

1 **Linkages between stratospheric ozone, UV radiation and climate change**

2 **and their implications for terrestrial ecosystems**

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35 **Abstract**

36
37 Exposure of plants and animals to ultraviolet-B radiation (UV-B; 280-315 nm) is modified by
38 stratospheric ozone dynamics and climate change. Even though stabilisation and projected recovery
39 of stratospheric ozone is expected to curtail future increases in UV-B radiation at the Earth's
40 surface, on-going changes in climate are increasingly exposing plants and animals to novel
41 combinations of UV-B radiation and other climate change factors (e.g., ultraviolet-A and visible
42 radiation, water availability, temperature and elevated carbon dioxide). Climate change is also
43 shifting vegetation cover, geographic ranges of species, and seasonal timing of development, which
44 further modifies exposure to UV-B radiation. Since our last assessment, there is increased
45 understanding of the underlying mechanisms by which plants perceive UV-B radiation, eliciting
46 changes in growth, development and tolerances of abiotic and biotic factors. However, major
47 questions remain on how UV-B radiation is interacting with other climate change factors to modify
48 the production and quality of crops, as well as important ecosystem processes such as plant and
49 animal competition, pest-pathogen interactions, and the decomposition of dead plant matter
50 (litter). In addition, stratospheric ozone depletion is directly contributing to climate change in the
51 southern hemisphere, such that terrestrial ecosystems in this region are being exposed to altered
52 patterns of precipitation, temperature and fire regimes as well as UV-B radiation. These ozone-
53 driven changes in climate have been implicated in both increases and reductions in the growth,
54 survival and reproduction of plants and animals in Antarctica, South America and New Zealand. In
55 this assessment, we summarise advances in our knowledge of these and other linkages and effects,
56 and identify uncertainties and knowledge gaps that limit our ability to fully evaluate the ecological
57 consequences of these environmental changes on terrestrial ecosystems.

58 3.1 Introduction and overview

59
60 The structure, function and diversity of terrestrial ecosystems are being modified by ongoing
61 changes in the Earth's climate, and these complex changes are becoming increasingly evident with
62 time.¹⁻³ An assessment of the effects of depletion and recovery of stratospheric ozone and
63 associated changes in ultraviolet-B radiation (UV-B, 280-315 nm) on the terrestrial biota must,
64 therefore, consider the role of climate change in the response of these organisms and ecosystems.
65 In some regions, stratospheric ozone depletion is itself contributing to climate change with the result
66 that ecosystems are being affected by the consequent ozone-driven changes in temperature and
67 precipitation.^{4, 5} Prior assessments have considered the effects of stratospheric ozone depletion in
68 the context of climate change and have reported on some of the ways in which climate change can
69 potentially interact with ozone depletion and UV-B radiation to modify terrestrial ecosystem function
70 and composition.⁶⁻⁸ In this assessment, we report on progress made since the last one⁸ and
71 examine and further explore recent findings that document interactive effects of ozone depletion,
72 UV-B radiation and climate change on terrestrial organisms and ecosystems, including cultivated
73 species and highly managed ecosystems (e.g., agroecosystems). We emphasise effects that have,
74 at least to some degree, been demonstrated to occur in nature, but also identify areas where
75 potential effects on terrestrial ecosystems could occur in the future. Where possible, areas of
76 uncertainty are addressed, and the significance of findings is placed in a context relevant to policy
77 makers.

78
79 Ecologically significant linkages between stratospheric ozone depletion, climate change and UV
80 radiation are diverse, sometimes bi-directional, and, in certain cases, exhibit important feedbacks to
81 the climate system (Fig. 1). However, climate change is increasingly contributing to changes in the
82 timing and duration of UV-B radiation exposure, independent of ozone dynamics. These changes
83 can occur in a number of ways (see section 3.7). One avenue involves climate change-driven shifts
84 in cloud cover, which is increasing in some regions (usually wetter areas), while decreasing in
85 others (usually drier regions).^{1, 4} Similarly, climate change-driven effects on vegetation (e.g., forest
86 die-back or shrub invasions) can increase or decrease the UV exposure conditions of understory
87 plants and animals. As a result of warmer growth conditions and altered timing of seasons, many
88 plants are initiating growth and flowering earlier in the year,^{9, 10} while certain animals are adjusting
89 their timing of breeding and migration.^{11, 12} As UV-B radiation varies seasonally (Fig. 8), a change in
90 the timing of important life-cycle events can easily affect their exposure to UV-B radiation. In
91 addition, the geographic ranges of many plants and animals, including wild and domesticated
92 species, are shifting to higher elevations and latitudes in response to climate change.^{1, 2, 13-}
93 ¹⁵ Because of existing natural altitudinal and latitudinal gradients in solar UV radiation,^{4, 16-18} these
94 changes in geographic ranges can potentially increase (at high elevations) or decrease (at high

95 latitudes) the amount of UV-B radiation received by organisms. Unlike ozone depletion, all of the
96 above climate change-driven effects are modifying organisms' exposure to the full solar radiation
97 spectrum at the Earth's surface, including UV-B as well as UV-A (315-400 nm) and visible (400-700
98 nm) radiation. At the same time, plants and animals are being exposed to novel combinations of UV
99 radiation with other abiotic (e.g., changing day length, and fluctuating temperatures) and biotic
100 factors (e.g., competitors, pests, and pollinators). Because of these complexities, it is necessary to
101 consider how organism and ecosystem responses to UV-B radiation are modified by concomitant
102 changes in other regions of the solar spectrum (i.e., UV-A and visible radiation) as well as
103 simultaneous changes in a diverse range of abiotic and biotic factors.

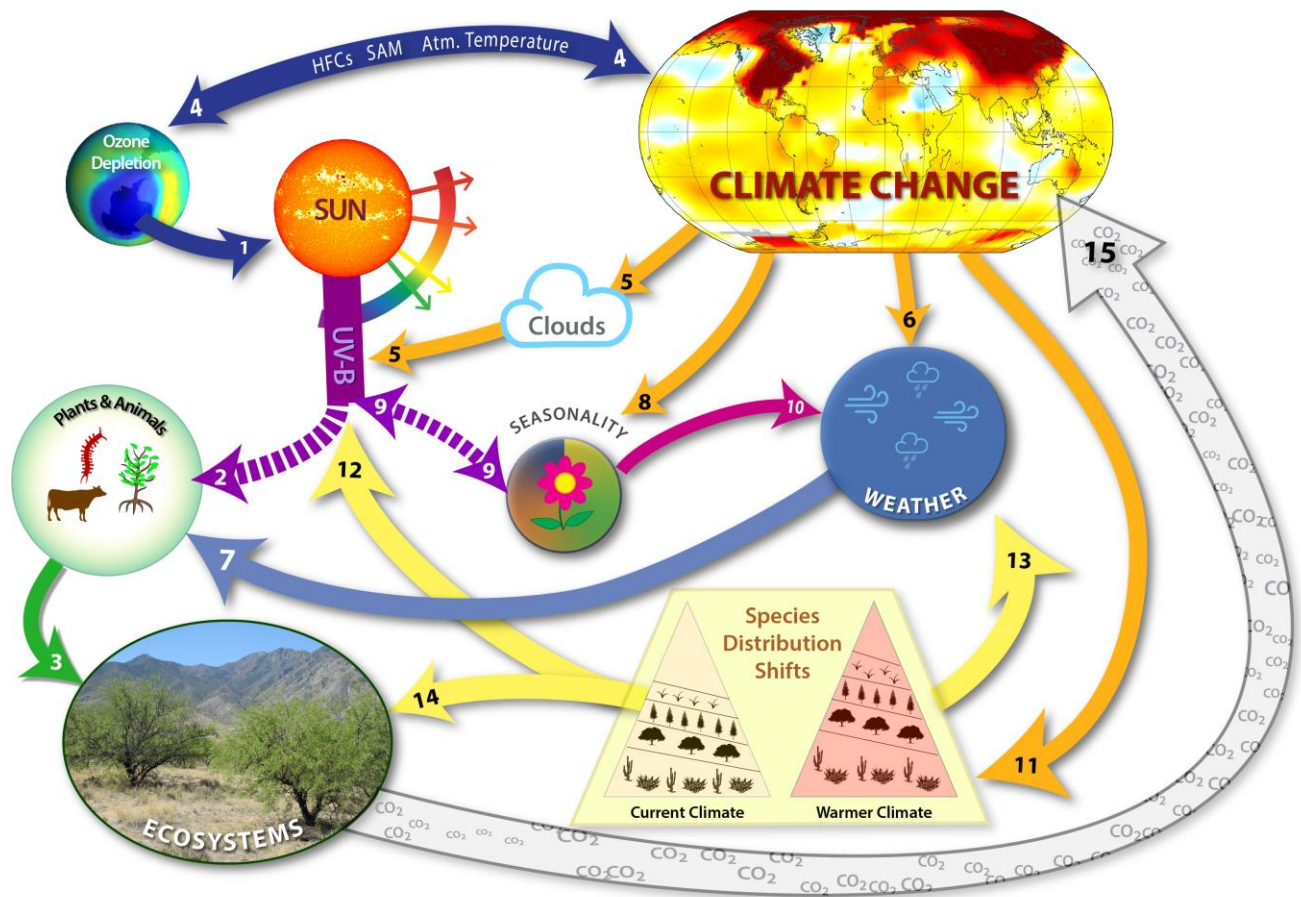
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105 Solar UV radiation (UV-B and UV-A) is known to affect the growth and performance of terrestrial
106 plants and animals (see sections 3.3 and 3.4). The shorter wavelengths of UV radiation (mostly in
107 the UV-B range) may cause cellular damage, and this can lead to changes in an organism's
108 morphology, physiology, and biochemistry. Concurrent exposure to longer wavelengths (e.g., UV-A
109 and/or visible radiation), however, can often reduce the negative effects of UV-B radiation.¹⁹ In
110 addition, both UV-B and UV-A radiation are important sources of information for plants and animals.
111 This radiation is perceived by specific photoreceptors, which trigger a range of responses. Many
112 animals sense UV radiation and avoid exposure to prolonged periods of high UV-B radiation.^{20, 21}
113 These behavioural responses together with physiological mechanisms can mitigate some of the
114 negative outcomes of high UV-B radiation. In some animal species (e.g., insects and birds), UV
115 radiation is used as a visual cue that enhances foraging, mate selection or other behavioural
116 activities.²¹ By comparison, land plants are sessile (rooted to their growth medium) and require
117 sunlight for photosynthesis and growth. Their primary response to changing UV radiation conditions
118 typically involves acclimating or adapting to these changes using biochemical and physiological
119 mechanisms. However, like animals, plants can sense UV radiation in their surroundings, which has
120 adaptive value.²²

121
122 Many initial studies following the discovery of the Antarctic ozone hole (as reviewed by Aphalo, *et al.*
123 ²³, Björn ²⁴, Barnes ²⁵) emphasised the direct, detrimental effects of increased UV-B radiation on
124 plants, especially important food crops. However, most evidence to date indicates that, under
125 realistic exposures, the direct, damaging effects of high UV-B radiation on photosynthesis, plant
126 productivity and crop yield, are relatively minor.^{7, 26-30} More recent studies have focused on
127 understanding how plants a) respond to UV radiation against the backdrop of a rapidly changing
128 climate in conjunction with current and projected stratospheric ozone dynamics; and b) perceive the
129 UV-B radiation and what role this radiation plays in regulating growth and development.³¹⁻³⁴ At
130 present, it is widely accepted that UV-B radiation can have beneficial as well as unfavourable effects
131 on plants.^{27, 35-37} In some cases, reduced exposure to UV-B radiation can even have negative

132 consequences for plant performance, pest defence,³⁸ and food quality.³⁹ Thus, projected recovery of
133 stratospheric ozone to levels that may exceed those in the recent past (i.e., 1970's;^{4, 40}), means that
134 there is a need to fully evaluate how organisms and ecosystems will respond to the increases and
135 decreases in solar UV-B radiation that occur in conjunction with a rapidly changing climate.

136
137 Climate change alters regional weather patterns, including temperature and precipitation, and these
138 changes can directly affect plants and ecosystems by altering moisture availability and critical
139 thermal conditions for growth, reproduction and survival. Of interest in this assessment, however, is
140 how climate change-driven plant responses are modified by UV radiation (see section
141 3.3). Exposure to UV-B radiation can enhance plant tolerance to some abiotic factors (e.g., water
142 and temperature stress)⁴¹, while other factors may alter the sensitivity of plants to UV radiation.
143 However, these effects are complex and often dependent upon specific growth
144 conditions.⁴² Understanding how plants respond to changes in UV radiation against this backdrop of
145 changes in multiple environmental variables is thus challenging but necessary in the context of
146 future environments (e.g., Virjamo, *et al.*⁴³). These UV-climate change interactions are particularly
147 relevant for agroecosystems, where crop yield, food quality, pest and disease resistance and overall
148 vulnerability to climate change can have significant impacts on food security (see section 3.5).

149
150 The effects of changes in incident solar UV radiation (UV-B and UV-A) on ecological communities
151 and ecosystems are largely a consequence of impacts on primary producers (i.e, plants).⁴⁴⁻⁴⁶ These
152 higher-level ecological effects include changes in plant-plant interactions (competition), herbivory,
153 pest-pathogen interactions and the decomposition of dead plant matter (litter) (see section 3.6).
154 Although initially minor, some of these community and ecosystem effects may accumulate over time
155 (e.g.,Robson, *et al.*⁴⁷) or be amplified by processes such as competition.⁴⁸ For certain crop species,
156 exposure to UV radiation can elicit changes in pest/pathogen defence that may have positive
157 consequences for the productivity and sustainability of agroecosystems.^{38, 45, 46}



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 160 **Fig. 1.** Conceptual diagram illustrating known linkages between stratospheric ozone depletion, UV radiation and climate change on terrestrial organisms and ecosystems. Stratospheric ozone depletion alters UV
 161 radiation (primarily UV-B; arrow 1), which in turn directly affects plants and other organisms (arrow 2). The
 162 effects on organisms can then alter the function and structure of ecosystems (arrow 3). Ozone depletion can
 163 alter the climate, and climate change can affect ozone depletion via several avenues (arrow 4). Certain ozone-
 164 depleting substances (e.g., hydrofluorocarbons (HFCs) and others) are potent greenhouse gases that can
 165 enhance global warming. Stratospheric ozone depletion in the southern hemisphere is directly altering climate
 166 via changes in the Southern Annular Mode (SAM) in addition to other climate changes. Resultant shifts in
 167 climate zones alter regional rainfall and drought and thereby change cloud cover; in turn, the changing cloud
 168 cover can increase or decrease exposures of organisms to UV radiation (arrow 5). Climate-related changes in
 169 weather patterns (arrow 6) alter temperature and precipitation patterns, which can directly modify plant growth
 170 and development, and the way in which plants respond to UV-B radiation (arrow 7). Climate change (including
 171 altered UV-B exposure) is also changing the seasonal timing of development (e.g., phenology of flowering or
 172 bud break; arrow 8), such that wild plants and crops develop at times of the year when UV radiation can be
 173 either greater or less than prior to current rapid climate change (arrow 9). These phenological changes further
 174 expose plants to novel combinations of UV radiation and other abiotic and biotic factors (arrow 10). In
 175 response to climate change many organisms are shifting their ranges to higher elevations and latitudes (arrow
 176 11). As with phenological shifts, these changes in geographic ranges can potentially increase (elevation) or
 177 decrease (latitude) exposures to UV radiation (arrow 12), as well as subjecting organisms to new
 178 combinations of UV radiation and other abiotic factors (arrow 13). As species migrate to different
 179 environments they also encounter new combinations of competitors, pests and pollinators that may alter
 180 important ecosystem processes such as herbivory and competition (arrow 14). Alterations in certain
 181 ecosystem processes, such as decomposition, can modify soil carbon storage and emissions of carbon
 182 dioxide and other greenhouse gases to the atmosphere (arrow 15). Image of stratospheric ozone shows total
 183 ozone over Antarctica (October 2017, Source: <https://ozonewatch.gsfc.nasa.gov/>). Climate change map
 184 indicates surface temperature anomalies for February 2017 compared to the base-period of 1951-1980
 185 (Source: <https://data.giss.nasa.gov/>). Sonoran desert ecosystem photograph by P.W. Barnes.
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188 One important ecosystem-level effect of changes in UV radiation and climate is the altered
189 decomposition of plant litter, which can result in a positive feedback to the climate system, thereby
190 contributing to climate change. Photodegradation is the process whereby UV radiation, together with
191 shorter wavelengths of visible radiation, drives the photochemical break-down of plant litter, and this
192 results in the release of carbon dioxide and other gases to the atmosphere (Fig. 7).⁴⁹⁻⁵¹
193 Photodegradation can also modify the chemical make-up of litter, thereby promoting or facilitating
194 the activities of microbial decomposers (bacteria and fungi; i.e., photo-facilitation). This results in
195 increased microbial and soil respiration, and contributes additional carbon dioxide to the
196 atmosphere.⁵²⁻⁵⁴ At present, considerable uncertainty remains regarding the quantitative significance
197 of photodegradation of terrestrial plant litter, and its effects on soil carbon storage and atmospheric
198 carbon dioxide concentrations. However, it is clear that this process is an important driver of
199 decomposition in many ecosystems, especially drylands (grasslands, deserts, and savannas).^{54, 55}
200 In some of these dryland ecosystems, the relative importance of UV-driven photodegradation may
201 increase with climate change as precipitation decreases and temperature increases.⁵⁶ Changes in
202 climate and land-use may also affect photodegradation and litter decomposition indirectly via
203 changes in the structure and species composition of vegetation, and occurrence of fire and soil
204 erosion (see section 3.6.3 and Sulzberger, *et al.* ⁵¹).

205
206 There are several linkages between ozone depletion and climate change that are ecologically
207 important but which do not directly involve changes in UV radiation. On the one hand, climate
208 change can modify stratospheric ozone depletion by perturbing temperature dynamics between the
209 stratosphere and troposphere.⁵⁷ Conversely, it is now apparent that ozone depletion in the southern
210 hemisphere is directly contributing to climate change (Fig. 2).⁴ Specifically, ozone depletion appears
211 to be changing regional atmospheric circulation patterns in the southern hemisphere which, in turn,
212 affect weather conditions, sea surface temperatures, and frequency of wildfires.⁵⁸⁻⁶² These changes
213 together with changes in UV-B radiation can have several consequences for terrestrial ecosystems
214 (see section 3.2, Fig. 3, and Table 1).⁵ While ozone depletion in the northern hemisphere may be
215 associated with similar, but smaller, climate shifts⁴, to our knowledge there are no reports linking this
216 to ecological impacts.

217
218 Finally, a better understanding of how terrestrial organisms and ecosystems might respond to
219 changes in UV radiation in the context of modern climate change is coming from studies examining
220 how plants and animals have adapted to changing UV radiation and climate conditions in the past.
221 These historical studies, however, require some knowledge of how UV radiation has changed over
222 geological time periods. In the absence of satellite or ground-based measurements of UV radiation,
223 some investigators have attempted to reconstruct past UV radiation climates using biological

224 indicators as proxies for ground-level UV radiation. Section 3.8 evaluates progress made in the
225 development of pollen grains and spores as bioindicators of past UV conditions.

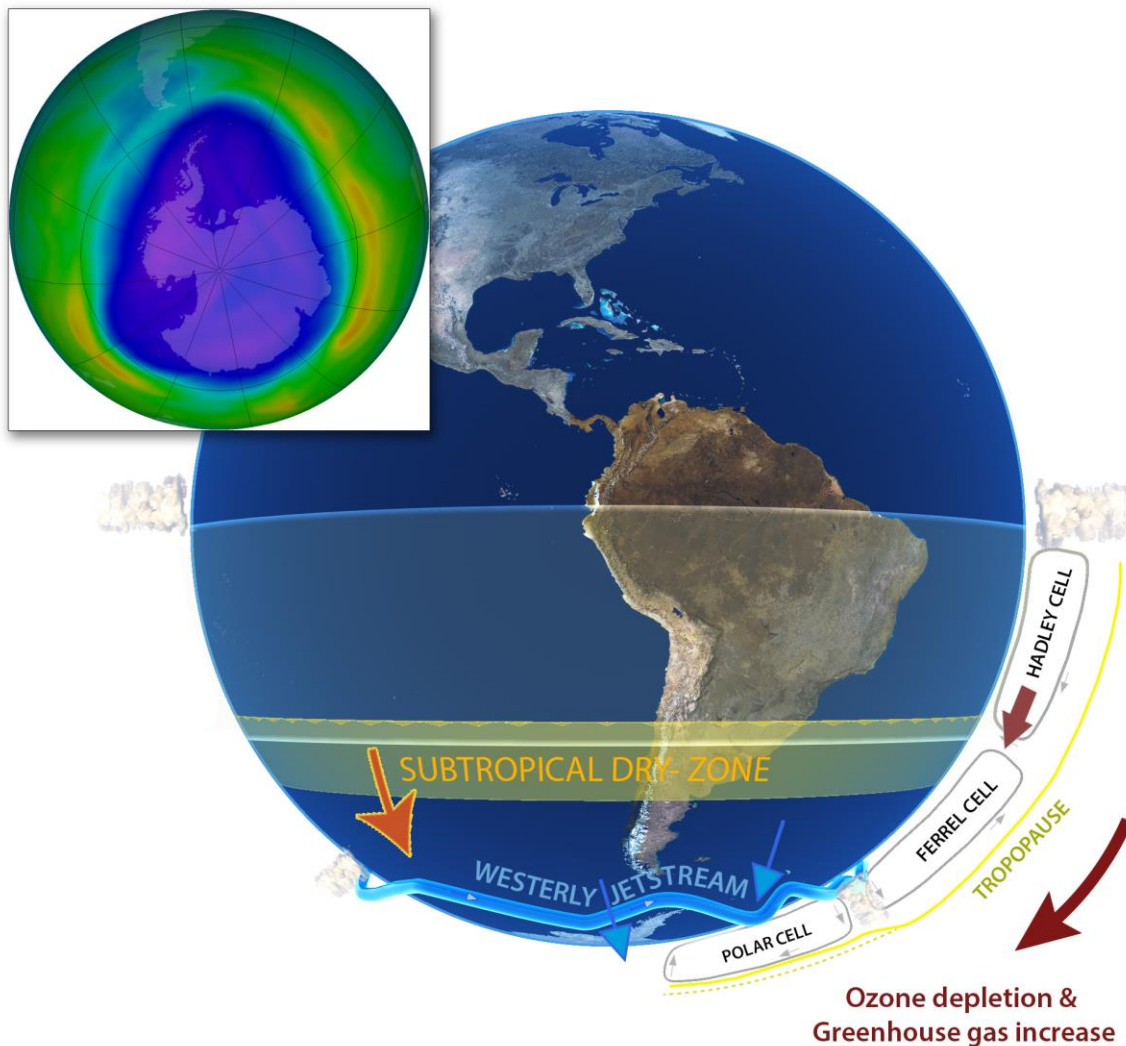
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228 **3.2 Ecological impacts of ozone depletion-driven changes in climate in the** 229 **southern hemisphere**

230

231 Stratospheric ozone depletion has led to large changes in southern hemisphere climate (as detailed
232 in Bais, *et al.* ⁴, Robinson and Erickson III ⁵, Bornman, *et al.* ⁸). These are manifested in a mode of
233 atmospheric variability, the Southern Annular Mode (SAM or Antarctic oscillation), which describes
234 the difference in pressure between 60° and 45° S. The SAM describes the strength and latitudinal
235 position of the westerly wind belt (i.e., jet stream) around Antarctica (see also, Robinson and
236 Erickson III ⁵, Bornman, *et al.* ⁸). Ozone depletion is linked to a highly positive phase of the SAM,^{63, 64}
237 corresponding to an increased pressure difference between mid- and high latitudes and a
238 contraction of the westerly wind belt towards Antarctica (Fig. 2). The effects of this change in
239 atmospheric circulation, which extend across the southern hemisphere, are summarised in the
240 following sections. The sections emphasise how these changes in climate link to stratospheric
241 ozone depletion (see also Bais, *et al.* ⁴), affect abiotic drivers (e.g., wildfires) and the contingent
242 responses of southern hemisphere ecosystems. The implications of these climate shifts for marine
243 and aquatic ecosystems are described in Williamson, *et al.* ⁶⁵



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Fig. 2 The Antarctic ozone hole (inset) and its impact on southern hemisphere atmospheric circulation. Stratospheric ozone depletion and resultant cooling over Antarctica has caused the tropopause to lift, allowing the Hadley Cell (dark red arrow) and the westerly jet stream to tighten and shift towards the South (blue arrow). The speed of the jet has also increased (see Robinson and Erickson III⁵ for details). The polar shift in the jet and its increased strength changes atmospheric and oceanic circulation throughout the southern hemisphere consistent with a more positive phase of the Southern Annular Mode (SAM; see text for explanation). Over the past century, increasing greenhouse gases and then ozone depletion over Antarctica have both pushed the SAM towards a more positive phase, and the SAM index is now at its highest level for at least 1000 years.⁶³ As a result, high latitude precipitation has increased and the mid-latitude dry zone has moved south (orange arrow). As the ozone layer recovers, increased greenhouse gas forcing will likely take over and the position of the jet is thus predicted to remain in this more southerly location. Figure adapted from Robinson and Erickson III⁵ and Perlwitz⁶⁶, with ozone 'hole' over Antarctica, 17th September 2006, reproduced from NASA Ozone Watch.⁶⁷

260 Changing concentrations of stratospheric ozone have been linked to changing surface
 261 temperatures, altered wind and ocean circulation patterns and changing precipitation patterns,
 262 causing increased rainfall or drought, the latter leading to increased risk of wildfires. As presented in
 263 our last assessment, terrestrial⁸ and aquatic ecosystems⁵ including biogeochemical cycling⁶⁸ have
 264 been affected by these changes across the southern hemisphere. Sections 3.2.1 and 3.2.2 give a

265 brief summary of the climate changes ascribed to ozone depletion and then address the implications
266 of these changes for ecosystems in the southern hemisphere.

267
268 The UNEP Science Assessment Panel (SAP)⁶⁹ notes that since their last assessment,⁷⁰ further
269 research has confirmed the impact of changes in stratospheric ozone on the tropospheric and
270 surface climate of the southern hemisphere and has, in some cases, allowed better quantification
271 and attribution of the changes. Stratospheric ozone depletion is assessed to have been the
272 dominant driver of changes in atmospheric circulation across the southern hemisphere from the mid-
273 latitudes to the tropics during austral summer (December-February) over the period 1960 to 2000
274 when stratospheric ozone was decreasing; while in other seasons, greenhouse gas emissions play
275 a comparable role to stratospheric ozone depletion. As stratospheric ozone recovers, its effect on
276 circulation should diminish; however, climate change is predicted to increasingly contribute to
277 changes in atmospheric circulation.^{4, 71, 72}

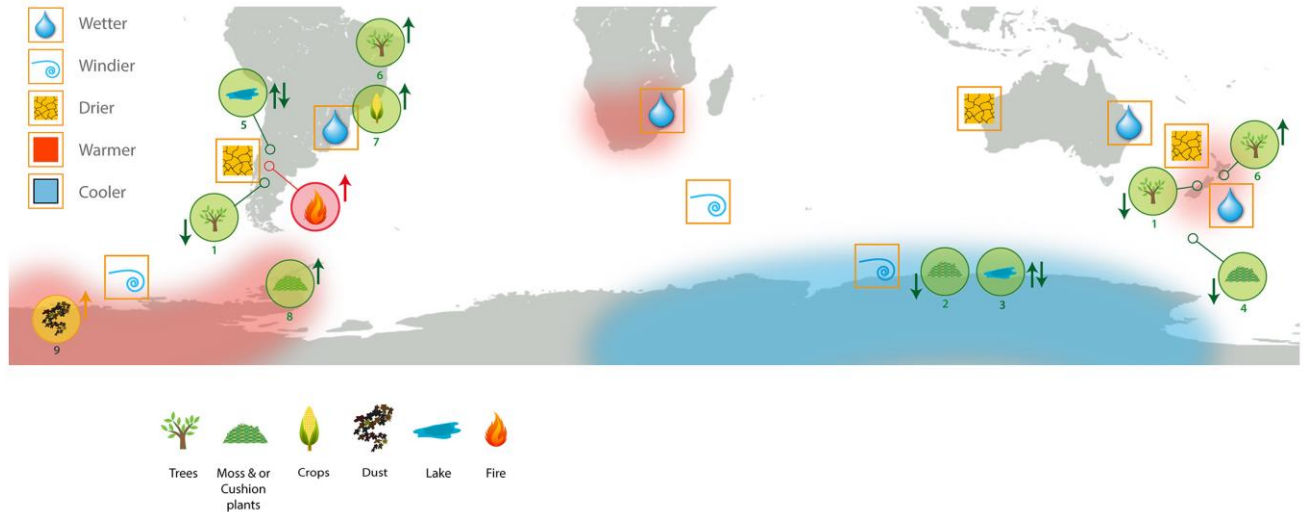
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279 The major changes in mid-latitude and tropical circulations driven by stratospheric ozone depletion
280 include the poleward shift of the mid-latitude jet (Fig. 2), the shift to an increasingly positive phase of
281 the Southern Annular Mode (SAM) and the poleward shift of the sub-tropical Hadley Cell (Fig. 2).^{39,}
282 ^{69, 73} Between 1980 and 2000, the westerly jet shifted south during summer by approximately one
283 degree of latitude. Since 2000, the jet has shifted north in summer, although this reverse trend is not
284 statistically significant.^{69,74} A meta-analysis⁷⁵ supports stratospheric ozone depletion as the
285 dominant driver of the Hadley Cell summertime expansion over the period 1979 to late 1990s.

286 287 **3.2.1 Changes to southern hemisphere regional rainfall related to stratospheric ozone** 288 **depletion, and ecosystem responses to fluctuating water availability: extreme rain, drought** 289 **and fires**

290
291 Changes in both extratropical and sub-tropical austral summer rainfall have previously been linked
292 to the position of the mid-latitude jet and thus to stratospheric ozone depletion (Figs 2, 3).^{4, 5, 8, 70, 76, 77}
293 South-East South America (northern Argentina, Uruguay, southern Brazil and Paraguay) has
294 experienced one of the largest increases in rainfall worldwide (Fig. 3; Table 1A)⁷⁸ with a 30%
295 increase in summer rainfall over the past 50 to 100 years. While this increased rainfall appears to be
296 the result of anthropogenic emissions of greenhouse gases,^{79, 80} the relative contributions from
297 greenhouse gases and ozone depletion to these changes have not yet been resolved (see also, Wu
298 and Polvani⁸¹, Zhang, *et al.*⁸²).

299
300 The SAM has been identified as the leading cause of changes in summer rainfall, surface
301 temperature, and the diurnal temperature range in East Africa^{83, 84}, and these authors highlighted the

302 effects of stratospheric ozone depletion. Over the period 1961-1996, the position for the South
 303 Pacific Convergence Zone (a region of abundant precipitation, stretching from New Guinea towards
 304 southern hemisphere mid-latitudes) has changed, with increasing rainfall on the northern edge and
 305 decreases to the south.⁸⁵ This shift in precipitation appears related to stratospheric ozone
 306 concentrations, with models that isolate the impacts of ozone recovery suggesting a reversal of
 307 these effects as stratospheric ozone recovers. These shifts in rainfall patterns can have negative
 308 and positive effects on ecosystems, populations and individual species.



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 311 **Fig. 3** Map of the southern hemisphere showing how stratospheric ozone depletion affects the climate and
 312 environment, and the effects of these abiotic changes on terrestrial ecosystems and populations. Symbols
 313 show types of organism, ecosystem or entity affected (see legend), with numbers referring to Table 1 C,
 314 which provide species and location details. Arrows indicate direction of effects on biodiversity, up =
 315 positive effects, down = negative effects, two-way arrows indicate changed biodiversity.
 316

317 **Table 1** Summary of how stratospheric ozone depletion affects the climate and environment (A) likely
 318 consequences, (B) the effects of these abiotic changes on terrestrial ecosystems, and (C) populations across
 319 the southern hemisphere. Regions affected and references are provided. Numbers (C) refer to locations in
 320 Fig. 3.
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A. Changes in southern hemisphere climate driven by stratospheric ozone depletion	Regional examples	References
<u>Changing regional precipitation</u>		4, 71, 86
Wetter	South East South America (Northern Argentina, Uruguay, southern Brazil and Paraguay)	78, 87
Wetter/Drier	New Guinea, southern hemisphere mid-latitudes wetter in the north and drier to the south Hydroclimatic variability over the Amazon Basin	85, 88
Drier	Chile, declining stream flows, consequences for ecosystem health and hydroelectric power	89
More extreme precipitation	South-eastern South America extreme Summer rainfall Heavy rain events in Madagascar	78, 81, 90-92
<u>Changing ocean and atmospheric circulation</u>		4, 71
Shifting location of wet and dry zones	Shifts in summer rainfall patterns, Australian summer - increased rainfall on mainland south east coast and decreased rainfall in western Tasmania. Sub-tropical dry zone also shifted towards the South Pole	83 93 73, 91, 94-96
Increasing surface wind-stress	Southern Ocean Leads to year-round stronger surface ocean warming Could enhance loss of Antarctic sea ice but see Bais, <i>et al.</i> ⁴ Alters mixed layer depth affecting nutrients	65, 97-99
<u>Temperature</u>		4, 71
Lower temperatures	Decrease in summer temperatures over East Antarctica, southeast and south-central Australia and inland areas of the tip of southern Africa. Eastern Tropical Pacific cooler	60, 96
Warmer temperatures	Much of Southern Africa warmer Warmer surface temperature and changed diurnal temperature range in East Africa Summer extreme temperatures, Australia, South America, Southern Africa	83, 96

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B. <u>Likely indirect consequences of changes in southern hemisphere climate</u>	Resulting from	References
Changing cloud patterns	Latitudinal shifts in the Hadley and Polar Cells	⁹⁴ . See Bais, <i>et al.</i> ⁴ for

	mean that cloud cover has also shifted southward with ozone depletion	implications for exposure to UV radiation
Fire	Changes in precipitation can alter fire regimes; e.g., central and southern Chile	51, 62, 100, 101
Dissolved organic matter (DOM)	Changes in precipitation affect run off and quantity of DOM in water bodies	See Williamson, <i>et al.</i> ⁶⁵ for details
Breakdown of litter	Changes in precipitation and temperature influence breakdown rates of litter	See Sulzberger, <i>et al.</i> ⁵¹ for details
Air quality	Weather [temperature, wind (transporting pollutants), rain and cloudiness] affects air quality with consequences for health of humans, other animals and plants	See Wilson, <i>et al.</i> ¹⁰² for details
Weathering of materials	Increased ambient temperature shortens the life of plastics and wood exposed to UV radiation, and their outdoor service lifetimes. Changing moisture also affects these processes	See Andrady, <i>et al.</i> ¹⁰³ for modes of action

325

C. Drivers of change for terrestrial plants and ecosystems (number of marker on Fig. 3)	Biological effects	Location	References
Decreased water availability			
1	Less precipitation associated with decreasing growth of trees and restricted forest distribution	West New Zealand, South West S. America	104, 105
2	East Antarctic drying. Moss beds exhibit changing species composition. Reduced growth, more plant stress and death.	Windmill Islands, East Antarctica	106-108
3	Lakes are becoming more saline leading to biodiversity changes		
4	Drying caused more than 80% dieback of cushion plant and moss fellfield communities	Macquarie Island	109
Increased water availability			
5	Less salinity causes changes in lake fauna	Eastern side of the Andes	110
6	More precipitation associated with increasing growth of trees	East New Zealand, Eastern South America	104
7	Expansion of agricultural zones with more precipitation	South East S. America	111 78
8	Moss beds and other biodiversity more productive due to warmer wetter conditions and more land	Antarctic Peninsula	112-114
Increased wind speeds			
9	Risk of increased dust and potential propagule inputs into Antarctica (negative if introduces non-native species)	West Antarctic, Antarctic Peninsula	115-118

326
327 **Ecosystem responses to fluctuating water availability.** Shifting atmospheric circulation cells
328 (Hadley, Ferrel and Polar cells, see Fig. 2) alter regional precipitation across the southern
329 hemisphere, causing some areas to receive more moisture and others to become drier. In
330 Patagonia, declines in tree growth have been linked to reduced water availability (Fig. 3; Table
331 1B).¹⁰⁴ In the extreme south of South America extending into Antarctica, lichens are an increasingly-
332 dominant component of the terrestrial biota.¹¹⁹ Lichens are extremely tolerant of desiccation, but
333 nevertheless the combination of high wind speeds and high irradiance, including increased UV-B
334 radiation due to ozone depletion, have been shown to affect their colonisation on trees in
335 Patagonia.¹²⁰ However, lichens grow very slowly,¹²¹ so responses to specific climatic changes can
336 take a long time to detect. Less seasonal precipitation and a reduced diurnal temperature range
337 were the dominant factors driving aridity and limiting the distribution of high-elevation woodlands of
338 *Polylepis tarapacana* (a rose family tree species of high conservation value, found in the South
339 American Altiplano). Models predict that by the end of this century almost half of the potential
340 habitat of this species will be lost due to increased aridity.¹⁰⁵
341
342 Decreased precipitation in this region of South America has led to reduced stream flows in Chile,
343 with adverse effects on aquatic and terrestrial ecosystems as well as the production of hydroelectric
344 power.⁸⁹ Since the 1960s, warming and associated drying at mid- and high-latitudes to the west of
345 the Andes have resulted in increased forest fires (measured from fire scars in tree ring records).⁶²
346 During the 2016–2017 fire season, more than 500,000 hectares burned in central and southern
347 Chile (between ~29°S and 40°S), driven by a long-lasting drought linked to the positive SAM that
348 was amplified by El Niño–Southern Oscillation (ENSO) conditions. Given that the positive phase of
349 SAM is predicted to continue, it is likely that increased wildfire activity in southern South America will
350 continue throughout the 21st century.⁶²
351
352 Several other regions of the southern hemisphere have experienced wetter summers⁴, leading to
353 increased tree growth in eastern New Zealand¹⁰⁴ and expansion of agriculture in south-eastern
354 South America (Fig. 3; Table 1B).⁷⁸ The eastern side of the Andes has experienced wetter
355 conditions with associated biodiversity changes. For example, changes in fauna (ostracods and
356 chironomids) from lake sediments in El Toro Lake (40°S, 70°W) indicate that the lake has become
357 fresher (less salty) as a result of increased precipitation since the middle of the 20th century,
358 associated with the positive phase of SAM.¹¹⁰
359
360 Increasing extremes of precipitation have also been linked to SAM-related changes. Rainfall
361 patterns in the southern Amazon Basin have been reconstructed from tree rings of *Centrolobium*

362 *microchaete*⁸⁸ and the findings suggest that the fluctuations between drought and extremely wet
363 seasons seen from 1950 to the present day may be unmatched since 1799.

364
365 **3.2.2 Changes in surface temperatures as a consequence of stratospheric ozone depletion**
366 **and implications for terrestrial ecosystems**

367
368 Recent studies^{122, 123} suggest that warming of West Antarctica and the Antarctic Peninsula may fall
369 within the range of natural climate variability.¹²⁴ This warming had previously been linked to
370 anthropogenic emissions of greenhouse gases and stratospheric ozone depletion.^{5, 8} Stratospheric
371 ozone depletion could account for between a quarter and one third of summer and autumn cooling
372 over the rest of the Antarctic continent (see Robinson and Erickson III⁵). However, our confidence in
373 any attribution or projections of climate warming over this region is limited by the large biases
374 inherent in the models used. Depletion of Antarctic stratospheric ozone over Antarctica has possibly
375 offset a substantial portion of the summer warming that would otherwise have occurred (due to
376 increasing greenhouse gases) in eastern Australia, southern Africa and South America (Fig. 3).⁹⁶
377 These changes in temperature are likely to have affected (positively and negatively) life cycles of
378 plants and animals, potentially leading to mismatches between plants and their pollinators (see
379 section 3.7.3). Cooler temperatures over East Antarctica have likely slowed the melting of ice
380 sheets. As stratospheric ozone concentrations recover, the extent of this amelioration may be
381 reduced with potential implications for the climate and populations of these regions as well as further
382 afield.

383
384 In western Antarctica, along the Antarctic Peninsula and on nearby islands, increasing
385 temperatures⁶⁰ were associated with increased productivity of terrestrial ecosystems (microbial
386 productivity, plant growth rates and carbon accumulation in moss beds) from the 1950s to the turn of
387 the century.¹¹⁴ There is some evidence that the direction of these changes has reversed since 2000,
388 consistent with recent cooling in this region.^{114,125,126} However, as noted above, the relative
389 contributions of stratospheric ozone depletion vs increasing greenhouse gases to temperature
390 changes is still unresolved because recent studies suggest they are not beyond the range of natural
391 variability (see above and Bais, *et al.*⁴).

392
393 On the opposite side of the continent, in the Windmill Islands of East Antarctica, decreased water
394 availability since the 1960s, linked to decreasing temperatures and increasing wind,¹⁰⁷ has resulted
395 in changes in biodiversity in both Antarctic moss beds¹⁰⁶ and lakes,¹⁰⁸ with species composition
396 changing to reflect the newly drier moss beds and more saline lakes. In addition, these East
397 Antarctic plant communities are becoming more stressed as a result of drying, resulting in
398 increasingly moribund moss.^{106, 127, 128} This is one of the first studies¹⁰⁶ to document ecosystem-level

399 changes in Antarctic terrestrial plant communities, which are correlated with the SAM and potentially
400 linked to stratospheric ozone depletion and climate change. Further north, widespread (>80%)
401 dieback of cushion plants (*Azorella macquariensis*) and mosses, on sub-Antarctic, Macquarie
402 Island, was primarily attributed to reduced water availability as a result of higher wind speeds, more
403 sunshine hours and therefore higher evapotranspiration since the 1970s. The authors estimate that
404 from 1992 to 2008 these plant communities suffered accumulated water deficit for 17 years.¹⁰⁹ This
405 dieback of Antarctic and sub-Antarctic vegetation is similar to the “*Arctic browning*” observed in the
406 Arctic in response to extreme climate events.^{129, 130}

407
408 ***Interannual variability.*** Two studies have linked interannual variability of springtime Antarctic
409 ozone to summer changes in surface temperature and rainfall in the southern hemisphere.^{96, 131} The
410 SAP 2018 report⁶⁹ concludes that interannual variability in springtime ozone at both Poles may be
411 important for surface climate, but the extent of this connection is not fully understood.

412
413 Stratospheric ozone-driven climate change has widespread and far-reaching effects on terrestrial
414 and marine ecosystems (see Williamson, *et al.* ⁶⁵) across the southern hemisphere. A better
415 understanding is needed of the relative contributions of stratospheric ozone, greenhouse gases and
416 interannual variability in order to determine the ecological or biological change attributable to
417 stratospheric ozone depletion vs that due to these other climate factors. Nevertheless, we have
418 only included studies in this section where a strong signal of ozone depletion or summer SAM has
419 been associated with an ecological effect.

421 **3.3 Plant response to UV radiation and interactions with climate change** 422 **factors**

423
424 There is now a basic understanding of UV-sensing and UV-signaling in plants, as well as the
425 consequences for gene-expression, physiology, biochemistry, plant growth, fitness and nutritional
426 quality. Potentially, UV-B radiation can damage plants through effects on DNA, the photosynthetic
427 machinery, and other cellular targets. However, UV-B-induced plant defence responses, including
428 up-regulation of photorepair processes, antioxidant capacity, and UV-screening, are thought to be
429 effective in the prevention of damage to plants by UV-B radiation under most natural conditions.
430 Nevertheless, effective prevention and repair do not imply that UV radiation has no effect on plants.
431 Acclimation to UV radiation and climate change factors can modify plant growth and development,
432 which, in turn, has consequences for ecosystem functioning (section 3.6), nutritional quality and
433 food security (section 3.5). Thus, understanding plant response to UV radiation and some of the
434 interactive effects of climate, is of fundamental importance for evaluating effects of UV-B radiation
435 on terrestrial ecosystems.

436

437 3.3.1 Limitations to current studies investigating interactive effects

438

439 Much of our understanding of plant responses to UV radiation began with single-factor experiments
 440 in laboratories, greenhouses, and controlled environment chambers that did not account for
 441 interactive effects from multiple climate factors. Overall there is evidence that conditions in artificial
 442 environments may unrealistically accentuate the negative effects of UV-B radiation on plant growth.
 443 For instance, such studies are often conducted in growth chambers or greenhouses where lamps
 444 are used as the principle source of UV-B radiation and the ratio of UV-B radiation to
 445 photosynthetically active radiation (PAR, 400-700 nm) is far above that generally found in field
 446 conditions. We illustrate these limitations for some recent controlled-environment studies (Fig. 4).
 447 Note that only 16 of the 49 studies surveyed provided sufficient UV and PAR data to be represented
 448 as data points in the figure.

449

450 It is important to use the knowledge from these studies to design experiments for testing the results
 451 at more expansive scales of space and time. Laboratory results may be scaled up by progressively
 452 moving to more realistic conditions in controlled environments and then to field experiments (e.g.,
 453 Flint and Caldwell ¹³²). Another scaling approach is to design experiments moving from our common
 454 organism-centered methodology to a community or ecosystem perspective, where interactions,
 455 feedbacks, and their relative magnitudes under realistic conditions are examined.¹³³ Some recent
 456 studies have investigated the effects of UV-B radiation in combination with other climate change
 457 factors, such as drought, temperature, carbon dioxide, and tropospheric ozone (e.g., Martinez-
 458 Luscher, *et al.* ¹³⁴, Wijewardana, *et al.* ¹³⁵, Mao, *et al.* ¹³⁶). For this assessment we evaluated the
 459 experimental studies and methodological protocols,¹³⁷ resulting in the exclusion of some studies in
 460 our summary findings.

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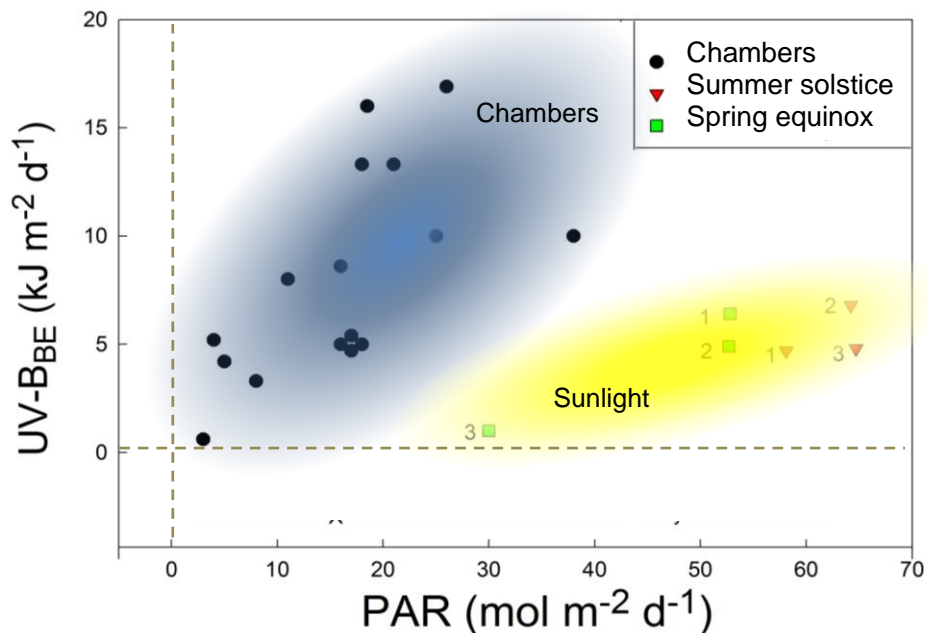
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472



474 **Fig. 4** Studies conducted in growth chambers (blue) are still using unrealistic ratios of photosynthetically
 475 active radiation (PAR, 400-700 nm) to biologically effective UV-B radiation (UV-B_{BE}; data were reported using
 476 the generalized plant action spectrum of Caldwell¹³⁸ (more commonly used in these studies than the action
 477 spectrum of Flint and Caldwell¹³⁹) compared with natural sunlight (yellow). Growth chamber experiments are
 478 represented by black circles within the blue shading. Solar irradiances within the yellow shading represent the
 479 summer solstice (red triangles) and spring equinox (green squares). Ambient PAR is from Ritchie¹⁴⁰ and
 480 ambient UV-B_{BE} was computed with the TUV calculator:
 481 http://cprm.acom.ucar.edu/Models/TUV/Interactive_TUV/. Latitudinal locations are indicated by numerals: 1.
 482 Equator (0°), 2. Tropic of Cancer (23°N), and 3. 55°N. A total of 49 peer-reviewed papers on growth chamber
 483 studies from the years 2011-2017 were surveyed; 16 are represented as data points in this figure and 33
 484 could not be represented, because they either lacked radiation data or it was not measured in a manner
 485 comparable to the other studies.

486

487 3.3.2 The UV-B photoreceptor and signaling pathways

488

489 The existence and nature of a specific UV-B photoreceptor in plants, the protein, UVR8, initially
 490 came to light in 2011.¹⁴¹ Since this discovery, a basic understanding of UV-sensing, signaling and
 491 function has emerged that has improved our knowledge of the molecular mechanisms underlying
 492 UV defence and acclimation in plants.^{22, 34, 141}

493

494 UVR8-mediated perception of UV-B radiation contributes to up-regulation of the expression of genes
 495 that encode components of the phenylpropanoid biosynthesis pathway, photorepair of DNA
 496 damage, and enhanced antioxidant capacity.²² Penetration of UV-B radiation into leaves depends
 497 on the concentration of flavonoids and other phenolics in the epidermis, as well as plant anatomical
 498 and morphological characteristics that vary among species. Most of the UV-B radiation is strongly
 499 attenuated as it passes through the epidermis, although it has been measured in some herbaceous
 500 plant species in deeper-lying tissues (mesophyll layers), with 18-41% epidermal transmittance.^{142, 143}
 501 Given that the UVR8 protein has been detected in most plant tissues investigated, including roots, it
 502 is currently difficult to pinpoint in which plant tissues perception of UV-B radiation takes place in
 503 plants growing in sunlight. Tissue-specific analysis of UVR8 activity has revealed that the UV-B-
 504 induced UVR8 signalling pathway in epidermal and mesophyll cells is involved in hypocotyl
 505 elongation, while UVR8 expression in the epidermis contributes to cotyledon expansion.¹⁴⁴ Thus, the
 506 UV-B-induced response appears to be partly mediated by tissue-autonomous signaling, although
 507 inter-tissue signaling may also be involved.¹⁴⁴ The role of UVR8 is not simply limited to protection
 508 from UV-B radiation. There is now strong evidence that UVR8-mediated signaling extends to
 509 processes such as stomatal function, de-etiolation (greening response of plants), entrainment
 510 (alignment with) the circadian clock, phototropism, and defence against pathogens.³⁴ These
 511 findings, mainly on the model plant, *Arabidopsis thaliana* (a type of cress), provide a frame of
 512 reference for the study of the multifaceted role of UV-B perception through photoreceptor(s) in the
 513 regulation of plant growth and development in the much more complex natural environment. This

514 frame of reference can also be used for other plant species that are likely to follow a variety of
515 strategies to acclimate and adapt to their habitats.

516
517 While much attention has been given to elucidating UVR8-mediated processes, UVR8 is not the
518 only UV-B sensing mechanism in plants. There are also UVR8-independent signaling pathways,¹⁴⁵
519 for example, arising from oxidative stress and via UV-B-mediated DNA damage,¹⁴⁶ including
520 generation of cyclobutane pyrimidine dimers (CPD, one of the main types of DNA damage).
521 However, CPD photolyase, which repairs the damage, is predominantly regulated in a UVR8-
522 dependent manner in plants exposed to UV-B radiation. There is evidence that the UVR8-mediated
523 signaling pathway regulates the scavenging capacity of reactive oxygen species (ROS),¹⁴⁷ and the
524 production of nitric oxide in response to UV-B-induced stress.¹⁴⁸ These latter molecules may
525 themselves play a role in signaling.¹⁴⁸

526
527 Thus, plant responses to UV-B radiation likely involve multiple UV signaling pathways. Moreover,
528 components of these UV-mediated signaling pathways interact with other stress-induced signaling
529 pathways, such as those activated by other wavelengths of light, exposure to drought, extreme
530 temperatures, and other factors associated with climate change.

531 532 **3.3.3 UV-B-mediated signaling, crosstalk and cross-tolerance**

533
534 There is still a lack of information and understanding concerning the effects of UV-B radiation in a
535 complex environment where plants are simultaneously or sequentially exposed to multiple
536 environmental factors that can modify plant growth and development.

537
538 In principle, the simultaneous application of treatments involving changes in two environmental
539 factors can lead to additive, synergistic, antagonistic or no effect. It is particularly relevant from an
540 agronomic perspective that acclimation responses induced by changes in one environmental factor
541 can confer cross-tolerance (including priming responses) or cross-sensitivity to another factor.
542 Exchange of information between distinct plant-signalling pathways can broaden the spectrum of
543 responses to one particular environmental factor. For example, high levels of PAR and UV-B
544 radiation generally increase the accumulation of flavonoids, with synergistic effects occurring in
545 some cases when plants are exposed to a combination of both variables.^{149, 150} Such increases of
546 protective pigments with antioxidant activity potentially enhance the tolerance of a plant to a variety
547 of unfavourable conditions.

548
549 Cross-talk also occurs when UV-B-mediated signalling cascades interact with signalling pathways
550 induced by biotic variables, e.g., bacteria. This cross-talk can sometimes lead to a shift in other plant

551 defences at the expense of the UV-induction of protective mechanisms, such as the accumulation of
552 flavonoids.¹⁵¹ In this case, the UV-B-induced genes of the flavonoid pathway are suppressed by the
553 bacterial elicitor, flg22 (a peptide), which in turn drives the immune response against the
554 bacterium¹⁵² by stimulating pathogen-protective compounds called phytoalexins. In other cases, UV-
555 B radiation can increase plant resistance against pathogens and pests, by increasing the
556 accumulation of metabolites involved in plant defence against multiple stress factors (reviewed in
557 Ballaré¹⁵³). Other examples of cross-talk where UV-B radiation is implicated in plant stress
558 responses include changes in some plant hormones, such as auxin, cytokinin, gibberellic acid,
559 brassinosteroids and jasmonic acid.¹⁵⁴⁻¹⁵⁶ UV-cross-talk involving the hormone abscisic acid can
560 result in increased plant tolerance to water stress, extreme temperatures, or salinity. Some of these
561 aspects are evaluated in the next section.

562
563 The interactions between UV-signalling and other signalling pathways imply that subtle molecular
564 effects of UV-B radiation may potentially extend to many aspects of growth and development, with
565 implications for ecosystems including agricultural systems under conditions of current and future
566 climate change.

567 568 **3.3.4 Plant and ecosystem response to potential interactive effects of UV-B radiation and** 569 **climate change factors**

570
571 Exposure to changing environmental conditions can directly affect plant growth and may also drive
572 changes in phenology (section 3.7.3) and shifts in the distribution ranges of species (section 3.7.1).
573 Here we will specifically explore interactions between UV-B radiation and certain key abiotic climate
574 variables. In comparison to studies on interactive effects of UV-B radiation and drought and/or
575 temperature, far less is known about interactive effects of UV-B radiation and elevated CO₂ on
576 plants.

577
578 ***UV radiation and drought.*** The potential for plant responses to UV radiation and drought to be
579 complementary has been the subject of research because seasonal droughts are usually coincident
580 with, or follow, periods of prolonged sunny weather, implying high exposure to UV radiation. An
581 example of such synergies comes from an experiment with silver birch (*Betula pendula* L.) seedlings
582 subjected to treatments combining solar UV-B radiation and water stress outdoors in southern
583 Finland. In this investigation, leaf and whole plant water potential responded to the combination of
584 ambient UV-B radiation, conferring resistance to drought, which was visible through reduced wilting
585 and lower mortality beyond that of UV-B radiation or water stress alone.⁴¹ Plant responses to the
586 combinations of UV-B radiation and drought should be considered when selecting agricultural
587 crops, as plant responses to these factors can have consequences for crop quality.¹⁵⁷

588
589 Additional research provides evidence for synergies in response to drought and UV-B radiation.^{158,}
590 ¹⁵⁹ However, both the mechanisms and outcome of response to combinations of water stress and
591 UV-B radiation are often inconsistent. To some extent, the seemingly contradictory results reflect
592 differences among studies in the timing and levels of drought and UV-B radiation applied to the
593 plants. Sequential exposure to two environmental variables can allow the first to elicit a response
594 that primes the plant for the second, resulting in cross-protection. In contrast, simultaneous
595 exposure may weaken plant defences.¹⁶⁰ In this context, it should be noted that few, if any existing
596 studies have adequately reproduced natural combinations of exposure to UV-B radiation and
597 drought as well as their relative timing, and therefore results from these studies need to be carefully
598 evaluated for their relevance (see Fig. 4).

599
600 Reduced cloudiness is expected to lead to increases in UV-B radiation and future seasonal droughts
601 in Mediterranean ecosystems.^{161, 162} A study, where solar UV radiation was filtered in a
602 Mediterranean ecosystem under normal and reduced rainfall, showed plants to be tolerant of UV-B
603 radiation independently of the rainfall regime and seasonal climatic conditions. In this case, the
604 species tested were evergreen Mediterranean shrubs with tough thick leaves high in phenolics.¹⁶³
605 Thus, life history, together with exposure protocols, choice of species and dose-dependency will all
606 determine the outcome of the interactive effects of drought and UV-B radiation.

607
608 Perhaps the most important complication in attempting to understand the interactive effects of
609 drought and UV-B radiation, is that both variables alone induce complex responses, and any
610 simultaneous exposure to both variables will result in an amplification of that complexity. Cross-
611 protection is multifaceted and likely to involve decreases in leaf area and possibly stomatal gas
612 exchange, increases in leaf and cuticle thickness, as well as enhanced concentrations of
613 antioxidants, flavonoids and potentially a range of other secondary metabolites such as proline and
614 volatile terpenes.¹⁶⁴ Osmotic stress-induced upregulation of the UVR8 transcript and protein levels
615 might also contribute to interactive effects of drought and UV-B radiation.¹⁶⁵ This complexity can
616 also be observed in a study where, only in the presence of ambient UV radiation did drought
617 increase canopy temperature and result in decreased accumulation of above-ground biomass in a
618 grassland ecosystem.¹⁶⁶ Thus, interactive effects of drought and UV-B radiation need to be
619 considered in the context of prevailing and future conditions, particularly warming temperatures.

620
621 **UV radiation and temperature.** On balance, rising average air temperatures associated with
622 climate change are expected to affect the growth and survival of many plant and animal species,
623 and perturb many ecosystem processes. In addition to changes in average temperatures, extremes
624 in temperature have increased in frequency and magnitude,¹⁶⁷ which can have severe local and

625 regional consequences. Changes in seasonal weather patterns and sky conditions are bringing
626 periods of high temperatures, which are often accompanied by high solar radiation including UV-B
627 radiation to many regions. However, extreme cold temperatures can also be accompanied by high
628 UV-B radiation, particularly at high elevations and latitudes in springtime where UV-B radiation
629 reflected by the snowpack¹⁶⁸ often supplements the irradiance received by organisms exposed to
630 the sun.¹⁶⁹ The combinations of UV-B radiation and temperature can affect plant acclimation
631 processes (see below), which are important in terms of understanding the response of ecosystems
632 to climate change, how future agroecosystems will be managed, as well as how vegetation itself
633 affects air quality and climate.¹⁰²

634
635 Exposure to high UV-B radiation and elevated temperatures elicits a variety of chemical responses
636 in plants. For example, UV-B radiation can induce production of volatile hydrocarbons, such as the
637 isoprenes,¹⁷⁰ and this has been associated with heat tolerance mediated by membrane stabilisation.
638 Typically, isoprene emission occurs in woody plants, contributing to air pollution and global carbon.
639 Global annual emissions of isoprene are estimated to be equivalent to 300 Tg carbon yr⁻¹ (=300 x
640 10¹² g C yr⁻¹) with changes depending on climate change and land-use.¹⁷¹ Isoprenes, as well as
641 other plant-produced biogenic volatile organic compounds such as monoterpenes, have an
642 important effect on atmospheric composition, and ultimately climate. Exposure to elevated
643 temperature combined with UV-B radiation can cause more isoprenes to be emitted than under
644 elevated temperature alone, as was found for European aspen.¹⁷² UV-induced isoprene production
645 is synergistically enhanced in response to higher temperatures, and this has significant implications
646 for both plant thermotolerance and plant-herbivore interactions.¹⁷³

647
648 An outdoor field experiment in Finland found that UV-B radiation enhanced accumulation of
649 condensed tannins in aspen, but this increase was negated by 2°C above ambient temperature
650 treatment in the spring and summer.¹⁷⁴ This process may directly impinge on herbivory, given that
651 tannins act as defence compounds that inhibit digestion (also see section 3.6). In willow, the same
652 combination of UV-B radiation and temperature produced a similar pattern of effects on the
653 accumulation of phenolic compounds.¹⁷⁵

654
655 It is well known that both the total content and composition of flavonoid compounds in plant leaves
656 can be modified by a number of environmental factors including UV radiation, and high and low
657 temperatures.¹⁷⁶⁻¹⁸⁰ For example, kale (*Brassica oleracea* var. *sabellica*) exposed to a low
658 temperature of 5°C accumulates almost twice as much of the polyphenol, kaempferol-3-O-
659 sophoroside-7-O-glucoside, as plants at 15°C. Such stimulatory effects may also completely mask
660 UV-B-induced accumulation of flavonoids, as was seen in an outdoor study where plants under low
661 temperatures accumulated high concentrations of UV-screening pigments, and this response was

662 unaffected by the UV-exposure regime.¹⁸⁰ However, the profile (or composition) of the polyphenols
663 is also modified, whereby kale plants at 15°C accumulate *ca* 25% more kaempferol-3-O-caffeoyl-
664 sophoroside-7-O-glucoside but 30% less kaempferol-3-O-sophoroside-7-O-glucoside.¹⁷⁸ At present,
665 the function of these changes in phenolic profiles are not clear, although some of the compositional
666 changes result in compounds with higher antioxidant activity. Since flavonoids are considered
667 desirable by the food and nutrition industries (see also sections 3.5.2 and 3.5.3), an understanding
668 is needed of changing phenolic profiles under different environmental conditions.

669

670 **3.4 Perception of and response to UV radiation in animals**

671

672 UV-B radiation has the potential to damage tissues in animals, but many animals, like humans,¹⁸¹
673 have mechanisms that protect against the potentially deleterious effects of UV-B radiation.
674 Nonetheless, there are reported cases of UV-induced injury in animals (see section 3.4.1; and
675 Bornman, *et al.*⁸). Apart from UV damage, many animals perceive UV radiation and can use these
676 cues to lessen exposure to intense UV radiation. Also, some animals use UV radiation as a source
677 of information for mate selection, foraging, predator avoidance, and other behaviours. Traditionally,
678 an anthropocentric or human-centric perspective has resulted in a narrow definition of “visible light,”
679 appropriate only for human vision. However, it has long been known that many species have vision
680 that encompasses different wavelengths of the spectrum, sometimes including the UV region.
681 Animals known to have UV vision include species of insects, amphibians, reptiles, birds and
682 mammals.²¹ While advances have been made in understanding the mechanism of UV vision in
683 animals, it is unclear how changes in the UV environment, as a consequence of changes in
684 stratospheric ozone and climate change, might alter the UV sensory responses of these organisms
685 (section 3.4.2).

686

687 **3.4.1 UV radiation damage to animals**

688

689 Ultraviolet-B radiation is known to be potentially deleterious to a wide variety of terrestrial animals.
690 Under controlled conditions, it has been shown that UV-A and UV-B radiation can damage the skin
691 and eyes of various amphibian species (e.g., newts, frogs, bullfrogs, treefrogs), with the potential to
692 negatively affect their foraging ability and fitness (reviewed by Blaustein and Kats¹⁸², Bancroft, *et al.*
693¹⁸³). For example, in South America there are indications that land-use and climate change may lead
694 to increased exposure to UV radiation in the habitats of frog species, e.g., *Hypsiboas curupi* and
695 *Hypsiboas pulchellus*.¹⁸⁴⁻¹⁸⁶ However, while UV radiation may impair vision and cause DNA damage
696 to frogs, it is not considered at present to be among the most important environmental factors
697 contributing to the reduced fitness and abundance of several frog species in this region.¹⁸⁷

698

699 3.4.2 UV vision in animals and ecological implications in changing environments

700
701 The eyes of insects and mites have specific rhodopsin photoreceptors that perceive UV radiation,¹⁸⁸
702 which may be important in avoiding excessive UV radiation.²⁰ In other insects, such as damselflies,
703 UV-reflecting wings appear to play a direct role in mate recognition by creating visual signals of sex
704 and age.¹⁸⁹

705
706 Birds have UV-A vision and photoreceptor UVS-cones (sensitive to wavelengths longer than 355
707 nm), which may assist in foraging and mate choice.²¹ For instance, woodpeckers use visual cues in
708 the UV-A region to forage on decaying wood, which differs in UV-absorption according to the extent
709 of its fungal colonisation. Changes in the amount of UV radiation in the environment (e.g., due to
710 changing weather patterns or forest cover) may affect visibility of these fungi and hence alter the
711 behaviour of woodpeckers foraging for them. Changes in mutualisms of this sort have broad
712 consequences for ecosystem function.¹⁹⁰ In other birds, UV-absorbing melanin in their feathers has
713 been linked with sexual selection but also UV-protection and thermoregulation, and UV protection
714 over wide geographic gradients.¹⁹¹ Many bird species display strong sexual differentiation
715 (dichromatism), creating specific patterns through both melanin accumulation and UV-reflectance of
716 feathers.¹⁹² UV patterning¹⁹³, including UV-absorbance and reflectance, are not limited to feathers
717 and their putative role in mate selection, but are also used in a much broader range of visual
718 recognition processes. For example, UV-reflection of bird eggs attracts aerial predators.^{193, 194}
719 Conversely, UV-absorbing melanin in egg shells may protect eggs from UV-B radiation directly and
720 reduce their visibility to predators, although the dark pigmented colour may cause overheating in
721 some environments. Across a variety of species, including a palmate newt (*Lissotriton helveticus*),
722 the expression of SWS1 opsin, a UV-photoreceptor in the eyes of animals, is UV-dependent^{195, 196};
723 furthermore, plasticity in expression of the photoreceptor depends on the habitat of population
724 origin. This suggests that changes in the amount of UV radiation in the environment during the
725 development of these newts could affect visual sensitivity in the UV region.^{197, 198}

726
727 The role of UV-B radiation has been relatively well-studied in the case of lizards. Lizards kept in
728 captivity are routinely exposed to low background levels of UV-B radiation to enhance vitamin D
729 synthesis and their overall health.¹⁹⁹ UV-reflectance of lateral blue spots in male lizards has a clear
730 role in male-male interactions, including the processes of mutual assessment.²⁰⁰ If two males have
731 an equal signal from their UV-reflecting throat patch, their behaviour towards each other is more
732 aggressive.²⁰¹

733
734 At present, evidence for an ecological role of UV vision in animals is steadily increasing, but detailed
735 information of the functional role of UV-absorbing or reflecting tissues often remains a matter of

736 speculation. There is also a lack of information on the dose-response of UV-visual recognition
737 processes. Thus, it is not known how changes in stratospheric ozone and climate change-driven
738 alterations in exposures to UV radiation will influence visual cues in animals or whether altitudinal or
739 latitudinal gradients in UV radiation might affect migration or range shifts in these animals.
740 Nevertheless, understanding of UV vision in animals is of direct relevance in the context of food
741 security and specifically plant-pest and plant-pollinator interactions.

742

743 **3.5 Food security and agricultural ecosystems**

744

745 At mid-latitudes and the tropics, there are indications of recovery of ozone in the upper stratosphere.
746 However, the total ozone column, which is the metric of greatest relevance for terrestrial
747 ecosystems, has not yet started to recover. Because of increasing concentrations of greenhouse
748 gases, the total ozone column over mid-latitudes will be larger by the second half of the 21st century
749 compared to the time prior to the release of the ozone depleting substances into the atmosphere.
750 Changes in total ozone over the tropics will be relatively small and will depend on emission
751 scenarios and climate change-related phenomena.^{4, 39} Nevertheless, the relatively high levels of UV
752 radiation that occur in the tropics and at high elevations, together with ozone-independent, location-
753 specific factors such as decreasing concentrations of aerosols, less cloud cover and changes in
754 land-use,⁴ mean that crops may still be subject to significant changes in exposure to UV radiation.
755 Some areas will also receive less UV radiation where pollution levels continue to be high, including
756 increasing frequencies of smoke from forest fires.⁶⁵ These levels of complexity can affect
757 agroecosystems with respect to growth, development and survival. It is in this context that crop plant
758 and agricultural responses to UV radiation and climate change will be assessed here. Particular
759 attention is given to plant defence mechanisms, implications of genotype, and crop quality mediated
760 through changes in plant biochemistry.

761

762 **3.5.1 Linking UV radiation and climate effects to food security**

763

764 The interactive effects of UV radiation, climate change, and changes in land-use and management
765 practices, are likely to have consequences for agriculture and food security. For example, these
766 factors can modify crop yield and quality, pest and disease resistance and overall vulnerability or
767 adaptation to the environmental changes (Fig. 5). From the human intervention perspective, clearing
768 of land for increased agricultural production to cope with growing populations, leads not only to
769 increased exposure of agroecosystems to UV radiation, but also to poorer quality soils and soil
770 erosion. In areas receiving increased UV radiation, plants may more readily express acclimative
771 mechanisms against disease, herbivores, and other environmental stresses. Farmers and growers

772 are also becoming increasingly interested in the advantage of UV-induced stimulation of desirable
 773 secondary metabolites, such as the polyphenolics, in order to achieve improved crop response to
 774 stress conditions, including drought, pests and diseases.^{45, 202-206}

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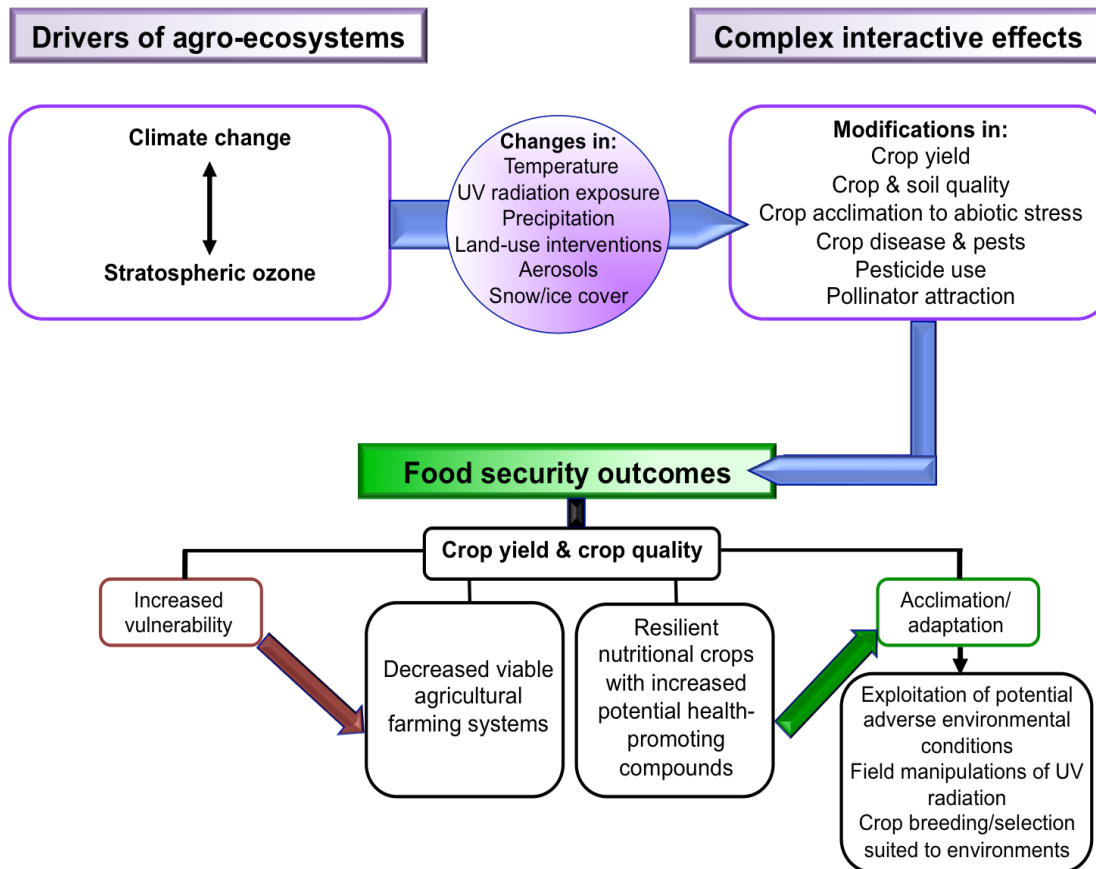
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796 3.5.2 Effect of genotype and environment on crop yield and quality

797

798 The degree of plant acclimation to stress conditions is often dependent on cultivar or genotype,^{177,}
 799 ^{207, 208} as well as location and growth conditions.^{177, 209-211} Environmental conditions and genotype
 800 have been shown to be key factors that determine crop plant response and yield, and are indicative
 801 of the general phenotypic plasticity of plants (changes in morphological, physiological and metabolic
 802 attributes). The roles of both the environment and genotype are especially important when
 803 assessing current and future plant acclimation to stressful environments, including locations
 804 exposed to high levels of UV-B radiation, low rainfall and extremes of temperature (e.g., Andean
 805 Altiplano and Tibetan Plateaux). Thus, research investigating the 'environment x genotype'
 806 response of crop plants is important for selection of genotypes suitable to particular environments
 807 and levels of UV-B radiation. The composition, concentration and antioxidant activity of
 808 polyphenolics change according to plant exposure to elevated UV-B radiation and vary strongly with



793 **Fig. 5** Examples of current and evolving drivers of change on food security, showing the effects of
 794 linkages between changes in stratospheric ozone and climate.

795

809 plant genotype.^{177, 212} The selection of responsive genotypes or cultivars can be used to improve the
810 nutritional status of a crop, because of the potential benefits of antioxidants (conferring free radical
811 scavenging capability) and other plant components.²¹³ These benefits may include the potential for
812 reducing the risk of health-related diseases such as cardiovascular disease and Type 2 diabetes.²¹⁴⁻
813 ²¹⁶

814

815 **3.5.3 Importance of secondary metabolites in agro-ecosystems**

816

817 Ultraviolet-B radiation regulates the accumulation of numerous secondary metabolites, including
818 flavonoids and other compounds derived from the phenylpropanoid pathway. These metabolites are
819 important for plant growth and development, as antioxidants, UV-screening pigments, herbivore and
820 pathogen deterrents, as well as serving as pollinator attractants and improving nutritional quality,^{217,}
821 ²¹⁸ flavour, visual appeal and desirability of many foods.^{8,45,219} and references therein,²²⁰⁻²²⁴ However,
822 exposure to UV-B radiation may cause both desirable and less desirable changes in nutritive
823 properties. For example, UV-B radiation can decrease protein content in some crops or increase
824 essential fatty acids not synthesised by humans and other animals (i.e., polyunsaturated linoleic and
825 linolenic acids), while decreasing other beneficial fatty acids, such as the monounsaturated oleic
826 acid, as was found in a study on soybean seeds.²²⁵

827

828 The UV-B-induced regulation of phenolic compounds can occur under low levels of UV-B radiation
829 in many plant species, including in a range of economically important crops in which these
830 metabolites contribute to food quality and/or value. For instance, UV-B radiation mediates increased
831 accumulation of the potentially nutritionally-valuable flavonoid compounds, quercetin and
832 kaempferol, in grape berry skins.²²⁶ The phenolic composition of grape berry skins can also change
833 along latitudinal gradients. This was shown in a study where these flavonoid compounds were
834 favoured in the south compared with the north (from 36.7°N Jerez, Spain to 50°N Geisenheim,
835 Germany), a change which positively correlated with overall solar radiation across multiple
836 European sites.²²⁷ This finding suggests that field manipulation of the exposure of grapes to UV-B
837 radiation and other fruit crops could be exploited to enhance desirable characteristics. Such field
838 manipulations are already in development.^{45, 228-230}

839

840 Although UV-B radiation can affect food quality, this does not only involve phenolics, but a much
841 broader range of metabolite classes including UV-regulated terpenoids, aromatic esters and
842 others.²³¹ In peaches exposed to UV-B radiation, levels of the flavour-related monoterpene, linalool,
843 decrease, while concentrations of sesquiterpene (E,E)- α -farnesene increase.¹⁷⁰ Volatile isoprenes
844 have also been associated with thermotolerance (see section 3.3.4). Specific glucosinolate
845 compounds may also accumulate in plants exposed to UV-B radiation,²³² and may lead to the

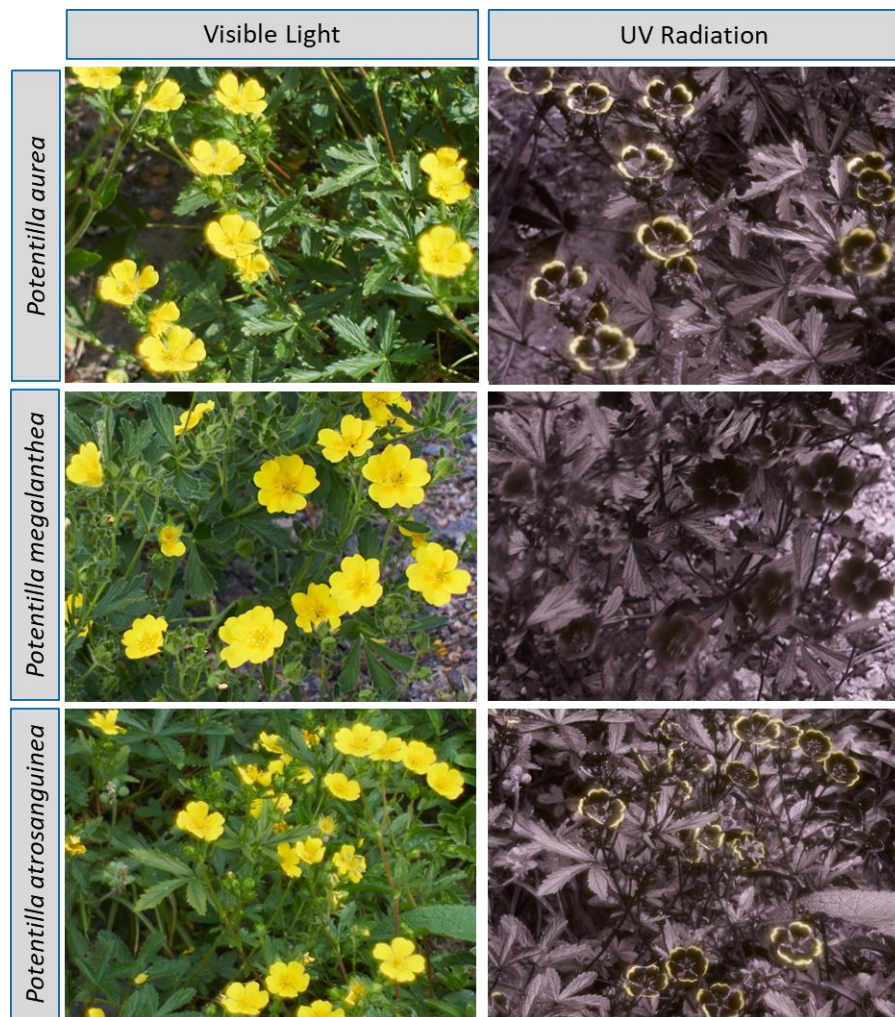
846 production of certain defence compounds against herbivory, creating another link with observations
847 of reduced herbivory in plants exposed to UV-B radiation (see section 3.6.2), although the degree of
848 resistance to herbivory under UV-B radiation may also be dependent on the type of herbivore.^{(173;}
849 and section 3.5.4)

850
851
852 Decreases in UV-B radiation in southern South America and Australasia as the stratospheric ozone
853 layer recovers⁴, may have negative effects for plants and agricultural crops in some cases. For
854 example, as noted above, since UV radiation generally enhances production of plant secondary
855 metabolites that deter many plant herbivores¹⁷³, a decreased induction of these polyphenolics may
856 result in increased herbivory and plant disease. It follows that from an environmental and food safety
857 perspective, reduced cross-protection against herbivores, resulting from decreased UV-induced
858 accumulation of phenolic compounds in crop plants under projected lower future UV-B radiation
859 exposures, may result in increased pesticide use.³⁸ There is also evidence that UV radiation can
860 promote the breakdown of certain pesticides (e.g., fenitrothion²³³, triazophos^{234, 235}).

861 862 **3.5.4 Potential effect of UV radiation on the visibility of crops to insect pests and pollinators**

863
864 As well as being herbivores, insect pests are the main carriers of plant viruses, which are a major
865 cause of plant disease and restrict yields through decreased plant vigour.²³⁶ In agricultural and
866 horticultural environments, reductions in UV radiation, whether through climate change (e.g.,
867 cloudiness, aerosols, forest fires) or deliberate intervention (e.g., the use of UV-attenuating screens,
868 plastic films or nets), can reduce visibility of crops for some insect pests. However, certain pests,
869 such as whitefly, aphids and thrips may be more damaging to crops in environments with UV
870 radiation compared with environments where UV radiation has been attenuated or reflected,^{236, 237}
871 although exceptions have been reported.^{7, 238} On the other hand, some beneficial insects such as
872 pollinators, are more effective in environments containing UV radiation, allowing them to use floral
873 cues such as UV-absorbing/reflecting nectar guides (reviewed by Llorens, *et al.* ²³⁹). The floral
874 patterns produced by nectar guides can be species-specific as found in the genus *Potentilla* where
875 flowers of species from different regions of its distribution appear similar in the visible spectrum but
876 differ in their UV nectar guides, presumably as an adaptation to attract different pollinators (Fig. 6).

877



878
879 **Fig. 6** The three *Potentilla* species with different origins growing together in Helsinki Finland: *Potentilla*
880 *atrosanguinea* var. *argyrophylla* (Himalayan cinquefoil) originates at high elevations; *Potentilla megalanthea*
881 is from Japan; and *Potentilla aurea* is European. While looking similar in the visible spectrum their flowers
882 have very different UV-absorbing and reflecting nectar guides that are visible to insect pollinators. UV
883 photographs were taken with a filter blocking visible radiation but transmitting in the UV-A as far as 325 nm.
884 Photographs by T.M. Robson and P.J. Aphalo.

885 These effects of UV radiation on insects have implications for crop yields and the use of
886 agrochemicals to control pests. However, in controlled environments growers must balance the
887 benefits of UV radiation for plants providing higher food quality^{240, 241} against any potential costs in
888 terms of the visibility of the plants to pests such as fruit flies (*Drosophila suzukii*²³⁵) thrips and
889 aphids.^{206, 242}

890
891 Thus, the interplay of changing levels of UV-B radiation and increased frequency of extreme
892 weather events is likely to add to the current and projected vulnerability of agriculture with
893 consequences for food security (Fig. 5). The key climate drivers together with UV-B radiation that
894 modify plant development and yield are usually temperature and water availability.²⁴³⁻²⁴⁵

895 Consequently, the capacity of plant acclimative mechanisms to adjust to the rapidly changing
896 conditions will become increasingly important.

897

898 **3.6 Ecosystem functioning**

899

900 Terrestrial ecosystems can be modified in several ways by the interactive effects of ozone depletion,
901 UV radiation and climate change. Below, we consider recent findings that address the impacts of
902 these interactions between plants (plant-plant), plant-herbivore, pest-pathogen, and litter
903 decomposition. Some of these processes, particularly litter decomposition, are important in
904 biogeochemical cycles. The consequences of alterations in these ecosystem processes for nutrient
905 cycling and climate change are addressed more fully by Sulzberger, *et al.*⁵¹.

906

907 **3.6.1 Plant-plant interactions**

908

909 Plants interact with one another in positive (facilitation) and negative (competition) ways and these
910 interactions can ultimately change the composition of plant communities and their development
911 following disturbance (succession). Competition between crops and weeds is also an important
912 process affecting agricultural productivity and can require considerable labour and economic
913 investment in weed control. Past studies have shown that enhanced UV-B radiation can shift the
914 balance of competition between crop and weed species, and that these changes are linked to
915 differential effects of UV-B radiation on plant morphology, which then alters competition for light
916 within plant canopies (reviewed in Barnes, *et al.*⁴⁸). Similarly, exposure to ambient UV-B radiation
917 has been shown to change species composition in alpine plant communities, and these changes
918 were also associated with differential effects of UV-B radiation on plant height and leaf area.²⁴⁶
919 Modelling studies confirm that these differential effects of UV-B radiation on plant growth and
920 morphology can lead to shifts in competitive relationships among species.²⁴⁷ At least some
921 modifications to shoot morphology are likely mediated by the UV-B photoreceptor, UVR8.^{22, 141}
922 Plants appear to use UVR8, along with other photoreceptor proteins (e.g., phytochromes), to sense
923 changes in the light environment caused by the proximity of other plants.^{248, 249} Low light conditions
924 (shade) inactivate UVR8, which then results in plant resources being redirected from defence to
925 rapid growth.²⁴⁹ However, while this strategy helps the plant to compete for light with its neighbours,
926 it also makes it more vulnerable to the attack of pathogens and pests (reviewed in Ballaré¹⁵³ Ballaré
927 and Pierik²⁵⁰; see section 3.6.2 below).

928

929 **3.6.2 Herbivory and plant-pathogen interactions**

930

931 Plant responses to UV-B radiation have consequences for organisms at various trophic levels or
932 positions along the ecological food chain from producer to consumer. Solar UV-B radiation-induced
933 reductions in herbivory have been well-documented in the field, and when this occurs, may be
934 proportionally much larger than the effects of UV-B radiation on inhibiting plant growth (reviewed in
935 Ballaré, *et al.*⁷). However, there are also instances where herbivory increases with UV-B radiation
936 (see section 3.5.4). Herbivorous insects can perceive solar UV-B radiation,²⁵¹ although many of the
937 inhibitory effects of UV-B radiation on insect herbivory and pathogens are thought to be indirect (i.e.,
938 mediated by changes in host-plant chemistry; reviewed in Ballaré¹⁵³). More limited evidence
939 indicates that solar UV-B radiation can reduce infection by some plant pathogens. This increased
940 pathogen resistance was shown in experiments where plants were pretreated with different amounts
941 of UV-B radiation before inoculation with a pathogen.²⁵²

942
943 Shade-intolerant plants often down-regulate or decrease their defences against pathogens and
944 pests in those leaves that are exposed to shade or shade signals (such as a low red to far-red ratio,
945 R:FR),²⁵³⁻²⁵⁶ presumably allowing for resources to be redirected into growth responses to avoid
946 shade. According to this interpretation, plants growing in patchy canopies use solar UV-B radiation
947 as a “gap” signal to adaptively regulate their growth and defence phenotypes. The interplay between
948 shade signals (such as low R:FR perceived by phytochromes) and gap signals (such as high levels
949 of UV-B radiation) may optimise the allocation of resources between growth and defence (see
950 Demkura, *et al.*²⁵⁷ and reviews of Ballaré¹⁵³, and Mazza and Ballaré²⁴⁹).

951
952 Some of the changes in plant chemistry elicited by natural levels of solar UV-B radiation involve
953 compounds known to be important for plant interactions with other organisms (reviewed in Escobar-
954 Bravo, *et al.*¹⁷³, and Williamson, *et al.*²⁵⁸). Known defence-related compounds regulated by UV-B
955 radiation include phenylpropanoid compounds,²⁵⁹ isoflavonoids,^{260, 261} conjugated polyamines,²⁵⁷
956 cuticular waxes,²⁶² proteinase inhibitors,^{263, 264} and jasmonates,²⁶⁵ among others. These effects of
957 solar UV-B radiation on defensive chemistry can be considered as specific, presumably mediated by
958 specific UV-B photoreceptors. However, the role of UVR8 in mediating effects of UV-B radiation on
959 secondary compounds has so far been demonstrated only for flavonoids and other soluble phenolic
960 compounds.^{252, 266}

961
962 In spite of the effects of UV-B radiation on plant defence against several herbivores and certain
963 pathogens, the connections between UV-B radiation and the key hormonal pathways that regulate
964 plant defence (i.e., the salicylic acid (SA) and jasmonic acid (JA) pathways), require further
965 research. Early reports of effects of UV radiation on SA and expression of SA marker genes should
966 be interpreted cautiously, as many of those experiments used doses or wavelengths of UV radiation
967 not present in the terrestrial environment (such as UV-C, <280 nm), or unbalanced UV-B radiation

968 treatments (high UV-B radiation delivered against low PAR; see Fig. 4). Similar limitations apply to
969 early studies of effects of UV radiation on JA activity (reviewed in Ballaré¹⁵³).

970
971 Some well-characterised effects of UV-B radiation on plant defence come from experiments that
972 tested plant resistance to herbivorous insects, and necrotrophic pathogens (pathogens that kill their
973 host cells). This has led to follow-up work focusing on interactions with JA signaling. A few studies
974 have shown that genetic perturbations impairing JA synthesis can effectively cancel out some anti-
975 herbivore effects of solar UV-B radiation, leading to the suggestion that JA signaling is required for
976 those effects of solar UV-B radiation that increase plant resistance to herbivory.^{257, 267, 268} However,
977 UV-B radiation can also affect plant defence against herbivores and pathogens via mechanisms that
978 are not mediated by JA.²⁵² The positive effects of UV-B radiation on JA signaling have been
979 attributed to increased JA biosynthesis²⁶⁵ or sensitivity,²⁵⁷ but the molecular mechanisms linking
980 perception of UV-B radiation and JA signaling remain to be elucidated.

981

982 **3.6.3 Litter decomposition**

983

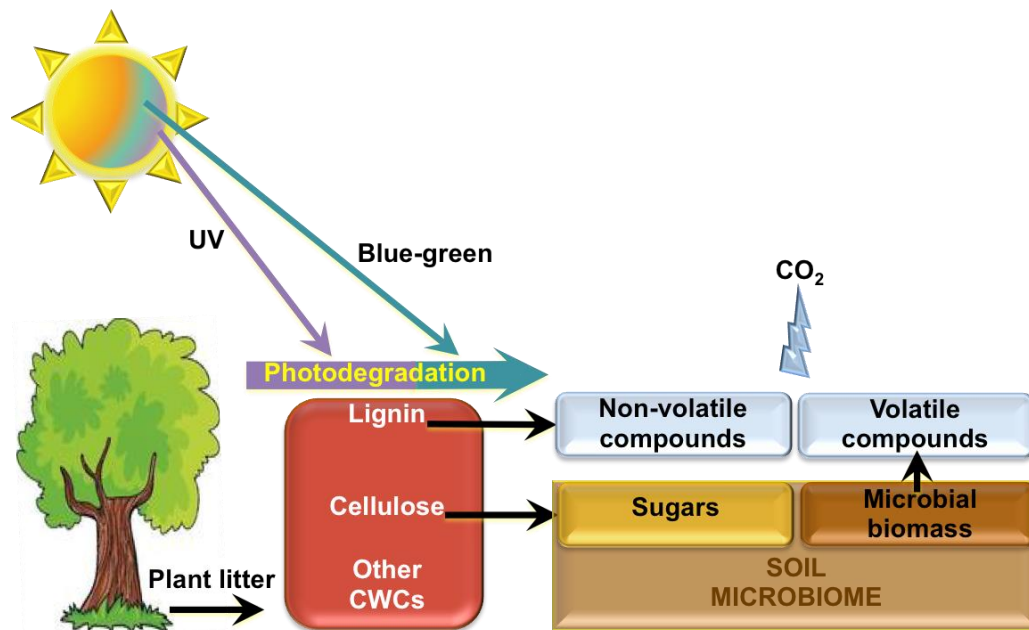
984 The decomposition of dead plant material (i.e., litter) drives the rate at which nutrients are recycled
985 and is a strong determinant of carbon storage and soil fertility in terrestrial ecosystems. In general,
986 the overall rate of decomposition is dependent on the temperature and moisture availability, which
987 affects the activity of decomposing micro-organisms (bacteria and fungi), as well as the type of plant
988 litter inputs (e.g., leaf vs woody tissue; evergreen vs deciduous leaves). Substantial evidence now
989 indicates that solar radiation (UV and short wavelength visible radiation) can also drive litter
990 decomposition via several mechanisms, with the net effect of these processes either accelerating or
991 retarding decomposition, depending on litter quality and environmental conditions. Climate change
992 will likely alter the importance that UV radiation plays in decomposition and regulating carbon
993 cycling in a number of terrestrial ecosystems.

994

995 Solar radiation in the UV and short-wavelength visible regions (blue and green light) can directly
996 break down the biochemical components of plant tissue, including relatively stable compounds, such
997 as lignin, which absorb UV radiation, through a process called photochemical mineralisation (Fig. 7;
998 ^{46, 269, 270}). These light-driven modifications in litter chemistry can, in turn, increase the ease with
999 which microbes can decompose litter.^{52, 54} This latter process is often called photo-facilitation or
1000 photopriming. However, solar UV radiation, especially shorter wavelength UV-B radiation, may also
1001 inhibit the activity of microbes and change the composition of the microbial community, which then
1002 works in opposition to photo-facilitation.^{270, 271} The net effect of these mechanisms is modified by

1003 environmental conditions (e.g., moisture availability) and the spectral quality of sunlight, which
1004 varies depending on ozone depletion, cloud cover, pollution, and plant canopy cover.

1005
1006 Recent studies have shown that photodegradation (photochemical mineralisation plus photo-
1007 facilitation) occurs in a variety of environments,⁵⁴ but the mechanisms and quantitative importance
1008 of this process in driving the overall decomposition of litter remains unclear in many cases. Since
1009 UV radiation can also inhibit microbial activity, a shift in spectral composition (i.e., UV-B:PAR ratios)
1010 would likely change the balance between photo-facilitation and microbial inhibition. This may be one
1011 reason why some experimental and modelling studies fail to detect a relationship between
1012 photodegradation and lignin content of litter.^{55, 271} Long-term studies indicate that increased rates of
1013 decomposition due to photodegradation become evident only in later stages of decomposition, as
1014 was found after 4 months for savanna litter in a controlled experiment,²⁷² and after 12 months in a
1015 semi-arid ecosystem.²⁷³ This suggests that the availability of substrates to microbes is only
1016 noticeably increased by photo-facilitation once readily-available substrates in fresh litter have been
1017 depleted. A diel time period (i.e., 24 h) appears to allow microbes to benefit from daytime photo-
1018 facilitation, possibly recovering during darkness, as well as utilising the extra humidity at night.^{272, 274}



1031
1032
1033 **Fig. 7** Conceptual model of the effects of solar radiation on litter degradation and microbial decomposition in
1034 terrestrial ecosystems. UV radiation and blue-green light cause the direct breakdown of lignin, cellulose and
1035 other plant cell wall components (CWCs), forming non-volatile and volatile compounds, such as carbon dioxide
1036 (CO₂), the latter being released to the atmosphere. This abiotic process is often referred to as
1037 photomineralisation. The changes in litter substrate resulting from photodegradation enhance the microbial
1038 breakdown of litter through a process called photo-facilitation. UV photons in sunlight may also directly inhibit
1039 the activity of decomposing microbes. Figure adapted from Ballaré and Austin⁴⁶.

1042 Field studies continue to show that photodegradation contributes most to the acceleration of litter
1043 decomposition in hyper-arid (annual precipitation <150 mm), arid, and semi-arid eco-systems.^{275, 276}
1044 In two contrasting locations on the Mediterranean steppe, UV radiation increased the decomposition
1045 rate of grass and shrub litter in a continental climate, but not in a high rainfall maritime climate.^{274, 277}
1046 These findings suggest that in drylands photochemical mineralisation dominates under the driest
1047 conditions, whereas photo-facilitation tends to dominate under slightly moister conditions. The
1048 acceleration of decomposition attributable to photo-facilitation can even be detected in sub-tropical
1049 and temperate environments in both litter and coarse woody debris.²⁷⁸ However, when moisture
1050 levels are favourable enough to support high microbial activity, UV radiation can have negative
1051 effects on decomposition, presumably because of direct inhibitory effects of solar radiation on the
1052 microbial populations.²⁷⁹

1053
1054 The majority of field photodegradation studies to date have been conducted in ecosystems
1055 occurring in dry (arid and semi-arid) rather than moist (mesic) climates.²⁷⁰ However, the interaction
1056 of moisture and photodegradation has recently been garnering attention.^{274, 276, 280} In moist, forested
1057 ecosystems, the amount of solar radiation reaching litter through the canopy can alter
1058 decomposition rates.²⁸¹ Different types and densities of canopy affect both the amount of radiation
1059 reaching ground level and its spectral composition.²⁸² This implies that shifts in vegetation type
1060 occurring because of changes in land-use and climate are likely to affect decomposition rates
1061 through photodegradation interacting with concomitant changes in temperature and moisture.²⁸³⁻²⁸⁵
1062 Typically, the encroachment of woody plants leading to conversion of grasslands to shrublands
1063 driven by climate change and/or land abandonment, will alter litter composition and chemistry. This
1064 will shift litter C:N ratios, affecting not only microbial activity but also photo-facilitation of litter and
1065 direct photodegradation.^{283, 286, 287} In addition to shifts in vegetation type, the exposure of litter to
1066 solar radiation will be determined by plant form and functional strategy. In habitats where standing
1067 dead litter remains on the plant, this will present a greater surface area exposed to sunlight than
1068 situations where litter falls to the ground becoming easily mixed with soil which then reduces
1069 photodegradation.^{273, 276, 288-290}

1070
1071 The structure and biochemical composition of litter produced by different plant forms plays a
1072 significant role in determining the underlying rate of decomposition. Hence litter with high lignin
1073 content may decompose slowly and be most affected by direct photochemical degradation.^{68, 291}
1074 However, variations in photodegradation among species independently of their lignin content,²⁶⁹
1075 suggest that other litter traits are also important (see Bais, *et al.*³⁹ for additional discussion). The UV
1076 radiation received by plants during growth can affect leaf morphology and the amount and
1077 composition of phenolic compounds that accumulate in the leaf epidermis,⁸ as well as affecting the
1078 rate at which leaves will break down. These traits may continue to modify leaf optical properties and

1079 hence the extent to which solar radiation penetrates the leaf during the early stages of
1080 decomposition.²⁹² Likewise, the depth and density of litter, its physical movement (e.g., by wind,
1081 rain) and the degree to which litter mixes with soil, will determine the surface area exposed to
1082 sunlight, factors that are likely to be highly important for photodegradation.^{269, 270}

1083
1084 The insight that recent research brings into the role of both UV radiation and short-wavelength
1085 visible light in photodegradation in humid temperate as well as arid biomes,^{56, 293} means that
1086 photodegradation has the potential to modify ecosystem processes (e.g., carbon cycling) across
1087 many biomes. This broader relevance compared with our past knowledge of photodegradation
1088 extends its scope to affect the biogeochemistry of terrestrial ecosystems under climate change and
1089 with future stratospheric ozone recovery.⁵¹

1090

1091 **3.7 Climate change is altering the exposure of organisms to UV radiation**

1092
1093 Previous assessments have focused on the effects of ozone-driven changes in UV-B radiation.⁸
1094 However, climate change is increasingly exerting a stronger control on UV-B and UV-A radiation
1095 received by organisms as a result of changing cloud cover, vegetative cover, shifting of geographic
1096 ranges of species, changing of seasonal timing of growth and reproduction, and migration. Some of
1097 the potential implications of these climate-driven changes in exposure to UV radiation for terrestrial
1098 organisms and ecosystems are addressed below.

1099

1100 **3.7.1 Species migration, UV radiation and climate change**

1101
1102 Plants and animals are shifting their ranges to higher latitudes and elevations in response to climate
1103 change and additional changes in distributions are expected to occur in the future.^{1, 2, 294} However,
1104 species vary in their potential rates of migration. For plants, short-lived, herbaceous species
1105 (grasses and forbs) generally shift geographic ranges more rapidly than long-lived, woody species
1106 (trees and shrubs).¹ Non-native (i.e., introduced) species of plants also appear to exhibit higher
1107 migration potentials than native (i.e., indigenous) species.^{294, 295} These climate change-driven shifts
1108 in geographic ranges will likely alter the exposure of plants to UV-B radiation, since UV-B
1109 irradiances generally increase with increasing elevation and decrease with increasing latitude^{16, 17,}
1110 ¹⁶¹. However, these changes in plant exposure to UV-B radiation will not occur in isolation of other
1111 environmental factors, since a number of abiotic (e.g., temperature and moisture) and biotic (e.g.,
1112 associated pests, pathogens and competitors) factors change with the migration of organisms to
1113 higher latitude and elevation.^{1, 296} Consequently, these shifts in geographical range will likely
1114 expose organisms to unique combinations of UV radiation and co-occurring environmental factors.
1115 To what extent UV radiation plays a role in influencing migration patterns and how plants and

1116 animals respond to different conditions of UV radiation in the context of these other environmental
1117 changes as they migrate, has received little attention to date (but see section 3.3). However, certain
1118 insights into these effects can be gleaned from studies comparing plant populations or ecotypes
1119 whose distribution naturally spans a range of latitudes or elevations.

1120
1121 Plants that are adapted to grow in high elevation environments (i.e., alpine) often accumulate more
1122 UV-screening compounds (e.g., flavonoids) and have other UV-protective mechanisms compared
1123 with those plants occurring at lower elevations.²⁹⁷⁻³⁰¹ These differences are likely the result of the
1124 combined effects of elevational changes in UV radiation, temperature and other factors.³⁰² As
1125 discussed in section 3.3.4, low temperatures induce the production and accumulation of flavonoids.
1126 This may then increase levels of UV-screening and protection against oxidative stress.³⁰³⁻³⁰⁵ High-
1127 and low-elevation plant populations may also differ their abilities to acclimate to changes in UV
1128 radiation.³⁰⁶ In wild potatoes (*Solanum kurtzianum*), populations grown at low elevation have
1129 relatively low constitutive (base-line) levels of leaf flavonoids but a high capacity for induction of
1130 flavonoids when UV radiation increases. In contrast, plants at high elevations have high constitutive
1131 flavonoid levels, but do not necessarily increase their UV-screening in response to supplemental
1132 UV-B radiation in experimental studies.³⁰⁷ Differential sensitivity to UV radiation of high vs low-
1133 elevation populations may also be due, in part, to population differences in DNA damage and repair,
1134 as has been shown for *Arabidopsis*.³⁰⁶

1135
1136 Whether there are differences in tolerance to UV radiation between native vs introduced species is
1137 unclear at present. For example, introduced populations of Chinese tallow tree (*Triadaca sebifera*),
1138 taken from south-eastern USA where the species was introduced in the 1700's, were shown to be
1139 more sensitive to UV-B radiation than native Chinese populations.³⁰⁸ By comparison, no differences
1140 were found in the sensitivity of seed germination to UV-B radiation in native vs introduced
1141 populations of *Verbascum* and *Echium* in New Zealand.³⁰⁹ Similarly, native and non-native species
1142 showed similar levels of UV-screening when growing in a high UV, tropical alpine location.³¹⁰
1143 However, UV-screening increased with increasing elevation and UV-B radiation in a non-native
1144 species (*Verbascum thapsus* (mullein)) but did not vary with elevation in the native *Vaccinium*
1145 *reticulatum* (ohelo). In contrast, similar levels of phenotypic plasticity (acclimation potential)
1146 between native (German) and non-native (New Zealand) populations of *Hieracium pilosella* with
1147 respect to morphological and growth response to UV-B radiation under growth chamber conditions
1148 have been found.³¹¹ Thus, while it is generally assumed that non-native species can acclimate more
1149 readily to environmental change than native species,³¹² it is unclear whether this generalisation
1150 applies to tolerance to UV-B radiation. Plants expanding their distribution into higher latitudes, would
1151 be expected to experience less exposure to UV-B radiation. As already noted, this may then lead to

1152 a decline in UV-screening compounds, antioxidants and other metabolites involved in photo-
1153 protection.³¹³

1154
1155 To date, relatively little research has exploited remote sensing to make quantitative assessments of
1156 plant responses to elevation and climate change. However, the potential to use this approach is
1157 apparent from remote sensing images of a 1-hectare area (from the Carnegie Airborne Observatory-
1158 2), using a high-fidelity visible-to-shortwave infrared (VSWIR) imaging spectrometer and dual laser
1159 waveform (LiDAR), which was calibrated against spectrophotometric measurements of leaf
1160 extracts.³¹⁴ This allowed a trend to be identified for increased phenolics with elevation (excluding the
1161 upper-most measurement point) using LiDAR images at the landscape scale in the Peruvian
1162 Andean rainforest. As this approach becomes more widely adopted, it will enable the resolution of
1163 large-scale relationships with topography and climate, allowing patterns in response to UV radiation
1164 and climate change to be mapped using remote sensing of large areas. Unmanned aerial vehicles
1165 (drones) are also increasingly being used to bridge the gap between satellites and ground
1166 measurements and to measure spectral reflectance at high resolution and under clouds.¹²⁷

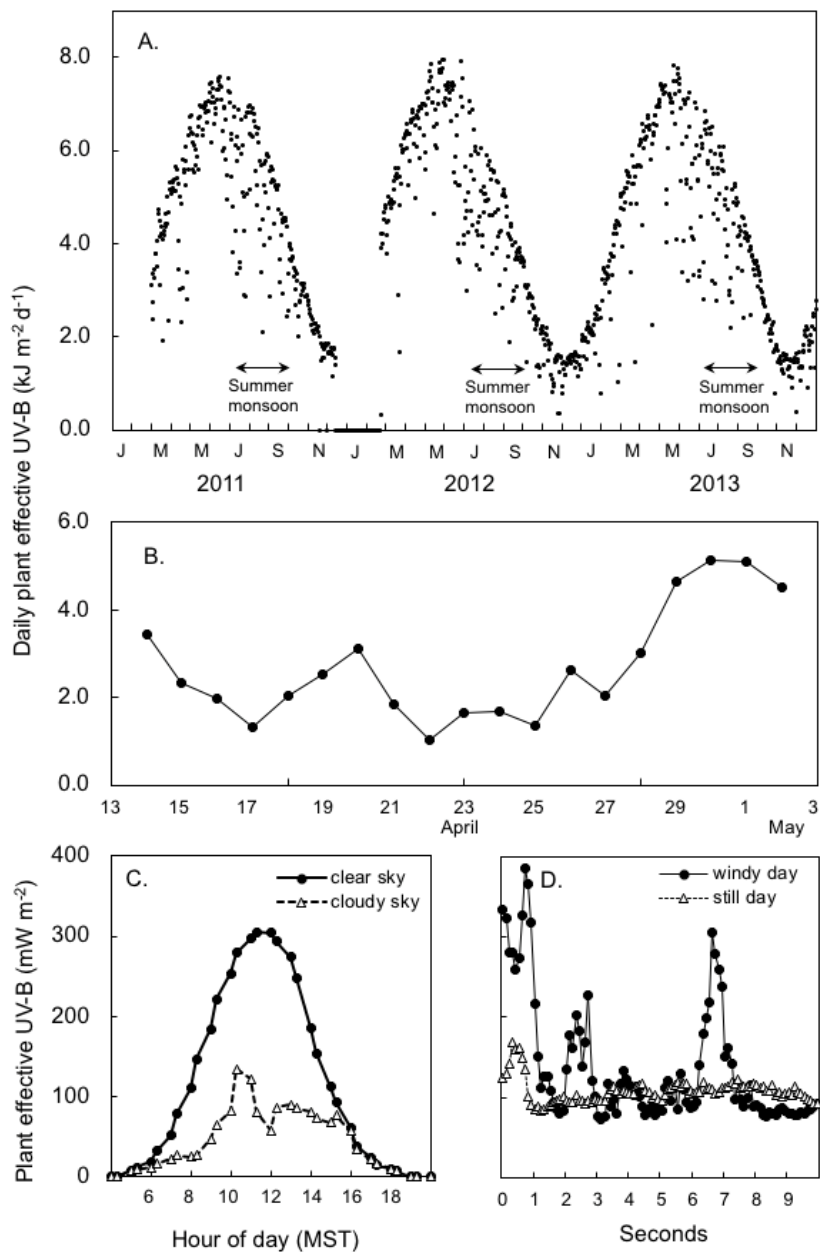
1167
1168 Ecosystems, and populations of plant species, including native species, have responded over the
1169 eons to changing environmental conditions. However, the recent rapid rate of climate change, in
1170 particular increasing temperatures and more frequent extreme weather events, are of concern in
1171 terms of the conservation of species and habitats.² Understanding the role of UV radiation in shifting
1172 distribution patterns and how readily plant populations can adjust physiologically and genetically to
1173 new UV radiation environments is therefore relevant to the conservation of biodiversity and the
1174 services that these natural ecosystems provide to humans.

1175

1176 **3.7.2 Clouds, canopies and plant response to fluctuating UV radiation conditions**

1177
1178 Climate change is altering cloud cover with some regions experiencing increased and other regions
1179 decreased cloud cover.^{1, 4} The effect of clouds on UV radiation also depends on the type of clouds
1180 ³¹⁵ as well as their position relative to the sun.³¹⁶ These changes in cloud cover alter the long-term
1181 (days to weeks) exposure of plants to UV radiation and they can also change the short-term
1182 (seconds to hours) dynamics of UV radiation received by plants. (Fig. 8; ³¹⁶) Whereas considerable
1183 attention has been given to understanding plant responses to changes in average UV radiation
1184 conditions that occur over long time periods (section 3.3; see also Bornman, *et al.*⁸ and Björn²⁴ and
1185 references therein), far less is known about plant responses to rapid fluctuations in solar UV
1186 radiation. A number of studies have, however, demonstrated that UV-screening levels in mature
1187 leaves can vary over the growing season³¹⁷, from one day to the next,³¹⁸ over the course of an
1188 individual day,³¹⁹ and in response to rapid changes in clouds.³²⁰ The changes in UV-screening that

1189 occur over the day are rapid (within minutes), reversible, and have been shown to be linked to
 1190 changes in the content and composition of UV-absorbing compounds (flavonoids and related
 1191 phenolics).^{319, 320} At present, the underlying mechanisms responsible for these rapid changes in UV-
 1192 radiation protection are unclear, as is the significance of these changes for plant growth and
 1193 function. These findings do, however, indicate that many, but not all, plant species can rapidly adjust
 1194 their UV-screening in response to fluctuations in UV irradiances.³²¹



1222 **Fig. 8** Variability in ground-level UV-B radiation at several locations over multiple time scales. Panel A shows
 1223 incident daily plant effective UV-B radiation in the Sonoran Desert, USA, over a 3-year period with annual
 1224 summer monsoon (rainy and cloudy weather) indicated. Panel B: daily plant effective UV-B radiation in
 1225 eastern Washington, USA, over an early spring period with heavy cloud cover followed by clear skies during a
 1226 time when the new leaves of many native plant species are emerging. Panel C: diurnal changes in plant
 1227 effective UV-B radiation under summer clear and cloudy skies in the Sonoran Desert. Panel D: changes in
 1228 instantaneous plant effective UV-B radiation in an understory location of a birch (*Betula pendula*) forest in

1229 Oxfordshire, UK, on one windy and one calm day. Fluctuations in UV-B radiation in Panel D are the result of
1230 wind-driven changes in canopy leaf flutter. Figure from Barnes, *et al.*³²² with permission.

1231

1232 The disruption of plant canopy structure (e.g., due to fire or drought-induced tree mortality) alters the
1233 amount and spectral composition of sunlight penetrating canopies (i.e., ratios of UV-B:UV-A:PAR),
1234 but the specific changes depend on the type of canopy and vertical position (e.g., crown vs
1235 understorey).³²³ Recent studies using array spectrometers have captured rapid changes in the sun-
1236 shade environment under canopies by recording multiple spectra every second.³²⁴ These
1237 measurements at high temporal resolution have confirmed findings from earlier studies^{282, 325, 326} that
1238 the spectral composition as well as total irradiance differs between sun flecks and understorey
1239 shade in forests and crop canopies. The importance of this fine-scale temporal and spatial variation
1240 in UV radiation in understorey environments for plant growth and development is not entirely clear at
1241 present (but see Krause, *et al.*³²⁷, Krause, *et al.*³²⁸). There is evidence, however, that plants use the
1242 total irradiance received or modulated as cues,³²⁹ which can prime them for seasonal or periodic
1243 changes. This may therefore be an important aspect of UV acclimation in understorey species that
1244 could lead to better adjustment to conditions of variable UV radiation resulting from modified
1245 overstorey canopies brought about by climate change.

1246

1247 Light tends to penetrate canopies more effectively under overcast or hazy sky conditions when the
1248 ratio of diffuse to direct radiation is higher, than under clear sky conditions.³³⁰⁻³³² Thus, cloudy
1249 conditions produce short-term increases in photosynthesis at the whole canopy level.³³³⁻³³⁵
1250 However, because leaves that develop in the sun are more efficient in using direct than diffuse
1251 radiation, and efficiency of leaves that develop in the shade does not differ significantly under
1252 changing sky conditions³³⁶, caution must be exercised in generalising from these results.
1253 Conclusions that plant productivity will be enhanced by projected increases in diffuse solar radiation
1254 resulting from manipulating aerosol levels in the atmosphere to reduce climate change (i.e.,
1255 geoengineering)⁴ must be viewed with a high degree of uncertainty because they will depend on the
1256 geographic location, on the extent of the reduction in incident irradiance and whether the increased
1257 canopy light-use efficiency from diffuse radiation is sufficient to offset this and persist in the long
1258 term.⁶⁹

1259

1260 Remote sensing of vegetation using satellites is routinely used to measure primary productivity and
1261 leaf pigments involved in photosynthesis; this technique has been used extensively for the scaling of
1262 ecosystem processes related to the carbon cycle.³³⁷ Most of these ecosystem process models have
1263 been developed for use in combining leaf-level and remotely-sensed data, but new possibilities to
1264 better understand canopy reflectance of UV radiation are being made possible by the capacity to
1265 extend these remotely captured images and spectral data into the UV range of the spectrum.

1266

1267 Radiative transfer models used to model canopy optical properties and determine the fate of solar
1268 radiation have not yet been extended into the UV range, e.g., the discrete anisotropic radiative
1269 transfer model.(DART³³⁸) These models can incorporate sub-models for leaf optical properties (e.g.,
1270 PROSPECT-D,³³⁹ and Fluspect-CX), which previously have been applied for optical estimation of
1271 chlorophyll and carotenoids but if extended into the blue light and UV-A regions could include
1272 estimation of anthocyanins³⁴⁰ and flavonoids. This may be facilitated by the new generation of those
1273 satellites designed for monitoring vegetation, which include the capacity to detect wavelengths
1274 spanning into the UV portion of the spectrum (from the European Space Agency, 270-370 nm for
1275 Sentinel-5 Satellite and Sentinel-5-precursor satellite). An alternative approach is to extend
1276 atmospheric radiative transfer models, such as libRadtran^{4, 341} and the tropospheric and visible solar
1277 UV radiation model (http://cprm.acom.ucar.edu/Models/TUV/Interactive_TUV/), to include radiative
1278 transfer through plant canopies or even greenhouse structures in the same way that DART and
1279 other radiative transfer models (RTMs) are being applied for the visible spectrum, or even coupling
1280 these two model types together. At the leaf level, both commercial sensors (e.g., Ocean Optics
1281 Jaz³⁴²) and custom-made devices (e.g., Robberecht and Caldwell³⁴³) have the capacity to measure
1282 leaf reflectance in the UV range in both broadleaved and needle-leaved plants.

1283
1284 In crop canopies, planting distance and crop species, or even the cultivar or variety planted, will
1285 dictate the canopy architecture and affect the spectral composition and total irradiance reaching the
1286 lower leaves. These decisions also have implications for how UV-B radiation affects plant growth
1287 and defence at the canopy level in agricultural crops (see Ballaré¹⁵³ and section 3.5.3). With a better
1288 understanding of the mechanisms by which plants in canopies respond to UV radiation as a part of
1289 the incident spectral irradiance over vertical profiles, we can make better-informed management
1290 decisions on species and cultivar selection for specific locations.

1291

1292 **3.7.3 Phenology and UV radiation**

1293

1294 The implications of warmer winters for the seasonal timing of development or phenology have been
1295 extensively studied, with findings consistently showing both the emergence of animals^{344, 345} and the
1296 onset of plant growth^{9,10} to occur earlier in the year there is less sunlight (and by definition less UV-B
1297 radiation). Although the molecular mechanisms controlling phenology are not fully understood³⁴⁶, it
1298 is known that organisms often use a variety of environmental cues to safeguard against mis-timing
1299 of development.³⁴⁷⁻³⁴⁹ Differences among life forms in their rate of response to temperature, which
1300 is usually the predominant cue, create the potential for a disruption of ecosystem processes through
1301 a mismatch in the timing of phenology among co-existing organisms such as plants and
1302 pollinators.^{350,351} It is likely that warmer temperatures will bring overwintering trees out of dormancy
1303 prematurely. This will produce an earlier spring bud-burst, possibly so early in the year that at high

1304 latitudes new leaves receive insufficient sunlight to develop as they normally would do later in the
1305 year.^{352, 353} This also implies that those plant defences partially regulated by UV-B radiation would
1306 be weaker and the benefit of pollinators UV-vision reduced.
1307 This forward displacement of phenology due to warming may also heighten the role of alternative
1308 phenological cues (e.g., daylength and spectral quality).^{354, 355} In particular, more research is
1309 required to better understand interactions between daylength (photoperiod) and cues related to
1310 spectral quality (i.e., changes in UV-B, UV-A, blue and red light), both of which are detected by plant
1311 photoreceptors. Alterations in the timing of spring phenology, particularly at high latitudes, may
1312 expose understorey plants to new light environments in early spring when freezing temperatures
1313 may limit their physiological acclimation capacity.

1314 1315 **3.8 Tracking changes in past UV radiation over geological timescales using** 1316 **the biochemical signatures of plants**

1317
1318 The long-term ecological effects of UV-B radiation over geological timescales are studied by
1319 palaeoecologists interested in retrospectively reconstructing solar UV-B radiation. Identifying a
1320 reliable proxy for tracking changes in UV-B radiation based on the biochemistry of pollen and
1321 spores, would help interpretation of the effects of UV-B radiation on terrestrial ecosystems.
1322 However, even then an additional calibration would be required to separate changes in total solar
1323 radiation from those of UV-B radiation, and it would be difficult to distinguish whether these changes
1324 resulted mainly from stratospheric ozone depletion or other environmental or astronomical factors.
1325 Improvements in analytical techniques have reduced the uncertainty associated with reconstructions
1326 of solar radiation based on the biochemistry of pollen from ice cores and lake sediments that track
1327 changes in past UV radiation over geological time scales.^{356, 357} These reconstructions may provide
1328 a better understanding of the evolution of the stratospheric ozone layer and its interaction with
1329 climate change.^{358, 359} However, the extent to which UV-absorbing compounds in pollen can be
1330 considered reliable indicators of the past UV-B radiation and reflect changes at high temporal
1331 resolutions, depends upon the causative temporally-stable relationship between the accumulation of
1332 these compounds in pollen and exposure to solar UV-B radiation being experimentally verified.³⁶⁰

1333
1334 The preserved outer walls of fossilised spores and pollen grains are made from sporopollenin, which
1335 is highly resistant to degradation over geological time scales and contains the phenolic compounds,
1336 para-coumaric acid and ferulic acid. Experiments using supplemental UV-B radiation have found the
1337 concentrations of these compounds to be proportional to the incident solar UV-B radiation received
1338 by the pollen.^{358, 361} Exploiting this relationship, Jardine, *et al.*³⁵⁹ reconstructed UV irradiance at Lake
1339 Bosumtwi, in modern-day Ghana, showing that over a 140-thousand-year period fluctuations in the

1340 concentration of phenolics from grass pollen contained in sediments corresponded with patterns of
1341 solar UV irradiance derived from changes in the Earth's orbit over cycles of 19-21 thousand years.
1342 The correlation between reconstructed UV-irradiance and phenolic concentration is also evident
1343 from pine pollen ³⁶² and spores of the ubiquitous clubmoss *Lycopodium*³⁶³ over broad latitudinal
1344 gradients, although this correlation is more robust across local elevational gradients.³⁶⁰ This is
1345 because seasonal and environmental variability and differences in UV-B radiation related to weather
1346 patterns (temperature and cloudiness) and canopy shade can confound the relationship.

1347 The lack of standardisation and inter-comparability of samples and sampling techniques is one
1348 impediment to the wider use of the above techniques. Improvements in the two analytical
1349 approaches used to detect phenolic compounds, i.e., Fourier-Transform (FT) high-throughput infra-
1350 red spectroscopy and thermally-assisted hydrolysis methylation (THM) with pyrolysis-gas
1351 chromatography mass spectrometry (THM-GC/MS), should allow researchers to obtain more
1352 detailed information from pollen samples.³⁶⁴⁻³⁶⁶ In the latter case, precision should also be improved
1353 by calibration of changes in phenolic compounds against a known concentration of a compound
1354 added to the sample as a standard or against another compound within the pollen that does not
1355 respond to changes in solar radiation.³⁶⁵ When used in conjunction with radiative transfer
1356 modelling,³⁶⁷ these approaches show promise in distinguishing past environmental gradients in UV
1357 radiation, such as that at the end of the Permian period (ca 250 million years ago),^{368, 369} from other
1358 climate changes across geographical gradients and long-time scales. This has the potential to
1359 improve our knowledge of the causes and consequences of stratospheric ozone depletion.

1360

1361 **3.9 Key gaps in knowledge**

1362

1363 Current gaps in our knowledge of the linkages between stratospheric ozone, UV radiation and
1364 climate change and their implications for terrestrial ecosystems are a direct consequence of the
1365 complexity of systems characterised by interactive loops that link climatology, meteorology and
1366 biology (Fig. 1). The challenge lies in developing integrated approaches to assess the effects of UV
1367 radiation against a complex background of rapidly evolving environmental conditions as well as
1368 human intervention behaviours. The way in which ecosystems respond to the often-interactive
1369 effects UV radiation and other climate change dynamics can have important consequences for the
1370 functionality and/or productivity of agricultural and natural ecosystems, but currently leave many
1371 unknowns. This emphasises the importance of studying combinations of those environmental
1372 factors that often change with UV radiation and which may modify the response of organisms to UV
1373 radiation in terms of acclimation and productive growth. Thus far, most research has concentrated
1374 on potential interactive effects of UV radiation with temperature and/or drought. Since climate
1375 warming continues to increase, a better understanding is needed of the effects of UV-B radiation

1376 and rising carbon dioxide together with other climate variables on natural and agricultural systems.
1377 This will then facilitate assessments of future outcomes for ecosystem functioning, conservation of
1378 species, and selection of environmentally suitable agricultural crops. While growth chamber studies
1379 can make valuable contributions to understanding some of the fundamental mechanisms of plant
1380 response to UV radiation, there is still a strong need for many growth chamber studies to be
1381 validated in the field for a realistic perspective of how organisms will actually respond in a more
1382 natural environment.

1383
1384 The balance between negative impacts and beneficial effects on organisms will determine the
1385 current and future adaptation and sustainability of terrestrial ecosystems. Changing exposure to UV
1386 radiation and climate change factors will affect plant resistance to pests and diseases, food quality
1387 and nutritional quality, as well as potentially modifying the behaviour of terrestrial animals. These
1388 changes may also affect visual cues contributed by UV radiation for certain animals. However, more
1389 information is required to evaluate the possible implications in the context of animal response to
1390 future environments and in plant-pest and plant-pollinator interactions, which will have a bearing on
1391 food security.

1392
1393 While qualitative analysis of responses to UV radiation and other variables is usually possible,
1394 quantitative analyses are often lacking due, in part, to the complexity of diverse and constantly
1395 changing biological systems. For example, it is difficult to quantify the importance of processes such
1396 as photodegradation and microbial breakdown of terrestrial plant litter for soil carbon storage and
1397 emissions at regional and global scales, and their potential contribution to global warming and
1398 nutrient cycling.

1399
1400 Climate change together with changes in land-use will very likely continue to have strong impacts on
1401 the exposure to UV radiation of ecosystems and terrestrial organisms, including human populations.
1402 On a global scale, there is currently insufficient information on the relative contribution and
1403 implications of stratospheric ozone depletion to climate change in the southern hemisphere, and
1404 how much can be attributed to natural variability. These interactive effects need to be evaluated for
1405 the way in which they may continue to modify ecosystem response differently in a future with a
1406 recovering stratospheric ozone layer. In addition, emerging findings from stratospheric ozone
1407 monitoring need to be taken into account for evaluating the possible implications of any sudden
1408 change towards the projected path of ozone recovery. This was recently illustrated in a report³⁷⁰
1409 suggesting that there are unexpected indications that emissions of the banned ozone-depleting
1410 compound, chlorofluorocarbon-11 (CFC-11), have increased. The magnitude and future significance
1411 of the responses of terrestrial ecosystems to increasing or decreasing UV radiation, either

1412 dependent or independent of stratospheric ozone depletion, and in the context of climate change,
1413 remain largely unknown.

1414

1415

1416 References

1417

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