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Review

A perspective on green, blue, and grey spaces, biodiversity, microbiota, and human health

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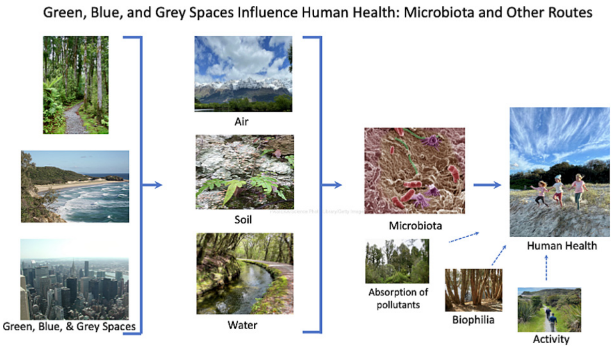
HIGHLIGHTS

- We are increasingly excluding ourselves from our wild spaces.
- There are health consequences of this loss of exposure to green and blue spaces.
- This loss is severing the connection between human and environmental microbiota.
- We need better tools to quantify aspects of exposure to environment.
- We need a major focus on increasing human exposure to the natural environment.

GRAPHICAL ABSTRACT



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ABSTRACT

Humans have lived from equator to poles for millennia but are now increasingly intruding into the wild spaces of other species and steadily extruding ourselves from our own wild spaces, with a profound impact on: our relationship with the natural world; survival of other species; pollution; climate change; etc. We have yet to grasp how these changes directly impact our own health. The primary focus of this paper is on the beneficial influence of proximity to the natural environment. We summarize the evidence for associations between exposure to green space and blue space and improvements in health. In contrast, grey space – the urban landscape – largely presents hazards as well as reducing exposure to green and blue space and isolating us from the natural environment. We discuss various hypotheses that might explain why green, blue, and grey space affect health and focus particularly on the importance of the biodiversity hypothesis and the role of microbiota. We discuss possible mechanisms and exposure routes – air, soil, and water. We highlight the problem of exposure assessment, noting that many of our current tools are not fit for the purpose of understanding exposure to green and blue space, aerosols, soils, and water. We briefly discuss possible differences between indigenous perspectives on the nature of our relationship with the environment and the more dominant international-science view. Finally, we present research gaps and discuss future directions, particularly focusing on the ways in which we might – even in the absence of a full understanding of the mechanisms by which blue, green, and grey space affect our health – begin to implement policies to restore some balance to our environment of with the aim of reducing the large global burden of ill health.

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Contents

1. Introduction . . . 2
2. Green, blue, and grey space . . . 2
   2.1. Green space . . . 2
   2.2. Blue space . . . 3
   2.3. Grey space . . . 4
3. How do green and blue space affect health? Some hypotheses . . . 5
4. How microbiota affect health: possible mechanisms . . . 5
5. Exposure routes . . . 7
   5.1. Aerosols . . . 7
   5.2. Soils . . . 8
   5.3. Water . . . 9
6. Exposure assessment challenges . . . 9
7. Indigenous perspectives . . . 10
8. Research gaps . . . 10
9. Future directions . . . 11

Author contributions . . . 12
CRediT authorship contribution statement . . . 12
Data availability . . . 12
Declaration of competing interest . . . 12
Acknowledgments . . . 12
References . . . 12

1. Introduction

The age-adjusted incidence of many NCDs (allergies, asthma, autoimmune disease, some cancers, diabetes, neurodegenerative diseases, cardiovascular disease, and other immunologic, metabolic, gastrointestinal, psychiatric and behavioral disorders) is rising (World Health Organization, 2014), with marginalized populations, including indigenous peoples (Ellison-Loschmann et al., 2009; Anderson et al., 2016; Moore et al., 2015), most affected. The causes remain largely unknown and prevention options are therefore often scant, not optimally effective, or both. Human interaction with the environment probably plays a key role. Indeed, colonization has resulted in massive and sudden changes to the living environments of indigenous peoples as access to traditional environments has been dramatically altered in favour of urban development.

Humans differ from most other species because of our ability to be largely unconfined to an ecologic niche — we have lived from the equator to the poles for millennia. As total population size has grown steadily, then rapidly, we have, almost paradoxically, increasingly confined ourselves into more densely packed living spaces, inventing and growing cities and then megacities.

Consequences of this capacity to live anywhere and the related growth of the human population include: our early acceptance of animals (domesticated and accidental – e.g., rodents) in our immediate environment; our increasing intrusion into the wild spaces of other species, including those with which we do not have an interaction history (e.g., bats); and the steady extrusion of ourselves from our own wild spaces. This has had, and continues to have, a profound impact on: our relationship with the other components of the natural world; the survival and extinction of other species; pollution of the air, soil, fresh water, and oceans; climate change; etc. What we have yet to grasp clearly is the way in which these changes in relationships to animals, plants, and microbes directly impact our own health.

The first two of these human practices are associated particularly with infectious diseases. Many endemic/epidemic human diseases are zoonoses acquired from animals that we have domesticated, e.g., diphtheria, measles, smallpox, mumps, rotavirus A (Wolfe et al., 2007; Dobson and Carper, 1996). The habit of intensive animal husbandry – pigs, various bird species, cattle, confined animal feeding operations, and live-animal markets – ensures that microorganisms endemic to these animal species are not only nurtured but potentially selected for robustness by use of antimicrobials (Liu et al., 2016) as well as allowed the opportunity for cross-species transfer (e.g., influenza viruses). The world is currently in the grip of a pandemic the like of which we have not seen for a hundred years. Although the immediate cause of illness in any one individual is clear – infection with SARS-CoV-2 – our understanding of the source of the virus, the timing of its emergence, and the nature of its spread is only partial. Intrusion upon the wild space of bats is likely to be at least part of the story.

Although what we have added to the human environment: high meat consumption, sugar, alcohol, tobacco, industrial foods, toxins, air pollution, industrial chemicals, etc., are appropriately cited as risk factors and causes of non-communicable diseases (NCDs), the losses associated with the third characteristic of current human existence, namely increasingly extruding ourselves from our own wild spaces, are likely to be equally important but are currently poorly understood. A steadily expanding number of studies has shown that proximity to the natural environment can beneficially influence our health (Hartig et al., 2014).

This paper does not attempt to be a full systematic review but instead provides a perspective on the relationships between green, blue, and grey space on the one hand and human health on the other. We focus on several critical research gaps: in particular, on important questions about what health benefits we derive from the natural environment and why. We specifically consider the role of environmental microbiota and potential exposure routes. We begin with a discussion of green, blue, and grey space, the spaces for which we have most data but we duly note that there are other parts of the natural environment that we need to explore in relation to health and that color-coding can lack nuance (Li et al., 2023). Thus, we have assembled empirical data and hypotheses that may explain the impact of ecosystem dislocation on human health. We also present some specific research and policy implications.

2. Green, blue, and grey space

Green and blue space often co-exist and the beneficial effects on health of green and blue space may be partially overlapping and partially different. However, this remains difficult to establish because most studies have focused exclusively on one or the other and few have considered both simultaneously. For the same reason, although green/blue and grey space often co-exist, for the purposes of what follows, we have presented each separately.

2.1. Green space

A recent review of the concept of green space noted that fewer than half of the more than one hundred journal articles that were examined had actually defined the term. These authors concluded that green space was largely used in one of two ways – to refer to nature generally or to refer specifically to urban vegetation (Taylor and Hochuli, 2017) – and suggested that it may be more useful in future for researchers to construct a definition of green space in the context of their own research. For the purposes of the current paper, we are similarly drawing on a spectrum of research that is focused across aspects and unspoken definitions of green space. As we are particularly concerned with the health impact of separation of humans from our own wild spaces, we regard green space as including urban, rural, and wilderness areas, which necessarily vary in size, characterized by a mix of vegetation, and inhabited or frequented to varying degrees by humans.

Although it has long been recognized that exposure to green space may have health benefits, with nineteenth century public parks in London, Paris, and New York (e.g. Central Park) specifically designed to ameliorate the adverse health effects of industrialization, it was not until late in the 20th century that empirical evidence became available to, at least partially, substantiate this. One of the first studies was a 1984 study by Roger Ulrich (Ulrich, 1984), which found that hospital patients with a view of an outside natural scene recovered more quickly from surgery and took fewer opioids.

Since this pioneering work, evidence has accumulated that exposure to green space is associated with improvements in health outcomes across the life course. At the beginning of life, multiple studies have shown that exposure to green space is associated with improved birth outcomes including higher birth weight (Dadvand et al., 2014; Markevych et al., 2014) as well as a lower probability of small for gestational age (Donovan et al., 2011) and premature births (Xiao et al., 2022).

During childhood, several studies have found that exposure to green space is inversely associated with immune diseases including asthma (Hartley et al., 2020; Donovan et al., 2018a) as well as childhood leukemia (Donovan et al., 2021). However, the evidence is mixed (Wu et al., 2022), which may be because of differences in exposure assessment (Parmes et al., 2020) or because exposure to green space may both protect against allergic diseases and also trigger symptoms in some susceptible individuals. The relationship is not simple and beneficial effects may be specific to the environment in which greenery is found. In a study of >40,000 Danish children, no evidence was found for lower asthma risk with higher biodiversity; indeed, overall green space was associated with higher asthma risk (Winnicki et al., 2022). Nonetheless, high exposures to urban green space were associated with lower risk of asthma, as also shown in other studies (Hartley et al., 2020; Donovan et al., 2018a; Parmes et al., 2020).

Exposure to green space is also associated with improved developmental, behavioral, and academic outcomes. Specifically, exposure to green space is associated with a reduced risk of ADHD in children (Donovan et al., 2019a) and can reduce symptom severity in those already diagnosed with ADHD (McCormick, 2017). Further, exposure to green space at school (Hodson and Sander, 2017) and at home (Donovan et al., 2018b) is associated with better performance on standardized academic tests. Finally, children who are exposed to more green space are at a reduced risk of developing autism (Wu and Jackson, 2017). A systematic review of green space (and blue space) and cognitive function in young people (0–18 years) found some evidence of beneficial associations but the heterogeneity of studies prevented any attempt at synthesis (Buczyłowska et al., 2023).

During adulthood, exposure to green space is inversely associated with many of the leading causes of mortality and morbidity including cardiovascular disease (Chen et al., 2020; Donovan et al., 2013), lower-respiratory disease (Donovan et al., 2013), cancer (James et al., 2016), and depression (Astell-Burt and Feng, 2019; Liu et al., 2019a). Individuals who lived in greener neighborhoods took fewer opioids in the 12 months – and lived longer – following hip arthroplasty (Donovan et al., 2019b). Long visits to green space have been associated with greater social cohesion and lower rates of depression and hypertension (Shanahan et al., 2016). In the elderly, exposure to green space is inversely associated with non-accidental mortality (Hyam, 2020; Donovan et al., 2022a) and Alzheimer's disease (Oudin, 2020). Although there are fewer studies specifically examining the health effects of urban green space than green space per se, a recent systematic review found a consistent inverse association between urban green space exposure and mortality, heart rate, and violence, and a positive association with mood, attention, and physical activity (Kondo et al., 2018).

As well as promoting good health across the life course, exposure to green space is inversely associated with nine of the top ten global causes of mortality identified by the WHO, which together account for 55% of the 55.4 million deaths worldwide (World Health Organization, 2020): ischemic heart disease (Wang et al., 2019); stroke (Asri et al., 2020); chronic obstructive pulmonary disease (Bauwelinck et al., 2021); lower respiratory infections (Shen and Lung, 2017); neonatal conditions (Donovan et al., 2011); lung cancers (Klompmaker et al., 2021); Alzheimer's disease and other dementias (Aitken et al., 2021); diabetes (Khan et al., 2021); and kidney diseases (Liang et al., 2022). Of the 10 leading causes of global mortality, only the incidence of diarrheal disease is not associated with exposure to the natural environment; even for this disorder, there is some evidence of a beneficial association with green space, as research has shown that greater upstream natural landcover is associated with a lower risk (Herrera et al., 2017).

Several studies (Ward Thompson et al., 2012; Mitchell and Popham, 2008; Moran et al., 2021) have found that exposure to green space may be “equigenic”, i.e., have the potential to reduce health inequity, although this has not been observed in all studies, with a recent systematic review reporting that some studies found that the inverse association with green space was greater for high SES and white women (Zhan et al., 2020). A complete understanding of this association will facilitate effective development of green space in deprived areas and other urban environments with large health inequities.

The reasons why green space, and the natural environment more generally, may be protective against such a wide range of health conditions are discussed below.

2.2. Blue space

Humans frequently express a high affinity with water, particularly the ocean. We live on, or close to, coasts, rivers and lakes, even though these have been dangerous, often lethal, places across time (Gaffney et al., 2020; McFadgen, 2007; IAEA, 2011).

Substantial parts of our history (5000–300,000 years) are to be found under water; sites submerged by the rise of the ocean following the last ice age (approx 12,000 years BP) have been found throughout the world (Gaffney et al., 2020; Beck et al., 2021; Wiseman et al., 2021; Smith et al., 2015; Gearey et al., 2017; Walker et al., 2020; Flemming, 2021); the ancient past that we know well is largely the history that the sea has not swallowed. Our migratory journeys out of Africa followed coastlines (Lopez et al., 2015; Pickrell and Reich, 2014), many of which have disappeared – even if that is not the way we currently draw the maps. Further back, stories often portray us, not as seacoast people, but only as wandering bands of smart hominids, patrolling the savannah from the edge of the forest, gathering plant foods and hunting and scavenging meat. This story ignores almost entirely the evidence of our persistent attachment to the sea. The ocean has always been a reliable source of: food of both animal and plant origin; of safety (many large predators — particularly most felines — do not swim); and of fresh water (inflowing rivers and streams). Certainly, after ocean levels stabilized around 7000 years BP, it was river deltas that saw the early rise of cities (Stanley and Warne, 1993; Stanley and Warne, 1997). Features of our biology (e.g., hairlessness, subcutaneous fat like seals and cetaceans, upright stance, and two-legged gait) fuelled Alistair Hardy's hypothesis that we are a semiaquatic ape (Hardy, 1960). This theory was popularized and explored further by Elaine Morgan (Morgan, 1973) as well as by others (Vaneechoutte et al., 2011), including critics (Langdon, 1997).

Whatever the truth of the aquatic-ape hypothesis, we remain attached to the sea. In fact, approximately 10% of the world's population (>600 million people) live in coastal areas that are less than 10 m above sea level and about 40% (almost 2.4 billion) live within 100 km of the coast. More crucially for the question being asked here (namely, how much impact has abandoning parts of the natural environment had on our health and well-being?), there is a body of evidence to show that blue space is good for us and some specific waters have established reputations as places of healing (Williams, 2010; Gesler, 1996; Foley, 2011).

A series of studies used national-survey data, almost all in high-income countries, to explore the relationship between blue space and health. An Australian study (Bauman et al., 1999) reported that people who lived in a coastal area were less sedentary and more physically active than those who lived inland. In New Zealand, findings suggested that beach access was associated with lower BMI and higher physical activity (Witten et al., 2008). In the UK, there was a small, but statistically significant gradient across coastal proximity and the likelihood of achieving recommended guidelines for physical activity (White et al., 2014). Also in the UK, living closer to the coast was associated with better self-reported general and mental health, partly mediated by on-land outdoor physical activity, primarily walking; there was also a relationship between nearby fresh water and better mental health (Pasanen et al., 2019). In the Netherlands, blue-space availability was related to a lower risk of mood disorders and anxiety; associations with blue space were stronger than those with green space (de Vries et al., 2016). A study of schoolchildren in Spain found that annual beach time was inversely associated with problem behavior and positively associated with prosocial behavior but showed no association with ADHD symptoms (Amoly et al., 2014). A study of 1100 residents in Shanghai found that living in proximity to a river was inversely associated with overweight/obesity (Ying et al., 2015). As coastal living is often more expensive than elsewhere, there may be confounding by social class in some of these findings.

Volker and colleagues conducted standardized interviews with more than 200 urban blue-space visitors in Germany (Völker et al., 2016). From these qualitative data, they noted that urban blue space induces restorative experiences, creates meaning, attracts urban dwellers, promotes physical activity, and diversifies health experiences in urban contexts.

A systematic review of quantitative studies of blue space and health (almost all cross-sectional and including some of the papers already discussed) (Gascon et al., 2017) concluded that the balance of evidence showed a positive association between higher exposure to outdoor blue spaces and benefits to mental health and well-being and higher physical activity. They noted that the paucity of the literature and the heterogeneity of study design and measures of both exposure and outcome made synthesis difficult.

Britton and colleagues undertook a systematic review of intervention studies (Britton et al., 2020). They concluded that blue-space interventions can have direct benefit for health, especially mental health and psychosocial wellbeing. Most papers reported a positive or weak association with health and wellbeing indicators. There were very few findings for physical health. More recently, Vert et al. undertook a randomized crossover study to assess psychologic and cardiovascular responses to exposure to blue spaces (Vert et al., 2020). Fifty-nine healthy adult office workers were randomly assigned to 20 min/day walking by a blue space or in an urban space or resting at a control site, 4 days/week, for 3 weeks. They reported that the subjects experienced statistically significantly improved well-being and mood immediately after walking in the blue space compared with walking in the urban space or when resting in the control site. Cardiovascular responses showed no statistically significant differences between blue- and urban-space walking.

2.3. Grey space

Unlike blue and green space, where we have focused primarily on the health-enhancing aspects of the environment, grey space – the urban landscape – largely presents hazards to health. More than half of the world's population now lives in cities, with fastest urbanization occurring in low- and middle-income countries (UN Department of Economic and Social Affairs Population Division, 2019). Several forces are at work: natural growth of the population, reclassification of rural land as urban, and migration to cities from rural areas (Buhaug and Urdal, 2013).

Urban intensification has resulted in reduced exposure to green and blue space and associated health-enhancing factors. In addition, grey space, largely made up of impermeable and hard surfaces such as concrete and tarmac, has further isolated us from the natural environment including soil, which hosts a wide range of microorganisms with known or suspected health benefits (von Hertzen and Haahtela, 2006; Liddicoat et al., 2019a; Keesstra et al., 2021; Giltrap et al., 2021; Samaddar et al., 2021; Smith et al., 2021; Li et al., 2018; Wall et al., 2015) (see below). This is compounded by many urban dwellers now living and working in high-rise buildings often tens to hundreds of meters above ground, with no or very little direct exposure to the natural environment (plants, animals, soil) and potentially distinctly different microbial exposures to airborne microorganisms as airborne microbial communities at height are likely to be different from those closer to the ground/soil (Giltrap et al., 2021; Zhao et al., 2022). Thus, grey space probably promotes dysbiosis, i.e., an imbalance of the human microbiota associated with poor outcomes across a range of health conditions (see below). Few studies have assessed associations between grey space and health directly. One study found inverse associations between green space and wheezing (hallmark symptom of asthma) and bronchitis in children, whereas grey space was associated with an increased risk of bronchitis (Tischer et al., 2017). A study of adults reported that grey spaces are associated with higher risk of allergy (Maio et al., 2022).

In addition to reduced exposure to the protective influence of the natural environment, urban environments may contribute directly to poor health. In particular, city infrastructure is unable to keep pace with rapid increases in population and, as a result, quality of life and even access to basics (e.g., food, shelter) of city dwellers is degrading; more than one billion people live in urban slums (UNFPA, 2007) and this will continue to increase, regardless of the optimism expressed by some (Rosling et al., 2018). This rapid growth puts ever-increasing strain on the natural resources and environmental services upon which cities rely; for instance, more than 30% of the world's largest cities depend for drinking water on catchment areas that are more or less nature reserves (Dudley and Stolton, 2003); recognising this, some megacities, such as Mexico City, have policies in place to protect forests and wetlands and to improve land management inside those water catchments (Tortajada, 2008). There is a wide spectrum of environmental hazards that are shared by essentially all urban dwellers; these have been researched and reviewed well elsewhere and include problems associated with urban violence (Cerdá et al., 2018); traffic (Recio et al., 2016; Thompson et al., 2020); the formation of heat islands (Manoli et al., 2019; Ziter et al., 2019) and possible remediation by trees (Iungman et al., 2023; Fu et al., 2022); air and water pollution (Liu et al., 2019b; Resongles et al., 2021; Fuller et al., 2022; Ural et al., 2022); increased access to, and consumption of, unhealthy foods (Willett et al., 2019) and alcohol (Griswold et al., 2018; Bryazka et al., 2022); accumulation of plastics (Guo and Li, 2020), heavy metals (Resongles et al., 2021; Gu and Gao, 2018), and persistent organic pollutants (Ouidir et al., 2019; Lee et al., 2010; Nair and Sujatha, 2012); noise pollution (Recio et al., 2016; Kim et al., 2012); light pollution (Dominoni et al., 2016; Bennie et al., 2015); etc. In addition, increasingly densely populated urban areas, combined with high mobility, increases the risk of pandemics, as we are currently experiencing with COVID-19.

Contemporary urban environments are also highly exposed to the risks associated with climate change and other environmental hazards, e.g., among six natural hazards analysed in 2012, the greatest and most common was flooding, potentially affecting almost half of the more than 60 cities with populations of ≥5 million people. Other identified hazards included cyclones, droughts, and earthquakes (UNDESA, 2012). Ecosystem degradation and resultant loss of services, including protection from flooding and storm surges, increase vulnerability to damage and costs of repair and remediation (Costanza et al., 2014), costs that will continue to rise with climate change.

The effects on human, animal, and plant health of many of these environmental hazards are increasingly well-understood (Cerdá et al., 2018; Manoli et al., 2019; Liu et al., 2019b; Fuller et al., 2022; Willett et al., 2019; Brumberg and Karr, 2021; Attina et al., 2016; Matsumoto et al., 2002; Kerr et al., 2017; Kotthoff et al., 2015; Sánchez-Bayo and Wyckhuys, 2019; Yamamuro et al., 2019). However, despite this recognition, few successful interventions have been developed or implemented and these problems will thus persist, with many worsening. This, combined with the increasing loss of exposure to the ameliorating effects of the natural environment, is likely to result in a further increase in incidence of many NCDs as well as communicable diseases. There is evidence that plants in cities may reduce some of these hazards; for instance, a US modeling study showed that urban trees remove an estimated 711,000 metric tons per year of air pollution and thus improve urban air quality (Nowak et al., 2006), arguing for a role of rewilding urban areas (discussed further below).

3. How do green and blue space affect health? Some hypotheses

An obvious explanation is that interaction with the natural environment drove our evolution; thus, we prefer biologically diverse environments and derive mental benefits from them: the “Biophilia Hypothesis” (Aerts et al., 2018). Consistent with this hypothesis, Kaplan draws a distinction between the degree to which we require directed attention for many aspects of our lives, noting that natural settings meet the requirements of a restorative environment and thus reduce the fatigue of directed attention and re-establish our effectiveness (Kaplan, 1995). Further, there is a surprisingly strong relationship between greenness and social cohesion – whether self-reported (Liu et al., 2019a; de Vries et al., 2013; Dzhambov et al., 2018) or measured objectively via voter turnout (Donovan et al., 2022b). Social cohesion, in turn, is an important predictor of total mortality (Holt-Lunstad et al., 2010).

Physical activity, facilitated by green and blue space, is an established contributor to better human health (Hartig et al., 2014) although the relationship between green space availability and physical activity is weak (Di Nardo et al., 2010). Further, and as noted above, absorption by plants of noxious agents, e.g., air pollution, may also reduce risk (Nowak et al., 2006). A fourth explanation involves the “Dilution-effect Hypothesis”, which relates particularly to infections: in more diverse environments, there are multiple targets for any infectious agent, resulting in lower infection per unit time (Aerts et al., 2018). These hypotheses probably explain some benefits but do not identify clear explanations – or mechanisms – for the consistency of the findings across multiple environmental settings and agents and over such a wide spectrum of disease processes.

In addition to the opportunities for physical activity and exposure to improved air quality in all settings, a key element linking these diverse environments is exposure to beneficial microbiota. Thus, there is a fifth possibility, called the “Biodiversity Hypothesis”, which postulates that reduced environmental (and dietary) biodiversity results in decreased diversity of the environmental and human microbiota and that this, in turn, increases the risk of allergic, autoimmune, and other inflammatory, immunologic, and metabolic conditions (Hanski et al., 2012; Haahtela et al., 2013; von Hertzen et al., 2011; Hanski, 2011). This hypothesis is an extension of the Hygiene Hypothesis (Strachan, 1989), which postulates that the rise in allergic diseases is due to reduced infections and exposure to microbes. The Biodiversity Hypothesis is based on epidemiologic observations linking: the diversity of animal exposures found in farm environments or domestic environments for pets; the diversity of plant exposures; and the diversity of human exposure (more siblings) to a reduced risk of allergies and other NCDs (Brooks et al., 2013).

Much of what follows is focused on the Biodiversity Hypothesis and particularly on the beneficial roles of microbiota – outdoor (soil, air, water), indoor, and human – discussing mechanisms and routes of exposure.

There is some empirical evidence that green space is associated with higher diversity of microorganisms in the environment (Flandroy et al., 2018), as well as differences in abundance of particular taxa (Kirjavainen et al., 2019). In particular, several studies have demonstrated that more diverse plant communities support greater microbial diversity (Kowalchuk et al., 2002) and affect the composition of airborne bacteria (Lymperopoulou et al., 2016). Also, exposures to an environment with higher vegetation diversity have been shown to affect the composition of the skin microbiota and this, in turn, was associated with risk of allergy (Hanski et al., 2012). Similar patterns are observed in samples from farms (Stein et al., 2016; Ege et al., 2011), households with pets, and buildings with large numbers of plants (Mahnert et al., 2015). In fact, a necessary condition for diverse microbial exposure is a habitat for microbes that is itself diverse; plants are one important source of such a habitat (Vorholt, 2012).

Regarding blue space and microbes, currently there is little more than an unexplored hypothesis (Moore, 2015; Grellier et al., 2017) that sea air carries aerosolized potentially beneficial compounds (for more on aerosols and water, see below) but it is also the case that the ocean carries a vast and diverse microbiota that resembles that of the human colon (Sunagawa et al., 2015). Clearly, there is need of much work in this area.

Much of the research examining the relationship between environmental microbial exposure and health has been done using household dust (a proxy of indoor air exposures) from homes, particularly farming homes. Such studies found greater microbial diversity, as well as microbes associated with animals rather than those associated with humans (Douwes et al., 2008; Wickens et al., 2002). In Finland, a farm-like dust-microbial-profile index has been developed (FaRMI: the Farm-home-Resembling Microbiota Index), with children raised in non-farm homes with a greater FaRMI index having a lower prevalence of allergic diseases (Kirjavainen et al., 2019): those raised in homes with uppermost-quartile FaRMI had a 60% reduced risk of asthma (odds ratio (OR) 0.4 (95%CI 0.2–0.8)) compared to those born in lowest-quartile FaRMI homes. This was confirmed in a separate study from Germany involving non-farm homes (Ege et al., 2011). FaRMI-associated protection was independent of diversity, suggesting that specific species are important for immune protection; FaRMI dust was associated with suppression of bacterial-cell-wall-induced pro-inflammatory cytokines, suggesting tolerance; and microbial taxa typical of soil were abundant in high-FaRMI indoor-dust microbiota, suggesting soil microbe exposures may exert a beneficial effect (Kirjavainen et al., 2019).

Although not extensively studied, there is further evidence suggesting links between green/blue space and indoor air microbiota. In particular, Dockx et al. observed statistically significant associations between indoor microbial diversity indices and nearby residential green space (Dockx et al., 2021). Bacteria were directly associated with green space: 0.08 Shannon-index (measure of diversity) units increase per interquartile range (IQR) increase in green space within a 50 m buffer. Fungal diversity was directly associated with high-growing vegetation and inversely related to low-growing vegetation. These are important observations as humans spent a large part of their time indoors, e.g. in the US, people spend, on average, 87% of their time indoors (Klepeis et al., 2001). To explore other evidence of this changing attitude to the natural world, Kesebir and Kesebir studied aspects of popular culture in English from the turn of the 20th century (works of fiction, song lyrics, and films) and concluded that, since the 1950s, references to nature have been decreasing steadily, whereas references to the human-made environment have not (Kesebir and Kesebir, 2017); both our behavior and our focus have changed.

4. How microbiota affect health: possible mechanisms

The assumption that biodiversity loss – resulting from modern life, urbanization, and climate change – leads to reduced diversity of exposure to environmental microbiota and increased risk of disease has only recently begun to be tested (Aerts et al., 2018; Flandroy et al., 2018; Parajuli et al., 2018). However, we have co-existed and co-evolved with commensal (including gastrointestinal, lung, and skin) microbiota at least since the beginning of hominin history. Indeed, microbiota appear early in multicellular life and colonized mammals (Rook, 2021) when the intestinal chitin barrier gave way to a mucosal niche (Nakashima et al., 2018). Microbiota have effects on: i) immunity and the maintenance of homeostasis and tolerance to environmental exposures, determined by, as yet, poorly defined microbial-host interactions that may occur in a narrow time-window in early life (Gensollen et al., 2016); ii) the nervous system via neurotransmitter-like compounds (Johnson and Foster, 2018); and iii) the endocrine system (Clarke et al., 2013).

Various organ microbiota may modify the relationship between environmental exposures and lifestyle factors (e.g., obesity, glucose metabolism) and cancer (Nicholson et al., 2012; Greiner and Backhed, 2011), although the mechanisms have yet to be elucidated. *Staphylococcus epidermidis* protects skin against inflammation, infections, and cancer through interactions with keratinocytes, T-cells, and other skin microorganisms (Stacy and Belkaid, 2019). Changes in gut microbiota may play a role in neurodegeneration through alterations in intestinal permeability (and subsequent bacterial translocation) (Berk et al., 2013); this may lead to systemic inflammation and sub-optimal macrophage/microglial function (Thevaranjan et al., 2017). The gut microbiome may also alter neurodevelopmental and neurodegenerative outcomes such as Alzheimer's disease (Vogt et al., 2017) and Parkinson's disease (Killinger et al., 2018) through changes in host immunity, etc (Killinger et al., 2018). Gut bacteria produce neurotransmitter compounds that can influence behavior and mental health (Johnson and Foster, 2018) and there is some population-scale evidence for links between microbiome and mental health (Valles-Colomer et al., 2019) and Autism Spectrum Disorder (Sharon et al., 2019). Finally, changes in human microbiota, through use of antibiotics, may alter susceptibility to a range of communicable diseases via immunomodulatory pathways (Gensollen et al., 2016). In fact, there is a growing body of evidence to link antibiotic use (Velicer et al., 2004), airway microbiota (Jin et al., 2019), and gut dysbiosis (Biragyn and Ferrucci, 2018; Shi et al., 2023) to cancer etiology.

Infants at risk of asthma exhibited a transient dysbiosis during the first 100 days with reduced relative abundance of four bacterial taxa that were shown to ameliorate airway inflammation in mice (Arrieta et al., 2015). Early childhood probiotic supplementation, in a randomized clinical trial, was associated with statistically significant reductions in atopic sensitization, eczema, and wheeze (Wickens et al., 2018). Protection against allergic asthma probably involves greater and more diverse exposure to microorganisms and may, through involvement of Toll-like receptors (TLR) (Medzhitov, 2001), direct innate and adaptive immunity away from the "imbalanced" T-helper 2 (Th2) immune response observed in allergy (Brooks et al., 2013) towards a more Th1-mediated response (Kaario et al., 2016) or modulation of regulatory T cells (Treg) or both (Schaub et al., 2009; Tumes et al., 2017).

Mouse models have shown that changes in microbiota are associated with both development of, and protection from, NCDs (Jin et al., 2019; Turnbaugh et al., 2006). An increasing number of human studies show similar findings (Turnbaugh et al., 2009); e.g., links have been described between diet, gut bacteria, and pathophysiologic changes on the one hand and carcinogenesis (Nicholson et al., 2012; Shi et al., 2023; Wirbel et al., 2019), metabolic conditions (Rosenbaum et al., 2015), and reproduction (Anahtar et al., 2018) on the other. Intestinal bacteria have been shown to be critical in regulating allergic responses to cow's milk (Feehley et al., 2019). Germ-free mice colonized with microbes from their natural, external habitat have been shown to model human physiology and disease (Rosshart et al., 2019) and, upon colonization with human fecal samples, helped to establish causal relationships between human gut microbes and NCDs (Sharon et al., 2019; Feehley et al., 2019). Exposure of mice to house dust from Amish and Hutterite homes recapitulates the substantial discrepancy in the prevalence of asthma in these two agricultural populations (Stein et al., 2016). Passive exposure is enough to influence gut-microbial composition and allergic responsiveness (Ottman et al., 2019), suggesting that several routes of exposure (airway, skin, gut) can impact immune systems and disease outcomes; it is unclear whether different routes influence pathways and outcomes differently and unknown whether direct colonization by environmental microorganisms is required (Seedorf et al., 2014).

Evidence for at least one specific beneficial mechanism associated directly with biogenic aerosols emerged from the study of the nasal application of cowshed dust. Stiehm et al. showed that cowshed-dust extract could release biologically active complement factor 5a (C5a) in the mouse lung (Stiehm et al., 2013). A protease from *Tenebrio molitor* larvae (mealworm) was used experimentally to release C5a, which damped important components of the allergic airway inflammation response, including infiltration of proinflammatory cells and Th2 cytokine secretion by lung cells. More generally, microbial colonization of mucosae is established as a critical factor for the maintenance of skin, lung, and intestinal homeostasis and barrier function in mice (Chen et al., 2018). In humans, close exposure to soil, air, and leaf litter in urban green spaces in 3 cities in different countries was associated with increased skin and nasal microbial diversity, with skin microbiota becoming more similar to soil microbiota after exposure (Selway et al., 2020). In contrast, dysbiosis may lead to allergy (Shukla et al., 2019; Iweala and Nagler, 2019). Precise effects of dysbiosis on epithelia and mucosae (barrier dysfunction vs bias towards allergic type 2 responses), timing and reversibility of dysbiosis (early-life vs adulthood), and potential pathogenic or pro-homeostatic/anti-allergic activity of environmental microorganisms in the context of allergy are largely unknown.

In a randomized controlled experiment, Liddicoat et al. showed that realistic exposures to trace-level dust from a high-biodiversity soil, compared to dust from low-biodiversity soil or no soil could change mouse gut microbiota (Liddicoat et al., 2019b). More specifically, a soil-derived butyrate-producer, *Kineothrix alysoides*, increased to a greater extent in the gut of the high-biodiversity-treatment mice. Further, the higher relative abundance of this rare organism correlated with reduced anxiety-like behavior in the most anxious mice (Liddicoat et al., 2019b), perhaps pointing to questions we can ask about green space, blue space, and grey space in relation to human mental health (Logan, 2015).

Adaptation to modern life, characterized by: marked population growth; increased urbanization, industrialization, and environmental pollution; increased use of monocultures, agrichemicals and antimicrobials (Potter, 2015); increased consumption of processed, energy-dense, nutrient-poor, and less diverse diets (Potter, 2018); and decreased physical activity (Bressa et al., 2017), may have resulted in substantial dysregulation of the environmental and human microbiota in many countries, potentially explaining (at least partially) the current global pandemic of NCDs (Liddicoat et al., 2016).

Blaser has argued that many of the chronic diseases seen in industrialized societies are a consequence of the loss of key members of an ancestral microbiota (Blaser, 2017). Sonnenburg and Sonnenburg specifically indict antimicrobials and a "Western" diet as shifting gut microbiota towards species that flourish in the presence of inflammation and towards microbes that live on mucus and away from fibre degraders. This results in loss of diversity and deterioration of function of microbiota with, again, an increase in NCDs (Sonnenburg and Sonnenburg, 2019). There are several papers that provide specific evidence of these differences across populations, most markedly between gatherer-hunter peoples and Western populations (Obregon-Tito et al., 2015; Smits et al., 2017). There are not only differences in taxa (Smits et al., 2017; Tett et al., 2019) but also complete loss of species (Obregon-Tito et al., 2015) and of seasonal variability (plausibly in response to changes in food sources) with the most variable taxa also showing the greatest loss in industrialized populations (Smits et al., 2017). Differences are particularly identifiable in infants (De Filippo et al., 2010; Yatsunenko et al., 2012). Most recently, Wibowo and colleagues have undertaken a large-scale de novo assembly of microbial genomes from authenticated human palaeofaeces samples (1000–2000 years old) with well-preserved DNA (Wibowo et al., 2021). Previously undescribed species represented almost 40% of the sequenced organisms. These ancient samples are more similar to non-industrialized than industrialized human gut microbiota with functional profiling identifying a markedly lower abundance of mucin-degrading and antimicrobial-resistance genes (Wibowo et al., 2021). Our understanding of the extent of person-to-person transmission of oral and gut microbiota and the influence of such transmission on health and disease is in its infancy (Valles-Colomer et al., 2023).

One of the important aspects of wild spaces is their dependence for stability on trophic cascades – especially the presence of apex predators that are central to ecosystem integrity. It has now been clearly established that the restoration of grey wolves to environments from which they had been exterminated (e.g., Yellowstone) and the recovery of whales following the cessation of regular and widespread slaughter, resulted, respectively, in marked improvements in riparian and forest habitats in Yellowstone (Ripple and Beschta, 2012) and food webs in the ocean (Savoca et al., 2021). What has been less appreciated is the fact that even apex predators have curbs on their numbers and that cascades are circular rather than linear: apex predators have microscopic predators and symbionts that are not necessarily bacteria (Matijasic et al., 2020). For instance, the newly introduced Yellowstone population of grey wolves are supported by large tracts of high-quality habitat and a ban on hunting but have also contracted viruses via spillover from resident canids. However, this did not cause die off but, along with near saturation of available territory, has resulted in some degree of control over population size (Almberg et al., 2012; U.S. Fish and Wildlife Service et al., 2012). Other reintroductions have fared less well (Thorne and Williams, 1988; Singer et al., 2008).

Animals (including humans) live in a world dominated by microbes (McFall-Ngai et al., 2013). Less understood are the roles of multicellular parasites and symbionts. Parasites that alter behavior, including Nematomorph or horsehair worms (*Gordionus* spp.) (Meguro et al., 2020), *Toxoplasma* (Berdoy et al., 2000), and *Ophiocordyceps* spp. (Andersen et al., 2009), are also important in wild places. The impact on human behavior of manipulative parasitic infection, for good or ill, is essentially unknown (Adamo, 2013). However, among other species, they can modify host behavior in ways that benefit the parasite (Hernandez-Caballero et al., 2022) and can be important more widely, e.g., horsehair worms can seek water, subsequently providing a food source for trout (although the worms escape) (Ponton et al., 2006). Indeed, this ecosystem cascade provides evidence that manipulative parasites can dramatically alter energy flow in natural systems (Sato et al., 2011). There is also evidence that increased risk taking induced by *Toxoplasma* can benefit infected grey wolves (Meyer et al., 2022).

In contrast, roles for parasites in influencing other aspects of human biology are better understood, particularly in relation to the immune system. Helminths are worms that infest as larvae, migrating to specific niches in lung, liver, intestine, and skin, where they develop and reproduce. They induce an IgE and eosinophil-dominated Th2-mediated immunity, which suppresses type 1 inflammation, generally resulting in control (rather than full clearance) of parasite load with minimal host pathology, which is more typically associated with Th1-inflammation. The same type 2 immune response is characteristic of asthma and allergy, except that it is now directed against innocuous environmental proteins. It is accordingly not surprising that the relationship between helminth infection and asthma is not straightforward (Bohnacker et al., 2020; Fernandes et al., 2019): overall, parasite infection is associated with an increased risk of asthma, as is infection with *Ascaris lumbricoides* (roundworm) but infestation with hookworm (predominantly *Ancylostoma duodenale* and *Necator americanus*) is associated with a much reduced risk of asthma (Leonardi-Bee et al., 2006). Perhaps clearer is the role of the loss of parasites in the etiology of inflammatory bowel disease, in which failure to acquire helminths and their eggs results in the absence of a mucosal Th2 response and overly active Th1 inflammation (Elliott et al., 2000). Rook has proposed the "Old Friends" hypothesis, which argues that contemporary widespread immunoregulation failure is associated with lack of exposure, particularly in the urban environment, to organisms, including helminths, from our evolutionary past (National Academies of Sciences Engineering and Medicine, 2023; Rook et al., 2005). Questions have been raised as to whether helminths are also relevant for cardiovascular disease (Lin and Loke, 2021). The possibility of a three-way interaction among microbiota, helminths, and mammalian host is emerging as a research question (Loke and Lim, 2015).

We are in danger, as food-webs disintegrate, of seeing the loss of parasites, particularly those of specialist hosts and hosts higher in the food chain (Lafferty, 2012). There is clear evidence that climate change is responsible for the decline of fish parasites over the last century (Wood et al., 2023). Given our patchy understanding of the role of parasites in animal (including human) health, we may understand the consequences of particular extinctions only after the fact.

5. Exposure routes

As noted above, environmental microbes probably explain, at least in part, the protective effects of green and blue space on health. Here, we will focus on three environmental exposure routes: air, soil, and water. Although diet is critically important for human gut health, it is only indirectly – through soil (Brown et al., 2022) – related to the protective effects of green/blue space and so will not be discussed in detail. The types, abundance, and diversity of microbes that live in green, blue, and grey space are likely to be different although, of course, there may be some overlap; thus, even when they operate through the same exposure route, say via aerosolization, they may have different effects on health. Relatedly, the physical characteristics of green, blue, and grey spaces are different, so, for example, the ways in which plant microbes move into the atmosphere may be different from the ways in which aquatic microbes move into the atmosphere. Much remains to be explored in this area.

5.1. Aerosols

Researchers have been writing about the relationship between air quality and human health for more than 2000 years. What is particularly interesting that, even as far back as Hippocrates,[1] the focus has almost always been on the deleterious consequences of poor quality air rather than the benefits of clean and clear air (Hippocrates, 1952).

Montaigne provides some contrast inasmuch as, writing in 1580, he impugned Paris and Venice, whose beauty he found greatly marred by their foul air but also noted, "*Physicians might*, *I believe*, *extract greater utility from odours than they do*, *for I have often observed that they cause an alteration in me and work upon my spirits according to their several virtues*; *which makes me approve of what is said*, *that the use of incense and perfumes in churches*, *so ancient and so universally received in all nations and religions*, *was intended to cheer us*, *and to rouse and purify the senses*, *the better to fit us for contemplation.*" (de Montaigne, 1580)

Foul air was, until quite recently, literally seen as the source of illness: "malaria" is Italian for "bad air". Our wish not to seem caught up in outmoded theories that attributed disease causation to miasmas from marshes may have made us slow to appreciate how much air pollution influences morbidity and mortality (Liu et al., 2019b; Schraufnagel et al., 2019; Strak et al., 2021) and even slower to understand the crucial role of aerosols in the transmission of virus particles (Morawska and Milton, 2020; Lewis, 2020).

A recent review summarises what we know about the detrimental and widespread impacts of particulates and pollen and even reminds us that we frequently neglect the impact of work practices on air quality (Lancia et al., 2021). However, it says nothing about possible beneficial aspects of aerobiology. Indeed, the notion that clean air and pleasant smells might have preventive or therapeutic value is largely confined to the relatively fringe areas of aromatherapy (Velasco-Rodriguez et al., 2019; Lin et al., 2019) and climatotherapy (Autio et al., 2002). Nonetheless, observational studies and trials have described the use of exposure to an alpine climate as an effective treatment for both atopic dermatitis (Vocks, 2006; Fieten et al., 2018) and asthma (Bersuch et al., 2017), the latter independent of sensitization status to pollen or house-dust mites.

The exposure routes (air, diet, soil, or some combination) and mechanisms remain to be fully elucidated, but studies in several settings have shown that children who grow up on a farm generally have a lower risk of asthma and allergy (Riedler et al., 2001; Perkin and Strachan, 2006; Douwes et al., 2007), though there are exceptions (Wickens et al., 2002). Various explanations have been proposed including microbial exposure (Ege et al., 2011), duration of farm exposure (Douwes et al., 2007), and consumption of unpasteurized milk (Perkin and Strachan, 2006). The inverse association persists into adulthood (House et al., 2017). Stein and

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[1] It is of more than passing interest to consider exactly how much data Hippocrates accumulated to make his unequivocal statements about the patterns of health and disease and their association with place and season.

colleagues have reported that, although Amish and Hutterite have similar genetics and lifestyles, the prevalence of asthma and allergic sensitization was, respectively, 4 and 6 times lower in Amish compared with Hutterite children. The median bacterial endotoxin level in Amish house dust (a proxy of airborne exposure) was almost 7 times higher than in Hutterite house dust (Stein et al., 2016). Differences in the microbial composition of house dust and major differences in innate immune cells between children of the two groups were also reported. One key difference is that Amish follow traditional practices whereas the Hutterites use an industrialized approach to farming. That does not immediately provide an explanation for the profound difference seen in both immune responses and atopic disorders but it may be relevant that a study covering four agricultural regions across Europe showed that increasing land-use intensity reduced soil foodweb diversity, functional diversity, and taxonomic diversity (Tsiafouli et al., 2015).

Gilles et al. draw attention to the multiplicity and complexity of influences – genetic, psychologic, environmental, and lifestyle – on the risk of atopic disorders. One particular piece of the puzzle is air quality; they discuss roles for both beneficial bioaerosols and anthropogenic air pollution (Gilles et al., 2018). That aspects of air quality are relevant can be inferred from the study of Muller-Rompa and colleagues who showed that the inverse association between farm exposure and asthma and atopy persisted to a maximum radius of 100 m from a farm and thus existed not only for those raised on farms but also those living nearby. They noted that traditional farms, with a broader diversity of microbial exposure, mainly contributed to the inverse association with asthma (Muller-Rompa et al., 2018).

As noted earlier, plant microbial communities are an important source of airborne microbes. For example, a study comparing plant microbes to airborne microbes found that plant microbial communities are indistinguishable from airborne microbes 50 m downwind of a plant, but upwind microbes are unique (Lymperopoulou et al., 2016). Therefore, as several studies have demonstrated that more diverse plant communities support greater microbial diversity (Kowalchuk et al., 2002), it is likely that airborne microorganisms are also more diverse in areas with more plant diversity. To put this in perspective, there are 391,000 known vascular plant species with a total leaf area of 1,017,260,200 km^2 (twice the world's land area) supporting $\sim10^{26}$ bacterial cells (Vorholt, 2012), thus probably being a substantial contributor to the overall airborne microbial exposure. On the other hand, and as a consequence, grey space is likely to be associated with reduced microbial diversity and load, as suggested by a study that found that the diversity of total bacteria, Proteobacteria, Actinobacteria, Bacteriodetes, and Firmicutes brought into households by foot traffic were inversely associated with built-area density (Parajuli et al., 2018). Higher densities of vegetation within residential environments has been associated with higher bacterial diversity in outdoor ambient air (Styles et al., 2023). Conversely, the relative abundance of pathogenic bacteria was increased with greater built-area coverage (Parajuli et al., 2018), thus suggesting that densely built areas may result in lower exposure to diverse, and potentially protective, environmental microbiota and higher exposure to pathogenic bacteria. Wild birds and animals have also been shown to have urban signatures in their microbiota (Maraci et al., 2022; Teyssier et al., 2020; Gurbanov et al., 2022). Aerobiota are stratified by height, with the implication that adults vs. children, walkers vs. wheelchair users, and high-rise apartment dwellers vs single-story house occupants, may experience different exposures even in the same setting or geographical location (Robinson et al., 2021; Robinson et al., 2020).

Not only metabolic and immune responses but cognitive reactions to aerosols and smells may also be relevant to health. The relationship between memory and the sense of smell gets its greatest boost from the writings of Marcel Proust (Proust, 1983) who described how a madeleine dipped in tea unexpectedly triggered a long-forgotten extremely detailed childhood memory. It is only recently, however, that we have understood how the sense of smell works (Buck and Axel, 1991); much remains to be explored.

5.2. Soils

Human health is deeply dependent on soil because approximately 40% of the world's land surface is dedicated to the production of human food and animal feed, with around 12% in crop agriculture and 25% in grazing lands (Diaz et al., 2018). People have directly managed (and mismanaged (Montgomery, 2012)) soils via agriculture for 8000–12,000 years across the globe (Zeder, 2011; Barton et al., 2009; Kuijt and Goring-Morris, 2002; Pringle, 1998; Levetin and McMahon, 2008; Riehl et al., 2013; Cubry et al., 2018; Lyons et al., 2016). For perhaps 10 times that period, soils have been indirectly managed through gathering and hunting (Mercader, 2009; Arranz-Otaegui et al., 2018; Mariotti Lippi et al., 2015). Humans have long been geomorphic agents (Hooke, 2000; Hooke, 1994; Wilkinson, 2005). What we ignore at our peril is how important management of land and soil is for: land degradation itself, desertification, climate change (especially greenhouse-gas fluxes), and food security (Intergovernmental Panel on Climate Change, 2019).

As is clear from the discussion above on farming practices and allergy, there are important consequences of the impacts of soil on air that both enhance and impair wellbeing. Soil may impair air quality through being a source of particulates and gaseous pollutants. Dust on smaller (quarrying, agriculture) and larger scales (natural or as a result of poor land management) also have negative effects on human health (Giltrap et al., 2021). Other deleterious contaminants of soil include heavy metals (Jiang et al., 2020), persistent organic pollutants, and potentially pathogenic biologic agents (Brevik et al., 2020). In contrast, soil supports the growth of vegetation that improves air quality in a variety of settings, both natural and human-made (Barwise and Kumar, 2020). It acts as a carbon sink, contributing extensively to amelioration of rising atmospheric carbon dioxide (Lal et al., 2021).

Soil is a major source of microorganisms in terrestrial ecosystems and is home to the most diverse and complex microbiome on earth (Banerjee and van der Heijden, 2022; Fierer and Jackson, 2006). As already noted, humans are exposed, both directly and indirectly, to soil microbiota through: diet; inhalation, outdoors and indoors, of soil-derived dust particles (people and pets bring soil into the house via shoes/paws or attached to skin/fur and particles may enter through the air); ingestion via hand-to-mouth behavior (particularly in young children); and drinking water that has passed through soil. In addition, some humans, like many other animals, choose to consume soils. Several hypotheses have been proposed to explain geophagy (conscious consumption of soil or clay): a means to balance out nutrient deficiencies; protection against ingested pathogens or toxins; or an attempt to allay hunger. In an extensive and detailed review, Young et al. evaluated these hypotheses using almost 500 accounts of human geophagy as well as more than 300 papers on geophagy in other mammals, birds, and reptiles. They concluded that human geophagy – which is often of carefully selected and prepared soils with a high clay content but low in micronutrients – is best explained as providing protection from dietary chemicals, parasites, and pathogens (Young et al., 2011). It is particularly common in children (Young et al., 2011) and in pregnant women (Young et al., 2011; Njiru et al., 2011). It has long been associated with poverty and deprivation (Anon, 1897) and is clearly a rational or desperate response to food shortage, whether disaster-related, seasonal, or induced by colonization. Geophagy has also been described as frequently missed compulsive behavior associated with mental disorder (Rose et al., 2000).

As a consequence of these various exposure routes, soil and human microbiota are probably closely and actively inter-related, although this has not been well-studied. There is some indirect evidence showing that neighborhood soil type is associated with nasal and oral microbiota in humans (Pearson et al., 2020). Providing further indirect evidence, skin microbiota of animals have been shown to be associated with soil microbiota (Ross et al., 2018) and, in an experimental setting, it has been shown that soil microorganisms can be transferred to the rodent intestine (Seedorf et al., 2014). Also, a recent study showed that fecal microbiota of gardening families differed from that of non-gardening families, with changes in the gut microbiota (in gardening families) being observed over the course of the gardening season, again suggesting a link between soil and human microbiota (Brown et al., 2022).

There is also more direct evidence linking soil, commensal microbiota, immune function, and health. A 28-day long placebo-controlled double-blind intervention trial that exposed children aged 3–5 years to playground sand enriched with microbially diverse soil (Roslund et al., 2022) found changes in skin and gut microbiota, which in turn were associated with favorable immune modulation. An Australian linkage study found that people living in areas with soils of high cation-exchange capacity (a surrogate of soil microbial diversity) had a reduced risk of infectious and parasitic diseases, particularly in less affluent areas (Liddicoat et al., 2018). As noted above, a mouse study showed that airborne exposures to trace-level dust from a high biodiversity soil altered gut microbiota, with abundance of one particular soil microbe (*Kineothrix alysoides*) being anxiolytic in the most anxious mice (Liddicoat et al., 2019b). Another experimental study in mice showed that exposure to soil modified the gut microbiota and increased the immune response towards a Th1 response, resulting in reduced Th2-type allergic response (Ottman et al., 2019). In contrast, there is also evidence that ingested soils can interfere with bioavailability of micronutrients and act as a pathway for ingestion of helminths and heavy metals (Abrahams et al., 2006), increasing health risk particularly for children (Geissler et al., 1998) and pregnant women and fetuses (Njiru et al., 2011).

Evidence that soil-borne microorganisms play an important direct role in the development and regulation of the human immune system adds considerably to our understanding of the way in which the environment influences disease, including allergy and asthma. There is a microbiota-gut-brain axis: the gut microbiota composition and microbiome-driven signaling pathways have roles, not only in host immune system development and function (Roslund et al., 2020; Mishra et al., 2021; Wastyk et al., 2021), but also in human behavior (Johnson and Foster, 2018; Hsiao et al., 2013; Kim et al., 2017; Vuong et al., 2020; Willyard, 2021; Wu et al., 2021; Smith et al., 2019) and even in evolution (Moeller and Sanders, 2020). The diversity, cross-talk, and complexity of soil and human microbiota are intimately linked (Haahtela et al., 2013; Haahtela, 2019).

Ferris and Tuomisto make the point that understanding soil health and its capacity to provide ecosystem services requires that we understand species diversity, functional diversity, and knowledge of abundances of organisms that provide ecosystem services (Ferris and Tuomisto, 2015). Samaddar et al. and Wall et al. provide some related insights, noting that there is a very wide diversity of soil microbial life that acts as a defence against both plant and human pathogens. They take a further step and tie this broader perspective on the relationship between soil and health back to the need to maintain the health of the soil (Samaddar et al., 2021; Wall et al., 2015). Lucretius reminds us that we have known that we reduce that health by agricultural practices for more than two millennia:

> *She first spontaneously, of Herself, produced for mortals goodly corn crops and joyous vineyards;of Herself, gave sweet fruits and glad pastures, which now rarely attain any size, even when nurtured by our labour.We exhaust the oxen and the strength of the husbandmen.We wear out our iron.After all our labour, we are scarcely fed by the tilled fields, so stingy are they of their produce despite our work.Now, the aged ploughman shakes his head and sighs and sighs to think that the labours of his hand have come to nothing. When he compares the present with the past, he often praises the fortunes of his father and harps on the themeof how the men of old comfortably supported life on a scanty plot of ground – each allotment of land then was far less than now*[2].

Aldo Leopold put it more succinctly: “We abuse land because we see it as a commodity belonging to us. When we see land as a community to which we belong, we may begin to use it with love and respect” (Leopold, 1949). We have paid little attention to a land ethic (Leopold, 1949); we have paid even less attention to the relationship between soil and human health. As with air quality, we often think of the environment generally as a source of insults rather than positive influences: we discuss toxic exposures rather than the presence or absence of beneficial exposures.

There is now widespread awareness of the direct toxic effects of biocides on insect, animal, and human health (Ouidir et al., 2019; Attina et al., 2016; Sánchez-Bayo and Wyckhuys, 2019; Potter, 2015; Zhang et al., 2019; von Ehrenstein et al., 2019; De Long and Holloway, 2017; Weidenmüller et al., 2022; Potts et al., 2016; Lind et al., 2019; Kuehn, 2010; Defois et al., 2018; Rohr, 2021; Tanner et al., 2011; Douwes et al., 2018). What is less well appreciated is the impact of these compounds on microbial life (Clair et al., 2012; Kurenbach et al., 2017; Jørgensen et al., 2018), particularly soil microbes (Jacobsen and Hjelmso, 2014; Lo, 2010), and the resultant deleterious impact on plant, animal, and human health (Samaddar et al., 2021). Agricultural intensification and nitrogenous-fertilizer use are also associated with loss of soil microbial diversity (Tsiafouli et al., 2015; Wang et al., 2018). In contrast, cover cropping improves soil microbiodiversity (Kim et al., 2020).

5.3. Water

Although we know less about the influence of water on human microbiota than we know about soils and aerosols, some data are beginning to emerge on the influence of drinking water and about the nature of microbes in the ocean.

Vanhaecke et al. examined the relationship between drinking water source (bottled, tap, filtered, or well) and intake and oral and gut microbiota, using data from the American Gut Project public database (a self-selected citizen-scientist cohort initiated by UC San Diego) on more than 3000 fecal samples and around 300 oral samples (Vanhaecke et al., 2022). Drinking water source was one of the key contributing factors that explained variation of gut microbiota across participants. Subjects drinking mostly well water had higher fecal α-diversity, higher *Dorea*, and lower *Bacteroides*, *Odoribacter*, and *Streptococcus* than the other groups. Those with low intake of water differed from those with high intake, including showing a higher abundance of *Campylobacter*. No associations were found between oral microbiota and drinking water.

Tara Oceans (Sunagawa et al., 2020), an international, multidisciplinary project focused on establishing the complexity of ocean life across comprehensive taxonomic and spatial scales, systematically collected approximately 35,000 ocean samples using standardized protocols. In a recent paper, they presented data from 243 ocean microbiome samples, collected from three depth layers at 68 locations (representing all main oceanic regions except the Arctic) and undertook metagenomic Illumina sequencing (Sunagawa et al., 2015). Their aim was to characterize epipelagic (upper open ocean) and mesopelagic (~200-1000 m) waters across the globe, generating an ocean microbial-gene reference catalogue with >40 million sequences from viruses, prokaryotes, and picoeukaryotes (planktonic eukaryotes ≤ 3.0 μm). They demonstrated that there was vertical stratification of species, with the open-ocean community composition mostly driven by temperature rather than other environmental factors or geography. They also found that >73% of species abundance is shared with the human gut microbiota; the connection, if any, remains unclear.

6. Exposure assessment challenges

Many of our current tools are not fit for the purpose of understanding exposure to aspects of green space, blue space, aerosols, soils, and water in relation to human health. Currently, exposure assessment of green space usually involves the use of the normalized difference vegetation index (NDVI), a greenness index derived from satellite imagery, land-use data, or both. Although this gives a measure of greenness, it provides, at best, a crude exposure measure, with little ability to differentiate among vegetation types or among species/genera/families within the same

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[2] Lucretius: De rerum natura, Book 2, Lines 1152-1174. Translation by HAJ Munro (slightly modernized) Encyclopaedia Britannica Chicago 1952.

vegetation type (Donovan et al., 2019a). This is an important limitation as grass is unlikely to offer the same benefits as mature trees with the same NDVI value; similarly, monocultures are unlikely to provide the same benefit as equally green complex ecosystems (with associated diverse fauna and microbiota). We have established this in a previous asthma study, which showed protective effects for native vegetation but neighborhood exposure to exotic monoculture species (gorse, pine) increased asthma risk (Donovan et al., 2018a). These issues are particularly relevant for studies that rely exclusively on NDVI; if combined with land use data, then this is of lesser concern, although most land-cover data distinguish only between broad categories of vegetation and cannot, for example, identify the mix of species within a broad category of vegetation. In addition, the most commonly used sources of land-cover data often have a coarse spatial resolution. For example, the National Land Cover Database in the US has a resolution of 30 m. This combination of broad categories of vegetation along with coarse spatial resolution mean much remains unknown about the association between vegetation types and health. Although remote-sensing, including Light Detection and Ranging (LiDAR), combined with other measures of ecological diversity hold promise (Labib et al., 2021; Donovan et al., 2019c; LaRue et al., 2018), this is a complex (but not impossible) issue to resolve.

Another potential approach is the use of biomarkers. Peters and colleagues provide a useful framework for considering the way in which the environment can damage human health, identifying eight intermediate physiologic biomarkers of environmental insults (Peters et al., 2021). If, in addition, we were to develop biomarkers of optimal function, not just dysfunction, such a framework might be employed to monitor both environmental insults and beneficial exposures.

Exactly how aerosols trigger memories, how they might work to improve or impair health, how inhaled toxins induce torpor without lasting damage (Blackstone et al., 2005) remain mysterious. More generally, how we might establish a science of identifying and assessing beneficial aerosols seems a worthy endeavor— and yet one more way to improve our understanding of what we have lost by being separated from the wild. Further, what is more broadly important about the study that identified a specific pathway by which cowshed dust (and thus traditional farming practices) might act to suppress allergic responses (Stiehm et al., 2013) is the fact that it opens the door to exploring other pathways and, ultimately, the development of interventions that mimic or supplement naturally occurring beneficial bioaerosols.

A systematic review of quantitative studies of blue space and health noted the problem of defining both blue space (ocean, rivers, lakes, etc) and the appropriate distance/access metric, the latter of which is equally relevant to green and grey space (Gascon et al., 2017). Further, we lack environmental maps of microbiota distribution across human and wild space, including not only in soils and woodland but also air quality and airborne microbiota associated with blue space (fresh water and ocean) and green space, although some global data are starting to emerge (Sunagawa et al., 2015; Senghor et al., 2018; Kuang et al., 2016; Likhitrattanapisal et al., 2021; Ma et al., 2016; Kumar et al., 2016). Similarly, although some studies are available, we lack understanding of the differences in distribution of human microbiota within human populations, including across traditional/industrial farmers, those who garden regularly, suburban populations, urban apartment dwellers, etc.

7. Indigenous perspectives

Indigenous perspectives on the nature of our relationship with the environment – green, blue, and grey space – are likely to be different from the more dominant international science view. For example, an established model of Māori health promotion (Māori are the Indigenous people of Aotearoa New Zealand) is derived from the imagery of Te Pae Māhutonga (also known as the Southern Cross); each of the four central stars represents key foundations of health (Durie, 2004). One of these is Waiora – environmental protection – which sees humans as part of the environment, guardians but not owners or managers. The connection of Indigenous Australians to Country (which is not just land) is similar and the health of both individuals and society is deeply entwined with the health of the environment (Burgess et al., 2005).

Secondly, some Indigenous Peoples rightly take the view that colonization has disrupted and often impaired the natural balance of the environment with the widespread introduction of exotic flora and fauna (Black et al., 2022) although views are often complex and nuanced (Reo and Ogden, 2018). More centrally, colonization has disrupted the association between people and their ancestral lands, just as an uncaring consequence of alienation of land for agricultural, pastoral, and extractive industries (Gislason and Andersen, 2016) but some places even saw the deliberate exclusion of Indigenous Peoples from their own wild spaces (Binnema and Niemi, 2006). All this has increased inequality and social injustice (Griffiths et al., 2016), as well as the health gap (King et al., 2009) between Indigenous and colonizing peoples. It has also disrupted the informed management of the environment, which is slowly, sometimes painfully, being reasserted (Eriksen and Hankins, 2014). Even as steps are taken, on the one hand, towards better conservation of the natural world and, on the other, towards return of ancestral lands to Indigenous guardians, some new disparities arise (Moorcroft, 2016a; Moorcroft, 2016b). However, some new concepts of social justice and new capabilities can also emerge from the struggles of Indigenous Peoples for better control of their lives and lands (Schlosberg and Carruthers, 2010).

Thirdly, the biodiversity hypothesis is frequently so fundamental to an indigenous world view that casting it as a hypothesis can seem odd in the "we already knew that" sense (Lambert and Mark-Shadbolt, 2021; Harmsworth and Awatere, 2013). It is becoming increasingly clear that the management of land, the security of food systems, and our relationship to nature generally all need to incorporate more indigenous knowledge than are currently the dominant practices (Antonelli, 2023; Brondízio et al., 2021; FAO, 2021; Wehi et al., 2019; FAO and FILAC, 2021; Sidik, 2022). Encouragingly, with mainstream scientists increasingly interested in the links between the natural environment and human health (until recently this remained a relatively niche area of contemporary international health research) this is now starting to happen, albeit at a modest rate. The growing indigenization of the academy – especially in North America, the Asia/Pacific region, and South America – has also seen increasing inclusion of indigenous views and analysis in our research agendas (Hoskins and Jones, 2022).

8. Research gaps

The biodiversity hypothesis is compelling, but the underlying mechanisms remain largely unclear. In particular, although there is evidence that humans, animals, plants, and the environment constantly exchange microbiota, this complex interaction remains poorly understood. Indeed, differences in human microbiota diversity are plausibly associated with differences in diversity and overall abundance of environmental microorganisms (Zhao et al., 2022; Flandroy et al., 2018; Kirjavainen et al., 2019; Stein et al., 2016; Ege et al., 2011; Mahnert et al., 2015; Pearson et al., 2020; Vanhaecke et al., 2022; Dannemiller et al., 2016; Zhou et al., 2018) and there is likely to be cross-talk between environmental and human microbiota; however, there are few data that describe how microbiota are distributed in the world or how the composition of the microbial subset in one environmental microhabitat overlaps with, and influences, the composition in another (Kowalchuk et al., 2002; Lymperopoulou et al., 2016; Parajuli et al., 2018). For instance, there is often no hard border between green space and blue space as many green spaces have blue components (e.g., a river or a pond in a city park). The possible interaction between these components is worthy of study.

At the moment, although some slender data exist on health benefits of specific microorganisms or groups of organisms in gut, skin, and airway, little is known about the types of environmental microbes that are associated with beneficial health outcomes. it is highly likely that bacterial diversity, rather than the presence or absence of specific taxa may be more important (Deckers et al., 2021). Understanding how different microbial (and parasite) patterns arise, change, and interact within and between all settings from the landscape to human organs should provide important information on the mechanisms by which microbial and parasite communities influence health and disease. Whether ocean-borne microbiota interact with, or otherwise affect, human health is unclear but the similarity of species abundance in the two very diverse settings suggest that it is worthy of study. Further, microbes that live in green, blue, and grey space and the physical characteristics of these spaces plausibly differ in their separate and combined impacts on human health.

It is not clear the range over which green and blue space impact health. Most studies use arbitrary circular buffers around participants' residential address ranging from 50 to 500 m (Akaraci et al., 2020; Rojas-Rueda et al., 2019). We do not know whether the spatial extent of the protective effect of green spaces varies for different health outcomes and different vegetation types. In addition, most studies use Euclidean distances, but network distance may be more appropriate for some mechanisms and diseases.

What does urban living do to the pattern of macro- and microbiodiversity with which we have co-evolved and, until recently, usually co-existed (Fig. 1)? A very important outcome (via public-health action) has been much reduced early-childhood mortality, but there are several markedly deleterious consequences: i) reduced exposure to green space, blue space, and soil; ii) disrupted infrastructure of the macro-diverse environment, namely soil, air, water, etc.; iii) increased exposure to agents that: a) increase disease (e.g., tobacco); b) disrupt human microbiota (e.g., antimicrobials); and c) do both (e.g., Western diet). All of this leads to deranged human and environmental microbiota.

The research questions that arise from indigenous perspectives are likely to look different; for instance, can we explore the disrupted balance and establish whether there are different human health consequences of exposure to indigenous versus exotic flora? We already have some hints that this is so given the different association between asthma and gorse and pine versus native vegetation (Donovan et al., 2018a).

There are other research gaps, including: what constitutes healthy human microbiota? How can microbial dysbiosis lead to such a diverse range of disease states? How do various human microbiota interact with other known risk factors? How do various human microbiota change when exposed to different environments and stimuli: diets, chemicals, antibiotics, and lifestyle? How do human microbiota modulate host immunity – and vice versa? How does the gut microbiota influence metabolic regulation and dietary intake? How can we study the impact of parasites, their loss from populations, and their interaction with microbiota? How does exposure to the natural environment affect human microbiota in urban areas? How does the extensive use of household- and agri-chemicals affect human and environmental microbiota? Will approaches to altering the human microbiota in disease (e.g., fecal transplants; use of probiotics) be safe and effective in reducing disease risk? How does this sort of research programme mesh with research on wider questions around macrobiodiversity, species loss, environmental degradation, and climate change?

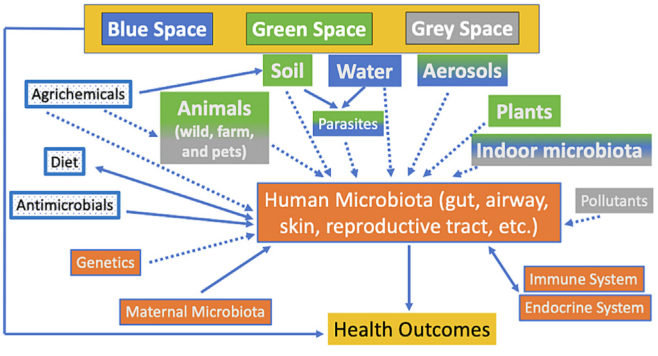

Fig. 1. The color backgrounds of the various exposure classes (animals, soil, water, aerosols, indoor microbiota, pollutants) link the exposures to green, blue, and grey spaces. Other ambient exposures that directly or indirectly influence microbiota are also shown. Relevant aspects of human biology are indicated in orange-colored boxes. The solid lines identify better established relationships; the broken lines identify many of the important knowledge gaps in the relationships between green, blue, and grey space and human health.

This last question brings us face-to-face with some of the central questions of our time and the slowly dawning realization that each of these problems cannot be successfully addressed without also dealing with the others; we are rapidly approaching a time when we will exceed all of the planetary boundaries and be faced with multiple tipping points, moments in time in multiple systems when the way back is no longer simply a matter of reversing course (Steffen et al., 2015; Seekell, 2016; Barnosky et al., 2012; Scheffer et al., 2009; Dai et al., 2012; Ritchie et al., 2021; Armstrong McKay et al., 2022; Solé and Levin, 2022).

9. Future directions

We have focused extensively on the possible role of microbiota in seeking to explain the very extensive range of health outcomes that are clearly beneficially influenced by aspects of the natural environment – and we and others are committed to exploring the relevant mechanisms further. Nonetheless, as we noted above, we acknowledge several other hypotheses that are worthy of further exploration, particularly noting the seminal observation of Ulrich (Ulrich, 1984) that patients with a view of an outside natural scene recovered more quickly from surgery which, in turn, stimulated further work on the role of workplace windows and even photographs in improving aspects of job stress (Leather et al., 2016), stress recovery (Ulrich et al., 1991), and work satisfaction as well as cognitive function (Berto, 2005; Berman et al., 2008) and self-reported health and wellbeing (Leather et al., 2016; Kaplan, 1993).

Even with the changes in the human condition of the last 150 years and the spectacular disruption that the Anthropocene has ushered in (Lade et al., 2019; Waters et al., 2016; Mottl et al., 2021), it is difficult to fully register how much has changed and how rapidly we are approaching catastrophe. Further, although we currently lack the tools to completely understand, if we focus on what we *have* lost, some actions come into view.

Our communities are shaped by external forces and also, perhaps too slowly, by awareness of those external forces. That awareness can provide us with a stimulus to develop and improve resilience. Local control over decisions regarding ecosystems and natural resources – particularly meeting places, town squares, parks, forest, other wild lands, and waterways – will allow us to better protect natural capital and improve human wellbeing in a sustainable way. Cities have a diverse set of problems associated with the density of the population but that also means that cities house the knowledge, skills, technology, creativity, and wealth to work towards solutions.

Many human-health benefits accrue via green and blue space whereas many toxic and deleterious exposures are found in grey space. It follows from this that approaches to amelioration might involve members of urban communities transplanting themselves to less dense population centres – increasingly possible with growing acceptability of flexible working places and time. However, more realistic for the vast majority of urban humanity would be both decreasing the toxicity of cities and increasing green and blue space within urban settings.

One review on nature-based interventions summarized 27 green-prescription, wilderness-therapy, green-gym, or outdoor-exercise studies and argued for further research to identify the factors that influenced their effectiveness (Shanahan et al., 2019). A review of reviews showed strong evidence for an association between improved affect – as well heat reduction – and urban natural environments (van den Bosch and Ode, 2017). An encouraging observational study in Glasgow, Scotland involved a 17-year longitudinal natural experiment that followed the impact on all-cause mortality of taking a canal – and its green and blue spaces – from complete dereliction to regeneration. There was an overall decrease in mortality over time (regression coefficient = −0.032, 95% confidence interval (CI) [−0.046, −0.017]) with a closing of the gap in mortality between less and more affluent areas. The annual rate of decrease in mortality rates was largest in the 0–500 m buffer zone closest to the canal, with smaller decreases found in buffer zones further out. A similar pattern of results was found following adjustment for deprivation (Tieges et al., 2020). A Finnish proposal called "Nature Step", identified several components that could improve our nature-relatedness: i) strengthening connections with natural environments and increasing physical activity; ii) increasing consumption of fresh fruit, vegetables and water; iii) linking natural elements with childhood and elderly care; and iv) focusing research on ecosystems and their health effects to allow better evidence-based interventions and approaches (Haahtela et al., 2019).

Although many knowledge gaps remain, some local and national strategies and policies have been developed – or are in the process of being developed – to rewild urban areas or increase people's exposure to the natural environment or both. For example, the UK government recently (Jan 2023) announced their Environmental Improvement Plan that aims to restore wildlife habitats (500,000 ha of wildlife habitat and 400 miles of river) and have every household live within a 15-minute walk of green space such as woodlands, wetlands, parks, and rivers (currently, 2.8 million people in the UK live more than 10 min from a green space) (Harvey and Horton, 2023; Briggs, 2023). If achieved, this may have a positive impact on public health in the UK. However, green space in the UK is generally defined as any land with vegetation, which may include sports fields, farmland, etc.; therefore, unless ecologically diverse, these spaces may not, on their own, be sufficient to enhance the health of the environment and its population. Large urban rewilding projects, integrating the natural environment into densely populated urban landscapes, have been developed and implemented in several major cities, including Vancouver, Canada (Environmental Education and Stewardship Task Force and Working Groups, 2014); Singapore (Hwang and Jain, 2021) (https://issuu.com/yhwang111/docs/rewilding_singapore_publication_final_reduced); Wellington, New Zealand (https://www.visitzealandia.com/About); Milan, Italy (https://www.bloomberg.com/news/features/2021-10-22/urban-rewilding-aids-biodiversity-climate-resilience); and Haerbin City, China (https://landezine.com/qunli-national-urban-wetland-by-turenscape/). Related to urban rewilding, and relevant to the way in which we reduce the planetary and human burden of grey space, urban agriculture (Dorr et al., 2023; Jha et al., 2023) worldwide, may provide ecosystem services valued at US$80–160 billion annually via food production, pollination, climate regulation, soil formation, energy savings, nitrogen fixation, etc (Clinton et al., 2018). Urban agriculture has positive impacts on food security, poverty, community development and resilience, social justice, job creation, and the economy, thus contributing to several UN Sustainable Development Goals: no poverty, zero hunger, sustainable cities, and climate action (Brevik et al., 2020). Education about these relationships is also important (Brevik et al., 2019).

Compared with the problem of our survival if we were to return to our mythical "natural state" (Graeber and Wengrow, 2021), approaches to remediation of urban environments – greening cities – would be a useful start (Nowak et al., 2006; South et al., 2018; Brown et al., 2018; Wolf et al., 2020; Song et al., 2019) and is almost certainly easier than cleaning up the current mess. We could encourage the organized development and expansion of small-scale urban agriculture and an increase of blue space and green space in cities, paying special attention to specificity and quality, not just quantity (Stevenson et al., 2020). Improving urban design has potential benefits on mental and physical health (Geschke et al., 2018; Ignatieva et al., 2008; Zari, 2017; Buszkiewicz et al., 2021) and may provide some creative spaces to tackle the really big questions that still face us.

Author contributions

Potter et al. A perspective on green, blue, and grey spaces, biodiversity, microbiota, and human health

CRediT authorship contribution statement

John D. Potter: Conceptualization, Writing – original draft, Writing – review & editing, Funding acquisition. **Collin Brooks:** Writing – review & editing, Funding acquisition. **Geoffrey Donovan:** Writing – review & editing. **Chris Cunningham:** Writing – review & editing. **Jeroen Douwes:** Conceptualization, Writing – review & editing, Funding acquisition.

Data availability

No data were used for the research described in the article.

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

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