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Review

Disease-mediated ecosystem services: Pathogens, plants, and people

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Despite the ubiquity of pathogens in ecological systems, their roles in influencing ecosystem services are often overlooked. Pathogens that infect primary producers (i.e., plants, algae, cyanobacteria) can have particularly strong effects because autotrophs are responsible for a wide range of provisioning, regulating, and cultural services. We review the roles of pathogens in mediating ecosystem services provided by autotrophs and outline scenarios in which infection may lead to unexpected outcomes in response to global change. Our synthesis highlights a deficit of information on this topic, and we outline a vision for future research that includes integrative theory and cross-system empirical studies. Ultimately, knowledge about the mediating roles of pathogens on ecosystem services should inform environmental policy and practice.

Highlights

Pathogens are ubiquitous in nature, and they can play crucial roles in ecosystem processes.

Pathogens mediate many ecosystem services on which humans rely. Pathogens that infect autotrophs (e.g., plants, algae, and cyanobacteria) may be especially important to human well-being because these hosts are fundamental to ecosystem function.

While infectious disease is inherently negative from the perspective of infected hosts, pathogens infecting autotrophs can have positive or negative effects on ecosystem services.

Global change induces shifts in pathogen prevalence and disease severity, which may lead to unexpected outcomes for ecosystem services.

Understanding how pathogens impact ecosystem services can fundamentally improve our ability to make environmental decisions for a sustainable future.

Pathogens mediate ecosystem services, and their effects may shift in response to global change

Microbial **pathogens** (see Glossary) infect all organisms, including **autotrophs** that form the base of ecosystems by capturing carbon and energy [1,2]. Although **infectious disease** is typically studied from a host-centric perspective, the effects of pathogens extend far beyond the scale of infected host individuals to impact ecosystem processes. For example, fungal pathogens infecting grassland plants [3,4] and viruses infecting marine phytoplankton [1,5] mediate primary productivity and global carbon (C) cycling. The effects of pathogens on ecological processes are inherent in all systems, yet we have a limited understanding of how pathogens impact ecological function beyond their direct effects on hosts [6].

Critically, human societies rely on **ecosystem services** that are provided by autotrophs and hence, influenced by autotroph pathogens (Figure 1). Although the negative effects of pathogens on hosts that provide **provisioning services**, such as crop and timber production, are well studied and may inform management decisions [7,8], the effects of pathogens on other ecosystem services are often overlooked. For example, despite the importance of ocean and grassland productivity to C cycling and climate regulation [9,10], pathogen effects on these **regulating services** are typically omitted from ecosystem models and environmental decision-making processes.

Understanding how pathogens mediate ecosystem services is especially critical in the context of anthropogenic changes to the environment. Global changes in temperature, atmospheric carbon dioxide (CO_2) concentrations, precipitation patterns, and eutrophication contribute to changes in infection **prevalence** and **disease severity** in aquatic and terrestrial systems [11–14]. Shifts in disease patterns can lead to unexpected outcomes in ecosystem responses to global change, although this potential is not well understood. Following the recognition that global change is

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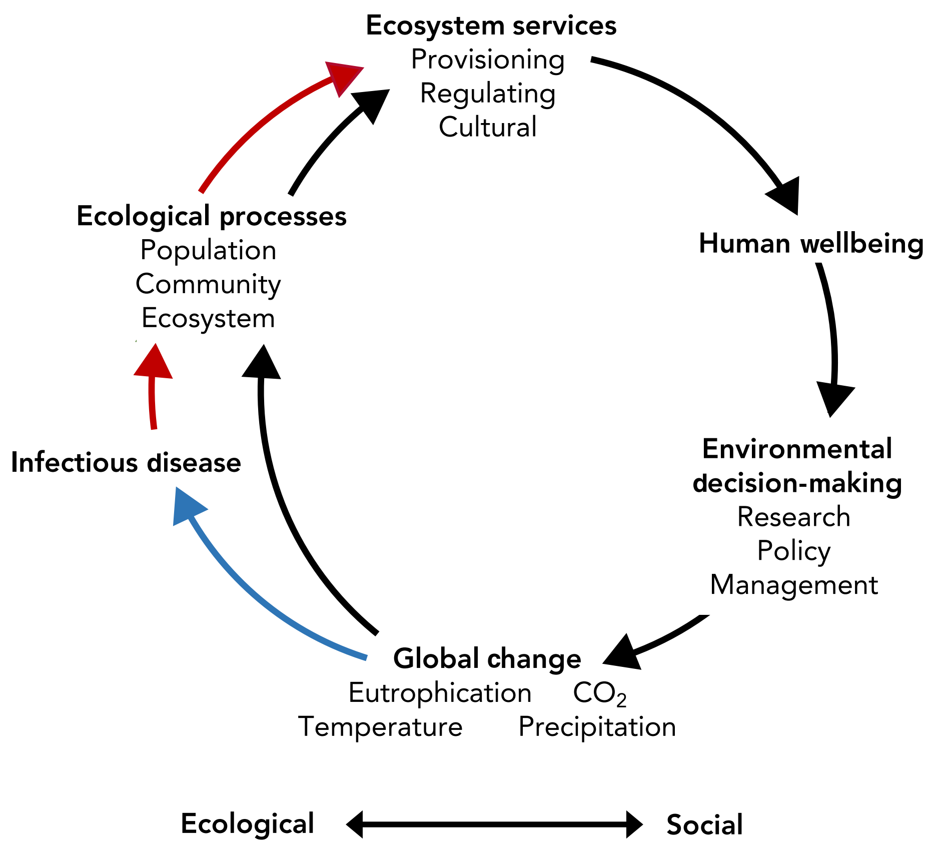
(A)



(B)

Diagram component	Traditional discipline or sector
→ Traditional socioecological paradigm	Environmental policymakers, resource managers, individual practitioners
→ Anthropogenic change impacts infectious disease	Disease ecologists
→ Infectious disease impacts ecological processes and ecosystem services	Disease ecologists, agronomists, aquaculturists, foresters

Trends in Ecology & Evolution

Figure 1. Ecological and social processes link global change, infectious disease in autotroph hosts, and human wellbeing. (A) Traditional perspectives (black arrows) on the processes linking environmental decisions, global change, ecosystem services, and human wellbeing omit explicit consideration of pathogens. However, anthropogenic changes to the environment can impact infectious disease dynamics in nature (blue arrow), and pathogens mediate many ecological processes and ecosystem services (red arrows). (B) The socio-ecological system depicted in (A) spans multiple sectors and scientific disciplines. Expanding the traditional paradigm to incorporate the effects of pathogens on ecosystem services requires improved communication and collaboration among these groups. Ultimately, understanding how pathogens mediate ecosystem services in the context of global change should inform environmental research, policy, and management practices.

degrading the quality of many ecosystem service categories [15], understanding the roles of pathogens in mediating these changes is critical.

Here we review evidence that pathogens mediate provisioning, regulating, and **cultural services**. This discussion inherently includes pathogen effects on **supporting services** (e.g., nutrient cycling, primary productivity) [15], which underlie all other ecosystem service categories and generally have indirect effects on humans. We focus on pathogens infecting autotroph hosts across freshwater, marine, and terrestrial systems to reflect the importance of primary producers to ecosystem services (Figure 2). While infectious disease is inherently negative from the perspective of autotroph hosts, the effects of pathogens infecting autotrophs on ecosystem services range from positive to negative (Figure 3). We also review evidence that global change leads to shifts in the prevalence or severity of infectious disease in autotrophs and outline scenarios in which these shifts will impact ecosystem services (Figure 4).

Through this synthesis, we aim to raise awareness among ecologists, socio-ecological scientists, and environmental decision-makers about the frequently overlooked effects of pathogens on ecosystem services. While scientists and practitioners currently address separate aspects of global change research and sustainability initiatives (Figure 1B), we argue that improved communication and collaboration among these groups is required to fully understand the complex, **socio-ecological system** that links anthropogenic activities, pathogens, and human wellbeing. Understanding the breadth of pathogen effects on ecosystem services is critical to the development of environmental policy and sustainable management strategies.

Provisioning services

Infectious disease directly decreases the quality of many provisioning services by reducing yields in food crops, fuel crops, and timber. Because these products have market value, the effects of pathogens on these provisioning services are relatively well quantified and sometimes inform management decisions [7,8]. However, pathogens that infect autotrophs also mediate provisioning services through less obvious mechanisms, including indirect impacts on livestock, fisheries, and drinking water.

Food provisioning: agriculture, aquaculture, and fisheries

Nearly 40% of Earth's most productive land is used for agricultural crops and livestock grazing, generating food and biofuels [16,17]. In this context, pathogens that infect autotrophs cause massive annual losses in the production of crops and livestock fodder. A recent estimate suggests that pathogens cause global yield losses of 14-21% for five major food crops, and these losses may be even higher in regions facing substantial food insecurity [18]. The detrimental effects of disease on crop yields can be exacerbated by agricultural monocultures and low genetic diversity in crop systems, which generally increase susceptibility to pathogens [19]. For example, the low number of potato cultivars grown in 19th-century Ireland contributed to the devastating potato late blight caused by the oomycete pathogen *Phytophthora infestans,* which led to the starvation of approximately 1 million people and the emigration of roughly 2 million more [20]. In addition to the effects of disease on crop yield, fungal infection can decrease food quality through the accumulation of mycotoxins in crops [21]. Many mycotoxins are carcinogenic to humans and have been linked with a range of other health problems [22]. Mycotoxins occur in the diets of a large fraction of the world's population and are especially damaging where reliance on contaminated corn, cereals, and nuts leads to chronic exposure [22].

Management strategies aimed at controlling crop disease, including pesticide application, crop rotation, and planting resistant cultivars, play important roles in global food security [21].

Glossary

Autotroph: Organism that produces organic compounds by capturing inorganic carbon and nutrients, thereby driving primary productivity. We focus on photosynthetic autotrophs that are terrestrial (trees, grasses, cultivated crops) or aquatic (algae, cyanobacteria, seagrasses).
Carbon (C) fixation: The process by which autotrophs capture inorganic carbon (carbon dioxide, CO_2) through photosynthesis
Carbon (C) sequestration: The capture and long-term storage of carbon in soil, living plants, or the ocean
Cultural services: Ecosystem characteristics that provide nonmaterial benefits to people through aesthetics, recreation, tourism, spirituality, education, science, or history
Disease severity: Individual-level estimate of pathogen burden or damage to an infected host
Ecosystem services: Benefits that humans derive from ecosystems, including provisioning, regulating, cultural, and supporting functions
Harmful algal bloom: Proliferation of microalgae or cyanobacteria in freshwater and marine ecosystems that negatively impacts human, animal, or ecosystem health
Infectious disease: Host condition resulting from pathogen infection; inherently negative from the perspective of the host
Pathogen: Causative agents of infectious disease in host organisms and mediators of ecosystem processes; includes viruses, bacteria, fungi, and oomycetes
Prevalence: Percentage of hosts within a population that are infected by a particular pathogen; used as a measure of population-level pathogen incidence
Provisioning services: Material products obtained from ecosystems, including food, fresh water, and wood
Regulating services: Ecosystem processes that maintain environmental conditions favorable to human life, including C cycling, climate regulation, and natural hazard regulation
Socio-ecological system: Tightly linked social and ecological subsystems that mutually impact one another
Supporting services: Ecosystem processes that support the production of all other ecosystem services and generally have indirect effects on humans (e.g., nutrient cycling, primary productivity)

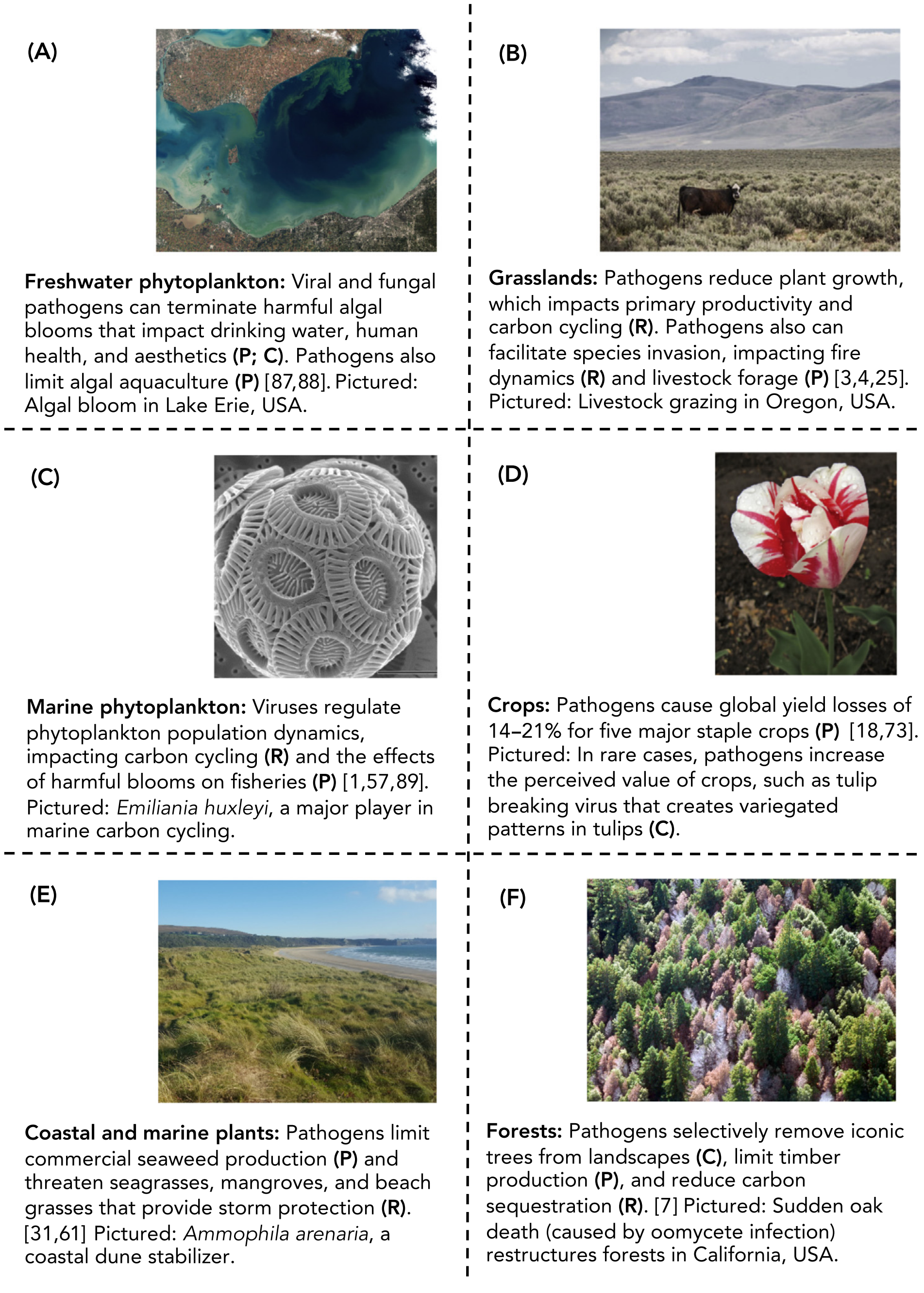


Figure 2. Pathogens that infect autotrophs mediate services provided by many ecosystems. Pathogens mediate provisioning (P), regulating (R), and cultural (C) services in (A) freshwater phytoplankton, (B) grasslands, (C) marine phytoplankton, (D) agricultural crops, (E) coastal and marine plants, and (F) forests. Open access photograph credits: (A) Public domain, https://commons.wikimedia.org/wiki/File:Toxic_Algae_Bloom_in_Lake_Erie.jpg; (B) CC-BY-2.0, https://www.flickr.com/photos/blmoregon/34757550354/in/photostream/; (C) CC-BY-2.5, https://commons.wikimedia.org/wiki/File:Emiliania_huxleyi_coccolithophore_(PLoS).png; (D) CC-BY-2.0, https://www.flickr.com/photos/jsjgeology/26555382654; (E) CC-BY-4.0, https://en.wikipedia.org/wiki/Ammophila_arenaria; (F) Public domain, https://commons.wikimedia.org/wiki/File:SOD_Mortality_of_Tanoak_in_Marin_Co._CA._(5812704234).jpg [1,3,4,7,18,25,31,57,61,73,87–89].

Host perspective: The effects of pathogens on hosts are inherently negative. Infectious disease reduces host fitness.	Human perspective: Depending on value of autotroph hosts to humans, pathogen effects on ecosystem services range from negative to positive.
(–) Pathogens limit the growth of food crops.	**(–)** Yield reductions threaten food security **(P)**.
(–) Pathogens infecting trees can selectively remove species from a landscape or cause extensive forest mortality.	**(–)** Iconic species are lost and landscapes are transformed **(C)**. Timber production declines **(P)** and forest fires may be more severe **(R).**
(–) Viruses cause continuous mortality in marine phytoplankton.	**(?)** Phytoplankton are key to marine carbon cycling and global climate regulation. The value of virus mediation of global climate is unknown **(R)**.
(–) Plant pathogens can limit the fitness of invasive species or native species, thereby impacting competition.	**(?)** Disease may limit or facilitate species invasion and mediate many services impacted by invasive species **(P, R, C)**.
(–) Fungal pathogens cause mortality in freshwater cyanobacteria, which can limit, terminate, or prevent algal blooms.	**(+)** Suppression of harmful algal blooms improves drinking water quality **(P)**, as well as aesthetics and recreation **(C)**.
(–) Tulip breaking virus (TBV) weakens bulbs and limits propagation.	**(+)** TBV creates variegated colors in flowers that increase their market value **(P)** and have inspired art **(C)**.

Key: (–) Negative effects; (?) Unknown effects; (+) Positive effects

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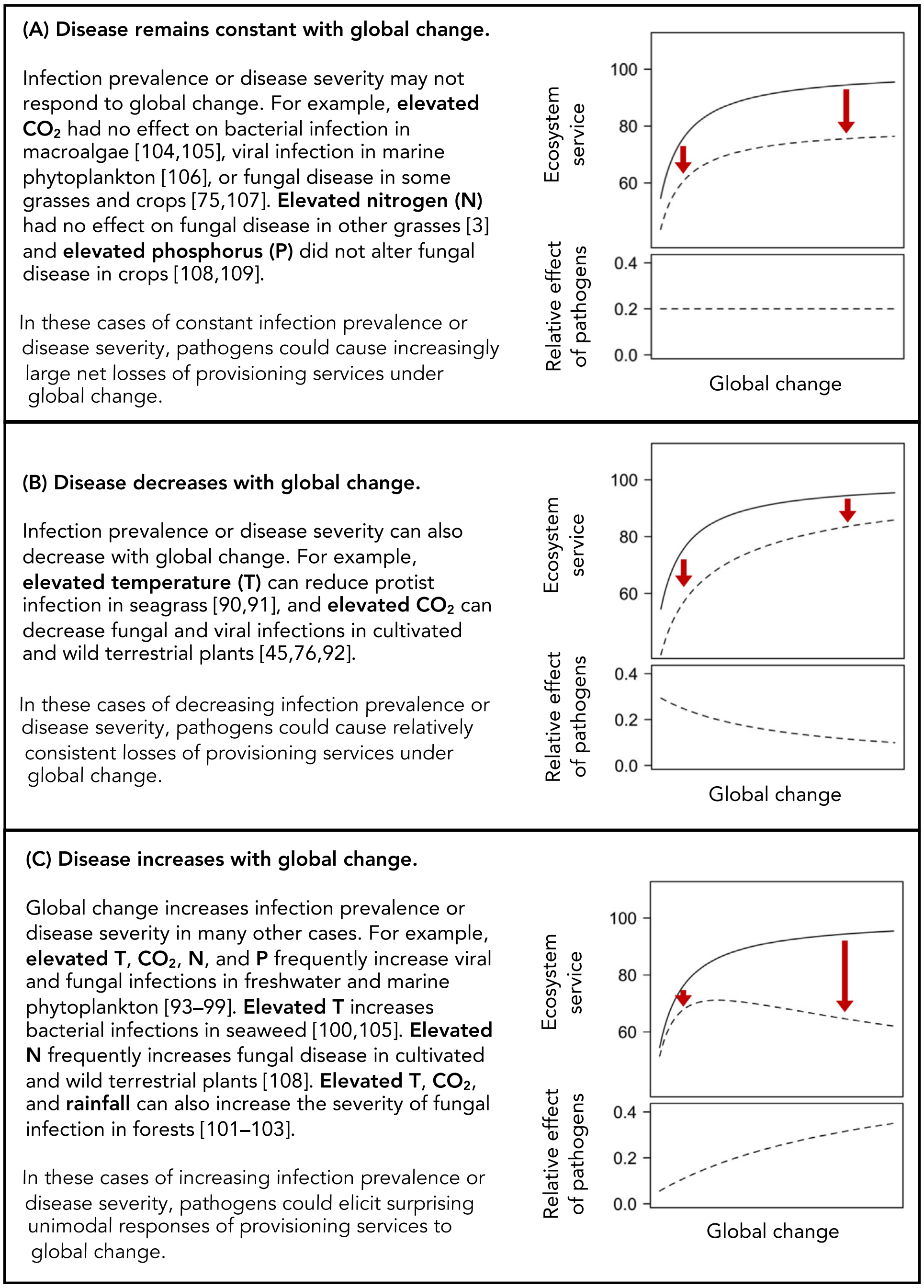
Figure 3. The value of autotroph disease is a matter of perspective. From the perspective of autotroph hosts (left column), infectious disease is inherently negative to fitness. From a human perspective (right column), pathogens infecting autotrophs have positive and negative effects on provisioning (P), regulating (R), and cultural (C) services.

However, some of these practices can have unintended, negative effects on other ecosystem services, such as the extensive environmental and human health costs of pesticide use [23]. Therefore, pathogens infecting food crops negatively impact ecosystem services directly by reducing yield and food quality and indirectly by precipitating management decisions that harm other ecosystem services.

Similarly, pathogens infecting grassland plants impact livestock production through direct and indirect effects on forage quality. In addition to their effects on human health, mycotoxins are harmful to livestock that consume contaminated grasses and other cereal crops [24]. Pathogens also can alter forage quality indirectly by driving shifts in grassland species composition. For instance, barley and cereal yellow dwarf viruses mediated the invasion of California's formerly native, perennial-dominated grasslands by non-native, annual grasses [25]. This invasion shortened the growing season for high-quality livestock forage and reduced forage nutritional value [26,27].



Trends in Ecology & Evolution

Figure 4. Pathogens mediate the effects of global change on ecosystem services. We outline three hypothetical ways in which infection prevalence or disease severity may respond to global changes in temperature, atmospheric CO_2, nutrient inputs, precipitation, or other factors. Infection prevalence or disease severity may **(A)** remain constant, **(B)** decrease, or **(C)** increase with global change (bottom panels). We assume here that the relative effects of pathogens on ecosystem services are proportional to infection prevalence or disease severity. These three responses lead to qualitatively different expectations for pathogen-mediated ecosystem services in response to global change (top panels). For simplicity,

(Figure legend continued at the bottom of the next page.)

In aquaculture, microalgae are grown to produce biofuels and dietary supplements [28]. Similar to agricultural monocultures, the use of monoclonal systems makes industrial microalgae production highly susceptible to pathogens [29]. The production of macroalgae (i.e., seaweed) for food has expanded rapidly over the past decade [30], and disease outbreaks caused by bacteria, fungi, and oomycetes have caused yield losses of up to 30% [31].

Pathogens infecting autotrophs also can benefit provisioning services. For example, the rapid growth of algae in marine ecosystems can lead to the formation of **harmful algal blooms**. Toxins produced by harmful algae can accumulate in shellfish produced for human consumption and contribute to fish kills [32]. Viruses and protists that infect harmful algae can prevent or limit bloom development [33,34], thus improving fisheries provisioning services.

Freshwater provisioning

Harmful algal blooms also occur in freshwater ecosystems [35], where they reduce drinking water availability and create health hazards for humans and domestic animals through toxin production [35,36]. As in marine systems, pathogens can control or suppress freshwater algae by causing continuous mortality in cyanobacterial hosts. Both viral and fungal infections are common during cyanobacterial blooms [37], with viruses removing up to 97% of potential cyanobacterial production [38]. Pathogens that infect marine and freshwater phytoplankton demonstrate the wide range of effects that autotroph disease can have on ecosystem services (Figure 3). While pathogens infecting algae have negative effects on provisioning services in algae-based aquaculture, pathogens infecting harmful algae in natural ecosystems also can have positive effects on fisheries, aquaculture, and drinking water quality.

Forest provisioning: timber and other products

Forests provide a wide array of provisioning services, such as timber, pulp, and food production [39]. Pathogens including fungi, oomycetes, viruses, and bacteria are integral to the natural functioning of forests through their effects on succession, tree diversity, decomposition, and wildlife habitat [7,40]. While these effects of native pathogens may contribute positively to a range of ecosystem services provided by forests, the spread of non-native pathogens can be extremely damaging to forests and their associated services [7,41]. For example, the iconic American chestnut (*Castanea dentata*) was nearly removed from eastern North American forests in the 1900s following the introduction of the fungal pathogen *Cryphonectria parasitica.* The chestnut blight that ensued led to a massive decline in American chestnut cover in forests across its range (from a historic 36% cover to less than 1%) and caused a loss of high-quality timber and nuts that were used as building materials and food for humans, livestock, and wildlife [42].

Regulating services

Pathogens impact many regulating services, the ecosystem processes that maintain environmental conditions favorable to human wellbeing. In contrast to the relatively well-quantified effects of pathogens on provisioning services, pathogen impacts on regulating services are often indirect and not well characterized. Nevertheless, pathogens shape critical services, such as the regulation of climate and natural hazards.

we outline a scenario in which a provisioning service (e.g., crop yield) is expected to increase and plateau in response to human activity (e.g., fertilization) in the absence of pathogens (top panels; unbroken lines). Pathogens reduce productivity (top panels; broken lines), and the magnitude of these deviations (red arrows) reveals the impact of pathogens on ecosystem services. While this general schematic is applicable to understanding how shifts in infection prevalence or disease severity impact any ecosystem service, note that predictions for how other ecosystem services are produced in response to global change (top panels; unbroken lines) vary among systems and that pathogens also benefit ecosystem services in some scenarios [3,45,75,76,90–109].

Carbon cycling and climate regulation

Pathogens infecting autotrophs in grasslands, forests, and oceans fundamentally mediate C cycling, and therefore climate regulation, through their effects on host physiology and population dynamics. In grasslands, pathogens impact the rates at which plants capture atmospheric CO_2 (**carbon fixation**), which has immense global importance because grasslands fix an estimated 0.5 Pg C each year [43] and store around 20% of global C stocks [44]. For example, fungal infection can reduce leaf-scale photosynthetic rate in grasses by more than 50% [45], which contributes to 30-40% reductions in grassland primary productivity and thus C fixation [3,4]. Grassland pathogens also impact C cycling indirectly by impacting species composition. For example, the virus-mediated shift from native perennials to non-native annuals in California grasslands [25] has been implicated in a 40 Mg/ha decline in soil C storage [46].

Carbon fixation by forests counterbalances approximately 30% of global C emissions [47], with old growth forests taking up ~0.85 Pg C annually, and the regrowth of forests following disturbance taking up an additional ~1.3 Pg C [48]. Pathogens can dramatically shift the capacity of a forest to fix and store C. Tree mortality from beech bark disease (caused by the fungus *Cryptococcus fagisuga*) and Dutch elm disease (caused by the fungus *Ophiostoma novo ulmi*) cause respective annual losses of 1.121 and 2.386 Tg C from living biomass in United States forests [49]. The long-term effects of non-native pathogens on forest C cycling depend on how forest communities respond following disease disturbance. Beech bark disease led to a decline in the cover of American beech (*Fagus grandifolia*) and an increase in sugar maple (*Acer saccharum*) in the New York Catskills region [50]. The relatively rapid replacement of American beech by sugar maple and the functional similarities between these two species led to no change in the net primary productivity of afflicted forests. However, this disease-driven shift in community composition led to a 40% decrease in the rates at which forest soils release CO_2 [51].

Marine phytoplankton fix 30-50 billion metric tons of C annually and are responsible for ~40% of Earth's annual **C sequestration** [52]. Viruses cause continuous mortality of marine phytoplankton and are estimated to mediate the recycling of more than a quarter of the C fixed by oceans [53]. Carbon released from dead phytoplankton can be recycled to fuel primary productivity or feed grazers [54,55] or can be exported to deeper parts of the ocean [56]. Marine viruses also promote cloud formation through the production of sea spray aerosols, which include viral particles and dead phytoplankton [57]. Viruses therefore impact the marine C cycle through multiple pathways [53], indirectly mediating atmospheric CO_2 and global climate.

Natural hazard regulation

Aquatic and terrestrial autotrophs can regulate the impacts of natural hazards on human society. For example, coastal plants such as seagrasses, mangroves, and beach grasses mitigate flooding and erosion in coastal areas, and these protective services will become increasingly critical with predicted increases in storm frequency [58,59]. Seagrasses mitigate the severity of coastal storm damage by dissipating wave energy, reducing current strength, and stabilizing sediment [58], but these services are threatened by pathogens. *Zostera marina* is the dominant seagrass of the northern hemisphere, but many populations have declined throughout its range over the past century [60]. Pathogens such as the oomycete *Phytophthora gemini,* the prevalence of which reaches as high as 74% in *Z. marina* populations across the North Atlantic, may be contributing to this decline by reducing seed germination and seedling development [61]. Similarly, the non-native beach grass *Ammophila arenaria* plays a critical role in dune stabilization and shoreline protection on the west coast of North America [59]. Soil pathogens reduce the growth and development of *A. arenaria* in its native range [62], and the introduction of these pathogens into its non-native range could thus potentially reduce coastal storm protection.

Pathogens infecting forest and grassland plants can impact the frequency and intensity of wildfires. Virus-mediated changes in California grasslands [25] are widely associated with increases in the intensity and frequency of fire regimes [63,64]. Similarly, California forests that have been invaded by the oomycete pathogen *Phytophthora ramorum* have experienced more severe fires following the accumulation of dead plant material [65], and fire and disease synergistically cause tree mortality that exceeds the losses expected from either of these disturbances individually [66].

Cultural services

The effects of pathogens on cultural services are difficult to quantify because these intangible services depend on local value systems and often go unmeasured. Nonetheless, pathogens infecting autotrophs play key roles in mediating a range of cultural services.

Disease can transform landscapes through the removal of dominant, iconic species. For example, American chestnut was a culturally important species (in addition to its timber and food value) prior its decline from chestnut blight, as evidenced by its role in poetry such as Longfellow's *The Village Blacksmith* [67]. On the west coast of North America, disease threatens another iconic species: the coast redwood (*Sequoia sempervirens*). While redwoods are usually resilient to wildfire, more severe fires in areas of California invaded by *P. ramorum* have led to unexpected redwood mortality [66]. In contrast, viruses and fungi that infect freshwater cyanobacteria can improve landscape aesthetics, recreation, and property values [37,38] by reducing the occurrence of toxins and malodors produced during harmful algal blooms [68,69].

In some cases, the effects of plant disease on crop yield and food safety may combine with social factors to cause cultural upheaval. For example, social disarray and political reform followed the death or emigration of a quarter of Ireland's population due to potato late blight in the 19th century [70]. Crop disease also can shape culture through less obvious means, such as its potential role in the Salem witch trials of the late seventeenth century. The physiological symptoms that can result from consumption of mycotoxins in contaminated grain have been implicated in the behavior of women accused of witchcraft and subsequently executed [71], although this hypothesis has been disputed [72]. In rare cases, pathogens can add value to the cultural value of plants. Tulip breaking virus, the earliest known transmissible plant viral disease, causes variegation in tulip flower color. The aesthetic appeal of infected tulips has been evident since the 17th century, when these flowers began to serve as inspiration for Dutch painters and poets [73].

Pathogens mediate the effects of global change on ecosystem services

Anthropogenic activities have degraded most categories of ecosystem services [15], and understanding of the mechanisms behind these changes will inform environmental decisions [74]. While global changes in temperature, atmospheric CO_2, nutrient inputs, precipitation, and other factors contribute to shifts in pathogen prevalence and disease severity [11–14], we know relatively little about how these changes in disease will impact ecosystem services.

Critically, pathogens may lead to unexpected outcomes in how ecosystem services respond to global change (Figure 4). Infection prevalence or disease severity may remain constant (Figure 4A), decrease (Figure 4B), or increase (Figure 4C) in response to global change. This response will determine whether the magnitude of pathogen effects on ecosystem services shifts under global change. For example, pathogens may contribute to a net decrease in ecosystem services that depend on primary productivity (e.g., crop yield), even in scenarios where infection prevalence remains constant under global change (Figure 4A). Pathogen effects may be especially important when infection prevalence or disease severity increase with global change, which may drive an unexpected, unimodal response in ecosystem services (Figure 4C). While increased infection prevalence or disease severity would negatively affect ecosystem services in situations where hosts benefit society (e.g., crops or beach grasses), increased disease could also positively impact ecosystem services in systems where hosts are harmful (e.g., cyanobacterial blooms).

While the examples in Figure 4 address individual effects of temperature, nutrients, CO_2, and precipitation on autotroph disease, these environmental variables are changing simultaneously and may interact to impact disease. For example, elevated temperature and CO_2 interact to promote fungal disease severity and mycotoxin production in a range of food crops [75]. Furthermore, despite ample evidence that global change impacts infectious disease in autotrophs, the effects of altered infection prevalence or disease severity are rarely extended to explicitly consider impacts on ecosystem services. While global change research on crop disease inherently includes consideration of food provisioning [75–77], the unknown effects of global change on disease in other systems are likely to play substantial and potentially unexpected roles in the long-term sustainability of ecosystem services.

Concluding Remarks and Future Perspectives

Advancing knowledge at the intersection of global change, disease, and ecosystem services represents a critical scientific frontier. Progress on this topic will require the prioritization of fundamental and applied research questions (see Outstanding Questions) as well as improved communication and collaboration among scientists and stakeholders (Figure 1). We have outlined many examples in which pathogens substantially mediate ecosystem services and the potential for global change to alter these effects. While we have not conducted an exhaustive review of empirical evidence, our synthesis highlights a deficit of studies making the full link from global change to pathogen effects on ecosystem services.

We encourage additional empirical research on pathogen mediation of ecosystem services. Understanding of the mechanisms linking global change, disease, and ecosystem services across systems will support the development of integrative theory that incorporates the roles of pathogens into ecological processes. For example, models describing ecosystem C dynamics are critical to the understanding of global climate, yet such models traditionally do not account for pathogen impacts on autotroph growth, survival, or decomposition rates. New models accounting for the effects of pathogens on C flux and the reciprocal effects of ecosystem properties (e.g., atmospheric CO_2) on disease transmission could fundamentally improve our ability to understand ecosystem C dynamics and climate regulation.

The roles of pathogens as mediators of ecosystem services may be complicated by complexities of disease ecology that we have not covered in this review. For example, global change can alter evolutionary processes in host-pathogen interactions [78], which may correspond to changes in how pathogens mediate ecosystem services. While many examples included in this synthesis focus on the effects of single-pathogen infections, coinfection by multiple pathogens is common [79] and may influence disease effects on ecosystem services. Finally, invasions of non-native pathogens and other forms of disease emergence constitute another important, ongoing form of global change that we did not exhaustively cover in this synthesis [80]. Thus, a clear knowledge gap is whether invading pathogens have qualitatively different effects on ecosystem services compared with native pathogens.

Although we focused this review on disease in autotroph hosts, pathogens and parasites mediate ecosystem services through direct and indirect impacts on other trophic levels. For example, the direct effects of livestock disease on food provisioning are relatively well understood [81], but

Outstanding Questions

Pathogens, Ecosystem Services, and Global Change

- How do multiple global change fac tors interact to impact the effects of pathogens on ecosystem services?
- Can global change lead to qualitative shifts in the effects of pathogens on ecosystem services (e.g., from posi tive effects of pathogens on services to negative effects)?
- Does incorporating the effects of pathogens into models on how ecosystem services (e.g., C seques tration) respond to global change critically alter model predictions?
- How will global change impact evolutionary processes in host-pathogen systems, and what will be the consequences for ecosystem services?

Host-Pathogen Interactions and Eco system Services

- What characteristics of host-pathogen systems or ecological systems predict the importance of disease to ecosystem services?
- Can the biomass of infected hosts within a system be used to predict the relative magnitude of pathogen effects on ecosystem services?
- How does coinfection impact pathogen mediation of ecosystem services?
- Do pathogen invasions lead to qualitatively different effects on ecosystem services compared to native pathogens?
- Do autotroph-pathogen interactions impact ecosystem services provided by higher trophic levels?

Pathogen Impacts on Ecosystem Services in PPolicy

- What strategies can be implemented to increase communication and collaboration among scientists, decision makers, and other stakeholders about the role of pathogens in ecosystem services to improve environmental research, policy, and practice?

disease in large herbivores also mediates regulating services in less obvious ways. Roundworm infection in lambs causes a 33% increase in the production of methane, a major greenhouse gas [82], and viruses infecting wild herbivores can impact ecosystem C storage [83]. Autotroph-pathogen interactions may also impact ecosystem services provided by higher trophic levels. For example, fungal pathogens that reduce phytoplankton blooms also provide food for zooplankton [84]. Such trophic links involving pathogens are likely to contribute to food web stability [85], supporting services provided by higher trophic levels, such as fisheries.

Beyond these knowledge gaps, there is a need for more effective communication between scientists and decision-makers, managers, and other stakeholders to translate research into practical strategies to protect and optimize ecosystem services in the face of global change. Policy and management decisions based on incomplete knowledge of complex, socio-ecological systems can lead to unintended consequences for sustainability [86], and pathogens may generate some of these negative outcomes. Management strategies meant to limit the negative effects of infectious disease on production systems are common in agriculture [8] and forestry [7]. Developing management strategies to optimize pathogens impacts on other ecosystem services presents a greater challenge, especially in systems where we lack fundamental information about how pathogens mediate ecosystem processes.

Overall, this review demonstrates the need for an expansion of the paradigm through which we view and study pathogens to include their roles as regulators of ecosystem services. This expansion will improve our predictions of how ecosystems will function under future environmental scenarios, which is critical to optimizing the sustainability of ecological systems and the services they provide.

Author contributions

Author order is random between first and last. R.E.P. led manuscript development and completion. R.E.P., E.T.B., E.W.S., A.T.S., T.F., A.L.G., D.B.V.d.W., and L.A.W. developed the text and figures. All authors contributed to the initial framing of the manuscript and to the completion of the final version.

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