess likelihood of O_3 being a threat by planting a small area with a known O_3 sensitive species. • Collaborate with scientists to deploy O_3 diffusion tubes and/or wireless sensor networks (can be through citizen science approaches) to monitor ambient O_3 levels and/or register instances of O_3 injury through the Ozone Injury App (https://icpvegetation.ceh.ac.uk/get-involved/ozone-injury/record). • Collaborate with scientists to screen tolerance and/or sensitivity of species to O_3, potentially using low-cost charcoal filtered air equipment to assess current impacts of ambient air. • If using irrigation to aid establishment, avoid O_3 episodes.	• Raise awareness of O_3 as a threat to the achievement of restoration goals, including in relation to scaling up seed supply. • Stimulate efforts to map areas, communities, and ecosystems, and restoration interventions, most at risk from tropospheric O_3 pollution • Raise awareness of useful sources of information on tropospheric O_3 e.g. the Tropospheric Ozone Assessment Report (TOAR). • Raise awareness of the co-benefits of climate change and air pollution mitigation options, while being mindful to not oversimplify given the biochemical and biophysical feedbacks of restoration interventions.