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# Solar ultraviolet radiation in a changing climate

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**The projected large increases in damaging ultraviolet radiation as a result of global emissions of ozone-depleting substances have been forestalled by the success of the Montreal Protocol. New challenges are now arising in relation to climate change. We highlight the complex interactions between the drivers of climate change and those of stratospheric ozone depletion, and the positive and negative feedbacks among climate, ozone and ultraviolet radiation. These will result in both risks and benefits of exposure to ultraviolet radiation for the environment and human welfare. This Review synthesizes these new insights and their relevance in a world where changes in climate as well as in stratospheric ozone are altering exposure to ultraviolet radiation with largely unknown consequences for the biosphere.**

In the early 1970s, Molina and Rowland proposed that chlorofluorocarbons, widely used as refrigerants and propellants, would reach the stratosphere and catalyze the destruction of ozone molecules there[1]. In 1985 evidence of an 'ozone hole' over Antarctica was first published[2] and its progression over the ensuing years has been captured in images that have become symbols of human influences on the global environment.

Large-scale depletion of stratospheric ozone and high levels of ultraviolet (UV) radiation have been avoided by the unprecedented success of the Montreal Protocol on Substances that Deplete the Ozone Layer, signed in 1987. The Montreal Protocol remains the only treaty ever ratified by all members of the United Nations. This unusual consensus on an environmental issue was driven by concerns that life on Earth was at risk, a concern that is supported by recent analyses of the 'world avoided' scenario of what could have happened without the Montreal Protocol[3,4]. The actions taken under the protocol have also made the single largest contribution to the mitigation of climate change so far, because many of the ozone-depleting substances (ODS) are also greenhouse gases (GHGs)[5].

## Ozone and the Montreal Protocol

Solar radiation is essential to life on Earth, but its UV component may also damage both living organisms and non-living matter. UV radiation is usually divided into three wavelength bands: UV-A (315–400 nm), UV-B (280–315 nm) and UV-C (100–280 nm). UV-C radiation is potentially the most damaging, but is completely filtered out by the Earth's atmosphere and does not reach the surface. The Earth's surface is also largely protected from the most damaging short wavelength UV-B radiation due to absorption by stratospheric ozone. UV-A radiation passes through the atmosphere with little attenuation and thus is the largest component of ground-level solar UV radiation. Although generally less harmful than UV-B radiation, UV-A radiation has important effects on tropospheric chemistry, air quality, and aquatic and soil processes, as well as being mutagenic and causing immune suppression in humans[6].

Implementation of the Montreal Protocol has drastically curtailed production of chlorofluorocarbons and other ODS[7]. It has thus successfully reduced depletion of stratospheric ozone and associated increases in ground-level UV-B radiation. However, the long lifetimes of many ODS in the atmosphere mean that substantial ozone depletion still occurs over the Antarctic, and is expected to continue for several more decades[8]. Stratospheric ozone loss has also been observed over the Arctic[9], with 2011 showing the largest depletion ever recorded[10]. This major depletion event was caused by a combination of unusually low stratospheric temperatures, ODS-derived chlorine in the stratosphere and a change in circulation patterns that delayed the seasonal transport of ozone from the tropics[10].

During the twenty-first century, upper stratospheric ozone is projected to increase due to the reduction in ODS and continued cooling from the increasing concentrations of GHGs. In the lower stratosphere, ozone is projected to decrease[11], offsetting the effect of upper stratospheric cooling. The net effect of these changes on terrestrial UV radiation is complex, as additional factors, such as increasing concentrations of carbon dioxide ($CO_2$) and other GHGs, begin to play an ever-increasing role in determining levels of stratospheric ozone and cloud cover. For example, by 2100, models predict that UV radiation will have increased in the tropics

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(where the current UV radiation is already intense), and to have decreased at polar latitudes (where the current UV radiation is generally less intense)[12].

## A different world

A different world has evolved after 26 years of the Montreal Protocol. The phase-out of ODS is projected to lead to recovery of stratospheric ozone. However, additional climate-related changes in the incident UV radiation at Earth's surface may result from changes in cloud, snow and ice cover, land-use, and atmospheric and oceanic circulation, and will vary regionally. Circulation patterns, such as the North Atlantic Oscillation, account for a high proportion of the variability in the total ozone column[13]. Such patterns are predicted to be altered by the accumulation of GHGs with subsequent changes in UV-B radiation levels at Earth's surface. These changes will, in turn, alter sinks and sources of $CO_2$ and other trace gases that will affect future climate warming.

The unequivocal warming of the climate system[14] may have important impacts on future stratospheric ozone depletion independently of the concentration of ODS in the atmosphere. Increasing concentrations of GHGs cause a radiative cooling in the stratosphere, and extremely cold polar stratospheric winters are responsible, in part, for the Antarctic and Arctic spring ozone depletions[15,16]. Denitrification of the chlorine reservoir (chlorine nitrate, $ClONO_2$) occurs on the surfaces of polar stratospheric clouds and this process is a major reason for the observed 2011 Arctic spring ozone loss[10,16]. The response to global warming is particularly rapid in the Arctic[17]. Moreover, global warming may also affect stratospheric ozone by increasing the atmospheric water content and its rate of transport through the cold tropopause (the troposphere–stratosphere boundary)[18]. Water vapour is a key component of stratospheric chemistry and may influence stratospheric temperatures and winds. It is involved in ozone destruction by accelerating the gas-phase hydrogen oxides ($HO_x$) catalytic cycle, and by increasing the surface area of stratospheric aerosol particles on which ozone-depleting halogen molecules can be activated.

Models suggest that in the first half of the twenty-first century, levels of UV radiation at Earth's surface will be determined by the recovery of stratospheric ozone, while in the second half, changes in UV radiation will be dominated by changes in clouds and GHG-induced transport of ozone[12]. These climate-driven changes are projected to markedly influence the amount of UV radiation received at Earth's surface. For example, by 2050, sunburning or erythemal UV irradiance (primarily in the UV-B region of the spectrum) is projected to decrease by 2–10% at mid-latitudes, and by up to 20% at northern and 50% at southern high latitudes, relative to 1980 levels. By the end of the twenty-first century, erythemal UV irradiance is projected to remain below 1960 levels at mid-latitudes, be reduced at high latitudes (particularly in the Arctic) by 5–10% due to increases in clouds[19], but to increase in the tropics by between 3 and 8% due to decreases in clouds and ozone, caused by increasing GHGs[12] (Fig. 1). Improvements in air quality, especially reductions of aerosols, may in the future result in higher UV radiation levels at Earth's surface. In the Arctic, there may be increases in sea-salt aerosols from the larger open-ocean area, as well as reductions in surface albedo due to the loss of sea ice[20,21], resulting in lower surface UV irradiance.

Unexpected effects of ozone depletion on climate are becoming increasingly apparent, highlighting the complexity of Earth's climate system. Ozone depletion over Antarctica has caused a poleward shift in the Southern Hemisphere circulation, resulting in increased precipitation in the subtropics (15–35° S)[22]. As stratospheric ozone recovers, an opposing effect is expected and subtropical regions are likely to become drier. It is still uncertain whether the effects on precipitation patterns from ozone recovery and increasing GHGs will cancel each other, or whether one will dominate over the other, and if or when this balance will be established[23]. However, Polvani and colleagues[24] suggest that the effect of ozone recovery will be more important than that of increasing GHGs during the next 50 years. The beneficial and detrimental effects of UV radiation in the context of this rapidly changing and complex ozone and climate forcing are addressed below.

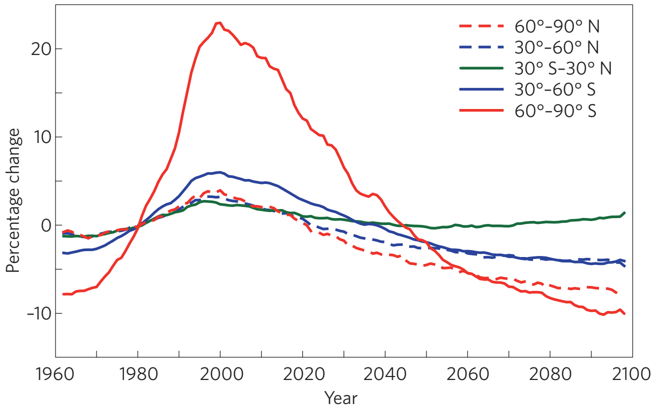

**Figure 1 | Observed (pre-2010) and projected changes in annual mean erythemal (sunburning) clear-sky UV-B radiation at Earth's surface, relative to 1980, for different latitude bands.** Figure updated with permission from ref. 33.

## An atmospheric regulator

Solar UV radiation has a profound influence on the chemical composition of the atmosphere, contributing both to cleaning of the atmosphere and to the generation of photochemical smog. These seemingly opposite effects are actually two aspects of the same chemical system. At its essence, atmospheric cleaning relies on increasing the reactivity of emitted pollutants to shorten their lifetimes. However, the higher reactivity also means that these transient compounds are often more toxic to humans and ecosystems.

UV radiation initiates this chemistry by breaking some relatively stable molecules into highly reactive fragments, and subsequent reactions involving oxygen and water generate hydroxyl (OH) radicals. These strongly oxidizing OH radicals have a beneficial cleaning effect as they remove many of the gases emitted at Earth's surface, including some important GHGs. The lifetimes and atmospheric quantities of these gases are controlled by the concentrations of OH radicals[25], which are in turn sustained by the UV radiation transmitted through the stratosphere to the troposphere[26]. This coupling between stratospheric and tropospheric photochemistry is a powerful mechanism, not only for the removal of present-day emissions, but also for maintaining the long-term stability of the atmosphere against major perturbations in emissions. Such perturbations would eventually propagate to the stratosphere, where they would probably decrease ozone and increase transmission of UV radiation, thus increasing the production of tropospheric OH and ultimately accelerating the removal of the pollutants, re-establishing the global oxidation capacity[27].

On shorter temporal scales, the partly oxidized intermediates of this UV-initiated chemistry constitute photochemical smog, a complex mixture of gases and condensed particles (aerosols) that reach concentrations detrimental to health in many urban areas. Poor outdoor air quality causes increased hospitalizations[28], with several million premature deaths globally in 2010 (ref. 29), as well as damage to crops[30]. Apart from ozone and $NO_2$, photochemically produced pollutants of major concern include particles containing nitrate, sulphate and various organics. Higher levels of

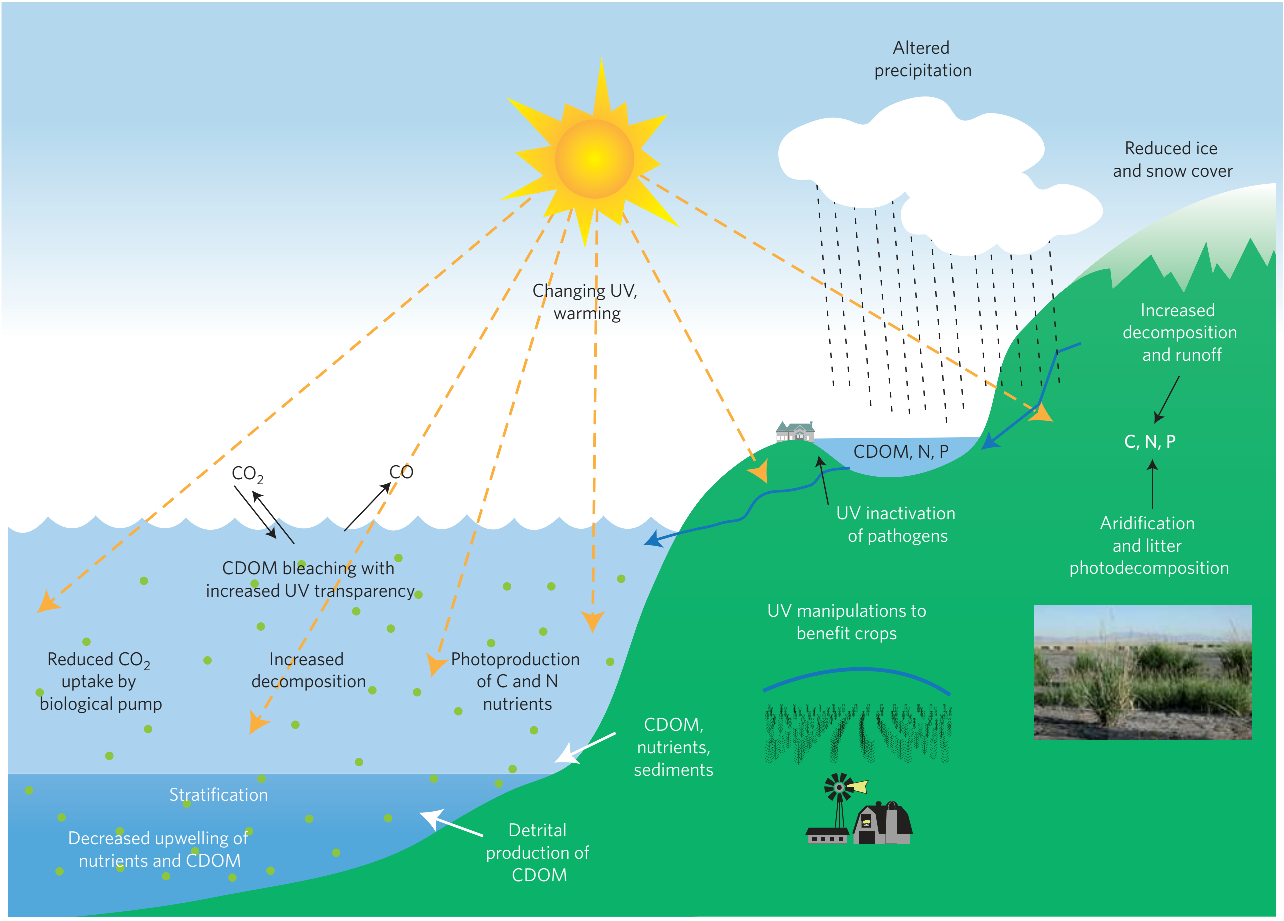

**Figure 2 | Conceptual model of aquatic and terrestrial processes that are possibly influenced by interactions between ultraviolet radiation and climate change.** On land, thawing of ice, snow and permafrost can result in increased exposure of dissolved organic matter (DOM) to ultraviolet (UV) radiation that stimulates the release of $CO_2$ and methane via DOM mineralization. Aridification caused by climate change is accompanied by increased UV radiation at soil surfaces that causes increased degradation of senescent plant material and litter with release of $CO_2$ and nutrients. Manipulations of UV radiation in agro-ecosystems using, for example, UV-modified plastic coverings or altering of canopy architecture are being used to increase crop quality and production. Exposure to UV radiation also helps reduce human diseases in lakes and the coastal ocean by disinfecting pathogens in surface layers. Coloured dissolved organic matter (CDOM) controls the transmission of UV radiation into aquatic systems. Photobleaching of the CDOM, which contributes to increased exposure of phytoplankton to UV radiation, occurs particularly efficiently in thermally stratified waters. This phenomenon, coupled with reduced nutrient and CDOM upwelling caused by stratification, reduces the efficiency of the biological pump. UV-induced breakdown of aquatic organic matter also can stimulate microbial activity and influence metal speciation that affects the air–water exchange of $CO_2$ and trace gases such as carbon monoxide and nitrous oxide. Inset image courtesy of the US Departement of Agriculture Agricultural Research Service.

both UV-A and UV-B radiation may intensify local and regional photochemical smog episodes, even while cleaning the global atmosphere more effectively.

The interactions of the tropospheric photo-oxidation system with the physical climate are numerous and complex. While OH radicals limit the abundance of some GHGs, such as $CH_4$ and halogenated hydrocarbons, the subsequent reactions can produce tropospheric ozone, which is itself a strong GHG. As production of ozone in the troposphere requires the presence of nitrogen oxides ($NO_x$), it is likely that tropospheric ozone has increased substantially since pre-industrial times[31] and has contributed to radiative forcing. Globally averaged OH concentrations tend to increase in response to more intense UV radiation and larger $NO_x$ emissions, but decrease in response to higher hydrocarbon emissions, so even the direction of net past (and future) changes remains uncertain[32]. Sulphate and organic aerosols affect solar radiation directly by absorption or scattering, or indirectly by modifying the formation, optical properties and lifetimes of clouds. Taken together, the direct and indirect effects of aerosols have been identified as one of the largest uncertainties in the radiative forcing of climate[32]. Increased cloudiness would generally decrease UV radiation reaching Earth's surface[33], but may enhance the radiation at higher altitudes by reflection from clouds below and to the sides[34].

## Terrestrial ecosystems and UV–climate interactions

The projected future changes in precipitation, vegetation cover and agricultural intensification will influence the balance between the detrimental and beneficial effects of UV radiation and their bidirectional interactions with climate change. This will have important implications for ecosystem processes and food production.

Globally, the negative effects on plant biomass of increases in UV-B radiation as a result of stratospheric ozone depletion have been minimal[35]. In fact, the reduction in plant growth caused by increased UV-B radiation in areas affected by ozone decline since around 1980 is unlikely to have exceeded 6% (ref. 35). Plant acclimation and adaptation mechanisms, such as increased production of UV-screening phenolic substances and morphological changes, are likely to have contributed to the relatively small impact of changes in UV-B radiation on growth[35], although these responses can be species and region specific. Although plants found in naturally high UV radiation environments (for example, tropical or high alpine) produce more UV-absorbing compounds ('sunscreens'), those endemic to low UV radiation environments may be more vulnerable to damage[36]. The mechanisms that mediate these acclimation responses in plants are being elucidated, including the identification of a specific UV-B photoreceptor[37].

Solar radiation, in particular UV-B, can be a positive regulator of plant defence systems against a broad spectrum of insect pests and pathogenic microorganisms[38]. This has been demonstrated in field experiments where significant increases in the severity of attack by a wide range of invertebrate herbivores occurred when solar UV-B radiation was attenuated using filters (reviewed in ref. 35). This beneficial role of UV-B radiation in resistance to pests is sometimes caused by increased activity of hormonal pathways responsible for the coordination of plant immunity, such as the jasmonate pathway[39]. Exposure to UV-B radiation intensifies the jasmonate immune response, so that the magnitude of defence induced by herbivore attack is increased[39]. In other cases, resistance is conferred by secondary metabolites that the plant synthesizes in response to UV-B radiation, for example, phenolic compounds[40]. Importantly, some of these UV-B-induced secondary metabolites may also have roles in human nutrition because of their antioxidant properties[41].

Utilization and modification of plant defence responses, which are activated by UV-B radiation, may help to improve crop health in agricultural systems[38]. In addition, manipulation of UV radiation in horticultural systems has provided an understanding of the potential positive effects of UV radiation, which can also be exploited to increase food production and quality. For example, UV-enhanced production of polyphenolics and other compounds can be used to enhance the nutritional quality of plant products and plant resistance to biotic stressors[38,42]. Pests and diseases can account for up to one-quarter of pre-harvest crop losses in modern agricultural systems[43], and standard chemical controls are becoming increasingly regulated due to their negative impacts on human health and ecosystems[44].

New insight into how UV radiation affects carbon and nutrient turnover has broadened our understanding of its impact in terrestrial ecosystems. For example, exposure to UV radiation can cause degradation of senescent plant material (such as leaf litter) and so stimulate the release of $CO_2$ and the mineralization of nutrients[45], especially in arid and semi-arid ecosystems[46]. Changes in vegetative cover due to human activity or climate resulting in aridification can increase UV irradiation at the soil surface, causing decreased carbon sequestration but increased nutrient release through accelerated degradation of senescent plant material. Climate interactions through permafrost thawing can result in exposure of dissolved organic matter (DOM) to solar UV radiation and, as a consequence, release of $CO_2$ and methane via DOM mineralization[47]. This process, coupled with other decomposition processes and increased fire incidence, can weaken the net $CO_2$ uptake of tundra, which is at present considered a carbon sink[20]. Reduction of $CO_2$ uptake by terrestrial ecosystems due to the combined effects of UV radiation and climate change may result in an UV-mediated increase in atmospheric $CO_2$.

Long-term effects of interactions between UV radiation and other concurrent environmental stress factors, such as water availability and high temperature, are unknown and will vary depending on geographical location, prevailing climate, ecosystem type[35] and agricultural practices[38]. Consequently, these strong stress conditions in combination may lead to decreased plant productivity and increased reliance on pesticides[38] as defence systems weaken[48]. In addition, changes in plant species in favour of more resilient species may compromise growth of current food crops.

## Aquatic ecosystems and UV–climate interactions

The extent and duration of periods of ice and snow cover on oceanic and inland waters have been decreasing in recent decades, altering the underwater light environment and potentially resulting in direct exposure of the aquatic environment to higher UV radiation[49]. The Arctic Ocean is expected to be ice-free during the summer within the next 30 years[20,50] and the average duration of ice cover on lakes in the Northern Hemisphere over the past 150 years has decreased by approximately 17 days[51]. Consequent increases in the exposure of aquatic ecosystems to UV and photosynthetically active radiation that result from these reductions in snow and ice cover[52] have the potential to create tipping points — shifts in photosynthetic versus heterotrophic organisms where community as well as ecosystem structure and function are fundamentally altered[49]. Shifts from multi-year ice-cover to annual ice-cover are increasing meltwater ponds on the surface of polar ice that reduce albedo and increase transmittance of UV radiation and photosynthetically active radiation by an order of magnitude[52]. This thinner and more spatially heterogeneous ice also allows more solar heat input into the ocean[52]. The effects of climate change on sources and sinks of the GHGs, particularly $CO_2$ and $CH_4$, have been estimated for the Arctic[20], but the potentially large interactions of these effects with changes in UV radiation levels are not well understood.

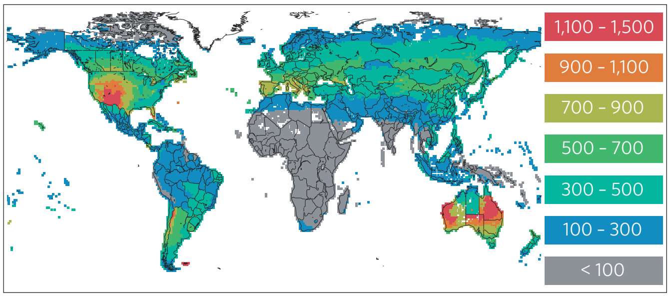

**Figure 3 | Projection of the total numbers of excess new cases of total skin cancer per million people per year avoided by the Montreal Protocol in 2030 compared with a reference population that takes account of population growth only.** Reproduced with permission from ref. 77.

Some of the interactive effects of UV radiation with climate change on aquatic ecosystems are linked to the coloured component of dissolved organic matter (CDOM), which absorbs sunlight, including UV radiation[53]. The CDOM mainly controls the transmission of solar UV radiation into aquatic ecosystems. Exposure to UV radiation accelerates degradation of organic matter, including CDOM, to produce trace gases, such as $CO_2$ and carbon monoxide, as well as biologically labile substances that affect microbial processes in aquatic systems (Fig. 2)[54].

Alterations in UV radiation linked to climate change have a variety of effects on phytoplankton and coral assemblages in the upper layers of aquatic ecosystems. The degradation of CDOM leads to a loss of colour and UV absorbance. This 'photobleaching' occurs particularly efficiently in thermally stratified waters of lakes and oceans where it results in greater exposure to UV radiation in surface waters. Enhanced exposure to UV radiation, coupled with reduced upwelling of nutrients into the upper layers of stratified aquatic systems can have a negative impact on phytoplankton. This would then reduce photosynthesis and hence the efficiency of the biological pump, which is the $CO_2$ fixed by phytoplankton and the subsequent transfer of the organic matter to deeper layers of the ocean through sedimentation[53]. CDOM in the open ocean is a by-product of biological degradation of dead phytoplankton, so that a reduced concentration of phytoplankton will drive decreases in CDOM production, thus further increasing transmission of UV radiation into the ocean. Thus increased exposure to UV radiation may contribute to the observed reductions in phytoplankton biomass that have previously been attributed primarily to increasing sea surface

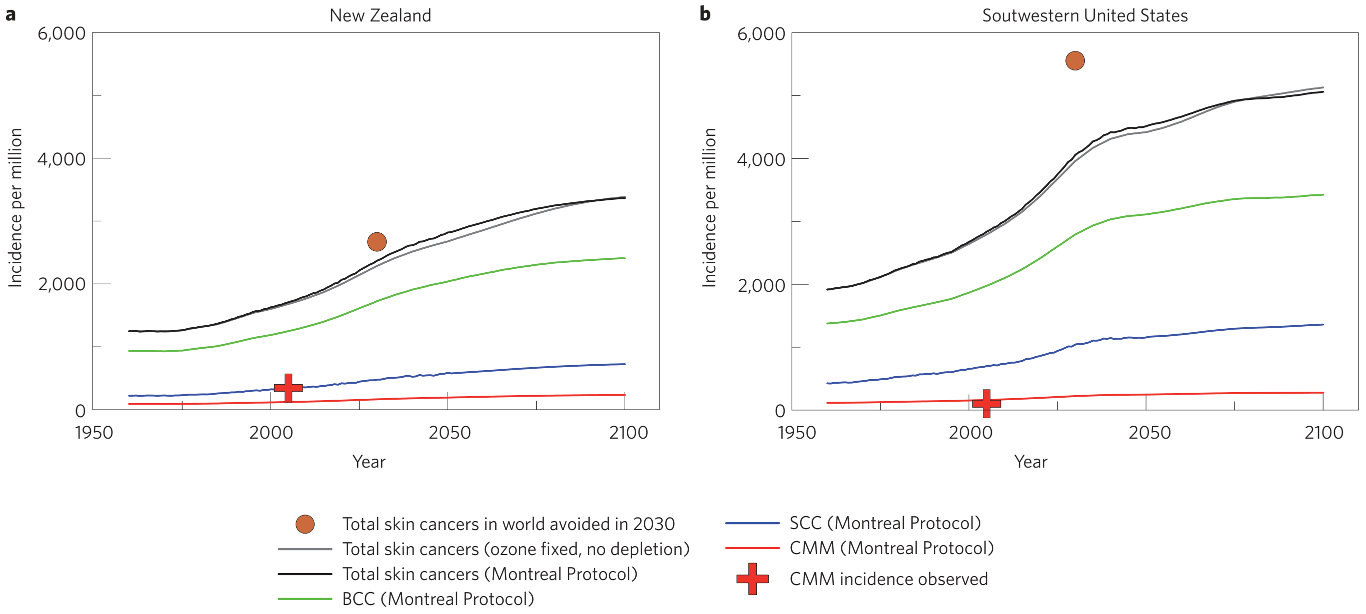

**Figure 4 | Predicted total skin cancer incidence per million population according to calendar year. a**, New Zealand and **b**, southwestern USA. The plots are not adjusted for changing demographics, and assume that the personal dose of ultraviolet (UV) radiation is a constant fraction of ambient UV radiation in all years and across all regions (data derived from predictive models in ref. 77). Note: skin cancer incidence models are derived from data available for Amsterdam in 1990. The red cross shows current cutaneous melanoma (CCM) incidence in both regions. The models overestimate melanoma incidence in southwestern USA and underestimate melanoma incidence in New Zealand. Equivalent data for non-melanoma skin cancer, to check the model predictions, are not available. BCC, basal cell carcinoma; SCC, squamous cell carcinoma. Original figure by Richard McKenzie.

temperatures and thermal stratification that reduce nutrient upwelling[55]. Additional feedbacks occur through interactions with climate change (Fig. 2), such as the increased uptake of $CO_2$ by the oceans that has increased the acidity of the upper water layers and reduced the available carbonate used by corals, plankton and some algae to form UV-protective calcifications[56]. Ocean acidification also results in reduced availability of essential trace metals to phytoplankton[57].

Changes in UV radiation can affect aquatic microbial processes that are involved with GHG air–water exchange. UV-induced degradation of terrestrially derived DOM results in the formation of biologically labile forms of DOM and nitrogen, such as ammonia[58]. This process stimulates microbial activity in aquatic systems and the release of $CO_2$ via biotic DOM mineralization[59]. Furthermore, as the upper ocean warms up, the solubility and thus concentration of oxygen decreases. Also, increased rates of microbial decomposition caused by warming further reduce oxygen concentrations. These climate change-related reductions in oxygen concentration and increased deposition of reactive nitrogen will result in increases in oceanic production of nitrous oxide ($N_2O$), an important GHG and ozone-depleting gas[60].

Although increased UV-B radiation can negatively affect the growth and viability of many organisms in aquatic food webs[61], sensitivity to UV radiation has the beneficial effect of disinfecting pathogens. This process is facilitated by climate and UV-induced changes that alter exposure of surface-dwelling organisms through increased water transparency and stratification, and reduced ice and snow cover. For example, the human intestinal parasite *Cryptosporidium parvum*, which is frequently found in rivers, lakes and drinking water, is sensitive to solar UV radiation[62], and disinfection by the UV radiation of still tap water can occur rapidly[63]. Similarly, infection of the zooplankton *Daphnia dentifera*[64], and tadpoles of certain species of toad[65] with fungal parasites can be reduced by solar UV irradiation. At the same time, however, the observed increases in DOM in the surface water of glaciated landscapes across North America and Europe[66] reduce the disinfection potential of solar UV radiation for parasites and pathogens.

## Human health risks and benefits

Considerations of health risks were important drivers of the international consensus that is reflected in the Montreal Protocol. For example, exposure of the eyes to solar UV-B radiation is a cause of a range of eye diseases, including cortical cataract, pterygium and photokeratitis[67]. Similarly, irradiation of the skin is the major environmental risk factor for cutaneous melanoma (CM) and the non-melanoma skin cancers (NMSCs), basal cell carcinoma (BCC) and squamous cell carcinoma (SCC)[68]. Exposure to UV radiation causes both local and systemic immunosuppression[67] but boosts innate immunity by inducing the expression of antimicrobial peptides in the skin[69]. An important beneficial effect of UV-B irradiation of the skin is the production of vitamin D[70], the active form of which is a hormone required for bone health that also has multiple immunomodulatory functions.

NMSC is the most common human cancer, particularly in older age groups, with an estimated incidence of ~1,170 per 100,000 in the US population in 2006 (ref. 71). CM is less common. Across a range of countries, the annual incidence per 100,000 (age standardized to the world standard population) varies from 0.1 in Algeria, 4.3 in Latvia, 9.8 in the United Kingdom, 14.4 in Denmark, and 15.1 in the United States (42 states) to 52.9 in Queensland, Australia[72]. In Australia, CM is the most frequently registered cancer in women aged 17–33 years[73]. Importantly, over the past 40 years, the incidences of both CM and NMSC have increased rapidly in fair-skinned populations worldwide, due to the combination of changing population demographics (that is, ageing), and high levels of sun exposure during the second half of the twentieth century coupled with a long latent period from exposure to disease onset. Because of the large numbers, skin cancers are, collectively, among the most expensive cancers to treat in many countries[74,75].

Action to mitigate stratospheric ozone depletion occurred in a setting of rapidly increasing incidence of skin cancer and was followed by the introduction of sun protection programmes in many countries[76]. Modelling studies have estimated that even larger increases in the incidence of skin cancers[4,77] and cataracts[78] would have occurred under different scenarios without implementation of the Montreal Protocol and its amendments (Figs 3 & 4). Nevertheless, sun exposure behaviour is a key factor in the biologically effective UV radiation received. For example, the increase in ambient UV-B radiation over Europe since 1980 has been estimated at 5–10% (refs 33,79,80), while the incidence of skin cancers has increased by 50% or more[81]. This change has been attributed to more frequent sunshine holidays[82] with associated cheap air travel, wearing less clothing including hats when the sun shines[83], the perception that a tan is a sign of good health and affluence, and other behavioural factors[84].

At the same time, other changes in lifestyles in recent years may have contributed to the widespread vitamin D insufficiency that has been reported[85,86]. This has likely been a consequence of lower sun exposure in recent years[87,88], due to a combination of increased urbanization[89], more indoor living, and concerns about sun damage to the skin and eyes, although the importance of measurement issues in assessing vitamin D status cannot be discounted[90]. The importance of vitamin D for bone health is well recognized, but more recently vitamin D deficiency has also been implicated in a wide range of health outcomes, including internal cancers, autoimmune diseases, infections and psychiatric diseases[91]. Although there is biological plausibility for vitamin D having a widespread protective role[92], there are conflicting results from observational studies. In addition, mainly negative results have been obtained thus far from clinical trials of vitamin D supplementation in the treatment or prevention of various diseases, possibly through use of too low a dose, the trial not going long enough to be biologically relevant to the disease outcome and failure to account for genetic variation or to achieve adequate vitamin D levels. An alternative explanation is that low vitamin D status is a marker of ill health, rather than a cause of it[93] or that measured vitamin D status is a proxy for non-vitamin D benefits of sun exposure[94].

Skin cancer incidence is predicted to increase from the combined effects of ageing, higher UV radiation levels until ozone recovery, and past and current sun exposure behaviour[77] (Fig. 3). Sun exposure behaviour will be a major determinant of skin cancer risks in the future and this is likely to be altered by changing temperatures, cloud cover and patterns of precipitation, and outdoor air pollution. Warmer temperatures may be associated with a higher number of sunburn episodes (and thus skin cancer risk)[95]. However, more sun exposure in currently cooler climates, that is, higher latitudes, may also reduce vitamin D deficiency. Skin cancer genesis may be accelerated at higher temperatures or under conditions of higher humidity[96], providing a direct effect of climate change on skin cancer risk. The rate of cutaneous vitamin D synthesis may also increase with higher skin temperature[97]. Thus, the net balance of risks and benefits under climate change conditions is difficult to predict, but will vary regionally according to the combination of changes in levels of UV radiation and sun exposure behaviour.

Population movements due to rising sea levels, food scarcity or other climate-related factors may further alter the spectrum and balance between the positive and negative effects of solar UV-B radiation on health. For example, large movements of populations of darker-skinned climate refugees from low-lying (that is, affected by sea-surface rises) but high ambient UV radiation locations where a large proportion of the day is spent outdoors, to less sunny and cooler locations at higher latitudes, could potentially accentuate the current apparent 'epidemic' of vitamin D deficiency, with associated disease risks (compare with ref. 98).

## Remarks and perspectives

Recognition of ozone depletion and the resulting mitigation activities have had the unforeseen benefits of careful assessment and stimulation of research on stratospheric ozone, UV radiation and its effects over the past 26 years. The shift in research focus from investigations almost solely centred on the negative effects of UV radiation to a more balanced perspective of the multiple beneficial and adverse effects has occurred in a rapidly changing environment where the impacts of stratospheric ozone depletion are intricately coupled with those of climate change[99]. The Montreal Protocol has simultaneously protected the ozone layer and lessened the radiative forcing of climate warming, relative to a 'world avoided' scenario of increasing ODS that would — according to models — have resulted in both significantly higher temperatures and more intense surface UV-B radiation globally[100].

Yet the review presented here of the new knowledge and insights generated by the research response to the Montreal Protocol reveals that our understanding of the UV–ozone–climate links is far from complete. The downside is that the success of the Montreal Protocol has led to the perception that this is a 'problem solved' for research in this critical nexus that has broad, pervasive and important implications for the future of humans and the ecosystems on which they depend. New research is necessary to uncover the breadth of potential risks and benefits across the atmosphere and biosphere as a result of the coupled ozone depletion–climate change interactions. We have illustrated here that many of these interactions have coincident risks and benefits, so the potential for reaching critical tipping points becomes of considerable importance. Changes in climate may alter the geographic distribution of organisms, including humans, and also the vertical distribution of organisms in aquatic and terrestrial ecosystems, exposing them to different UV radiation environments and attendant positive and negative effects.

Responses to solar UV radiation are integral to how organisms function, but in a changing climate some of these responses will probably be modified, resulting in benefits to some organisms and ecosystems and deleterious effects on others. Importantly the interactive effects of a broad range of environmental factors can no longer be considered in isolation. The way in which we manage the environment and its natural resources, and the decisions taken on ODS and their substitutes, as well as GHG emissions, will determine the ultimate outcome of further interactive effects of UV radiation, ozone and climate. This integrative approach to the research is still in its infancy with many unanswered questions that require further investigation to improve our understanding of the complexities and their consequences for the biosphere.

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## Author contributions

All authors have helped to develop the paper. C.E.W., R.G.Z., R.M.L. and S.M. played major roles, equally contributing to the conceptualization and writing of the paper. J.F.B. provided content, organized and coordinated the paper and contributed comments and revisions on all the drafts. A.T.A. and C.L.B. contributed text to the terrestrial and aquatic sections. S.A.R. provided text and comments on the terrestrial ecosystems. M.N. contributed to the health section and provided comments on the drafts. B.S. made contributions particularly to the biogeochemical sections. A.F.B. and R.L.M. contributed input to the UV effects and the atmosphere. D.P.H. provided input to the aquatic section. N.D.P. helped with the initial drafts and writing.

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## Competing financial interests

The authors declare no competing financial interests.