

Microorganisms and Climate Change: A Not so Invisible Effect

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Abstract: The effect of climate change on flora and fauna has been widely discussed for years. However, its consequences on microorganisms are generally poorly considered. The main effect of climate change on microbiota is related to biodiversity changes in different regions of the planet, mainly due to variations in temperature. These alterations are resulting in a worldwide (re)distribution of pathogens, which was not considered a few years ago. They mainly affect different food chain sectors (such as agriculture, livestock and fishing), as well as human health. Hence, the spread of numerous animal and plant pathogens has been observed in recent years from south to north (especially in America, Europe and Asia), leading to the spread of numerous plant and animal diseases, which results in economic and ecological losses. In addition, global warming that accompanies climate change could also be related to emerging antibiotic resistance. However, the mitigation of climate change goes hand in hand with microorganisms, which can help us through different natural and industrial processes. Thus, this manuscript presents the direct and indirect effects of climate change on microorganisms described up to date and how they act on this worldwide phenomenon.

Keywords: climate change; microorganisms; fungi; bacteria; pests; diseases; global warming; antibiotic resistance; human health; animal health; plant diseases

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1. Introduction

Climate change is probably the main concern of the 21st century, which not only affects the weather people experience but also the air they breathe, the water they drink, the food they eat and even where they are able to live. In the last decades, extreme weather events have become frequent, and records are continuously being broken. Thus, the last few years have been the hottest on average as long as records have existed, and more than 400 weather stations all around the World have beaten their heat records in 2021 (reaching up to 48.8 °C in Italy on 20 July, 49.6 °C in Canada on 29 June or even 54.4 °C in the US on 9 July) [1]. The global annual temperature has increased by 0.08 °C on average per decade between 1880 and 1981, culminating in 2021 with a temperature of 0.84 °C above the average of the 20th century, according to the “2021 Annual Climate Report” of the NOAA (National Oceanic and Atmospheric Administration of the US Department of Commerce; <https://www.ncdc.noaa.gov/sotc/briefings/20220113.pdf>, accessed on 21 July 2023). In addition, the mean annual precipitation is expected to be lower in southern Europe and higher in northern Europe over the next few years, leading to warmer and drier climates, particularly in southern and central Europe during spring and summer. In short, an increase in the risk of extreme weather events, such as heatwaves, extreme rainfall and extended drought periods, in the years to come due to climate change is strongly suggested [2].

Climate change seems to be the result of both natural (Earth's magnetic field changes) and anthropogenic (e.g., methane and carbon emissions) factors [3,4]. It was first reported in 1824 by the French physicist Joseph Fourier [5], but it was not until 1975 that Wallace Broecker introduced the term "global warming" into the public domain [6]. Sixteen years later, the Intergovernmental Panel on Climate Change (IPCC) was formed to collate and assess evidence. Thus, climate change can be defined as the long-term alteration of temperature and typical weather patterns (including, but not only, temperature, rainfall and wind). These changes can cause an unprecedented loss of biodiversity and endangered life on Earth. However, although the loss of plant and animal species has been reasonably well studied and documented, the effects of climate change on microorganisms are generally overlooked [2].

Microorganisms date back to Earth's origin, at least 3.5 billion years ago [7], and they will undoubtedly exist well beyond any future extinction events. Their abundance and diversity ($\sim 10^{30}$ bacteria and archaea cells and $\sim 10^{12}$ microbial species) are the life support of the biosphere and the basis for maintaining healthy ecosystems [2]. They play a critical role in nutritional cycles, such as carbon and nitrogen, as well as in animal (including humans) and plant health, agricultural yields and food security. Thus, as climate change can intensify seasonal disturbances and lead to an increase in extreme events [8], it is reasonable to consider a possible effect on microbial biodiversity and its subsequent consequences [2,9,10]. Nowadays, the most studied effect of climate change on microorganisms refers to the increase in animal and plant pathogens due to the geographical expansion of numerous marine and terrestrial vectors, mainly because of global warming [2], as detailed throughout this work. However, the relationship between microorganisms and climate change is a two-way road, since microorganisms can directly affect climate change due to their involvement in greenhouse gas (GHG) synthesis and consumption, but they are part of the solution by acting as mitigation agents, and also their biodiversity is being affected by environmental modifications.

2. Impact of Climate Change on Microbial Diversity

Ecology aims to understand the generation and maintenance of biodiversity over time and space, where climate strongly conditions the structure and interactions inside communities, as well as their functionalities [11]. Thus, the impact of climate change on the ecosystems' inhabitants, including microorganisms, is expected to be significant and complex, although its quantification seems challenging [12]. Among all the environmental factors affected by climate change (e.g., alterations in precipitation patterns, drought stress and changes in radiation), global warming has a pervasive influence on the variation in soil microbial diversity, playing a primary role in shaping microbial diversity compared to other proposed environmental drivers by increasing the temperature in the surface soil and decreasing its moisture [13,14].

It is important to note from the outset that the effects of climate change on microbial communities in both terrestrial and aquatic environments are complex and, at times, even contradictory, with both deterministic and stochastic influences. On one hand, it has been widely reported that changes in temperature have an impact on microbial biodiversity at various levels (e.g., geographical range, phenology, distribution or abundance) [13]. Microbial metabolism, population growth rate and species number increase exponentially with increasing temperature. In fact, bacterial and fungal diversity tends to decrease with increasing global latitude as temperatures decline [14]. However, variations in temperature can affect microbial biodiversity through several mechanisms. First, the most commonly reported mechanism is that increasing temperature leads to higher rates of metabolism, resulting in increased population doubling times [14] as well as the rates of ecological and evolutionary processes, including mutation, speciation and interactions (e.g., parasitism, predation, competition or mutualism among others) [12,14,15]. Therefore, if temperature drives the increase in microbial diversity, it can be expected that warming ecosystems (from tropical to alpine forests) will become more diverse and active, potentially

enhancing processes such as decomposition, nutrient cycling and carbon sequestration [14]. However, higher temperatures can also act as a deterministic filter, selecting more adapted microorganisms and constraining the stochastic drift and dispersal of species, ultimately leading to a decrease in the temporal scaling rates of soil microbial communities. In addition, microbial community responses to climate change greatly depend on microbial lineages and functional groups [12,15].

On the other hand, higher temperatures lead to an increase in the number of plant species, and this higher plant diversity allocates nutrients to belowground ecosystems, as there is a well-known correlation between microbial taxa richness and plant species diversity [14]. This shift in nutrient allocation could lead to changes in plant–microbe interactions, particularly affecting populations of plant growth-promoting rhizobacteria (PGPR) that rely on rhizodeposition [16,17]. In addition, the alterations in precipitation patterns and drought stress associated with climate change negatively impact the formation of a mycorrhizal mycelium in plant roots [16,18]. These changes in climatic conditions contribute to an increased incidence of environmental stresses, which can also enhance the activities of pathogens and heterotrophic microorganisms, leading to the redistribution of beneficial microbes across different ecological niches [16,17].

Despite the reported potential impact of climate change on microbial composition and interactions, most of the conducted studies have focused on specific regions and conditions (especially on terrestrial ecosystems). Therefore, given the complex interplay between microorganisms and their biotic and abiotic surroundings, information obtained from a single point in time provides only a snapshot of the microbial community, and it is unsuitable for ecosystem model simulation and interpretation. Further research is needed to fully comprehend this dynamic relationship.

3. Microorganism Involvement in Production/Consumption of Greenhouse Gases

The appearance of oxygenic photosynthetic cyanobacteria, 2.3 billion years ago, altered the course of evolution by allowing aerobic respiration and the development of complex multicellular life [19]. Since then, microorganisms have been involved in some of the most relevant events in recent history, such as the 1918 influenza pandemic (with a third of the world's population infected and 50 to 100 million deaths); the discovery of penicillin by Alexander Fleming in 1928 [20], allowing the beginning of the golden era of antibiotics; or the recent COVID-19 outbreak due to the SARS-CoV-2 coronavirus.

Microorganisms are simultaneously involved in the production and consumption of three main GHGs responsible for 98% of the increase in global warming: carbon dioxide (CO₂), methane (CH₄) and nitrous oxide (N₂O) [21]. First, microorganisms are part of a large global carbon cycle. They extract carbon from non-living sources and make it available to other living organisms, mostly from atmospheric carbon dioxide (carbon fixation). The best-known example of carbon fixation is photosynthesis, and, despite this process being mainly attributed to plants, half of the global CO₂ photosynthetic incorporation is performed by marine phytoplankton (e.g., *Vicicitus* spp. or *Emiliana huxleyi*) even though they only represent 1% of the photosynthetic biomass of the entire biosphere [2,19].

Secondly, methane is a simple hydrocarbon that is ~30 times more impactful than CO₂ as a GHG. While microbes are sources of CH₄ (between 70–90% of the total methane produced) as part of natural processes, some of their recent increase is due to changes in human activities. Methane is mostly produced “anthropogenically” (as a result of human activity) during agricultural practices (e.g., feed digestion in ruminants due to methanogenic archaea, rice paddies), as well as methanogenic microorganisms in landfills, coal mines and natural gas production. However, natural sources of methane also exist, such as anoxic sediments (oceans and lakes), wetlands, termite nests and soils [22]. In contrast, methane-consuming microorganisms are crucial for maintaining a worldwide balance, as these methanotroph species (which literally means “methane eaters”) are able to use this methane as an energy source [1,2,19,23]. Examples of well-known methanotrophs are the members of the genus *Methylococcus* or *Methylobacter* [22].

Finally, nitrogen is one of the most important gases in the atmosphere (~78%), which exists in numerous forms, such as NH_3 , NO and N_2O , although N_2 is its most habitual state. However, it is not directly available to plants and animals, and it enters the biosphere via biological fixation through different bacteria (such as *Azotobacter*, *Beijerinckia*, *Clostridium* or *Rhizobium*) or blue-green algae. Hence, marine fixation is 30% higher than terrestrial nitrogen fixation [19,23].

This brief introduction of microbial relevance in the GHG worldwide balance presents microorganisms as relevant players in climate change, but they also play several roles outside atmospheric gas control. Thus, the relationship between climate change and microorganisms (including bacteria, fungi, unicellular algae and protozoa) will be addressed point-by-point along different human sectors (e.g., industrial and health).

4. Microorganism-Mediated Effect on Productive Sectors

Climate variations (e.g., temperature increase, rainfall instability, glacial retreat, extreme weather events, etc.) have foreseeable impacts on certain industries. These impacts encompass technical concerns (e.g., power supply) or extend to more severe problems in sectors such as agriculture, forestry, livestock and commercial fishing, which are primary sectors of great economic relevance, whose global value grew by 73% between 2000 and 2019, reaching USD 3.5 trillion in 2018 [24]. Nowadays, farmers and scientists are already both turning their eyes to the use of biofertilizers and eco-friendly tillage practices in order to protect soil health, reduce GHG emissions and increase carbon sequestration [25]. However, the increase in outbreaks of several diseases, as well as the geographical expansion of different pathogens, is compromising the balance between eco-friendly activities and the way to face these new climate-change-derived risks [2] (Figure 1). Thus, the microorganisms involved in these processes play a crucial role as detailed below.

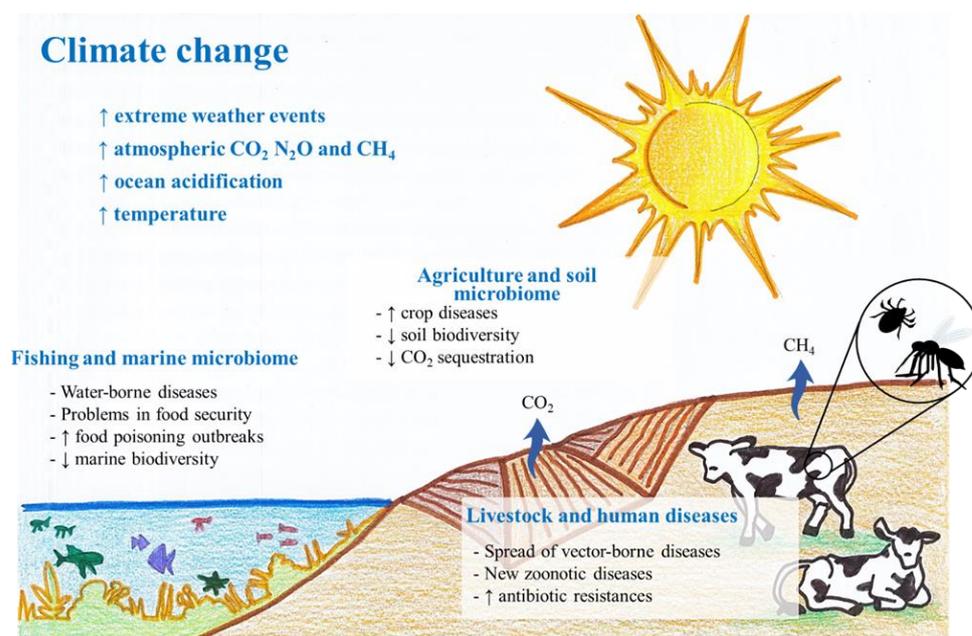


Figure 1. Main effects of climate change on microorganisms: (i) expansion and increase in water-borne diseases affecting fish and shellfish and causing an increase in food poisoning outbreaks and loss of marine biodiversity; (ii) expansion and intensification of pathogenic fungal infections in crops all around the world; and (iii) outbreaks of livestock diseases, emergence of new zoonotic diseases and increase in antibiotic resistance.

4.1. Agriculture and Soil Microbiome: Eternal Feedback

One of the most important worldwide primary sectors is agriculture, which relies on food production. The total production of crops increased by 53% between 2000 and 2019, yielding 9.4 billion tons in 2019 [26]. However, the variation in soil microbial communities influenced by climatic change affects the physiology, temperature sensitivity or plant growth rate, which jeopardizes the final yields and compromises the future of this sector [27]. The relationships among microorganisms, atmospheric gases and crops showcase an intricate feedback system. Discrepancies have been observed between short-term laboratory studies and long-term field experiments on how climate change affects soil communities and nutritional balances. These differences may be caused by several factors, including variations in environmental conditions, differences in experimental designs and the complexity of soil ecosystems [27–31].

Thus, increased temperatures accelerate microbial decomposition activities, leading to faster CO₂ emissions. As a result, soils will become a carbon dioxide source rather than a sink [27]. However, an increase in atmospheric CO₂ has been reported to stimulate rhizosphere-colonizing bacteria such as *Burkholderia* and *Pseudomonas* as well as plant-growth-promoting fungi, while non-rhizospheric species such as *Bacillus* were not stimulated. This CO₂ enrichment enhances the development of rhizobial populations and the increase in N-fixing microorganisms in controlled environments, although multiple resource limitations dampen rhizobial responses in natural systems. In contrast, high temperatures lead to drought, which reduces colonization by arbuscular mycorrhizal fungi [27,28].

In addition, temperature and soil humidity play a critical role in microbial-soil abundance, diversity and metabolic functionality, since climatic factors greatly modify the type and quantity of some plant species that predominate in a landscape. Thus, owing to the relationship between soil microbial biodiversity and the presence of certain plant species, this vegetal redistribution also affects soil microbial communities in a continuous feedback system [29,30]. Furthermore, the consequences of climate change on soil communities and nutritional balances depend on the specific soil type, vegetation cover and management techniques. As a result, the total effects of climate change on soil communities and nutritional balances seem logical but unclear [27,28,32].

4.2. Plant Pests' and Diseases' Effect on Agriculture and Forest: The Uncomfortable Travelers

The prediction of climate change effects on crop yields is being analyzed by means of several models, which, despite not being consistent with the final balances, predict multi-million dollar losses in numerous crops throughout the world as a result of pest and pathogen movement to new geographic locations [33–38]. In 2020, Delgado-Baquerizo and co-workers demonstrated that warming temperatures increase the presence of soil-borne fungal pathogens [39], and Bebbler and co-workers' study in 2013 reported that the poleward movement of numerous pathogens and pests of around 3 km per year has been underway since 1960 [40]. However, although there are certain difficulties in accurately quantifying the potential impacts of climate change on plant pests, crop production and risks to natural biodiversity [41,42], numerous bacterial and fungal diseases have already begun their geographical expansion, although most of them have not actually been related to climate change (Table 1).

Fungi annually destroy one-third of all food crops, including rice, wheat, maize, potatoes and soybean. The mitigation of this loss would have been enough to feed around 8.5% of the world population of seven billion in 2011 [38]. According to Chaloner and co-workers [43], Europe and North America, followed by some regions of Asia, are expected to be the most affected areas by the spread of non-commonly detected fungi as a result of the temperature increase, where the most economically devastating is *Magnaporthe oryzae* affecting rice and wheat [38]. Thus, some models create a devastating scenario for 2050, with a large increase in fungal infections throughout Europe, such as the following:

- Brown rust (mainly caused by *Puccinia recondita*), in the case of wheat, is forecast to increase its pressure on the crop by 20–100%, and yellow rust (caused by *Puccinia striiformis*) will increase by 5–20% in cold regions.
- Rice pathogens such as *Pyricularia oryzae* (the main cause of blast) and *Bipolaris oryzae* (or brown spot) are favored in all European rice districts, with the most critical situation in northern Italy (with an increase of close to 100%).
- In the case of grape, *Plasmopara viticola* (also called downy mildew) will increase by 5–20% across Europe, while *Botrytis cinerea* (or bunch rot) will have diverse impacts, ranging from a 20% decrease to a 100% increase in infection events [44].

Indeed, the spread of several agricultural diseases toward northern regions of Europe has already been reported:

- An increase in cases of diseases in leafy vegetable and cereal crops has already been reported in Italy, as a result of several pathogens' effect, such as *Plectosphaerella cucumerina*, *Alternaria* sp., *Fusarium equiseti*, *Myrothecium verrucaria*, *Myrothecium roridum*, *Phoma valerianellae*, *Pleospora betae*, *Peronospora belbahrii* and *Pythium ultimum*, as well as the appearance of new pathogens like different species of *Pythium* (*Pythium aphanidermatum*, *Pythium irregulare*, *Pythium dissotocum*, *Pythium coloratum*, *Pythium diclinum* or *Pythium lutarium*) and new species causing yellow rust or stem rust [44–46].
- Among the new infections that have been reported in recent years in southern Europe and the Mediterranean coast, different species of the fungus *Diaporthe* have been found infecting several citrus, and the bacterium *Xylella fastidiosa* has also been discovered in olive trees [47].

On the other hand, fungal infections of invertebrate hosts also require attention, not only because they are an important route of transmission of pathogens to new areas but also because they can boost agricultural crises due to ecological imbalance. Thus, a dramatic example is bee broods, which are susceptible to some fungal infections, like those caused by *Ascosphaera* and *Aspergillus*, and viruses, such as Deformed wing virus (DWV) or Varroa destructor virus-1 (VDV1). Thus, agricultural production is highly dependent on bee pollination, and infections may lead to unprecedented disasters (see below) [29,41,48].

Table 1. Geographical expansion of agricultural diseases reported in recent years.

Disease	Pathogen	Host	Origin	Spread and Development	Ref.
Ash dieback	<i>Hymenoscyphus fraxineus</i>	Ash trees	Asia	Asia, Europe and Africa	[49,50]
Bacterial blight or Bacterial leaf blight	<i>Xanthomonas oryzae</i>	Rice	Japan	Worldwide (especially Asia and Africa)	[51,52]
Bacterial canker	<i>Pseudomonas syringae</i>	Fruit trees	Depends on pathovar	Worldwide	[53,54]
Brown rust or Leaf rust	<i>Puccinia recondita</i>	Cereals (wheat, rye and barley)	Eastern Australia	Worldwide	[55,56]
Brown spot	<i>Bipolaris oryzae</i>	Rice	USA	Asia, Europe and South America	[44,57]
Bunch rot or Gray mold	<i>Botrytis cinerea</i>	Wide range	Unknown	Worldwide	[58]
Chestnut canker	<i>Cryphonectria parasitica</i>	Chestnut tree	Asia	North America	[59]
Disease dependent on the <i>Diaporthe</i> species	<i>Diaporthe</i> spp.	Wide range	Germany	Europe, Australia and Asia	[47,60]
Disease dependent on the <i>X. fastidiosa</i> subspecies	<i>Xylella fastidiosa</i>	Wide range	USA	South and North America and Europe	[47,61]
Downy mildew	<i>Plasmopara viticola</i>	Grape	North America	Worldwide	[62–64]
Dry root rot	<i>Rhizoctonia bataticola</i> (also <i>Macrophoma phaseolina</i>)	Chickpea	India	North America, Asia and Africa	[65]
Dutch Elm disease	<i>Ceratocystis ulmi</i> (also <i>Ophistoma ulmi</i>)	Elm	Asia	Worldwide	[66]
Fire blight	<i>Erwinia amylovora</i>	Apple, Pear and some Rosaceae	North America	Europe and Asia	[67]
Rice blast	<i>Magnaporthe oryzae</i> (anamorph <i>Pyricularia oryzae</i>)	Rice	Brazil	South America, Asia, Africa and Europe	[44,68]
Stewart's wilt	<i>Pantoea stewartii</i> (formerly <i>Erwinia stewartii</i>)	Corn	USA	Italy, Malaysia	[69,70]
Yellow rust or Stripe rust	<i>Puccinia striiformis</i>	Wheat	Transcaucasia (Armenia, Georgia and Azerbaijan)	Worldwide	[55,71]
Wheat blast	<i>Pyricularia graminis-tritici</i>	Wheat	Brazil	North and South America and Asia	[72]

The forest industry accounted for USD 244 billion in derivatives such as paper and paperboard, agglomerates or pellets in 2020 (<https://www.fao.org/forestry/statistics/80938/en/>, accessed on 21 July 2023). In the same way as agronomic soils, global warming is affecting the microbial communities of forest soils where a variation of just 5 °C unbalanced the relative abundance of soil microbiota in a field experiment (mainly fungi and some actinobacteria) [73]. However, the most visible problem today is the increase and expansion of pests and pathogens into new areas, which yield severe environmental and economic impacts, including the near-extinction of certain tree species, such as the following:

- Chestnut blight, caused by the pathogenic fungus *Cryphonectria parasitica*, native to Southeast Asia, which has killed more than 4 billion trees in the US to date.
- Ash dieback, caused by the newly identified *Hymenoscyphus fraxineus*, first detected in Asia, which has been recently detected in the UK and Northern Ireland [59].
- Dutch Elm disease, caused by *Ceratocystis ulmi*, a fungus responsible for its spread from Asia to Europe in 1918 that has killed millions of elms in Europe, western Asia and North America all throughout the 20th century [74].
- Needle blight of *Pinus contora* in north-western British Columbia, Canada, caused by outbreaks of *Dothistroma septosporum* as a result of a summer rainfall increase [75].

In summary, the causative agents of plant diseases are troublesome travelers that result in huge economic losses for the agricultural and forestry sectors, although obtaining realistic analyses seems complex.

4.3. Livestock and Climate Change: An Arthropoda Matter

The livestock sector is a capital pillar of the global food system, which, according to the FAO [24], represents 40% of the global agricultural output value and supports the livelihood, food and nutrition security of almost 1.3 billion people [24]. Although the increase in productivity efficiency helps to minimize the detrimental environmental impact of livestock, global farm-gate GHG emissions increased by 11% between 2000 and 2019, and around 55% of them are related to the livestock industry [76,77].

As in the agricultural sector, climate change could directly and indirectly influence livestock production in many ways: (i) growth performance, (ii) the yield and quality of the product, (iii) reproductive performance and (iv) health status. However, the main risk of climate change, as far as microorganisms are concerned, is an increase in fungal and bacterial diseases [76]. In addition, changes in temperature may trigger the secretion of stress hormones such as cortisol, which suppresses the immune system and favors pathogen infections, which also increases their transmission and expansion [78].

Pathogens' geographical extension is sometimes attributed to both anthropogenic and natural effects, including climatic factors and fauna and flora spread. Hence, the increased temperatures in the northern regions favor the expansion of numerous pathogen vectors (e.g., insects) that increase their chance to be established in new regions [79], promoting the geographic spread and increasing the incidence of some infections and diseases [80] (Table 2). The most climate-sensitive diseases are those transmitted by arthropods. Thus, the prevalence of tick-borne diseases has increased throughout Europe during the last decades [79]. In fact, 50% of tick species have the potential to expand their range worldwide, many of them being vectors of important animal diseases. These tick vectors that are already spreading north include the following:

Table 2. Geographical expansion of livestock diseases reported in recent years.

Disease	Pathogen	Vector	Host	Origin	Spread and Development	Ref.
Anaplasmosis	<i>Anaplasma phagocytophilum</i>	<i>Ixodes scapularis</i> , <i>Ixodes pacificus</i>	Sheep and cattle	Scotland	Worldwide	[81,82]
Babesiosis	<i>Babesia microti</i> , <i>Babesia venatorum</i> and <i>Babesia divergens</i>	<i>Ixodes ricinus</i> , <i>I. scapularis</i>	Mammals	Romania	Europe and North America	[83]
	<i>Babesia bovis</i> and <i>Babesia bigemina</i>	<i>Rhipicephalus microplus</i>	Mammals	Asia, Africa, South and Central America	Europe and North America	[84]
Bluetongue Virus	<i>Orbivirus</i>	<i>Culicoides imicola</i>	Ruminants	South Africa	USA, Canada, Australia, South and Central Europe	[85]
Canine Babesiosis	<i>Babesia</i> spp.	<i>Dermacentor reticulatus</i>	Mammals (especially cattle) and birds	Romania	Worldwide	[26]
Colorado tick fever	<i>Coltivirus</i>	<i>Dermacentor andersoni</i>	Mammals	Western US	Europe and North America	[86,87]
Ehrlichiosis	<i>Ehrlichia chaffeensis</i> and <i>Ehrlichia ewingi</i>	<i>Amblyomma americanum</i>	Mammals	Canada	North America and Europe	[88,89]
Leptospirosis	<i>Leptospira</i> spp.	Environmental transmission	Mammals	Japan and Europe	Asia, Australia, America and South Europe	[90,91]
Lyme disease	<i>Borrelia burgdorferi</i>	<i>Ixodes scapularis</i>	Rodents	USA	North America and Eurasia	[92–94]
Powassan virus disease	<i>Powassan virus</i>	Several tick species	Mammals	Unknown	North America	[95]
Q fever	<i>Coxiella burnetii</i>	<i>D. reticulatus</i>	Ruminants (cattle, goat and sheep)	Australia	Europe and North America	[96]
Rocky Mountain spotted fever	<i>Rickettsia rickettsii</i>	<i>D. andersoni</i>	Mammals	South and Central America	North America	[97]
	<i>Rickettsia parkeri</i>	<i>A. maculatum</i>			Central and North America	

- *Ixodes scapularis* and *Ixodes pacificus*, which transmit anaplasmosis disease, mainly caused by the bacterium *Anaplasma phagocytophilum* (formerly *Ehrlichia phagocytophilum*), which has also been reported in new regions worldwide [98]. In addition, they can also transmit the pathogen bacteria *Borrelia miyamotoi*, which has recently been reported in new areas of North America [81,82,99].
- *Dermacentor reticulatus*, which can transmit canine babesiosis, tularemia or Q fever [100,101]. Canine babesiosis is caused by the intracellular protozoan *Babesia* spp., and the number of reported cases has increased in northern countries, including Canada, Germany, Hungary, Switzerland and the Netherlands [26,78,95]. Q fever, meanwhile, is an important zoonotic disease caused by the bacterium *Coxiella burnetii*. It was originally described in Australia in 1933, although it began to spread across North America and Europe only two decades ago. In Europe, some cases were initially reported in southern countries such as France, Spain and Germany, although in recent years, significant outbreaks have been reported even in countries further north like the Netherlands [96].
- *Ixodes ricinus*, which transmits encephalitis and Lyme disease (borreliosis).

Another important group of vectors spreading to the north are mosquitoes, such as *Culicoides imicola*, which transmits bluetongue virus (BTV). It has spread northward from Africa and Cyprus causing BTV outbreaks (with high mortality and morbidity rates) in the Netherlands, Germany, Belgium, Luxembourg, Great Britain and other northern European countries since 2007 [80,85]. BTV is an infectious disease caused by an *Orbivirus* that mainly affects ruminants (especially sheep), but other non-ruminants can also be infected (e.g., shrews or dogs) [102,103]. In addition, changes in air currents associated with climate change can alter the dispersal of mosquitoes, leading to outbreaks of infectious diseases, such as leptospirosis and foot rot, although no confirmatory studies have been conducted to prove this [78].

On the other hand, although vector-borne diseases are prone to be impacted by global warming, other kinds of weather events (such as abundant rains, extreme drought or changes in air currents) may play an important role in their geographical expansion. These events have been extensively studied in processes such as El Niño events. After these extreme weather events, an increase in diseases, like Rift Valley fever, has been observed. This acute viral hemorrhagic fever is caused by a member of the genus *Phlebovirus*. It triggers high livestock morbidity and mortality and has traditionally been identified in sub-Saharan regions. However, there have recently been outbreaks as far north as the Arabian Peninsula and Asia, with the potential to spread further into Europe in the future [13,78,104].

In addition to the geographical expansion of vector-borne diseases, the ability of microbial pathogens to mutate and adapt to environmental changes is a significant factor in understanding the potential impact of climate change on livestock. For instance, in the case of Venezuelan equine encephalitis virus (VEEV), a single amino acid substitution in the envelope glycoprotein was observed (Ser → Asn), enabling the virus to adapt to a new efficient epizootic vector. This change occurred after a shift in the representative mosquito population, where the mosquito species *Ochlerotatus taeniorhynchus* became the most abundant after deforestation eliminated the habitats of *Culex taeniopus*, the previous principal mosquito vector. It serves as an example of viruses' rapid response to changes in their vector populations [80]. In addition, RNA viruses have no proof-reading, leading to a high evolutionary rate, mainly those with segmented genomes. The conservation degree of host receptors used by the pathogen is also important, and, although it is not directly affected by climate conditions, climate change could reduce the species barrier and facilitate contagion to new species through the invasion of new habitats [80].

Finally, apiculture is a livestock sector often forgotten when it comes to climate change. *Apis mellifera* is the most common species of honeybees in Europe and is the most valuable pollinator of agricultural crops worldwide [105–107]. However, they suffer from

a wide variety of bacterial, fungal and viral pathogens, as well as microsporidial or ectoparasitic mites. Among its most common diseases, European foulbrood (EFB), American foulbrood (AFB), chronic bee paralysis (CBP), sacral brood, calcareous brood and varroosis [108] are worth mentioning. Thus, different model predictions have described a positive relationship between temperature and the incidence of some of these important diseases [109], although they are not usually the focus of numerous analyses. Two of the most studied ones are chronic bee paralysis (caused by an unclassified bipartite RNA virus usually called chronic bee paralysis virus) [110] and American foulbrood (caused by the Gram-positive bacteria *Paenibacillus larvae*), whose expansion and intensification have already been reported despite the absence of models linking it to climate change [108,111].

4.4. Fishing and Marine Microbiome

Fishing and shellfish are relevant food industrial sectors. On average, a person eats approximately 20.5 kg of fish and shellfish every year. The 179 million metric tons of total seafood from 2018 landings had a farm-gate production value exceeding USD 401 billion, and global fish consumption has continued to increase at an average annual rate of 3.1% since 1961 (a higher rate than all other animal protein foods) [24,112]. However, marine animals are mainly ectotherms, and, as a result, they are particularly sensitive to changes in water temperature, which highlights the effect of global warming on this fauna. Over the past few decades, there has been a significant increase in temperature in the European seas, with warming rates four to seven times higher than the global average. This accelerated warming has important implications for marine life because it can disrupt migration patterns, reproductive cycles, food availability and species distribution [113].

Climate change may also affect other environmental factors such as seawater acidification, hypoxia, CO₂ accumulation, salinity or sea level modifications [114] (Figure 2). These changes disturb marine ecosystems, including microbial biodiversity, which has been under-researched for decades. Marine microorganisms account for 90% of marine biomass. They form the basis of marine food webs and are responsible for important biogeochemical cycles [115]. However, most of the ocean observation programs and studies do not target microbes [2,116], and the few reported just point to changes in the ocean's microbial biodiversity mainly due to the increase in water temperatures and sea acidification [117,118]. Therefore, Wang and co-workers [119] observed that warmer oceans will alter microbial communities, especially in thermally stable regions, and Hutchins and Fu [120] reported that ocean warming causes losses in microbial populations, leading to the predominance of a few earlier insignificant taxa.

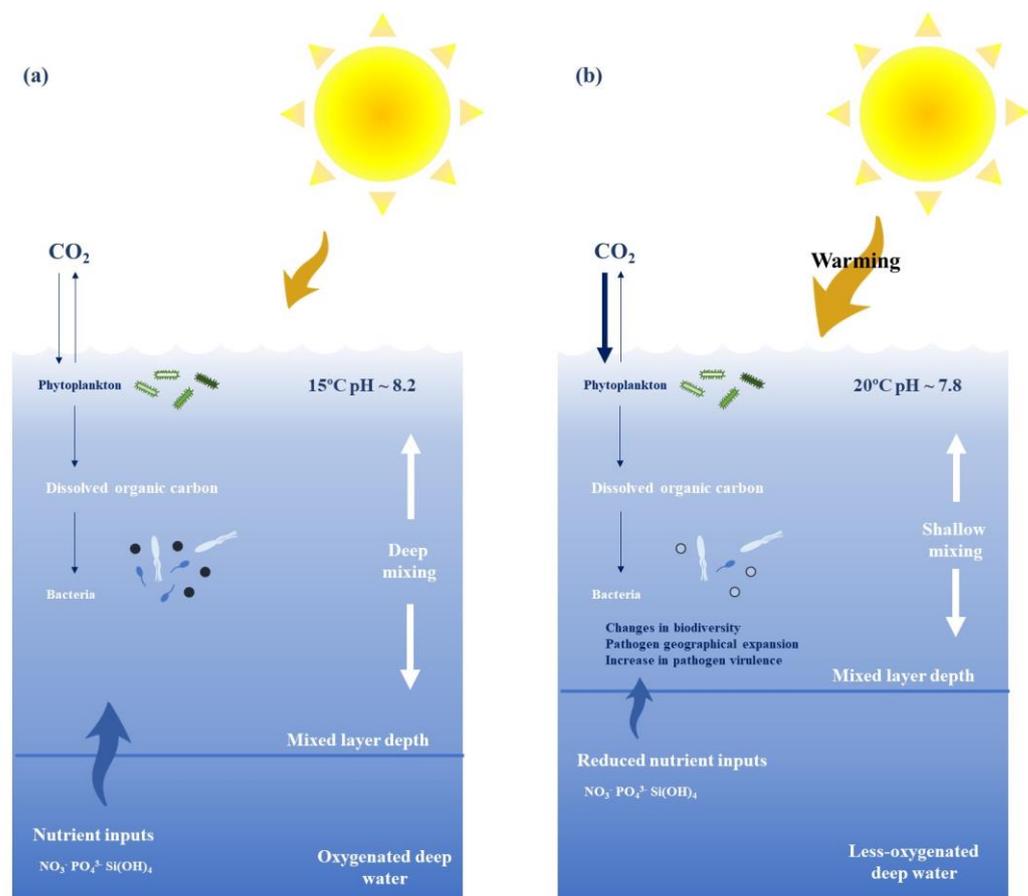


Figure 2. Main effects of climate change on key chemical and physical factors influencing the community composition of marine planktonic microorganisms. The current ocean (a) vs. the future one (b) after 2100. Among the changes that will have the greatest impact are (i) increases in atmospheric CO₂ uptake and, therefore, water acidification, (ii) increase in temperature, (iii) shallowing of the surface mixed layer, (iv) intensified stratification, leading to lower vertical fluxes of nutrients, and (v) reduction in oxygen both at the surface and in the underlying deep ocean. All these changes lead to changes in microbial biodiversity and expansion of both pathogen geographic ranges and pathogen virulence, inducing an increase in disease outbreaks and fauna and flora mortality.

To date, 25 viruses, 33 bacteria, 23 protists and 21 metazoans have been reported as the main causes of marine diseases in plants, corals, mollusks, crustaceans, echinoderms, fishes, turtles and mammals [114], although it is estimated that a greater part of the diversity in marine microbial biodiversity remains undiscovered, with less than 0.1% being described [121]. Thus, some studies have illustrated how marine warming alters host–pathogen dynamics, which can be described as follows:

- First, environmental changes like those caused by climate change may lead to stress in both fish and shellfish species, leading to lower immune responses against various pathogens and diseases [2]. Urchins are a clear example of this. Both tank and real-world experiments showed a strong correlation between mass mortality events and long-term elevated temperatures. While urchins experience thermal stress, leading to a decrease in the immune response (increasing infection rates) and fertility (minimizing population recovery) at higher temperatures, pathogens increase their replication and transmission rates [122].
- Second, a rise in temperatures leads to an increase in several marine pathogens' virulence by increasing their metabolism and inducing higher rates of transmission [122]. Such as the case of the host–pathogen interaction between *Pocillopora damicornis* and *Vibrio coralliilyticus*. At temperatures above 27 °C, pathogen virulence increases

because multiple virulence factors are upregulated, including extracellular proteases that cause lysis and mortality in *P. damicornis* [123].

- Third, pathogen geographical expansion comes with increasing temperatures. A shining example is *Perkinsus marinus*, a protist parasite of the eastern oyster *Crassostrea virginica* that has expanded its range from the mid-Atlantic to the northeast in recent decades, primarily due to increased winter water temperatures, since both *P. marinus* infection patterns and *C. virginica* immune response are dependent on the temperature [124,125]. In addition, *P. marinus* infection intensity increases above 20 °C, especially at temperatures close to 25 °C, and some models predict longer periods of sustained higher temperatures after 2100, which may allow the geographical spread of *P. marinus* and its establishment farther north along the coast [122]. Other cases come from the *Vibrio* genus, which includes more than 110 different species. Some of them are well-known animal and human pathogens, like *Vibrio cholerae*, responsible for cholera disease, which causes between 100,000 and 120,000 deaths every year globally. Zooplankton is one of the main environmental reservoirs of vibrios in aquatic environments, and some species can be found infecting molluscan and crustacean shellfishes, as in the case of *Vibrio parahaemolyticus* and *Vibrio vulnificus*. Both species are related to typical human infections associated with seafood consumption, and the risk area for both vibrio infections has greatly increased during warmer water temperature episodes in the last years [113,126]. A similar effect is expected in other aquaculture species due to *Vibrio harveyi*, which poses a great risk to some of the most important species in the fish market, such as rainbow trout (*Oncorhynchus mykiss*), Atlantic salmon (*Salmo salar* L.), Senegalese sole (*Solea senegalensis*), Japanese seabass (*Lateolabrax japonicus*), cobia (*Rachycentron canadum*) and common dentex (*Dentex dentex*), among others [127].
- Last, habitat expansion is likely to cause novel contact among populations, pathogens and vectors, potentially increasing interspecies infections. For example, *Brucella*, a group of Gram-negative bacteria and the causative agents of brucellosis. Novel species of *Brucella* named *Brucella ceti* and *Brucella pinnipedialis* have been reported to cause infection in marine mammals like cetaceans and seals, respectively [122].

On the one hand, although temperature is presented as the dominant climate change effect disrupting microbial marine communities, there are physical and chemical factors that may also affect infection and disease transmission in aquatic environments. A reduction in water salinity has the potential to significantly impact the immune response of host organisms. For instance, oysters exposed to low-salinity stress exhibited increased susceptibility to infection by *Vibrio alginolyticus*, resulting in higher mortality rates [128]. Similarly, ocean acidification can affect the immunological defenses of diverse organisms, such as urchins, mussels, oysters, finfishes, corals, bivalves and seagrasses. In addition, different studies have reported that *Vibrio tubiashii* grows better and increases its infectivity against mussels (*Mytilus edulis*) and hemocytes when exposed to low-pH conditions [114,129]. On the other hand, elevated partial pressures of CO₂ (usually known as hypercarbia) may impact the immune response by activating the complement system, activating the inflammatory response and down-regulating IgM expression. Thus, the joint effect of hypercarbia and temperature changes can alter the first and second lines of finfish defense, affecting their susceptibility to infections and diseases [114].

5. Human Health and Climate Change

Last but not least, human health is also affected by climate change effects. According to the World Health Organization, the epidemiology of infectious diseases constantly fluctuates in response to environmental changes and interactions among pathogens, hosts, reservoirs and vectors. The report of the IPCC (Intergovernmental Panel on Climate Change; <https://www.ipcc.ch/report/sixth-assessment-report-working-group-ii/>, accessed on 21 July 2023) indicates that an intensification in infectious disease outbreaks due to

climate change will be observed because several pathogens will spread to new regions and emerge in areas where they were previously under control. In addition, diseases that have never previously affected humans may “spill over” from animals, through a process known as zoonosis [130]. It properly fits the concept of One Health which recognizes the close connection between human and animal health and our shared environment (<https://www.cdc.gov/onehealth/index.html>, accessed on 21 July 2023). Thus, climate variation and its effect on human health can be considered directly due to the evolution and expansion of different disease vectors or indirectly through antibiotic resistance, which hampers microbial disease control.

5.1. Human Infective Diseases: Evolution and Expansion

Climate change can modify the relationship between humans and pathogens, thereby increasing their probability of contracting infections and diseases. Rising temperatures would modify the host immune system and boost the growth rate of pathogens, which supports their perpetuation and transfer [2,131] in a similar manner previously described for livestock. The most positively affected pathogens are those transmitted by vectors, food, air, water and other environmental agents [2]. Thus, the forecast for the near future is an increase in the infection transference and spread, as well as a change in the patterns of infectious pathologies due to rising temperatures, early changes of season and fluctuations in rainfall. For example, the spread of mosquito-borne diseases like dengue fever or Zika virus will be the result of increasing temperatures and changes in rainfall patterns, which lead to more breeding sites. In addition, infectious disease-causing pathogens are able to adapt to new climatic conditions that enhance their transmission and prevalence [132–134].

The impact of rising temperatures and the adaptation of pathogens to new conditions poses a significant threat, leading to the emergence of previously unrecorded human infectious diseases. A notable example is the Chikungunya virus, transmitted by mosquitoes, which causes fever and severe joint pain. Although it was initially identified in Tanzania in the 1950s, it has since spread to other parts of the world, including America and Asia [135,136]. Pathogens may develop thermotolerance as a survival mechanism in response to changing environmental conditions and their adaptation to new hosts. The acquisition of this thermotolerance involves various molecular and cellular mechanisms, such as (i) the activation of heat shock response genes encoding heat shock proteins (HSPs), (ii) DNA repair mechanisms, metabolic adaptations to optimize energy production and utilization at higher temperatures or (iii) gene regulatory network modulation and signaling pathways to coordinate the expression of heat-responsive genes [137]. As these pathogens adapt to higher temperatures, they acquire the ability to cross the mammalian endothermic barrier (which creates a zone of thermal inhibition to prevent infection), thereby adapting to the internal environment of the host. This, together with the increased population density of pathogens, poses a greater threat to human health and increases the likelihood of infection. For instance, certain strains of *Vibrio*, commonly found in coastal waters, have become more virulent in response to escalating ocean temperatures, leading to outbreaks of infections among individuals exposed to contaminated water or seafood. Additionally, pathogens preserved in Arctic permafrost may also resurface, causing diseases such as tularemia or anthrax, as old variants long forgotten by the immune system regain activity [138].

The effect of climate change on the expansion and proliferation of some human diseases is presented in this section based on their transmission manners (vector-borne, food-borne or waterborne diseases) (see Table 3 and Figure 3).

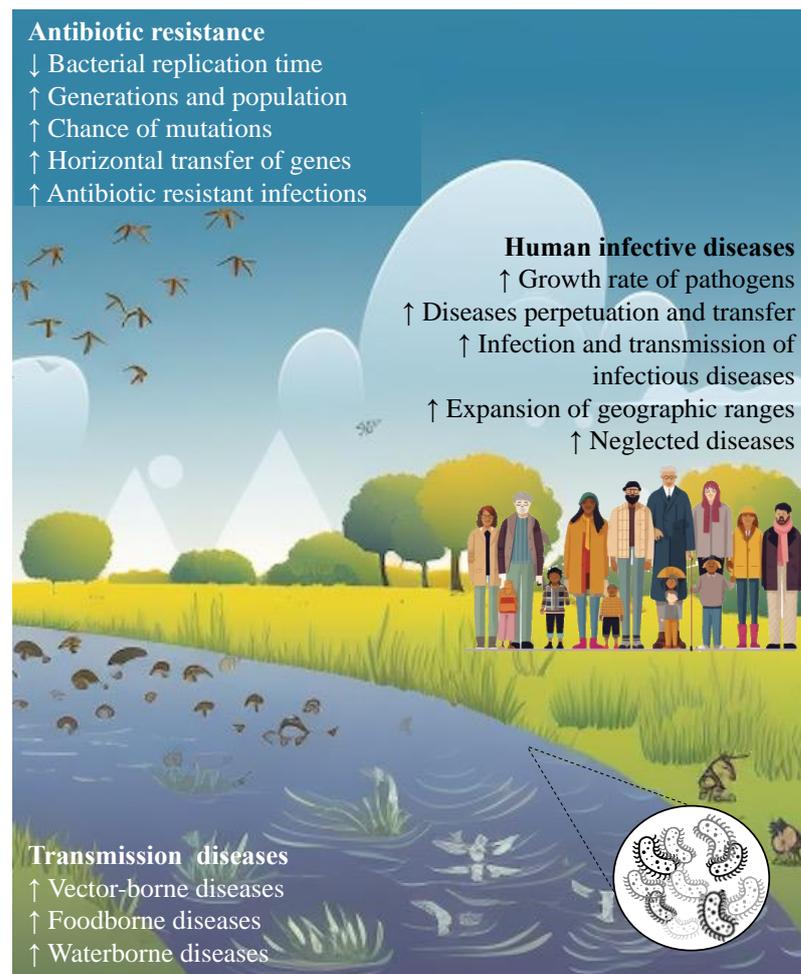


Figure 3. Summary of the main causes and effects of climate change on human health due to microbial global variations. White font: (up) factors that contribute to the worldwide increase in antibiotic resistance; (down) different sources of borne diseases. Black font: result on human health of the different factors presented in the manuscript.

5.1.1. Human Vector-Borne Diseases

The most important vector-borne diseases in Europe are caused by pathogens sensitive to climatic conditions because they are spread mostly by cold-blooded arthropods, which expand their geographic ranges owing to the effects of climate change (global warming, rainfall variations and extreme weather events) [2,130,138]. Vector-borne diseases account for more than 17% of all infectious diseases, causing 700,000 deaths every year worldwide. Although mosquitoes are the best-known disease vector in humans and animals, other arthropods, such as ticks, black flies, sandflies, midges, fleas and triatomine bugs, also act as relevant vectors and should be kept in mind [2,139–141].

The effects of climatic variations can be observed with the spread of some tropical diseases, such as dengue and Zika, both transmitted by mosquitoes of the *Aedes* family. Dengue transmission has increased since 1950 by 8.9% in the case of *Aedes aegypti* and by 15.0% when considering *Aedes albopictus*, reaching almost 4 billion people in over 128 countries at risk of contracting dengue [130,139,140,142]. In addition, there was a 50% increase between 2005 and 2015 in the number of deaths caused by dengue, which has become the most prevalent disease among travelers in Southeast Asia, surpassing malaria.

Table 3. Effect of climate change on the expansion and development of different diseases.

	Disease	Microorganism	Vector	Host	Origin	Spread and Development	Effects of Climate Change	Ref.
Vector-borne diseases	Chikungunya	Chikungunya virus	<i>Aedes albopictus</i>	Human	Tanzania	Asia and Africa		[139]
	Dengue	Dengue virus (DENV)	<i>Aedes aegypti</i> <i>Aedes albopictus</i>	Human	Africa	Tropical and subtropical areas and Europe	Increase in temperatures, changes in rainfall and increase in the number and severity of extreme weather events multiply the risk and the ranges of infection and the spread of diseases	[133,142]
	Leishmaniasis	<i>Leishmania</i> spp.	Female sand-fly	Human	Africa	Southern countries of the European continent		[138,139]
	Zika	Zika virus (ZIKV)	<i>Aedes albopictus</i>	Human	Africa	North America and South America		[138,139]
Foodborne diseases	Diarrheal disease	<i>Campylobacter</i> spp.	Contaminated food	Human	America	Worldwide	Temperatures rise favors the contamination of food by pathogens that cause diseases	[138,139]
	Salmonellosis	<i>Salmonella</i> spp.	Contaminated food	Human	America	Worldwide		[139,143]
Waterborne diseases	Cholera	<i>Vibrio cholerae</i>	Contaminated water	Human	Asia and Africa	Africa, Asia and North America	Increased precipitation can wash pathogens into waterways, while rising sea temperatures activate impulses for pathogen spread and development	[1,111, 112,117, 119,120]
	Leptospirosis	<i>Leptospira</i> spp.	Contaminated water	Human	Germany	Tropical and subtropical areas	Warmer temperatures and extreme weather events can create favorable conditions for the survival and persistence of <i>Leptospira</i> bacteria in the environment. Alterations in land use and deforestation can also increase human contact with animal reservoirs of leptospirosis	[2]

Thus, a 30-fold increase in dengue incidence over the last 50 years, as well as an extension in the geographic area of this disease, is a clear warning sign. Hence, forecasts estimate the future expansion of dengue, which will increase the risk of infection in the global population [138,144]. Currently, the greatest concern is the mosquito *A. albopictus*, which can spread from temperate regions to higher altitudes. This mosquito species is known to transmit diseases such as chikungunya and Zika viruses, making its presence a cause for heightened attention and concern. Some studies have related the spread of outbreaks to an increase in total viral load with an increase in the number and range of vectors, which is directly related to climate change [139,144–146].

Leishmaniasis, which is transmitted in warm environments by protozoa of the *Leishmania* genus, is moving into regions that are now temperate as a result of climate change, including areas of southern Europe such as Italy, Greece and Spain, as well as regions in South America, such as Argentina and Brazil [147–149]. In this way, the reproduction and survival of protozoa are advantaged because although the number of protozoa per cell does not increase, the concentration of these protozoa in the environment rises, since warm temperatures enhance their reproductive cycle. This has resulted in an alarming growth of cutaneous leishmaniasis in areas where this protozoa was not previously detected (because temperatures were much lower before), such as the southern countries of Europe, especially in Mediterranean countries such as Spain, Italy, France and Greece [138,139,150].

The effectiveness of disease transmission by a vector depends on the time taken for the vector to become infectious after encountering an infected host. Higher temperatures play a significant role in boosting efficacy. When temperatures are higher, the time between contact with the infected host and the vector becoming infectious is shortened. This shorter timeframe results in higher vector concentrations. As a result, there are more opportunities for the vector to transmit the disease within its lifespan, thereby increasing the overall transmission potential. Hence, the spread of vector-borne diseases is favored by rising temperatures, lengthening transmission seasons, increasing pathogen replication in the vector and increasing geographic range [2].

5.1.2. Foodborne Diseases

Nowadays, more than 200 types of foodborne diseases have been reported, most of which could be affected by climate change [139,143]. Approximately 420,000 deaths per year are caused by foodborne diseases, and an increase is expected because rising temperatures favor food contamination and pathogen establishment in new temperate regions [139,143]. In addition, the more humid the environment, the greater the survival of pathogens (such as *Trichinella* spp. and *Toxoplasma gondii*) and parasite eggs, larvae and cysts. The rainfall rises and its intensity, as well as the increase in floods, favor crop and food contamination because the air bacterial concentration is increased after a drizzle. Additionally, after a flood, wastewater is more likely to overflow, causing contamination of fresh produce [134,151].

Several examples of climate change effects on foodborne diseases have been described, such as an increase in *Campylobacter* infections due to rising temperatures and intense rainfalls [152]. According to a study carried out by Kuhn and collaborators in 2020 [152], there is a possible increase of between 3 and 20% in cases of *Campylobacter* infections if climate change is not delayed. In addition, salmonellosis, transmitted by *Salmonella* species, which activates reproduction at high temperatures, is another relevant concern. Global warming has been linked to an increase in *Salmonella* infections, and it is estimated that every degree of temperature rise would cause a 5% to 10% increase in *Salmonella* infections [139,143,153]. Morgado and co-workers, in 2021 [154], showed a direct relationship between warm temperatures, increased rainfall (especially during extreme weather events) and a rise in diagnosed cases of salmonellosis. In this way, higher temperatures can lead to increased bacterial concentrations, potentially resulting in more severe cattle

infections. This has significant implications for the food industry, as contaminated meat can contribute to outbreaks of salmonellosis in humans [128].

5.1.3. Waterborne Diseases

Increased rainfall can drive pathogens into waterways and overwhelm water treatment systems, causing different disease outbreaks. In addition, as presented in previous sections, the increase in sea temperature and salinity changes can cause the development and proliferation of numerous *Vibrio* species, such as *Vibrio cholerae*. Thus, it should be kept in mind that these temperature changes, no matter how small, can lead to significant alterations in host–pathogen relationships [133,139,153,155]. In addition, it must be considered that the spread and development of some pathogens (*Vibrio cholerae*, *Cryptosporidium*, *Leptospira* spp., etc.) can lead to the contamination of urban water, which can result in an increase in several diseases [156,157]. Most of these pathogens are transmitted by the fecal–oral route or indirectly through contaminated water, where they can survive for long periods, even though their nutrient access can be scarce [143,144]. An example is cholera disease, whose clinical impact has increased in recent years, mainly due to temperature and rainfall variations. In fact, it has been observed that each increased degree raises the risk of cholera infections by around 15–29% [144,158].

Other cases of waterborne infections are those caused by the toxic microalgae *Vicicitus globosus* (formerly *Chattonella globosa*), which contaminates the food chain through shellfish consumption. Hence, climate change has intensified the proliferation of this algae because of the increase in the concentration of CO₂ in water, driving an upsurge in food poisoning outbreaks [2,159]. Ocean acidification has also been linked to the formation of toxic algal blooms. Some species of algae, including *Emiliania huxleyi*, produce toxins when their environment changes due to acidification. These blooms can lead to the accumulation of toxins in the food chain, causing harm to marine organisms and potentially even to humans who consume seafood [159].

5.2. Antibiotic Resistance

The World Health Organization indicates antibiotic resistance as “one of the greatest threats to global health, food security and development today” (<https://www.who.int/en/news-room/fact-sheets/detail/antibiotic-resistance>, accessed on 21 July 2023). In recent years, antibiotic resistance has risen sharply to become a public health problem, with 23,000 people dying annually as a result of antibiotic-resistant infections. This health threat has been due to the wide variety of antibiotic applications (e.g., human and animal health, growth promotion in food-producing animals, disease prevention, crop-disease control as pesticides) in the last 80 years [160]. Worldwide, antibiotic consumption rose by approximately 39% between 2000 and 2015, and it is estimated that it will continue to rise up to 200% in a few years. These data, which are worrying for public health, were reviewed by Jim O’Neill (UK Prime Minister commissioned the Review on Antimicrobial Resistance) in 2014 [161], who reported that deaths from untreatable infections could reach 10 million annually after 2050. In addition, there was a reminder a few years later in 2019 from the IACG (Interagency Coordinating Group on Antimicrobial Resistance) hosted by the WHO (World Health Organization) with contributions from FAO and OIE (Organization for Animal Health) [162].

Latest studies relate antibiotic resistance spread to temperature increase because bacterial duplication time is accelerated, multiplying the chance of mutations, the horizontal transfer of genes (some of them related to antibiotic resistance) and infectivity [2,161,163,164] (Figure 3). Particularly, this increase in resistance has been notably higher in southern Europe, where climate change has led to a rise in minimum temperatures. As a consequence of this temperature increase in these southern countries, the intensification of antibiotic resistance has increased from 0.33% to 1.2% per year [163]. *Acinetobacter baumannii*, *Pseudomonas aeruginosa* and *Klebsiella pneumoniae* are examples of this peculiar connection between temperature and antibiotic resistance, which is currently causing serious

sequelae because some strains are hard to tackle with current antibiotic formulations [165,166]. In addition, the increase in deaths due to antibiotic-resistant strains of tuberculosis causes more than 2000 deaths annually [167].

Furthermore, it has been observed that the higher the temperature, the faster the new instances of resistance upsurge [163,168]. Thus, salmonellosis could increase both burden and morbidity due to global warming [169].

Another particular case is *Candida auris*, a new drug-resistant yeast species [167]. Its most enigmatic aspect is that it emerged simultaneously as a human pathogen on three continents in 2009, exhibiting antifungal agent resistance. One hypothesis is that the increase in environmental temperature increased the concentration of *C. auris* and favored the appearance of new mutations, including those for antibiotic resistance. In addition, seabirds acted as intermediate hosts and reservoirs, and it became a zoonotic disease after breaking the mammalian thermal barrier through adaptation to climate change. According to Casadevall's conclusions [135], *C. auris* was the first human pathogen to appear as a result of climate change [135,167].

The increase in temperature leads to higher growth rates and enhanced survival of pathogens, resulting in higher population densities. This, in turn, leads to an increased number of pathogens, which subsequently contributes to an increased occurrence of random mutations [138,170]. It is important to note that resistance to one stressor, such as higher temperatures, can provide protection against other stressors (e.g., antibiotics) [171]. This phenomenon is known as collateral resistance or cross-protection, which was studied by Rodríguez-Verdugo et al. in 2013 [172]. Interestingly, certain generations of *E. coli* have acquired antibiotic resistance despite never being directly exposed to them. Instead, resistance emerged owing to exposure to elevated temperatures. Both temperature and antibiotics influence the transcription of RNA polymerase, leading to the acquisition of mutations as a survival mechanism against heat stress, conferring also resistance to antibiotics [167,172].

Additionally, warmer environmental temperatures promote biofilm formation, mainly because of the decrease in oxygen solubility with increasing temperature. In response to these changing conditions, bacteria adapt their growth and behavior, transitioning from planktonic bacteria to biofilms. Within biofilms, bacteria enter a dormant state, enabling them to better tolerate the presence of antibiotics. Consequently, biofilms exhibit increased resistance to antibiotics. In the context of reduced oxygen availability, certain bacterial species can adapt their metabolism and form biofilms to enhance their survival and persistence. Biofilms provide protection and access to nutrients, allowing bacteria to thrive in oxygen-depleted environments [171]. In summary, microorganisms have the ability to adapt and persist by undergoing genetic mutations and selecting strains that are better suited to their environment. This includes developing resistance to antibiotics as a means of survival in the presence of these drugs [167].

6. Microbial Mitigation of Climate Change

Hitherto, this review has presented microbes as actors and recipients of climate change (e.g., GHG producers, crop destroyers or players in human and animal health concerns). However, although there are still a limited number of non-model studies focused on using microorganisms as a counterpart (mitigation agents) of global climate variation, some hope glimmers appear on the horizon. Thus, microbial support can be considered in a direct manner (e.g., plant biostimulants) or in an indirect way (e.g., helping in the transition to the circular bioeconomy (a way to maximize resource efficiency, reduce waste generation and promote the regeneration of natural systems) [173]).

The direct commitment of microorganisms to decreasing or slowing down climate change can be considered if those microbes are relevant players acting straightly against the causes or effects, such as the following:

- **Inoculants:** one of the main strategies to deal with the inevitable effects of climate change on crops is the use of biostimulants, which recover plant resistance and resilience to biotic and abiotic stresses showing low toxicity and avoiding the appearance of new resistant strains of pests and pathogens. Hence, the biofertilizer market has steadily increased in the last years, with Europe being the world industry leader [174]. Several microorganisms can act as biostimulants providing crop-limiting nutrients: (i) by nitrogen fixation (*Azospirillum*, *Azotobacter* or *Rhizobium*), (ii) mineral solubilization like phosphorus, potassium or zinc (*Pseudomonas*, *Bacillus* or arbuscular mycorrhiza) or (iii) siderophore production (*Pseudomonas* and *Acinetobacter*) [174,175].
- **Biofertilizers** tackle climate change concerns in different positions:
 - (i) Some microbial species have shown crop protection from warmer temperatures, such as *Paraburkholderia phytofirmans* in potato crops, *Bacillus* and *Azospirillum* species in wheat and soy or *Pseudomonas* species in wheat [174],
 - (ii) *Biofertilization* minimizes N₂O (GHG) emissions from soybean root nodules. Thus, bacterial strains with higher N₂O reductase activities (such as *Azospira* sp. or *Bradyrhizobium diazoefficiens*) may provide avenues for reducing N₂O emissions in such crops [176,177],
 - (iii) *Methanotrophic* bacteria are gaining attention as biofertilizers, since it has been estimated that they are able to consume approximately 40–60% of the methane produced in wetland environments. Thus, methanotrophs can be used in landfills and agricultural soils, ultimately helping to reduce atmospheric methane levels (e.g., *Methylococcus* or *Methylococcus* species) [22,178,179].
- Microorganisms are leaders in **carbon sequestration**:
 - (i) Several soil microbes contribute to carbon sequestration through different mechanisms, although certain microbes possess faster metabolic rates and, therefore, sequester carbon faster. It is possible to enrich soils with these species of interest through the introduction of microbial formulations respecting the environment, as well as by enhancing the capacity to collect carbon in agricultural soil [180].
 - (ii) In addition, studies on the production of biofuels at an industrial level by means of algae, which are one of the most powerful microorganisms for carbon fixation (1.83 kg of CO₂ is needed for each kg of dry algae biomass production), connect two relevant concepts of the circular bioeconomy. On the one hand, CO₂ sequestration is closely connected to the carbon credits that pollute the air, and on the other hand, the biomass produced by some of these algae genera (e.g., *Botryococcus* sp., *Scenedesmus*, *Neochloris*) is ideal for energy fuel production and multiple value-added products (e.g., feeds). Therefore, it would be a particularly interesting cycle, since concerns about the depletion of fossil fuels have increased general interest in recent years, and this process could be interesting not only from an ecological point of view for the biological sequestration of carbon from punctual sources but also from an economic one [181].
- **Livestock rumen:** manipulation of rumen microbiota and breeding programs has been proposed as a suitable solution to reduce methane emissions from cattle. The objective would be to obtain cattle lines producing less methane without affecting the health and productivity of animals [2].

On the other hand, the indirect involvement of microorganisms in the fight against climate change can be considered if those microbes work in the transition to the circular bioeconomy by helping to reintegrate residual materials or by-products in the production chains, as well as by supporting the degradation of recalcitrant material to their elementary components or biomolecules (e.g., as biomass to the environment), such as the following:

- The **Rs concept** is aimed at the transition to a circular bioeconomy by means of different wording that collects the spirit of the materials' reinsertion into the production system. Initially, three Rs were considered (Reduce, Reuse and Recycle); later, it was increased to six Rs (the three Rs plus Rethink, Refuse, Repair), and, nowadays, it continues increasing the number of Rs (the six Rs plus Refurbish, Remanufacture, Repurpose, Recover). In this context, the recent isolation of the poly(ethylene terephthalate) (PET)-degrading bacterium *Ideonella sakaiensis* [182], the description of epoxy-degrader microorganisms, such as *Pseudomonas putida* [183], or the description of the wax moth caterpillars (*Galleria mellonella*) as polyethylene degraders [184] have boosted the research on the biotechnological degradation of plastic. Excessive use of these materials increases plastic accumulation on land and sea. Microbes are the predominant organisms able to face this problem, the so-called plastic biodegradation [185]. The degradation to these basic molecular components presents the microorganisms or their enzymatic activities as relevant players in environmental sustainability.
- **New protein sources:** the search for new sources of protein to cover the increasing demand for meat protein has led to single-cell protein (SCP) development. In the first place, efforts have been made to convert plant protein into meat protein, getting low yields. Thus, the production of SCP was initiated, which are dried microbial biomass or the total amount of protein extracted from bacteria, yeasts, fungi or algae cultures [186]. A clear example is the production of burger patties from the fungal protein of *Aspergillus oryzae*, with similar organoleptic properties to meat burgers and rich nutritional content [187].
- **Bioremediation:** oil spills are one example of pollution that can have devastating effects on ecosystems and habitats. The bacterium *Alcanivorax borkumensis* thrives in hydrocarbon-rich environments and has been shown to play a crucial role in the degradation of oil spills [188]. This microorganism has been used in several bioremediation efforts, including the clean-up of the Deepwater Horizon oil spill in the Gulf of Mexico in 2010 [189].
- **Liquid-3:** Pollution is growing steadily around major urban centers. In 2021, Dr. Ivan Spasojević from the University of Belgrade launched Liquid-3 on the market, a 600-L tank filled with microalgae design to remove CO₂. The tank effect is able to replace two 10-year-old trees or 200 square meters of lawn (<https://liquid3.rs/>, accessed on 21 July 2023).

7. Conclusions

Doomsday scenarios have been a constant concern throughout the second half of the XX century and the beginning of the XXI. Thus, the “unsustainable” worldwide overcrowding in 60 s that could compromise food supplies (± 3.0 billion people in 1960 compared to ± 7.9 billion today) or the nuclear arms race of the Cold War between the United States and the Soviet Union, which kept the Doomsday Clock a few minutes before the midnight for several years (nowadays, it is 90 s to midnight (<https://thebulletin.org/doomsday-clock/>, accessed on 21 July 2023)), are two examples of theoretical, but fortunately non-fulfilled, risks for the humankind. Currently, climate change is a highly relevant concern at different levels all around the world that could be presented as the next doomsday scenario due to social controversy, which also affects the scientific community, with both pros and cons to climate change. However, what is sure is that microorganisms are rarely the focus of the analyses. They have not been considered in policy development, probably because of their immense diversity and varied responses to environmental changes, which make it a challenge to determine their role in the ecosystem. Nevertheless, based on scientific evidence, as it has been reviewed throughout this manuscript, numerous alarms have been raised in recent years due to the rise in the appearance and spread of several diseases throughout the world. Several pathogenic fungi and bacteria have already extended their geographical area of influence northward and are

advancing at a great speed through Europe and North America, with the immense economic losses that this entails. These pathogens not only affect the three most important food production sectors—agriculture, livestock and fishing—but human diseases (especially tropical) are also targeted, and the appearance of new ones (zoonoses) is relevant. The mitigation of these illnesses is complicated since they are climate-conditioned, and the appearance of new antibiotic resistance further complicates the resolution.

Nowadays, microorganisms can be used to bring some light to climate change concerns, and they should play a more relevant role. On the one hand, they can be used as reporters of the weather variations tracing the appearance, evolution or impact of non-common diseases at novel locations. On the other hand, their ability to decrease greenhouse gases, due to their involvement in the carbon (fixing atmospheric CO₂) and nitrogen cycles, is also remarkable and should be valued at its full potential. In addition, microbial involvement in the worldwide degradative tasks of recalcitrant compounds also presents them as relevant players in climate change mitigation.

The evolution of climate change, as well as the truthfulness and accuracy of the model predictions, highly condition the future results of climate variations and the role of microorganisms. However, although the hands of the Doomsday Clock point to midnight, the microorganisms will continue living here.

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