

# Interconnecting global threats: climate change, biodiversity loss, and infectious diseases



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The concurrent pressures of rising global temperatures, rates and incidence of species decline, and emergence of infectious diseases represent an unprecedented planetary crisis. Intergovernmental reports have drawn focus to the escalating climate and biodiversity crises and the connections between them, but interactions among all three pressures have been largely overlooked. Non-linearities and dampening and reinforcing interactions among pressures make considering interconnections essential to anticipating planetary challenges. In this Review, we define and exemplify the causal pathways that link the three global pressures of climate change, biodiversity loss, and infectious disease. A literature assessment and case studies show that the mechanisms between certain pairs of pressures are better understood than others and that the full triad of interactions is rarely considered. Although challenges to evaluating these interactions—including a mismatch in scales, data availability, and methods—are substantial, current approaches would benefit from expanding scientific cultures to embrace interdisciplinarity and from integrating animal, human, and environmental perspectives. Considering the full suite of connections would be transformative for planetary health by identifying potential for co-benefits and mutually beneficial scenarios, and highlighting where a narrow focus on solutions to one pressure might aggravate another.

## Introduction

We are experiencing profound planetary changes. The climate is now warmer than at any time in the past 125 000 years,<sup>1</sup> extreme climatic events are more frequent,<sup>2</sup> and global average temperature increases relative to the 1850–1900 average already exceed 1°C, and might top 1.5–2°C in the next two decades.<sup>3</sup> Natural habitat is increasingly fragmented and intact fragments are decreasing in size.<sup>4</sup> This change in climate and natural habitat is shifting species distributions and rearranging the composition of ecological communities, and an estimated 1 million species are at risk of extinction.<sup>5</sup> Simultaneously, we are witnessing widespread increases in the emergence, spread, and re-emergence of infectious diseases in wildlife, domestic animals, plants, and people.<sup>6,7</sup> These major environmental trends are often attributed to common anthropogenic drivers, including pollution, deforestation, and agricultural expansion (figure 1); however, although meta-analyses draw focus to the strength of connections between disease and the global pressures of climate change and biodiversity loss, the science that mechanistically links all three is insufficient.

The connections between biodiversity loss and climate change have been highlighted in recent intergovernmental global assessments (eg, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services [IPBES]–Intergovernmental Platform on Climate Change [IPCC] cosponsored workshop report,<sup>5</sup> the UN Global Environmental Outlook [GEO],<sup>8</sup> and WWF's Living Planet Report<sup>9</sup>), establishing a process of identifying common drivers and responses to inform policy and solution pathways.<sup>10</sup> The strong interconnections between infectious disease and biodiversity, and between infectious disease and climate change, are also increasingly well recognised.<sup>7,11</sup> There is now a pressing need to investigate

the expansion and effects of disease in humans, domestic animals, wildlife, and plants as primary and secondary drivers and as a consequence of biodiversity–climate relations.<sup>11,12</sup>

WHO's One Health initiative, IPCC, IBES, and GEO all recognise the need for a holistic approach to planetary health, but the three global pressures of climate change, biodiversity loss, and infectious disease are rarely considered together. We argue that considering the three pressures together is essential for identifying effective management solutions and mutually beneficial scenarios and for avoiding ecological surprises. For example, when implemented thoughtfully, nature-based solutions to manage biodiversity can have the co-benefits of improving health and mitigating climate change (panel),<sup>55</sup> but when designed poorly, might result in trade-offs, such as climate mitigation policy supporting the planting of non-native trees.<sup>56</sup> Furthermore, by investigating interactions among pressures, we can also gain new insights into system dynamics; for instance, amphibian declines could be explained by the interaction between extreme temperatures and infectious disease, but not by either pressure alone (panel).<sup>40</sup>

Here, we examine interactions among the three global pressures of changes in climate (encompassing shifts in the means, variability, seasonality, and incidences of extremes in climate variables, as well as changes in spatial and temporal correlations among climate variables), biodiversity *sensu lato* (defined as “the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems” by the Convention on Biological Diversity), and infectious disease. We focus on the science connecting these

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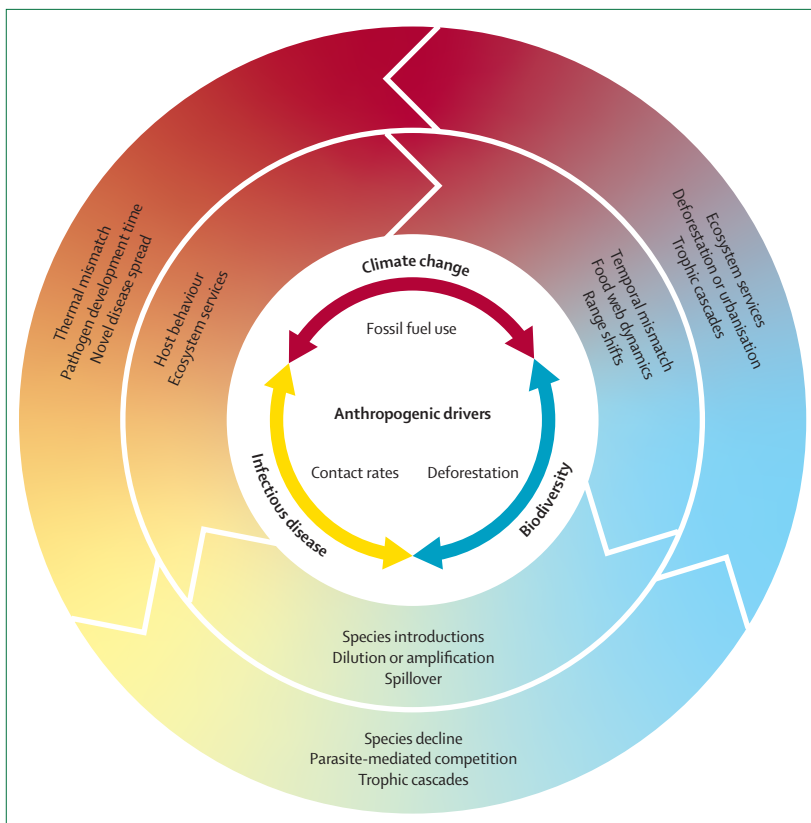
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For more on the Convention on Biological Diversity see  
<https://www.cbd.int>

three pressures, not their underlying root causes, including the social, political, and financial systems that frame them. Nonetheless, we suggest that a better understanding of interactions between pressures will aid in identifying more effective policy responses and solution pathways that address the primary axes that ultimately drive environmental change. Using case studies to illustrate the causal pathways between them (figure 2), we show that the mechanisms between some pairs of pressures are better understood than others, and that the body of research addressing all pairwise interactions is growing rapidly. We highlight that pairwise interactions between biodiversity and infectious disease have been extensively studied, although underlying mechanisms remain hotly debated, and that climate variability and change have major effects on both biodiversity and disease, although paths from biodiversity and disease to climate are less frequently observed and likely to be weak, at least over timescales that define the Anthropocene.



**Figure 1: Directionality of mechanistic links between climate change, biodiversity, and infectious disease** Anthropogenic drivers, such as fossil fuel use, deforestation and agriculture, and human population growth, are accelerating increases in global temperatures, losses of biodiversity, and infectious disease outbreaks. These three global pressures can be connected mechanistically (examples listed in the two outer rings illustrate directional links, shown by arrows, between pressures) with cascading consequences. In addition to linear paths linking pressures, these mechanisms can lead to feedback loops between pressures, stepping from one ring to the next. Mechanisms listed represent only a subset of the many possible mechanisms that connect pressures. The 2022 Intergovernmental Panel on Climate Change report provides examples of how the human system can be similarly integrated and connected to climate and biodiversity.

## Mechanistic links

### Climate change to biodiversity

Species can adjust to climate change by shifting in space (range shift), time (phenology), plasticity, or acclimation and evolutionary adaptations, or a combination of these.<sup>57,58</sup> Rapid changes in local climate and extreme climatic events (eg, heatwaves, floods, and hurricanes) can result in local extirpations, and even global extinctions,<sup>59,60</sup> reducing the richness of local communities. Climate-induced range shifts beyond historical distributions can additionally lead to novel community compositions without historical analogues,<sup>61</sup> reshaping species interactions (figure 2).

Changes in temperature and precipitation can impact resource production and the flow of energy through ecological networks. Warmer temperatures will additionally shift species' thermal ecologies, decreasing generation times, increasing metabolic needs, changing dispersal patterns, and altering seasonal phenologies.<sup>62</sup> These climate-induced changes can modify the strength of species interactions and the resilience of food webs,<sup>63,64</sup> which could cascade to species extirpations.<sup>65</sup>

### Biodiversity to climate change

In natural systems, greater biodiversity is generally associated with a reduction in the effects of anthropogenic drivers on the climate. For instance, more diverse and species-rich natural forests and grasslands have higher carbon sequestering potential (figure 2),<sup>66</sup> reflecting the general positive biodiversity–productivity relationship.<sup>67</sup> Conversely, loss of biodiversity through deforestation reduces carbon sequestration, and simultaneously increases greenhouse gas emissions by increasing plant biomass undergoing decomposition. Post-deforestation land is often used for agriculture or urban development, both of which contribute to global greenhouse gas emissions (17% and 60% of global greenhouse gas emissions, respectively).<sup>68</sup> Deforested lands left unmanaged typically undergo succession towards forest regrowth, but this secondary forest can have lower diversity, be more fire-prone, and provide fewer ecosystem services than the primary forest (figure 2).<sup>69</sup>

At local scales, changes in biodiversity due to loss of natural habitat, agricultural expansion, and urbanisation can alter the microclimate. Urban areas—urban heat islands—have higher air and surface temperatures compared with surrounding areas due to reduced vegetation and energy absorptive surfaces like concrete and asphalt.<sup>70</sup> Local extirpations that include the loss of a keystone species can have downstream effects that decrease the abundance of primary producers that are important for carbon sequestration. Much of the evidence supporting top-down effects, in which the loss of consumer diversity results in reduced primary productivity and carbon sequestration, comes from blue carbon (carbon stored in coastal or marine systems) literature, with ongoing debate on the role of blue carbon in climate-change accounting.<sup>71</sup>

In terrestrial systems, release of producers from top-down control can lead to greater biomass accumulation; however, although increased biomass is a temporary carbon sink, it can also exacerbate wildfires, leading to a net increase in atmospheric CO<sub>2</sub> emissions (figure 2).

### Biodiversity to infectious disease

Changes in biodiversity are often linked with a change in disease prevalence.<sup>72</sup> Greater biodiversity can decrease (have a dilution effect on) or increase (have an amplification effect on) disease exposure and incidence.<sup>72,73</sup> The amplifying and diluting effects of biodiversity on disease prevalence are complex, and probably capture multiple mechanisms, sometimes simultaneously.<sup>74</sup> Changes in reservoir host populations, specifically the introduction of new reservoir species or the increase in abundance of existing reservoir species, can additionally increase the potential for novel disease spillover,<sup>75,76</sup> and decreases in biodiversity can decrease pathogen prevalence if infected individuals die or migrate out of a population (figure 2), or if key reservoir or vector species are removed. Similarly, changes in vector abundance, as a result of ecological release, species introductions, or climate-induced range shifts for example, can also alter disease transmission, with either positive or negative effects on disease prevalence.<sup>77,78</sup>

In human-managed ecosystems, such as agricultural landscapes, a focus on enhancing productivity and efficiency has led to extensive planting of monocultures, which are vulnerable to disease outbreaks.<sup>79</sup> In contrast, the practice of adding biodiversity (agrobiodiversity) can enhance agricultural productivity by reducing crop losses<sup>80</sup>—for example, via the dilution effect or moderating the microclimate (figure 2). Increasing genetic or species diversity, specifically including disease-resistant host genotypes or promoting natural enemies of pests, can reduce the likelihood and severity of pathogen and pest outbreaks.<sup>81</sup>

### Infectious disease to biodiversity

Infectious diseases can cause population declines by reducing the development, fitness, and survival of their hosts, and pose a particular risk to already threatened and endangered species.<sup>82</sup> In turn, species declines can cascade to wider community impacts through competitive release, removal of top-down regulation, and loss of foundational species (figure 2).<sup>83</sup>

Not all pathways linking disease to biodiversity are negative. Disease maintains or promotes biodiversity through indirect (parasite-mediated) competition or by occupying a crucial role in a trophic cascade. Parasites increase biodiversity where frequency-dependent parasitism increases intraspecific competition relative to interspecific competition—this is known as the Janzen–Connell hypothesis—and when parasites are more detrimental to competitively superior or more abundant species (figure 2).<sup>84,85</sup> Evidence increasingly

## Panel: Connecting climate change, biodiversity, and infectious disease

### Malaria: climate to biodiversity to infectious disease

Human malaria, which results from transmission of *Plasmodium* parasites by *Anopheles* mosquito vectors, involves multiple vector and parasite species with varying climate responses and contributions to disease transmission.<sup>13,14</sup> Vector biodiversity affects malaria transmission through interspecific variation in competence, feeding behaviour, and seasonality.<sup>14–16</sup> For example, the presence of species that can aestivate during the dry season sustains high malaria transmission in arid climates such as the Sahel desert,<sup>17</sup> and both high abundances of anthropophilic vector species and co-occurrence of dry and rainy season vectors have been associated with increased disease prevalence in Kenya.<sup>18,19</sup> The climate has complex, non-linear relationships with vector and parasite species distributions and life history traits that contribute to disease transmission.<sup>20,21</sup> Precipitation affects the availability and stability of aquatic breeding habitats required by mosquitoes,<sup>22,23</sup> and temperature affects vector and parasite development rates as well as vector survival, lifespan, reproduction, and biting rates.<sup>24</sup> These climatic influences are reflected in malaria incidence patterns that follow rainfall and temperature gradients and seasonality,<sup>25</sup> and generate complex non-linearities that are not well captured by simple linear models.<sup>24,26</sup> Crucially, ignoring the diversity of *Anopheles* vectors, which are each characterised by distinct temperature dependencies (influencing developmental rates, biting rates, fecundity, etc), shifts forecasts of both the magnitude and direction of temperature effects on disease prevalence.<sup>27</sup>

### Amphibian declines: climate to infectious disease to biodiversity

Chytridiomycosis, a disease caused by the pathogenic chytrid fungus *Batrachochytrium dendrobatidis*,<sup>28,29</sup> is known to infect more than 1000 amphibian species, many of which are considered threatened by the International Union for Conservation of Nature.<sup>30</sup> Chytridiomycosis has resulted in mass mortality and amphibian biodiversity declines globally.<sup>31,32</sup> Climate change has multiple points of impact, including on host abundance, disease prevalence, and pathogen transmission;<sup>33,34</sup> however, responses of *B dendrobatidis* to temperature vary across species,<sup>35</sup> life stages,<sup>36</sup> and pathogen isolates.<sup>37</sup> For example, there is empirical evidence for increased *B dendrobatidis* prevalence in cold-adapted systems under unusually warm temperatures (and vice versa), as predicted by the thermal mismatch hypothesis,<sup>38</sup> which has mixed support,<sup>39</sup> driving amphibian declines in some warming habitats. Disease-driven declines in amphibians were thus only revealed when examining the interaction between climate (temperature extremes) and pathogen presence, whereas considering either in isolation fails to capture the crucial dynamics underlying declines.<sup>40</sup>

### Blue carbon: infectious disease to biodiversity to climate

Vegetated marine ecosystems often support high biodiversity and productivity.<sup>41</sup> These biodiverse regions provide crucial ecosystem services.<sup>42–44</sup> Radiocarbon dating in mangrove soil, salt marshes, and seagrass indicates that these habitats can store carbon for thousands of years;<sup>45–47</sup> however, biodiversity loss due to changes in marine and land use (eg, aquaculture and urban development) can release stored carbon, transforming these habitats into carbon sources.<sup>48,49</sup> The degradation of vegetated coastal ecosystems is estimated to release 0.45 billion tons of CO<sub>2</sub> a year.<sup>50</sup> Disease is one of several factors exacerbating biodiversity loss and decline in these productive ecosystems. Eelgrass wasting disease, for example, has caused large declines in eelgrass density across locations and time,<sup>51,52</sup> which reduces the habitat quality of eelgrass beds that support coastal biodiversity. Recent epidemics have been linked to increased temperatures.<sup>52,53</sup> The interactions between climate change and ecosystem health in these systems thus create a vicious cycle. In addition, because eelgrass growth is lower in disease-impacted systems, the ability to sequester carbon is also reduced, and ignoring disease status could mislead global estimates of blue carbon storage capacity.<sup>54</sup>

supports that parasites can also function as the top predator in trophic networks, either by directly killing their hosts or by mediating host behaviour, thereby altering the flow of nutrients within and between habitats.<sup>86,87</sup>

### Climate change to infectious disease

The effects of climate change on infectious disease are well studied but have largely focused on vector-borne diseases. Climate change can have a direct effect on disease prevalence by altering physiological processes

of the host, affecting immune activity, altering the pathogens or their vectors, and modifying generation times, development times, and fitness.<sup>88</sup> Increases in temperature decrease generation times for pathogens and vectors, in turn increasing disease spread and the potential for outbreaks;<sup>89,90</sup> however, the effects of temperature on infectious disease are often non-linear<sup>24,91</sup> and vary by parasite, host, and vector, depending on species' thermal optima and disease ecology.<sup>92</sup> Under the thermal mismatch hypothesis, parasites are suggested to have a broader thermal niche than their hosts, and thus

#### A

Climate to biodiversity	Biodiversity to disease	Case study	Pathway
Precipitation and food web dynamics	Dilution or amplification	Elevated precipitation increases resource production, which in turn increases reservoir species richness and abundance, amplifying Lyme disease	
Precipitation and food web dynamics	Dilution or amplification	Addition of host species with low reservoir competence to a community with low species richness reduces <i>Borrelia burgdorferi</i> infection in nymphal ticks, and in turn, Lyme disease prevalence	
Precipitation and food web dynamics	Vector population	Drought induces changes in water depth and patchiness, disrupting aquatic food webs, and control of larval mosquitoes by fish; the increase in mosquito populations and the concentration of avian hosts around remaining watering holes increases West Nile virus transmission	
Temporal mismatch	Migration	Climate induced shifts in the phenology of milkweed leads to changes in Monarch butterfly migration, which acts as a filter for diseased individuals; disease prevalence is higher at the end of breeding season than at overwintering sites	
Gradual climate change and species introductions	Novel disease spread	Permafrost melt releases active bacteria and viruses from thawing carcasses, leading to anthrax outbreaks	
Migration or range shifts	Spillover	Change in migratory behaviour of harp seals following increased sea ice melt leads to increased opportunities for disease spillover and outbreaks of phocine distemper	
Migration or range shifts	Dilution or amplification	Sea ice melt alters the migration of caribou, a seasonal disease escape strategy; increased contact between geographically separated ungulate species facilitates spillover of diseases into communities that were previously isolated	
Migration or range shifts	Dilution or amplification	Extreme wetness and dryness decrease richness of insect-pollinated plants, reshaping the distribution of their pollinators; increased length of pollinator foraging distances, and floral trait variation drive, increases pathogen transmission and disease intensity	

#### B

Climate to disease	Disease to biodiversity	Case study	Pathway
Novel disease spread and spillover	Trophic cascade	Severe storms and warmer water are associated with amoebiasis outbreaks in sea urchins; mass mortality of sea urchins releases kelp forests from predation, increasing local species richness	
Thermal mismatch	Parasite mediated competition	Shorter winters favour temperature dependent growth of <i>Geomyces destructans</i> , which is linked to white nose syndrome in bats, which reduces the abundance of dominant bat species in the community, favouring less dominant bat species	
Thermal mismatch	Extirpation	Cold-adapted and warm-adapted amphibian hosts are more susceptible to <i>Batrachochytrium dendrobatidis</i> fungus at relatively warm and cool temperatures, respectively; <i>B. dendrobatidis</i> infection has caused amphibian population declines and extirpation	
Thermal mismatch	Extirpation	Climate-related shifts in habitat suitability for white pine blister rust resulted in a decline in prevalence in arid regions and an increase in colder regions, causing host extirpation	
Temperature and physiology	Species decline	Temperature-dependent virulence of <i>Vibrio</i> spp is associated with coral bleaching and disease; coral declines are associated with fish biodiversity loss	
Temperature and physiology	Species decline	Warming temperatures increase the occurrence and severity of ranavirus, a disease linked to mass mortality events and population declines in the common frog, <i>Rana temporaria</i>	
Behaviour	Species decline	Drought increases foraging distances in the blue orchard bee, resulting in the increase of parasitism rates by the blister beetle and subsequent species decline	
Development time of pathogens	Extirpation	Decreased larval development times of the lung-dwelling nematode <i>Umingmakstrongylus pallikuukensis</i> in muskoxen ( <i>Ovibos moschatus</i> ) increases infection pressure, which cascades to elevated predation risk from polar bears	
Novel disease spread and spillover	Extirpation	Shifts in the timing of the end of the dry season, when Ebola outbreak risk is highest, lead to mortality-induced changes in local primate community assemblages	

(Figure 2 continues on next page)

C			
Disease to biodiversity	Biodiversity to climate	Case study	Pathway
Species decline or extirpation	Ecosystem services	The loss of keystone and mesopredators due to sea star wasting disease reduces kelp forest resilience; loss of kelp forest could reduce potential to capture and store (blue) carbon	
Species decline or extirpation	Ecosystem services	Eelgrass wasting disease and loss of eelgrass beds could reduce potential carbon sequestration	
Species decline or extirpation	Ecosystem services	The chestnut blight fungus, native to east Asia, essentially removed a dominant forest tree in the eastern USA; the death and decay of mature American chestnuts resulted in a pulse of released carbon and removed an important carbon sink	
Species decline or extirpation	Ecosystem services	The protozoan parasite <i>Haplosporidium nelsoni</i> influences shellfish populations, and epizootic outbreaks have led to large population declines; oyster beds provide a range of ecosystem services, including habitat for fish, water filtration, and shoreline protection	
Species decline or extirpation	Trophic cascade	Rinderpest reduced herbivore density in the Serengeti; decreased grazing released vegetation from top-down control and increased fires, shifting the habitat to a net carbon source	
Parasite mediated competition	Ecosystem services	Foliar fungal pathogens increase plant biodiversity by reducing above-ground plant biomass; reduced biomass might decrease ecosystem services, including carbon sequestration; however, more diverse grasslands are suggested to sequester more carbon	
D			
Biodiversity to climate	Climate to disease	Case study	Pathway
Agrobiodiversity and microclimate	Development time of pathogens	Height differences in more genetically diverse rice crop plantings modified temperature and humidity conditions and might have inhibited spore germination and mycelium growth of fungal blast ( <i>Magnaporthe grisea</i> ), reducing disease pressure	
E			
Biodiversity to disease	Disease to climate	Case study	Pathway
Species introductions and novel disease spread	Ecosystem services	Introduced non-native species and their pathogens (ie, <i>Cryptococcus fagisuga</i> ) cause beech bark disease, which can result in tree damage and death, reducing forest biomass and potential carbon sequestration capabilities	
Dilution or amplification	Ecosystem services	Tree diversity has a hump-shaped relationship with pest diversity (at low tree diversity, pests are amplified, and at high tree diversity, pests are diluted); mountain pine beetle infestation reduces forest biomass and carbon sequestration capabilities	
F			
Disease to climate	Climate to biodiversity	Case study	Pathway
Behaviour	Ecosystem services	Parasitic plants, such as <i>Striga hermonthica</i> —a parasite of sorghum—might modify their microclimate via high transpiration rates; forest microclimate influences soil microbial composition, impacting primary productivity, and plant communities	
Behaviour	Climate-induced biodiversity decline (various mechanisms)	The mitigation strategies used during the emergence of COVID-19 (eg, travel bans, social distancing, and suspended industrial production) also mitigated climate change by decreasing daily CO <sub>2</sub> emissions	

**Figure 2: Case studies illustrating mechanistic links connecting climate, biodiversity, and infectious disease**

A table with references relating to this figure can be found in the appendix (p 7).

should maintain thermal performance over a broader range of temperatures, driving outbreaks at temperatures at which host performance is diminished.<sup>93,94</sup> In some systems, thermal performance curves indicate that climate change might reduce disease burden over longer timescales due to a lower survival probability of infected hosts at higher temperatures.<sup>38,95</sup> Wider climatic shifts including changes in the length of wet or dry seasons can also alter disease dynamics by increasing or decreasing the time when the environment is suitable for transmission.<sup>93</sup>

In general, the relationships between climate change and non-vectored microparasites have not been as well studied, in part because of scale differences in dynamics (see Discrepancies in scale section). Nonetheless, seasonal weather patterns might alter host behaviour and

contact rates.<sup>96</sup> Thus, shifts in seasonality due to climate forcing can drive shifts in infection dynamics for diseases such as cholera.<sup>97</sup> Climate change can also more directly affect the spread of some airborne infections such as chickenpox (varicella) through changes in humidity.<sup>98</sup> Similarly, infection risk from fungal pathogens in plants is often closely linked to humidity or dew,<sup>99</sup> and dispersal of spores can be strongly weather dependent.<sup>100</sup>

Gradual climatic shifts, including polar ice and permafrost melting, could lead to disease spread by releasing pathogenic fungi and viruses, and providing new opportunities for spillover (figure 2). Hosts shifting distributions to track changing climate (see Climate change to biodiversity section) increase the potential for disease spillover between previously geographically distant species.<sup>76,101</sup> Climate-induced range shifts have

See Online for appendix



been predicted for pathogen vectors,<sup>102,103</sup> and shifting disease pressure with climate change has been the focus of much recent attention;<sup>104,105</sup> however, in many systems, which climatic factors limit the distribution of hosts and parasites is unclear, making it difficult to generate robust projections.<sup>88,106</sup> Extreme climate events, such as heat waves or deluges, modify disease pressure through induced stress responses and lowered host immunity. Extreme heat and drought can additionally have indirect effects on host immunological competence—for example, via food shortages. Extreme climate events also affect transmission dynamics. For instance, in environments with little water, droughts lead to more hosts congregating around scarce water sources, facilitating transmission of waterborne or environmentally transmitted diseases. Flash floods that cause damage to wastewater and potable water infrastructure can lead to an increase in transmission of waterborne pathogens in people.<sup>107</sup>

#### Infectious disease to climate change

Evidence for direct mechanistic links by which infectious disease alters climate is generally insufficient. Here, we speculate on some possible associations. Disease can modify the greenhouse gas emissions of wild and domestic animals—for example, livestock infected with helminths release more methane than their unparasitised conspecifics<sup>108</sup>—but knowing whether such relationships generalise or scale to a magnitude likely to affect global climate is difficult. In human systems, health care has a large and expanding carbon footprint;<sup>109</sup> however, when infectious disease occurs at a larger scale, as was the case for the SARS-CoV-2 pandemic, policies put in place by governing bodies (eg, stay-at-home orders and travel bans) could reduce transport-related CO<sub>2</sub> emissions.<sup>110,111</sup>

#### Key challenges to connecting climate change, biodiversity, and infectious disease

We have highlighted some of the many pairwise links between climate change, biodiversity, and infectious disease. There are varying degrees of empirical evidence for different links (figure 2), and the mechanisms between some pairs of pressures are better studied than others, but the volume of research linking pressures is growing. These pairwise mechanisms are often intricately interconnected, resulting in feedbacks and chains of interactions, as we illustrate in the case studies presented in the panel; however, they are rarely studied together.

What prevents studies of climate change, biodiversity, and infectious disease connectedness? Some impediments probably relate to research pedagogy, and other barriers reflect the practical challenges of working with complex systems and access to funding to support interdisciplinary research. Ecosystems are complex, dynamic, and non-linear. The current literature addressing mechanistic links among all three pressures thus comprises a tangled web of empirical, conceptual, and

synthetic studies, encompassing a myriad of ecological processes (figure 3). Changes in infectious disease, climate, and biodiversity are often impossible to experimentally manipulate at large scales. Most research investigating interactions among all three pressures is observational or based on natural experiments, and interactions are intrinsically difficult to analyse and interpret.

#### Multiple axes of variation

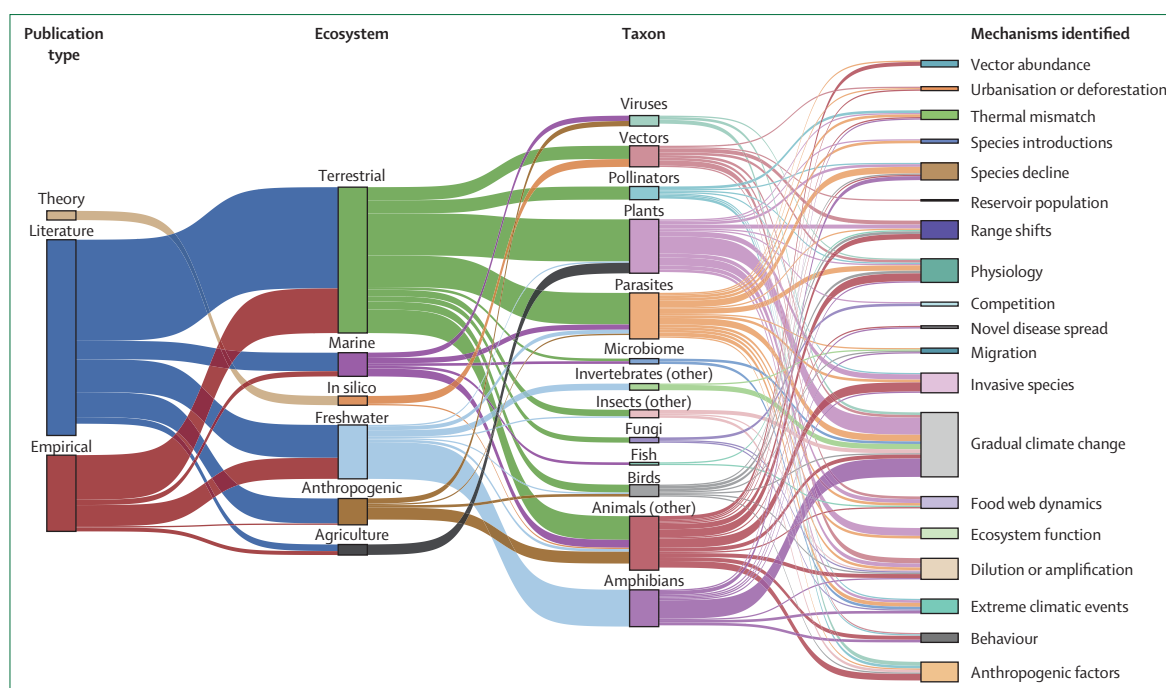
Climate, biodiversity, and infectious disease are measured in multiple ways, operationally tailored to specific questions. For example, numerous climate variables and their means, variability, and extremes can be calculated. Measures of biodiversity and disease are equally multifaceted,<sup>112</sup> and indicators of connectedness among the three pressures must consider unit scales ranging from local microclimate measures (eg, °C, millimetres, and metres per second) to indicators of decline and health in species biodiversity (eg, species richness, Shannon's entropy, Simpson's Diversity Index, phylogenetic diversity, expected heterozygosity, and International Union for Conservation of Nature Red List of Threatened Species classification) to transmission rates and measures of disease epidemiology (eg, susceptible populations, infected individuals, recovery rates, and R<sub>0</sub>). Even when units are compatible, collecting data in overlapping places and times can be difficult, although the increasingly widespread availability of remotely sensed environmental data and global databases of species occurrences is improving the outlook (see Overcoming barriers to research section).

#### Non-linearity

Trends describing human-caused changes to the environment are non-linear, and it is perhaps unsurprising that biological responses to these changes also show non-linearities. For example, phenological responses to recent warming appear to be slowing down<sup>113</sup> (although mechanisms remain debated<sup>114</sup>) and temperature effects on biological rates (eg, metabolic functions, life history, etc) are frequently described by non-linear curves that vary among species and traits.<sup>115,116</sup> Linear predictions will, therefore, often fail. Common machine learning tools, such as Random Forest, Neural Networks, and Support Vector Machines, allow the fit of complex non-linearities, but mechanistic models that capture underlying biological and physical process will be required for making predictions beyond the training data that inform them, which is crucial for robust future forecasting.<sup>117</sup>

#### Complex systems

The nexus of climate change, biodiversity of ecosystems, and the transmission of infectious diseases presents a complex system that confounds long-term predictability. Complex systems are networks of components without central control that can give rise to complicated



**Figure 3: Classification of 128 studies that discuss climate change, biodiversity, and infectious disease**

Each study was scored for publication type, ecosystem (focal habitat), taxon (focal organism), and mechanisms. The study-specific mechanisms described in each publication were assigned to the broader mechanism categories discussed in this synthesis. For example, studies that describe general increases in temperature and precipitation were included in the gradual climate change mechanism, whereas studies on extreme heatwaves were included in the extreme climatic events mechanism. Line width represents the number of studies. More details are provided in the appendix (p 4).

behaviours.<sup>118</sup> Crucially, complex systems exhibit emergent and self-organising behaviours that usually cannot be anticipated simply by understanding the properties of the constituent parts. The climate system is recognised as a complex system.<sup>119</sup> Agent-based model simulations are one approach to modelling complex systems. Agent-based models start with a set of beliefs about the rules governing the constituent subsystems and simulate (rather than solve for) the possible trajectories of the system; however, there are substantial challenges to using agent-based models for forecasting, including insufficient robustness to the underlying models, a tendency to overfitting, high computational cost and data demands, and scalability. Another approach, which is perhaps better suited to studying the climate–biodiversity–disease nexus, is to represent complex systems as sets of coupled non-linear differential equations. Here the challenge is an insufficient amount of realism and use of highly simplified models for the behaviour of the individual parts; however, more recently developed machine learning tools such as symbolic regression<sup>120</sup> and physics-informed neural networks<sup>121</sup> allow for the construction of more complex non-linear dynamical systems models informed by data (rather than theory).

### Discrepancies in scale

A mismatch in the temporal and spatial scales at which relevant mechanisms act creates an additional barrier to

studying the three-way interaction between pressures. Changes in biodiversity and infectious disease prevalence are commonly measured at the community and population levels, respectively, at timescales ranging from months to years and spatial scales ranging from metres to hectares. The large interannual and spatial variability in climate leads most estimates of climate change to be measured at large spatial and timescales (eg, decades), and complex processes shape how climate change filters down to alter the microclimates organisms experience.<sup>2,122</sup> If pressures interact at different scales, then it is also likely that no single scale will capture their full impacts.<sup>123</sup>

Because of this scale mismatch, it is unsurprising that the bidirectional interactions between biodiversity changes and infectious disease prevalence have been more thoroughly investigated, whereas the tripartite of interacting pressures that includes climate change is only rarely considered; however, both the independent pairwise interactions between biodiversity and infectious disease, and between biodiversity and climate change, (figure 2) are strongly supported. Furthermore, if changes in infectious disease prevalence or biodiversity are widespread, then their effects will be felt at much larger timescales. Examples of this are the elimination of the American chestnut in eastern US forests due to blight<sup>124</sup> and ongoing climate-driven impacts of white pine blister rust on western US forests,<sup>125</sup> narrowing the

mismatch in scales. Whether these effects propagate to impact the climate system, however, will depend on the unique role of extirpated species in their ecosystems.

Interactions between climate change (operating at large scales) and infectious disease or biodiversity dynamics (operating at finer scales) can also be affected through local environmental conditions created by the larger climate system. For instance, a warming climate can change the average temperature of disease vector habitats, affecting growth rates and carrying capacity, with implications for disease transmission (figure 2). Similarly, climate-induced range shifts can alter population abundances and local community composition, as documented in Thoreau's woods.<sup>126</sup> Thus, processes that propagate down from the climate system to biodiversity and disease transmission are both more prevalent and easier to detect than interactions of biodiversity and disease transmission that propagate up to the climate system.

Multiscale modelling provides a key method for better understanding the upscaling and downscaling of interactions. In multiscale models, dynamical transitions among states are commonly solved at two different space and time resolutions.<sup>123,127</sup> Changes in the fine-grained scale (here, changes to biodiversity and infectious disease prevalence) are studied at a high resolution and then aggregated to provide average changes of state that are relevant to the dynamics of the coarse-grained system. Solutions of the coarse-grained system are then obtained to provide initial states and boundary conditions for the next solution of the fine-grained system.

### Siloed research cultures

Current methods of research and education on climate change, biodiversity, and infectious disease do not facilitate thorough understanding of three-way interactions. Attempts to broaden cultures, as advocated in the 2022 IPCC report,<sup>128</sup> and to integrate animal, human, and environmental perspectives are captured in the One Health<sup>129</sup> and Planetary Health<sup>130</sup> approaches.

The US Centers for Disease Control and Prevention's One Health approach acknowledges the climate–biodiversity–disease interface: prioritising local, regional, and global workshops on disease emergence, connectedness of zoonotic spillover, likelihood of substantial effects on animal and human health, and coordination of medical networks. Gaps remain, however; for example, disease prioritisation in the USA—with priority diseases including rabies, salmonellosis, West Nile virus, plague, and Lyme disease—recognises shifts in range distributions attributed to habitat losses and fragmentation, yet climatic effects are not factored in.<sup>131</sup> Extensive policy plans that are in the works, such as the One Health Joint Plan of Action<sup>132</sup> launched by the Quadripartite organisations (the Food and Agriculture Organization, UN Environment Programme, WHO, and the World Organisation for Animal Health), advocate for joint consideration of animal, human, and environmental health systems, but we show that the

science has been lagging and the integration of climate impacts and feedbacks remains ambiguous.

Although many concepts central to planetary health are not new, by explicitly recognising the interconnections between climate, biodiversity, and human health, planetary health is a call for massive collaboration across disciplines and national boundaries. To be successful, however, funding bodies need to recognise and support such collaboration.

### Other challenges

We have highlighted some of the key challenges to jointly considering the intersecting pressures of climate change, biodiversity loss, and infectious disease; however, our list is far from comprehensive. In addition, each pressure is accompanied by its own unique list of challenges. Studies of infectious disease can be limited by restrictions on data sharing; disease incidence is frequently under-reported or biased, with different reporting standards over space and time; historical records are often sparse; and seroprevalence data can be unreliable. Studies of biodiversity change are difficult to compare because our indices often measure different axes of biodiversity; we still do not have data for most species, many of which have yet to be described; and ecological forecasting is in its infancy. Climate change science has progressed rapidly over recent decades, and advances in climate change attribution have been particularly useful in communicating impacts; nonetheless, working with data from climate models is not straightforward for non-experts, forecasts come with large uncertainties, the temporal resolution of model projections does not necessarily match to species lifecycles and activity patterns, and we are better at modelling some climate attributes (eg, mean temperatures) than others (eg, weather anomalies and extremes).

### Overcoming barriers to research

Challenges to evaluating the interactions among climate change, biodiversity, and infectious disease remain substantial. Interdisciplinary collaboration will be increasingly important; however, differences in methods, statistical frameworks, corpus of literature, and even language present barriers to effective interdisciplinary research.<sup>133</sup> Additionally, data that can be integrated across scales, capturing non-linear effects and feedback loops, and that can be projected forward in time, are needed. For instance, what types of data are needed to detect climate change effects is debated in biodiversity and climate change research,<sup>134,135</sup> what data and scale are best to evaluate relationships is debated in infectious disease and biodiversity research,<sup>72,136</sup> and how to integrate non-linear effects of temperature along with other concurrent drivers of disease dynamics is debated in climate change and infectious disease research.<sup>24,96</sup>

Addressing the intersection of climate, biodiversity, and infectious disease will require appropriate field observational data for all three pressures, collected at



relevant time and spatial scales, paired with experiments and mechanistic models (appendix p 2). Global efforts, such as the Global Biodiversity Information Facility, Group on Earth's Observations Biodiversity Observation Network, Global Forest Watch, the Integrated Ocean Observing System, the National Ecological Observatory Network, and the Ocean Biodiversity Information System, provide useful examples of large-scale data collection and curation. Citizen science data (eg, USA National Phenology Network and eBird), distributed experiments (eg, Nutrient Network), and Indigenous knowledge networks<sup>137</sup> represent novel and increasingly important types of information, but such data remain undervalued and need to be better integrated.<sup>138</sup>

Ultimately, we need to expand research frameworks to truly integrate climate and habitat changes, wildlife conservation, food security, and modern agricultural practices, considering both their direct and indirect effects as well as the feedback and non-linearities in the pathways that connect them. Expanding course curricula to advance core competencies (eg, integration of animal, human, and environmental sciences, and application of research to policy, public health, and clinical programmes),<sup>139</sup> and supporting interdisciplinary hiring clusters and research coordinated networks, will provide part of the solution.<sup>140</sup> In addition, we must motivate experts to work outside their given expertise, to build on and carry over inherent strengths to other fields. For example, predictive analytical models that are not typically applied in clinical areas of veterinary sciences would extend methods and concepts from ecology and environmental sciences. Likewise, advances in medical and veterinary fields, alongside their more immediate solutions focus, provide important grounding for ecological theory and practice.

## Outlook and future directions

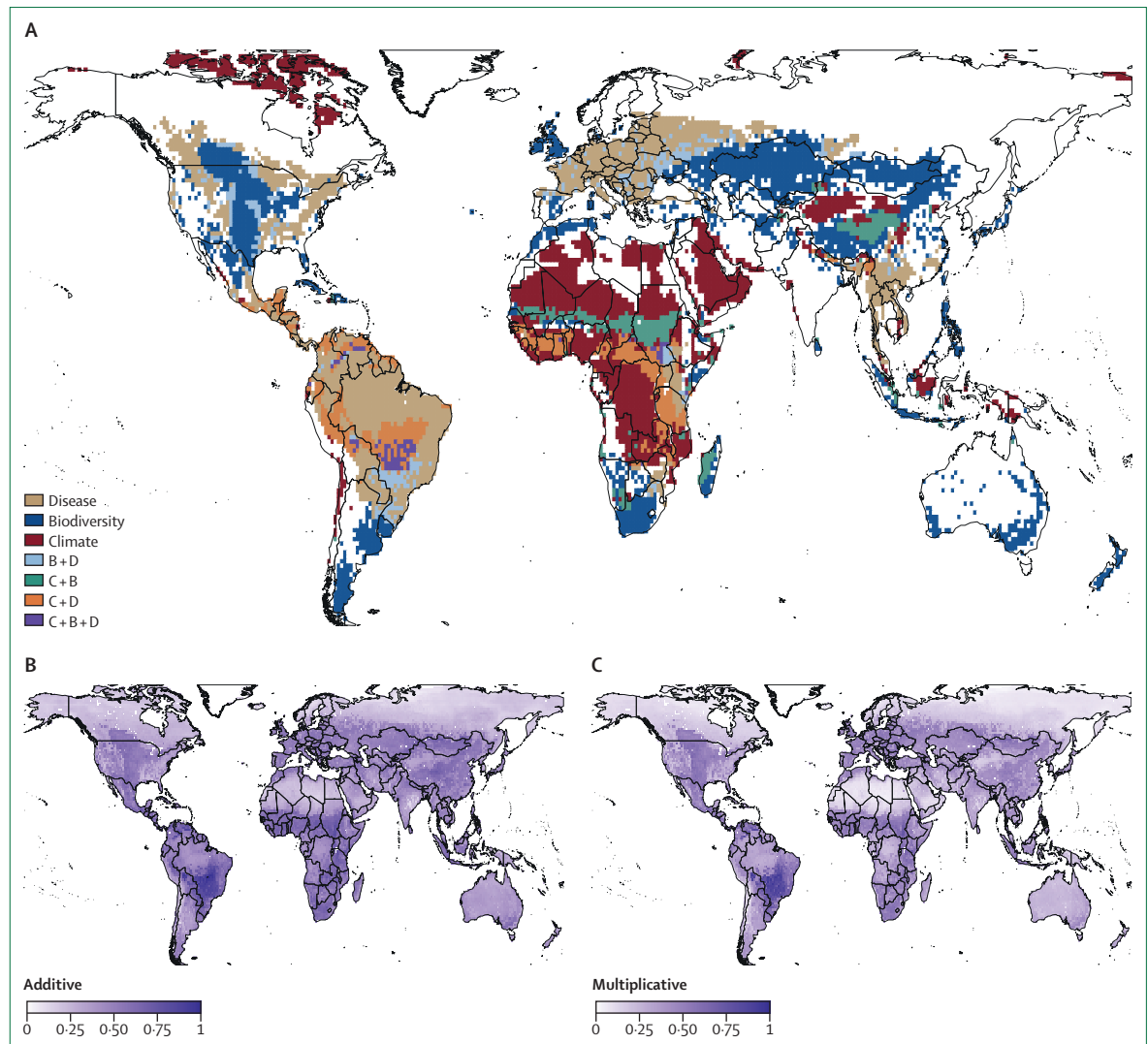
Urgency is increasing for major global action on climate change, biodiversity, and infectious diseases, and the international community has responded. The 2022 IPCC report, highlighting widespread human and environmental impacts of climate change that are already occurring and expected to accelerate without extreme and rapid changes in carbon emission mitigation, inspired calls for international policy shifts at the UN Climate Change Conference. The 2022 meeting of the Parties to the UN Convention on Biological Diversity resulted in the unprecedented commitment by participating countries to protect 30% of land and sea area by 2030, an action considered essential for safeguarding Earth's remaining biodiversity. The SARS-CoV-2 pandemic encouraged the establishment of various international pathogen surveillance and pandemic prevention initiatives (eg, WHO's Global Genomic Surveillance Strategy<sup>141</sup>). These combined efforts look to address the primary crises of climate change, biodiversity loss, and infectious disease, and increasingly, the connections between them.<sup>142</sup> By recognising the interconnectedness of these

crises, there is an opportunity to identify shared drivers and develop sustainable solutions with multiple co-benefits (panel),<sup>143,144</sup> however, doing so requires new approaches to scientific research and communication across disciplines.

Given the challenges, how can we advance research and policy at the interface of climate change, biodiversity, and infectious disease? Researching the interactions of all three global pressures is certainly more complex than studying them individually or in pairs; however, elucidating the full connectedness of climate change, biodiversity, and infectious disease might be possible by integrating theory and data across temporal and spatial scales using data-driven models. Such efforts could be transformative for planetary health, allowing the identification of mutually beneficial scenarios (eg, compared with continued planting of fast-growing tree monocultures, preserving older and more biodiverse forests stores more carbon and increases resistance to climate extremes and disease<sup>56</sup>) and, conversely, highlighting where a focus on solutions to one pressure can aggravate another (eg, tree planting in ancient grasslands to mitigate climate drives biodiversity loss and probably overestimates net carbon benefits<sup>145</sup>).

Empirical research that considers the mechanistic links among all three global pressures is currently aggregated in a few well studied systems: amphibian chytridiomycosis, forest health, and Lyme disease. For instance, chytridiomycosis in amphibians comprises approximately a quarter of the studies we identified that jointly address climate, biodiversity, and infectious disease measures. Our analysis considered more than 1.8 million publications, and shows the rarity of such integrative research. Although these few well studied systems provide useful case studies, expanding beyond them is urgently needed. Encouragingly, we show that a substantial body of research already addresses many of the pairwise connections in figure 2 (which we suggest presents more than a list of case studies; it serves as a guide for mapping how all three global pressures can be mechanistically linked by identifying adjacent pathways).

One approach for identifying where interactions between pressures could be important is to examine how they overlap in space or time. Although each pressure can be characterised along multiple dimensions by mapping the axes relevant to a specific mechanistic pathway on a common spatial or temporal scale, examining their intersection is then possible. For example, the intersection between climate and biodiversity loss might exacerbate risk of zoonotic spillover in central Brazil given the high richness of zoonotic hosts in that region, whereas low zoonotic host diversity might reduce risk of spillover in Australia, despite exposure to similar biodiversity loss and climate hazards (figure 4). Of course, such coarse scale approaches only provide a guide to potential interactions between pressures, and are unlikely to



**Figure 4: Geographical overlap of global pressures**

(A) Pressure hotspots, defined as cells falling within the upper 20% quantile of each pressure. (B) Global pressures combined additively (datasets rescaled to between 0 and 1). (C) Global pressures combined multiplicatively (datasets rescaled to between 1 and 2). In the additive (B) and multiplicative (C) panels, zero indicates absence of, and one indicates presence of, all three global pressures. Climate change risk is measured as the standard Euclidean distance across multiple climate metrics between a baseline period (1995–2014) and future period (2080–99) under the Shared Socioeconomic Pathway 2–4.5 scenario.<sup>146</sup> Biodiversity is represented as the inverse of the Biodiversity Intactness Index, which reflects the proportional loss of species richness in a given area relative to minimally affected baseline sites in 2005. Disease risk is represented by mammal zoonotic host richness,<sup>147</sup> a measure of both biodiversity and zoonotic infectious disease burden. More details are provided in the appendix (p 4). B=biodiversity risk. C=climate risk. D=disease risk.

accurately capture dynamics for any one particular system; for example, the loss of biodiverse native forests in Australia has been linked to increased aggregation of bats in human-managed gardens, leading to spillover of Hendra virus to horses.<sup>148</sup> Nonetheless, such approaches allow for scenario modelling—for instance, contrasting additive versus multiplicative or threshold-type interactions (figure 4). Improved data at appropriate scales, coupled with a mechanistic understanding of the connections among pressures, would allow for more fine-grained predictions, such as shifts in transmission of mosquito-borne diseases with warming,<sup>103,149</sup> and effects

of the chytrid fungus *Batrachochytrium dendrobatidis* on global amphibian declines<sup>40</sup> (panel).

### Open questions to improve our understanding of the interconnections among climate change, biodiversity, and infectious disease

Key questions need to be addressed to further advance the integration of climate change, biodiversity, and infectious disease research and to tackle the combined pressures they pose to ecosystem integrity and human wellbeing. Many questions relate to data synthesis and modelling, including how we can augment existing

### Search strategy and selection criteria

We conducted a series of literature searches via the Web of Science Core Collection for papers published between Jan 1, 1975, and Dec 31, 2022, using key search terms to identify papers on biodiversity, climate change, and infectious disease (see appendix p 3 for full details of search criteria). The searches were restricted to primary research articles and review papers, and excluded book chapters, conference proceedings, and data papers. Our search returned 1 878 560 primary research and review articles. Among individual drivers, infectious disease had the most publications (1 347 124), followed by climate change (282 122), and then biodiversity (235 048). Pairwise combinations of these global pressures returned far fewer publications: infectious disease and biodiversity returned 17 580 results, biodiversity and climate change returned 17 652 results, and infectious disease and climate change returned 4751 results. We identified 505 studies that matched our search terms for biodiversity and climate change and infectious disease, but only 128 studies discuss the mechanistic links (appendix p 5) connecting pressures. Only 29 papers quantified measures of climate change, biodiversity, and infectious disease, and seven of these were on a single disease system, *Batrachochytrium dendrobatidis*, the causative agent of chytridiomycosis in amphibians. More detailed search methods are described in the appendix (pp 3–4).

datasets to address data gaps in our understanding of the mechanistic pathways linking climate change, biodiversity, and infectious disease; at which temporal and spatial scales interactions between pressures are most likely to arise; and how the spatial coincidence of multiple pressures increases the likelihood of interactions. Crucially, we still do not know which climate axes, disease attributes, and dimensions of biodiversity are most likely to drive, and be affected by, three-way interactions among pressures, or whether interactions between pressures are mostly reinforcing or dampening. The final set of questions address future scenarios—for example, how artificial intelligence and machine learning tools and data streams (eg, genomics, remote sensing, and social network analysis) might contribute to improving models, and how future global change (eg, climate change, human population growth and movement, and habitat transformation) will shift interactions among pressures in addition to the intensity of the pressures. Answers to these questions will be needed to identify the solution pathways for policy and management strategies to maximise co-benefits.

We have focused our Review at the nexus of the intersecting pressures of climate change, biodiversity loss, and infectious disease. We have outlined the benefits of considering these three pressures together, and some of the costs of failing to do so. Ultimately, solution

pathways to jointly reduce pressures are needed and will require coordinated efforts in science and policy.<sup>10</sup> By better understanding the interactions among pressures, we can better map out the solution space. Identifying the most effective policy and socioeconomic levers to achieve transformative change will present new challenges at the interface of natural and human systems.<sup>5,128</sup>

### Contributors

TJD and JLG conceptualised the Review. MJF and AP-B conducted the search strategy and study screening. All authors drafted the Review. AP-B, LBB, TJD, JMD, MJF, JLG, and EAM critically revised the Review.

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