Review

Comparing the impacts of climate change on the responses and linkages between terrestrial and aquatic ecosystems
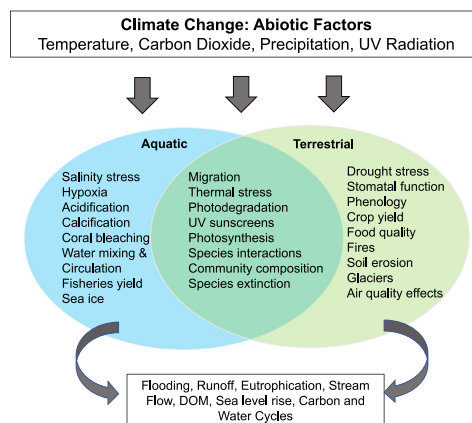
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HIGHLIGHTS

- Aquatic and terrestrial ecosystems are affected by anthropogenic climate change
- Organisms respond by poleward migrations and upward migration
- CO_2 negatively affects many aquatic organisms by ocean acidification
- Increased water temperatures result in shoaling of the upper mixed layer
- Changes in precipitation, hurricane frequency and rising seawater affect terrestrial habitats

GRAPHICAL ABSTRACT

ARTICLE INFO

ABSTRACT

Aquatic and terrestrial organisms are being exposed to a number of anthropogenically-induced environmental stresses as a consequence of climate change. In addition, climate change is altering various linkages that exist between ecosystems on land and in water. Here we compare and contrast how climate change is altering aquatic and terrestrial environments and address some of the ways that the organisms in these ecosystems, especially the primary producers, are being affected by climate change factors, including changes in temperature, moisture, atmospheric carbon dioxide and solar UV radiation. Whereas there are some responses to climate change in common between terrestrial and aquatic ecosystems (e.g., changes in species composition and shifting geographic ranges and distributions), there are also responses that fundamentally differ between these two (e.g., responses to UV radiation). Climate change is also disrupting land-water connections in ways that influence biogeochemical and hydrologic cycles, and biosphere-atmosphere interactions in ways that can modify how aquatic and terrestrial ecosystems are affected by climate change and can influence climate change. The effects of climate change on these ecosystems are having wide-ranging effects on ecosystem biodiversity, structure and function and the abilities of these systems to provide essential services.

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Contents

1. Introduction

Climate change is exposing terrestrial and aquatic organisms to a plethora of anthropogenically-induced stresses. These environmental changes are disrupting the biodiversity, structure and function of these ecosystems, compromising their abilities to provide food to humans as well as important ecological services (IPCC, 2014; Pecl et al., 2017; Scheffers et al., 2016; Williamson et al., 2016b). Both aquatic and terrestrial ecosystems exchange energy and water with the atmosphere and process key elements (e.g., C and N) that influence the climate system (Frank et al., 2015; Le Quéré et al., 2016). These ecosystems are also linked in a number of ways such that perturbations in terrestrial ecosystems have consequences for aquatic ecosystems and vice versa (Sulzberger et al., 2019). How are aquatic and terrestrial ecosystems similar and different in their responses to climate change, and how does climate change influence the linkages between these two distinct types of ecosystems?

Here, we compare and contrast how ongoing changes in important climate change factors (i.e., atmospheric CO₂, temperature, precipitation and solar UV radiation) are impacting aquatic and terrestrial organisms (Fig. 1). We further highlight important linkages between aquatic and terrestrial ecosystems that are being affected by these aspects of climate change. Our emphasis is on the effects and responses of primary producers in both types of ecosystems as these organisms play fundamental roles in the biogeochemical and biophysical processes that connect ecosystems on land and water, and also serve to bridge the biosphere with the Earth's climate system (Schlesinger and Bernhardt, 2013).

2. Global environmental changes impacting aquatic and terrestrial ecosystems

2.1. Atmospheric CO_2 increases

Atmospheric CO_2 concentrations have increased from 280 ppm in the pre-industrial era to >400 ppm at present (NOAA. Earth System Research Laboratory, 2017). Under a business-as-usual scenario (IPCC, A1F1 scenario) the value is expected to increase to about 750 ppm by the end of this century (IPCC, 2013). Currently the atmosphere holds about 735 Pg (1 Pg = 10^{15} g) carbon and the estimated fossil fuel reserves are about 7500 Pg. The terrestrial biomass amounts to 600 Pg carbon and vegetation on land assimilates about 62 Pg per year which it then releases back to the atmosphere when the vegetation decays. Aquatic ecosystems take up and release about the same amount of carbon even though their standing crop is only about 1% of that of terrestrial ecosystems (Falkowski, 2013). Human activity adds about 8 Pg
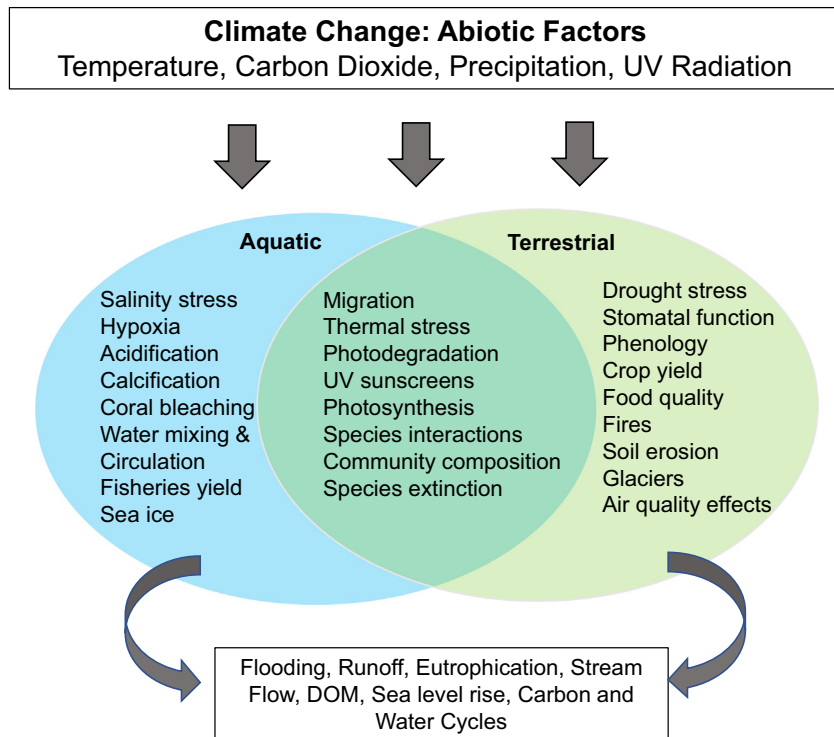

Climate Change: Abiotic Factors
Temperature, Carbon Dioxide, Precipitation, UV Radiation

Aquatic

Salinity stress
Hypoxia
Acidification
Calcification
Coral bleaching
Water mixing &
Circulation
Fisheries yield
Sea ice

Migration
Thermal stress
Photodegradation
UV sunscreens
Photosynthesis
Species interactions
Community composition
Species extinction

Terrestrial

Drought stress
Stomatal function
Phenology
Crop yield
Food quality
Fires
Soil erosion
Glaciers
Air quality effects

Flooding, Runoff, Eutrophication, Stream Flow, DOM, Sea level rise, Carbon and Water Cycles

Fig. 1. Effects of abiotic climate change stress factors affecting aquatic and terrestrial ecosystems and resulting consequences for organisms and ecosystems.

from fossil fuel burning and close to 3 Pg from tropical deforestation and altered land use per year (Cerri et al., 2018; Wang et al., 2017).

The oceans are a major sink for atmospheric CO_2 and therefore a global player partially mitigating increasing temperatures (Landschützer et al., 2014). The biological pump is the main mechanism for reducing the CO_2 concentration in the water: Aquatic primary producers, such as marine phytoplankton, incorporate CO_2; organic material from dead organisms and fecal pellets sediment to the deep sea bottom (Honjo et al., 2014). As a result of these processes, the ocean carbon sink has likely increased since pre-industrial times, but considerable uncertainty exists about the limits of carbon sequestration by the oceans, regional variation in carbon sink potential and how this sink will be influenced by climate change (McKinley et al., 2017).

Terrestrial primary producers sequester carbon in above- and below-ground biomass, with soils storing about twice the amount of carbon as standing vegetation (Scharlemann et al., 2014; Schimel, 1995). Climate change can have positive and negative effects on terrestrial primary productivity. Increases in net primary production in Amazon rain forests from 1982 to 1999 were attributed to decreased cloud cover and increase in solar radiation (Nemani et al., 2003). Others have attributed recent increased carbon uptake by tropical forests to rising atmospheric CO_2 conditions (Schimel et al., 2015). However, carbon uptake by forests can be reduced by increases in drought and temperature (Liu et al., 2018; Wang et al., 2013) and some ecosystems (e.g., Arctic tundra) may be transitioning form carbon sources to carbon sinks as a consequence of climate change (Jeong et al. 2018). Thus, significant uncertainties exist on the climate feedback effects of marine and terrestrial ecosystems (Schimel et al., 2015) and the implications of these changes for future rates atmospheric CO_2 change (Gaubert et al., 2018).

Increases in atmospheric CO_2 concentrations are currently influencing aquatic and terrestrial organisms albeit in different ways. In aquatic ecosystems, increasing CO_2 concentrations result in a change in water chemistry and a decrease in pH as these ecosystems absorb more and more CO_2. Presently, the oceans have absorbed >30% of the anthropogenically released CO_2 and the pH is predicted to drop by 0.4 units corresponding to an increase in H ions by about 150% by the end of this century (Gattuso et al., 2015). This ocean acidification affects the physiology of many organisms (Brennan and Collins, 2015) and interferes with the calcification of phytoplankton, macroalgae and many zoological taxa (Gao et al., 2018). Closely related with climate change and ocean acidification is deoxygenation and hypoxia (Keeling et al., 2009). About 94% of dead zones depleted of dissolved oxygen will occur in areas where the temperature increase is ≥2 °C (Altieri and Gedan, 2015). These dead-zones are influenced by land-use patterns up-stream (e.g., agriculture and urbanization) and (primarily run-off from nutrient-rich agricultural lands) and climate change-driven increases in precipitation and flooding that enhance nutrient loading and deposition of surface waters into coastal waters (Altieri and Gedan, 2014).

Carbon dioxide is the primary substrate for photosynthesis and CO_2 concentrations constitute a limiting bottleneck for many aquatic and terrestrial photosynthetic organisms. Therefore it has been assumed that photosynthetic carbon fixation should benefit from increasing concentrations (Kirschbaum, 1994). However, plants possessing C_4 photosynthesis (e.g., many tropical grasses and warm-season crops such as maize and sugar cane) have evolved mechanisms to concentrate CO_2 inside their photosynthetic cells and tissues, such that changes in ambient CO_2 concentrations generally have minimal effects on photosynthetic rates (Sage, 2003). Moreover, for plants that are responsive to increased atmospheric CO_2 concentrations (i.e., C_3 plants), it was found that though higher CO_2 concentrations foster the growth of young seedlings, productivity of adult plants was not affected. Also, drought and warming decrease the positive impact of elevated CO_2 concentrations (Broughton et al., 2017; Xu et al., 2014). Increasing atmospheric CO_2 concentrations have been found to significantly affect the plant

development and may decrease dry mass productivity. Competition for water could be one of the most important factors in the interaction between crop plants and weeds (Santos et al., 2017). Indeed, exposure to elevated CO_2 concentrations generally increases plant water use efficiency (the ratio of carbon uptake to water loss; (Wayne Polley et al., 2002)) which can then lead to altered soil moisture conditions, especially in moisture-limited ecosystems (e.g., deserts and grasslands; (Morgan et al., 2004). Indeed, some recent results indicate that increased CO_2 availability conferred increased drought resistance to some grasses in New Mexico and this may give these plants an advantage over other species (Drake et al., 2017). Indeed, shifts in plant community composition and increases in aggressive invasive species, rather than increases in primarily productivity may be more likely consequences of rising atmospheric CO_2 levels on terrestrial ecosystems (Körner et al., 2005; Mohan et al., 2006; Weltzin et al., 2003a).

Many aquatic photosynthetic organisms (phytoplankton and macroalgae) also possess a CO_2-concentrating mechanism based on the activity of an enzyme, carbonic anhydrase and an active transport of CO_2 and bicarbonate so that increasing concentrations are of no avail (Gee and Niyogi, 2017). In some cases elevated CO_2 concentrations may even decrease growth because of enhanced photorespiration and mitochondrial respiration (Mackey et al., 2015).

2.2. Temperature increases

The anthropogenically released CO_2, together with other radiatively important trace gases (e.g., CH_4, N_2O, halocarbons) is currently the dominant driver of global warming (Nick et al., 2013). The global mean surface temperature has reached ~0.9 °C above the long-term average before the industrial revolution and it is questionable that the targeted upper limit of 2 °C stated in the Paris Agreement can be met (Huang et al., 2017). This warming has large regional variation with temperature increases 2–4 times higher in the Arctic than the mean global temperature (Van Dinh and Nielsen, 2017).

All organisms have a permissive thermal window with upper and lower limits, and within those limits, temperature has a strong, non-linear effect on metabolic activities. This is true for both aquatic and terrestrial organisms. Marginal increases in temperature are generally expected to accelerate growth and development of organisms. Temperature is also an important environmental cue used by plants and animals to signal reproduction, senescence, migration, and other critical seasonal activities.

Corals dwell in habitats with temperatures close to their upper limit. Even though coral reefs are limited to <0.5% of the oceans they harbor about 25% of all marine species and provide important ecological and economic values (Albright, 2018). In the recent past several catastrophic bleaching events have decimated about 70% of all tropical reefs mainly due to elevated water temperatures (30–32 °C) augmented by massive El Niño periods (Eakin et al., 2016; Hughes et al., 2017). Despite serious endeavors to save the reefs by growing corals in nurseries, assisted evolution and freezing eggs and sperm in banks it has been estimated that only 10% of the tropical reefs will survive the rising temperatures by mid-century (Walker, 2017).

In contrast to sessile organisms, fish can escape the warming by moving polewards. As isotherms are migrating poleward (Gupta et al., 2015) and the Arctic is warming twice as fast as the global average many invasive species from temperate latitudes have been found to increase in abundance and distribution which results in community-wide shifts in species distribution, while Arctic fish species have retracted further North to the polar basin (Fossheim et al., 2015). Thus, climate change in conjunction with ocean acidification alters species composition and abundance which will affect fisheries which supports over 1.8 million jobs and contributes >200 billion USD in the US alone (Peterson et al., 2018). Also other species have been found to move from the tropics into the Arctic Oceans; e.g. plankton samples taken north of Svalbard showed an unusual abundance of tropical and

subtropical radiolaria (Bjørklund et al., 2012). The massive Arctic sea ice loss has opened up totally new ecosystems for phytoplankton and the food web building on them (Ardyna et al., 2014).

Increasing atmospheric temperatures are inducing many plant species to expand their habitats to higher latitudes and elevations (Dainese et al., 2017; Steinbauer et al., 2018). Species vary in their migration potentials (Körner et al., 2005) and, in some regions, non-native (alien) species appear too capable of migrating faster than native species (Averett et al., 2016). The shifts in distributions for some alien species may be facilitated by disturbance and land-use changes (Tanaka and Sato, 2016). Increasing temperatures also allow crop growing at higher latitudes. E.g. the productivity in low-temperature vineyards, such as in Eastern Germany has increased considerable during the last decades (Storchmann, 2018) and it may be feasible that wine growing will become possible in Scotland if the trend in climate change continues (Dunn et al., 2017).

As a result of warmer growth conditions and changes in the timing of seasons, many plants are also initiating growth and flowering earlier in the year today than they have in the recent past (Körner and Basler, 2010). Many animals are also emerging earlier or changing seasonal migration patterns (Cohen et al., 2018; Both and te Marvelde, 2007). These shifts in phenology and seasonal migration are exposing both aquatic and terrestrial organisms to novel combinations of abiotic (e.g., UV) and biotic factors (e.g, pollinators and pests) that can influence their growth and fitness (Rafferty, 2017). How these rapid changes in distributions will influence community organization and ecosystem function is largely unknown.

These temperature increases are also melting glaciers, sea ice, and altering cloud, wind and precipitation patterns. Although, increases in surface water temperature are smaller than that over dry land, these changes have far-reaching consequences as the oceans have a much greater heat storage capacity than land and absorb about 93% of the excess heat attributed to climate-change. Increases in ocean temperatures also result in stratification and shoaling of the upper mixed layer (UML), alteration in water mixing dynamics and sea level rise (Ehlert et al., 2017; Nick et al., 2013; Wang et al., 2015). In the Arctic the surface water temperature increase results in a massive loss in Arctic sea ice, and the Arctic Ocean is expected to be ice-free during the summer within the next three decades (Williamson et al., 2014). These changes could further accelerate warming as a consequence of reduced surface albedo.

The melting of land ice, together with the thermal expansion of ocean waters, are contributing to sea level rise and altering salinity in marine and coastal environments (Nicholls and Cazenave, 2010). Rising sea levels and tidal surges associated with tropical storms threaten to inundate and ultimately reduce the extent of coastal wetlands and mangrove swamps (Alongi, 2008). The intrusion of salt water into fresh water aquifers and coastal wetlands reduces coastal primary productivity (Neubauer, 2013) and can result in the replacement of highly productive fresh water plants by less productive salt tolerant species (Baldwin and Mendelssohn, 1998). These coastal wetlands and estuaries are critical nursery habitats for near- and off-shore fisheries. Consequently, disruption or loss of these ecosystems will have strong negative consequences for marine food production (Harley et al., 2006). These coastal systems are also important in protecting inland ecosystems from the destructive effects of storm surges and hurricanes (Costanza et al., 2008).

Changes in ocean temperatures, driven by greenhouse gas emissions and ozone depletion, are currently shifting wind and ocean circulation patterns in the Southern Hemisphere which in turn, influence regional precipitation patterns, drought, fire frequencies and vegetation growth in terrestrial habitats (Robinson and Erickson III, 2015). Some of these changes are acute in drylands (i.e., regions with arid and semi-arid climates) which are expected to experience even warmer temperatures than humid areas. Since drylands occupy over 40% of the land surface area on Earth (Prăvălie, 2016), the climate change-driven changes in vegetation composition and productivity have potentially large consequences for carbon cycling and storage (Ahlström et al., 2015), as well as the suitability of these landscapes to support grazing and dryland agriculture.

2.3. Precipitation and drought

The combination of increased temperatures, greater surface evaporation and reduced precipitation in some regions is increasing the occurrence and severity of droughts (Trenberth et al., 2013). In general, it would seem that drought would influence terrestrial organisms to a greater degree than aquatic organisms. Indeed, water is a fundamental ecological factor that limits the distribution of many terrestrial species, especially plants, and species vary greatly in their water requirements and abilities to tolerate moisture limitation (Pinheiro et al., 2002). However, the very survival of certain freshwater organisms (e.g. some fish species) depends critically on rainfall and runoff from terrestrial landscapes that determine stream flow and the persistence of seasonal ponds (Shattuck et al., 2013). Extreme precipitation events can also cause river flooding which can influence wetland plant productivity (White and Visser, 2016). For freshwater and estuarine systems, changing rainfall patterns can influence water quality and salinity which can then influence the productivity and composition of phytoplankton and aquatic plant communities (White and Visser, 2016).

The short-term effects of water limitation on land plants include stomatal closure, increases in stress hormones (e.g., ABA) and reduced capacities to transport water in conducting tissue (xylem) (Bray, 1997; Hsiao, 1973). These physiological changes lead to reduced photosynthesis, growth and crop yield (Osakabe et al., 2014). Longer-term exposure to water stress can shift patterns of root vs. shoot allocation, alter flowering and seed production, and in severe cases cause mortality (Pangle et al., 2015). At higher levels of organization, alterations in the amount and timing of precipitation are expected to have widespread impacts on species interactions, productivity and decomposition, and biogeochemical cycles in terrestrial ecosystems (Weltzin et al., 2003b). However, the magnitude and extent of these effects appear to vary with ecosystems, even within broad ecosystem types such as grasslands (Knapp et al., 2015). The causes of this differential sensitivity are unclear but may be related to species-specific functional traits and life history attributes.

There is now compelling evidence that increased drought in many ecosystems is indeed contributing to plant mortality (especially long-lived trees and shrubs) (Eamus et al., 2013; Pangle et al., 2015; Allen et al., 2010). However, the precise mechanisms causing mortality is sometimes unclear and may vary with species. For some species, mortality may be due to hydraulic failure and carbon starvation (McDowell et al., 2008). In other species, drought stress leads to weakened plant defenses against pests and pathogens which makes trees more susceptible to insect attack (Carnicer et al., 2011; Martinez-Vilalta et al., 2012). These changes increase standing dead material which then makes these systems more vulnerable to fire, which, in turn, results in the release of stored carbon into the atmosphere (Dale et al., 2001). Soil erosion and runoff can then accelerate in these ecosystems increasing the loading of dissolved organic matter in aquatic ecosystems (Williamson et al., 2016a).

Terrestrial vegetation plays a key role in the global hydrological cycle by releasing ca. 41 km^3 of water into the atmosphere per year (Chahine, 1992). This water ultimately returns as precipitation which contributes to stream flow and the recharge of soil moisture and underground aquifers. In moist ecosystems, the loss of forest cover resulting from deforestation or climate change can this have measurable negative effects for regional precipitation patterns (Coe et al., 2013). Increases in woody plant cover driven by changes in land-use and climate has been shown to reduce stream flow and ground water recharge in certain cases (Huxman Travis et al., 2005). In agricultural ecosystems, the increased use of water for crop irrigation to alleviate the effects of climate

change-induced drought can further reduce stream flow, the recharge of reservoirs and ground water levels (Elliott et al., 2014).

2.4. Solar UV radiation

In addition to the changes in atmospheric composition that contribute to global warming and climate change, ongoing changes in stratospheric ozone continue to influence surface levels of solar ultraviolet-B radiation (UV-B; 280–315 nm) (Bais et al., 2019). Ozone depletion is influenced by anthropogenically produced and emitted chlorinated fluorocarbons and other chlorinated organic compounds as well as temperature changes in the troposphere resulting from climate change (WMO, 2018). Ozone depletion can itself also influence climate change as noted above. At present, the ozone layer is showing signs of recovery because of the effects of the Montreal Protocol and its subsequent Additions and Amendments (Bais et al., 2018a). However, due to the long lifetimes of these substances in the stratosphere solar UV-B irradiances will only slowly decrease and may take till mid-century until they reach pre-1980s levels (Solomon et al., 2016).

In the future, changes in UV-B (as well as UV-A (315–400 nm) and photosynthetically active radiation (PAR; 400–700 nm) will likely be dominated by changes in cloud cover and aerosols (Bais et al., 2019; IPCC, 2014). Depending on region, these changes could increase or decrease UV exposures of both aquatic and terrestrial organisms. The UV exposures of understory plants will also change as plant canopies change as a result of changes in land cover (e.g., deforestation) and climate change (e.g., forest die-back from wild fires, drought and/or insect pests) (Predick et al., 2018). Climate change is also shifting species geographic ranges poleward and into higher elevations (IPCC, 2014; Pecl et al., 2017). For species migrating to higher latitudes these distribution changes will be associated with decreases in UV exposure (assuming no changes in cloud cover), whereas species migrating to higher elevations will likely experience increases in UV exposure (Blumthaler et al., 1997; McKenzie et al., 2001). The relative changes are expected to be greater for UV-B than UV-A (Caldwell et al., 1980; Nullet and Juvik, 1997). How these altered changes in UV exposures will influence migration processes is not currently known, but these changes in solar UV radiation have the potential to influence both aquatic and terrestrial organisms in a variety of ways that are both positive and negative.

In addition to these factors, climate change will alter exposures to solar UV radiation in other ways. Increasing temperatures result in ocean stratification and shoaling of the UML where most of the marine organisms dwell (Wang et al., 2015). This exposes the organisms to excessive solar visible and UV radiation (Gao et al., 2012). Most prokaryotic and eukaryotic aquatic primary producers have developed a number of mitigating strategies against damage by solar UV radiation including the production of UV-screeening substances such as mycosporin-like amino acids and scytonemin (Rastogi and Incharoensakdi, 2014). In addition, increasing temperatures facilitate the enzymatic repair of UV-induced damage to the DNA and the photosynthetic apparatus (Häder et al., 2015). Additional mechanisms against excessive exposure to solar UV are crust formation and vertical migration (Häder et al., 2015). Coastal ecosystems receive increasing amounts of dissolved organic material (DOM) from terrestrial run-off which has a strong absorbance in the UV region which protects organisms in these habitats (Bais et al., 2018a). However, coastal phytoplankton communities have been found to have a higher sensitivity to solar UV radiation than open ocean associations (Gao et al., 2018). Some organisms are more sensitive to solar UV than others and consequently the species composition changes substantially with changing environmental stress factors (Häder et al., 2014). To date, it is not possible to predict how aquatic communities will change in response to altered UV conditions.

Exposure to solar UV radiation (UV-B and UV-A) is well-known to influence the growth and physiology of terrestrial plants (Jordan, 2017; Verdaguer et al., 2017). While the shorter UV wavelengths (i.e., UV-B) are potentially deleterious to plants, there is little evidence to date indicating negative, detrimental effects of solar UV-B on plant productivity and crop yield (Ballaré et al., 2011; Fiscus and Booker, 1995; Searles et al., 2001). This likely reflects the fact that higher plants have evolved a number of mechanisms to protect themselves from UV-induced injury. One of the most widespread responses of plants to UV-B is the induction and accumulation of UV-absorbing compounds (flavonoids and other phenolic compounds) in epidermal tissue which serves to reduce the penetration of UV-B to underlying tissues (Caldwell et al., 1983; Day et al., 1994; Mazza et al., 2000). This response appears mediated, at least in part, by a UV-B photoreceptor in plants (UVR8) that orchestrates UV-B perception and the up-regulation of genes involved in flavonoid biosynthesis (Jenkins, 2014; Schreiner et al., 2017). This receptor has recently been identified also in green algae and mosses (Fernández et al., 2016). Some of these phenylpropanoid compounds are not only involved in UV protection, but also aid in protecting plants from pests and pathogens (Ballaré, 2014; Escobar-Bravo et al., 2017). At present, it is widely thought that UV-B can have both beneficial and negative effects on plants (Jansen and Urban, 2017; Neugart and Schreiner, 2018; Wargent and Jordan, 2013). Thus, even reductions in UV-B exposure have the potential to have negative, albeit indirect, consequences for the sustainable production and quality of food plants (Bais et al., 2018b; Ballaré et al., 2012).

The effects of UV radiation on ecosystems are largely mediated by effects on plants (e.g., insect herbivory as cited above). Most notably, the decomposition of plant litter has been shown to be accelerated by exposure to UV and short-wavelength visible radiation (Austin et al., 2016; King et al., 2012). Through the process of photodegradation UV contributes to the photochemical degradation of litter and the chemical modification of litter to enhance microbial decomposition (Baker and Allison, 2015; Ballaré and Austin, 2017). These effects appear most important in dryland ecosystems where high temperatures and low moisture limit the activities of decomposing microbes and where solar UV irradiances are high (Adair et al., 2017; Almagro et al., 2017). Although the quantitative importance of photodegradation in driving decomposition remains uncertain at present, it is clear that this process will be influenced by changes in land-cover and climate that alter the amount and quality of leaf litter produced in these ecosystems, their exposures to solar radiation and the activities of decomposing organisms that change with temperature and moisture conditions (Bornman et al., 2015). These changes, in turn, could potentially alter carbon storage and cycling, as well as atmospheric CO_2 levels (Sulzberger et al., 2019).

3. Conclusions

The growth and productivity as well as reproduction and development in both aquatic and terrestrial organisms are strongly affected by multiple external stress factors. How these organisms will respond to the simultaneous alterations in many of these environmental factors is poorly understood at present. While in the past often the effects of individual factors have been analyzed under controlled laboratory conditions it becomes more and more obvious that the additive, synergistic or antagonistic effects of all these factors in the environment have to be accounted for. For example, in certain cases, exposure to one stress can confer tolerance or sensitivity to another factor. This can happen when common signaling pathways are involved in the acclimation to environmental stress. For example, both visible and UV-B radiation can increase the accumulation of flavonoids with synergistic effects occurring when plants are exposed to both simultaneously (Barnes et al., 2013; Müller et al., 2013). Cross-tolerance may also exist between UV-B and drought, where UV-B can reduce the negative effects of drought on plants (Robson et al., 2015). In other cases, drought can decrease the adverse effects of UV-B (Araújo et al., 2016) but decreases the beneficial effects of elevated CO_2 (see above). Both temperature and CO_2 can also influence plant responses to UV-B (Randriamanana et al., 2015; Wijewardana et al., 2016). Understanding how plants respond to changes in multiple environmental variables is challenging but

necessary to fully evaluate how plants will respond to UV radiation in the context of future environments (Virjamo et al., 2014). Unfortunately, few studies have examined how plants respond to the combination of >2 or 3 factors at once. Understanding how entire ecosystems respond to the new, novel environments resulting from climate change is even more complex and may require fundamental changes in how ecologists conduct ecosystem studies (Schimel and Keller, 2015).

Since different organisms have different sensitivities toward individual stress factors, changes in species composition are inevitable when the stress increases. Elevated temperatures in conjunction with high nutrient availability often result in the development of harmful algal blooms (HAB) consisting of poisonous cyanobacteria or dinoflagellates (Hallegraeff, 2014; Paerl et al., 2014). Fossil records of dinoflagellate cysts indicate that altered stratification, ocean currents and nutrient availability resulting from El Niño events and changes in the North Atlantic Oscillation augment the occurrence of HABs (Hallegraeff, 2010). When inorganic nitrogen supply is limited the large pool of dissolved organic nitrogen as well as upwelling of deeper water can support HABs (Bronk et al., 2007). HABs are considered a nuisance in recreationally used waters and pose a threat to animal and human health (Dees et al., 2017).

In short, both aquatic and terrestrial ecosystems are affected by various stress factors induced by anthropogenic climate change. Since these factors can have additive, synergistic or antagonistic effects, ecosystem responses need to be analyzed under natural conditions taking into account all relevant stressors. Aquatic ecosystems have taken up about 93% of the anthropogenically generated excess heat but even though we monitor a rising temperature in both the atmosphere and the oceans. Responses of organisms are a poleward migration in both ecosystems and a upward migration of plants to higher elevations. Even though CO_2 is a limiting factor for photosynthesis, increasing concentrations have not been found to boost biomass productivity in either ecosystem. Rather it negatively affects many aquatic organisms since the resulting ocean acidification hampers calcification in phytoplankton, macroalgae and many zoological taxa including e.g. worms, shells and corals. Ozone-related elevated solar UV-B radiation has not been found to significantly affect productivity of terrestrial plants, but increased water temperatures result in shoaling of the upper mixed layer exposing the organisms dwelling there to excessive solar visible and ultraviolet radiation. Solar radiation levels in terrestrial ecosystems are mainly governed by changing cloud cover. Changes in precipitation (droughts and indundations), hurricane frequency and rising seawater affect terrestrial habitats. Predictions of consequences of further climate change stress factors indicate serious consequences for biomass and food production, species composition and extinction as well as ecosystem services all of which are of growing concern for a fast growing human population.

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