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Review article

Pathways linking biodiversity to human health: A conceptual framework

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A B S T R A C T

Biodiversity is a cornerstone of human health and well-being. However, while evidence of the contributions of nature to human health is rapidly building, research into how biodiversity relates to human health remains limited in important respects. In particular, a better mechanistic understanding of the range of pathways through which biodiversity can influence human health is needed. These pathways relate to both psychological and social processes as well as biophysical processes. Building on evidence from across the natural, social and health sciences, we present a conceptual framework organizing the pathways linking biodiversity to human health. Four domains of pathways—both beneficial as well as harmful—link biodiversity with human health: (i) reducing harm (e.g. provision of medicines, decreasing exposure to air and noise pollution); (ii) restoring capacities (e.g. attention restoration, stress reduction); (iii) building capacities (e.g. promoting physical activity, transcendent experiences); and (iv) causing harm (e.g. dangerous wildlife, zoonotic diseases, allergens). We discuss how to test components of the biodiversity-health framework with available analytical approaches and existing datasets. In a world with accelerating declines in biodiversity, profound land-use change, and an increase in non-communicable and zoonotic diseases globally, greater understanding of these pathways can reinforce biodiversity conservation as a strategy for the promotion of health for both people and nature. We conclude by identifying research avenues and recommendations for policy and practice to foster biodiversity-focused public health actions.

1. Introduction

Biodiversity comprises the diversity, abundance and identity of species, their genes and ecosystems (Box 1), and underpins ecosystem services that are essential for human health and well-being (Cardinale et al., 2012; IPBES, 2019; Mace et al., 2012). However, biodiversity is declining at an unprecedented rate (IPBES, 2019), threatening the quality of life of all humans, rich and poor. The COVID-19 pandemic has exposed the vulnerabilities of public health across the globe in response to unsustainable biodiversity management (IPBES, 2020). Yet, understanding of the specific aspects of biodiversity that are most relevant to human health and wellbeing (Box 2) remains limited in important respects. Of the large body of research on nature and human health, and in particular those studies that focus on health benefits derived through directly experiencing nature (e.g. Frumkin et al., 2017; Hartig et al., 2014), the majority focus on the spatial extent of greenspace near the home or the amount of time spent in nature, without distinction of its ecological characteristics (Collins et al., 2020; Schwarz et al., 2017; van den Berg et al., 2015). The extensive research on how nature benefits human health and well-being via pathways that do not involve direct experience, as through provisioning or regulating ecosystem services, also often lacks specifics on the biodiversity involved (Cardinale et al., 2012; Sandifer et al 2015). Accordingly, we see a need to further develop knowledge of the ways in which biodiversity matters for human health (Marselle et al., 2019b). A simplistic approach to measuring nature, for example as the amount of greenspace, has enabled a surge of new research and can serve as an important indicator for urban health planning goals. Yet, it does not enable a clear understanding of how human health is influenced by the presence of, contact with, or change in different manifestations of biodiversity.

The importance of the fundamental linkages between biodiversity and human health is increasingly recognized in global and regional policy development (Corvalan et al., 2005; Korn et al., 2019; Romanelli et al., 2015; Ten Brink et al., 2016). For example, the Convention on Biological Diversity (CBD) and the World Health Organization (WHO) are collaborating to promote awareness of the influence of biodiversity on human health and well-being (Convention on Biological Diversity, 2016). In recent years, evidence has emerged that contact with biodiversity is associated with both physical health (Aerts et al., 2018; Lovell et al., 2014; Romanelli et al., 2015) and mental health (Korpela et al., 2018; Lovell et al., 2014; Marselle et al., 2019a). These studies document a direct relationship between biodiversity and human health outcomes. However, they do not shed light on the causal pathways through which biodiversity may work to establish those relationships.

A key research need is, therefore, to unravel the specific causal pathways through which biodiversity affects human health (Aerts et al.,

Box 1
Biodiversity.

Biodiversity is defined by the Convention of Biological Diversity (CBD) as "the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and the ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems" (United Nations, 1992). We use biodiversity here in a broad sense to include the composition, configuration and diversity of specific species or habitats; the abundance and biomass of species; the functional traits of species (e.g. nutrient content, medicinal properties, colors, sounds, contagious properties); and the genetic composition and identity of particular species (e.g. lion, robin, ticks, oak). The term "biodiversity" will frequently be used in the text as shorthand for elements of biodiversity.

Biodiversity overlaps with but differs from three other broad and widely used concepts. *Nature* as defined by Hartig et al. (2014, p.208) refers to "physical features and processes of nonhuman origin that people ordinarily can perceive, including the "living nature" of flora and fauna, together with still and running water, qualities of air and weather, and the landscapes that comprise these and show the influence of geological processes". The term *greenspace* is defined as "land covered by vegetation of any kind. This covers vegetation on private and public grounds, irrespective of size and function" (World Health Organization, 2017a, p.2). Finally, bluespace refers to outdoor environments that prominently feature water, such as oceans and coasts, rivers, lakes, ponds (Beute et al., 2020).

These broad terms do not adequately support understanding of how variation in the ecological characteristics of *nature*, *greenspace or bluespace* relate to health. In contrast, *biodiversity* explicitly encompasses the details and qualities of living organisms and ecosystems. With its focus on biodiversity, the framework presented here can be used to facilitate research on the mechanistic understanding of biodiversity-human health relationships.

2018; Clark et al., 2014; Sandifer et al., 2015). Some specific causal pathways (e.g. nutrition, infectious diseases, microbiota) (Aerts et al., 2018; Sandifer et al., 2015) are better understood than others (e.g. cultural goods and values; Clark et al., 2014). Correspondingly, the complex interplay among known and potential pathways also remains understudied. This lack of mechanistic understanding of pathways linking biodiversity to human health limits application of nature-based solutions in public health, and influence on policy (Hough, 2014). In order to facilitate cross-sector policy and research integration on biodiversity conservation and public health (Korn et al., 2019), it is necessary to better identify and characterize the linkages between biodiversity and human health. A conceptual framework indicating the causal pathways through which biodiversity influences human health is needed for organizing and guiding health research. It should help to inform public health interventions, including nature-based solutions that entail biodiversity management for public health.

In this paper, we summarize the evidence linking biodiversity to human health and discuss the implications of this evidence for underlying causal pathways (for a detailed review of the literature, see Marselle et al., 2019b). We first introduce the conceptual model providing a framework for an understanding of biodiversity-health pathways, and then describe the four major components of our framework. Next, we discuss how to test each component of the framework with analytical approaches and existing datasets. Finally, we identify applications in policy and practice and outline future research frontiers.

Our conceptual framework is intended to inspire, organize and support the work of diverse environmental and health researchers and professionals, as well as the planned nexus assessment of the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) on the interlinkages of biodiversity, water, food and health (https://ipbes.net/nexus). Importantly, we think it can also support implementation of the UN 2030 Agenda for Sustainable Development, the EU Green Deal, the WHO-CBD partnership, and the development of the CBD post-2020 global biodiversity framework and its translation into regional and national policies and associated measures.

2. Conceptual framework relating biodiversity to health

2.1. Framework precursors, features and functions: A user's guide

The proposed biodiversity-health framework was generated during a three-day workshop in September 2019 with an international panel of 26 experts from different disciplines, including biology, biomedical sciences, ecology, environmental epidemiology, environmental psychology, geography, medicine, modern literature, public health, and statistics, as well as experts from conservation agencies and health authorities. This review article summarizes the discussions that consider the evidence linking biodiversity to human health from an interdisciplinary standpoint, focusing on the mediating pathways. In addition, we discuss the analytical approaches (Section 3) and data sets (Section 4) available to test the biodiversity-health framework, as well as recommendations for policy, practice and future research (Section 5). It is not intended to be an exhaustive review of the literature.

2.1.1. Consideration of other approaches, models, and frameworks

Currently, there is no framework that delineates the causal pathways by which biodiversity influences human health and well-being. To develop our biodiversity-health framework, we critically reviewed other published frameworks that deal with related issues to identify gaps and why a new conceptualization is needed. Here, we briefly discuss those frameworks and how we can build on them.

Recent years have seen a growing recognition of the interconnectedness of people and the environment as evidenced by three broad approaches linking the ecological environment and human health: Planetary Health, One Health, and EcoHealth (Assmuth et al., 2020; Buse et al., 2018; Lerner and Berg, 2017). The simplest definition of Planetary Health is "the health of human civilization and the state of the natural systems on which it depends" (Whitmee et al., 2015). As Planetary Health takes a high-level view of the health-environment relationship, focusing on population health and the health of natural ecosystems, this approach is better suited to identifying threats to human health than to understanding the mechanisms through which biodiversity both benefits and harms human health (Lerner and Berg, 2017). Our framework is also more specific and targeted than the Planetary Health approach by focusing on one aspect of the natural system – biodiversity – and its relationship with health at multiple scales, whether of the population or of the individual. The One Health and EcoHealth approaches both refer to the interconnections between the health of humans, animals and ecosystems. One Health, however, focuses on human and animal health (often domestic animals), with an emphasis on attaining optimal health through risk prevention (e.g. of zoonosis). In contrast, EcoHealth concentrates on sustainability and achieving better human health through better ecosystem health (Buse et al., 2018; Lerner and Berg, 2017). Whilst One Health and EcoHealth both consider biodiversity, it is not their primary focus, as it is in our framework. While we acknowledge that humans are merely one species among many on the planet, and healthy ecosystems are the foundation of human health, our approach differs from EcoHealth and One Health by focusing exclusively on outcomes related to human health.

In creating our framework, we also considered other models linking biodiversity to human well-being or quality of life, including the lens of ecosystem services (Díaz et al., 2018, 2015; Haines-Young and Potschin, 2012; Mace et al., 2012; Millennium Ecosystem Assessment, 2005; Potschin and Haines-Young, 2011). These models and frameworks, however, were designed to serve a broad range of functions and audiences and to guide policy development, and – interestingly – human health is rarely considered explicitly as an outcome (Ford et al., 2015).

Box 2
Health and Well-being.

Health is defined by the World Health Organization (WHO, 1948) as "a state of complete physical, mental, and social well-being and not merely the absence of disease or infirmity". A bedrock of the WHO's definition of health is the focus not only on factors that cause disease (pathogenesis), but also on factors that promote health and well-being (salutogenesis).

Physical well-being refers to the quality and performance of bodily functioning. This includes having the energy to live well, the capacity to sense the external environment, and the capacity to experience pain and comfort (Linton et al., 2016).

Mental well-being refers to the psychological, cognitive and emotional quality of a person's life. This includes the thoughts and feelings that individuals have about the state of their life, and their experience of happiness (ibid).

Social well-being concerns how well an individual is connected to others in their local and wider community. This includes social interactions, the depth of key relationships, and the availability of social support (ibid).

Moreover, they do not directly identify the specific pathways linking biodiversity to human health.

Our framework has a particular concern for utility in health research. With its focus on human health, our framework represents a narrower set of concerns than that of other frameworks, such as Planetary Health, One Health or EcoHealth (Whitmee et al., 2015). Our framework nonetheless implicates a wide array of methodological approaches and sources of data that can be used to address specific research questions and to explore different pathways and their co-action. As our aim was to develop a tool that facilitates research that addresses those pathways, the framework we put forward here builds upon three conceptual models that identified specific causal pathways linking nature to human health (i.e. Bratman et al., 2019; Hartig et al., 2014; Markevych et al., 2017). We discuss these next.

2.1.2. *Relationship to previous nature-health models*

In this section, we detail the strengths and weaknesses of three nature-health conceptual models and outline how they inform our biodiversity-health framework.

The Hartig et al. (2014) model of nature-health relationships identified groups of pathways through which the natural environment, and contact with nature, influences human health. The model distinguishes between the natural environment and contact with nature to acknowledge the importance of peoples' encounters with the natural environment and how they conceive of and experience nature. Contact with nature then feeds into four pathways: air quality; physical activity; social contacts; and stress reduction. The model also acknowledges that the strength and direction of associations between nature and health may depend on individual characteristics, such as age and gender, and on features of the broader context in which a person encounters nature, such as cultural practices and values. The model served to organize a review of extant research on already relatively well-described pathways. Hartig et al. (2014) noted that those pathways had largely been addressed separately in different scientific and professional fields, even though they were likely to be intertwined and work together in various ways. The authors also noted that their review did not seek to cover as-yet little-explored pathways.

To extend the representation of possible mediating variables, the Markevych et al. (2017) model grouped known and potential pathways in three broad domains by which greenspace could engender human health benefits. The three domains correspond to the three general functions of greenspace that relate to human adaptation: the 'reducing harm' domain relates to greenspace's ability to mitigate stressor exposures; the 'restoring capacities' domain relates to the ability of greenspace to restore resources that have been depleted in efforts to cope with stressors; and the 'building capacities' domain relates to the use of greenspace for instoration or development of resources that will help to better support coping. These three domains include Hartig et al.'s (2014) previously described pathways while also providing a means to organize them with novel pathways that might serve adaptation in similar ways. The diagram used to present the Markevych et al. (2017) model did not distinguish nature (or greenspace) from contact with nature, but textual pathway descriptions acknowledged the distinction.

Finally, the Bratman et al. (2019) model specifically considers the effects of natural features on mental health. The diagram used to present this model differs from those of Hartig et al. (2014) and Markevych et al. (2017) in that it submerges the different pathways into a succession of four steps (cf. Frumkin et al., 2017). Step 1, 'natural features', refers to the aspects of the environment (e.g. size, quality, type) that can influence mental health. Step 2, 'exposure', refers to the amount of contact with nature. Step 3, 'experience', focuses on the experiential aspects of nature exposure. Step 4, 'effects', refers to the potential mental health impacts that follow from a nature experience. Although the Bratman et al (2019) model do not distinguish mediating pathways in their model diagram, they do discuss commonly studied pathways in the accompanying text.

None of these three models addresses biodiversity in particular, nor do they systematically represent the potential adverse influences of nature/biodiversity on human health. In this way, our biodiversity-health framework expands upon these three models. We draw inspiration from Step 1 of the Bratman et al. (2019) model in order to clearly detail the measurement of biodiversity. From the Hartig et al. (2014) model, we distinguish between biodiversity and contact with biodiversity to acknowledge the potential importance of peoples' encounters with biodiversity. We further expand the contact with biodiversity component of the model using Steps 2 (exposure) and 3 (experience) from the Bratman et al. (2019) model. We then build on the Markevych et al. (2017) model by organizing pathways linking biodiversity to human health into domains defined with regard to their general role in adaptation. Finally, the Hartig et al. (2014) model informs our depiction of the potential for co-action of pathways in different domains and our specification of individual characteristics and features of the environmental and social context that can modify biodiversity-health relationships.

2.2. *Biodiversity and health conceptual framework*

The conceptual model (Fig. 1) underlying our framework shows how biodiversity, and contact with biodiversity, indirectly influences human health through pathways arranged in four domains defined in terms of adaptive relevance: (i) reducing harm (e.g. provision of medicines, decreasing exposure to air and noise pollution); (ii) restoring capacities (e.g. attention restoration, stress recovery); (iii) building capacities (e.g. facilitating physical activity, transcendent experiences); and (iv) causing harm (e.g. exposure to dangerous wildlife, infectious diseases or allergens).

Several novel features of our biodiversity-health framework warrant mention here. First, our framework focuses on the health effects of biodiversity rather than more frequently studied environmental entities (i.e. "nature" and "greenspace", Box 1). Biodiversity is considered with its different elements and hence with all its complexity (Box 1). Each component of the biodiversity-health framework has a critical focus on these specific elements of biodiversity. Second, the framework distinguishes between biodiversity and contact with biodiversity to acknowledge the importance of a person's exposure to and their experience of biodiversity (see Section 2.4). We also identify instances where biodiversity may influence human health without contact with biodiversity, particularly through the 'reducing harm' domain (see Section 2.5.1). We conceptualize the type of contact between the individual and specific elements of biodiversity, and the pathways leading to human health. This enables us to place more emphasis on understanding how the different facets of this relationship work and their respective positive and negative aspects. Third, we include the domain 'causing harm' to represent the ways through which biodiversity can have a negative influence on human health (see Section 2.5.4). Representation of both beneficial and harmful effects gives a more complete picture of human relationships with biodiversity. Finally, the biodiversity-health framework references both the environmental and socio-cultural context and individual characteristics that can moderate relations at every point in the process (see Section 3.2).

The present biodiversity-health framework refers to four intertwined domains of pathways that relate to human adaptation. Multiple pathways may work together simultaneously, with synergies and trade-offs. As such, it is important to consider how the effects realized through different pathways might stand in relation to one another, rather than treating them as independent (c.f. Dzhambov et al., 2018, 2020a; Zhao et al., 2010). Consider the interrelationships between pathways in the domains of 'causing harm' and 'reducing harm'. SARS-CoV-2, the virus responsible for COVID-19, is a dangerous, communicable zoonotic virus, most likely a result of contact with wildlife due to habitat loss (deforestation, agriculture, urbanization) (IPBES, 2020). Consequences for individual and public health are severe, as COVID-19 can lead to death

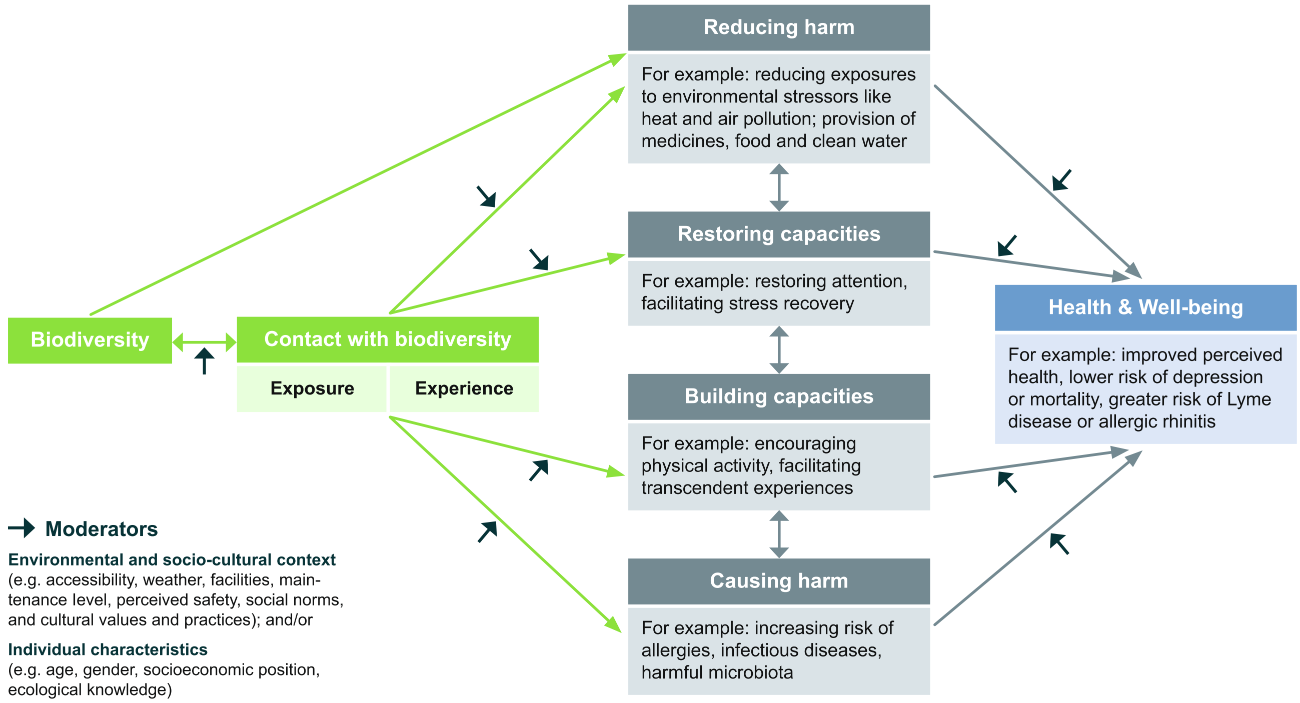

Fig. 1. Pathways linking biodiversity to human health and well-being. Four domains of pathways linking biodiversity and health involve contact with biodiversity (i.e., exposure and possibly experience). An additional pathway runs directly through the reducing harm domain, which implies that biodiversity may affect health without an individual or group having contact with biodiversity (e.g. biodiversity improving upstream water quality through bioremediation). Each domain may be related with all others (for ease of presentation, only adjacent relationships are shown). Two-headed arrows between the domains speak to the potential for reciprocal relationships. Associations between variables are subject to modification by the environmental and socio-cultural context or individual characteristics.

and collateral health damages from disruption of ordinary health care provisions and public health interventions. At the same time, though, the spread of the virus has prompted a reduction in travel that otherwise would generate harmful air pollution (He et al., 2020; Venter et al., 2020). This intertwining of multiple pathways emanating from one and the same feature of biodiversity necessitates interdisciplinary research. Researchers in different disciplines have already begun to study processes as depicted here and can encourage other researchers to join their efforts.

Below we describe the four components of the biodiversity-health framework. In Section 2.3, we discuss how to characterize and measure biodiversity (Component 1 of the biodiversity-health framework). In Section 2.4, we define a general component of many of the pathways of interest, contact with biodiversity (Component 2), as both exposure to (Component 2.1) and experience of (Component 2.2) biodiversity. In Section 2.5, we describe the four domains of pathways through which biodiversity influences human health (Component 3), namely: (i) reducing harm, (ii) restoring capacities, (iii) building capacities, and (iv) causing harm. In Section 2.6, we account for the human health effects of biodiversity (Component 4).

2.3. Biodiversity (Component 1)

This step characterizes the specific elements of biodiversity that potentially influence human health and well-being (see Box 1). Depending on the health outcome studied (e.g. allergic rhinitis, depression), researchers may measure the appropriate tiers of biodiversity — genes, species or ecosystems (Box 1). For example, genetic diversity may be important for investigating allergic rhinitis, while species abundance may be important for investigating depression (Marselle et al., 2020).

2.3.1. Measurement of biodiversity

2.3.1.1. Actual biodiversity. Biodiversity is currently measured in two ways: actual and perceived biodiversity (Fig. 2). Measurements of the actual biodiversity present at a location refer to the identity and number of species and individuals present and their functional characteristics, for example, the species richness, identity and abundance of street trees in a city district (see Supplementary Table 1). The amount of actual biodiversity that is present at a location will vary depending on the spatial extent of an area under observation (e.g. local, national, international) and the time of day and season of sampling (Kelling et al., 2019). Accuracy will depend on sampling intensity (spatial and temporal extent), and previous knowledge and experience of the observer (Kelling et al., 2019). Data on actual biodiversity can be gathered from a variety of sources (e.g. fieldwork, remote sensing) and operationalized in different ways (e.g. databases; for more information see Section 4).

Information on actual presence/abundance and trait values of species in an assemblage can be used to calculate measures of functional identity and diversity of the assemblage. Various parametric and non-parametric measures are available to assess actual species diversity or also genetic or functional diversity, with Shannon and Simpson Indices as common indices (Magurran, 2013). These assess the degree of heterogeneity, evenness or dominance within species assemblages.

2.3.1.2. Perceived biodiversity. When data on actual biodiversity are not available, a proxy measure may be used (Cameron et al., 2020). The proxy measure, perceived biodiversity, is a person's subjective assessment of the biodiversity that they think is present in an environment (Dallimer et al., 2012; Fuller et al., 2007). Similar to actual biodiversity, perceived biodiversity may also refer to the identity and number of species (i.e. species richness and species composition) and individuals present (i.e. abundance) and their functional characteristics (i.e. traits of individual organisms, such as size, color, life histories or behavior) or structural diversity (e.g. the physical architecture of plants in a park or

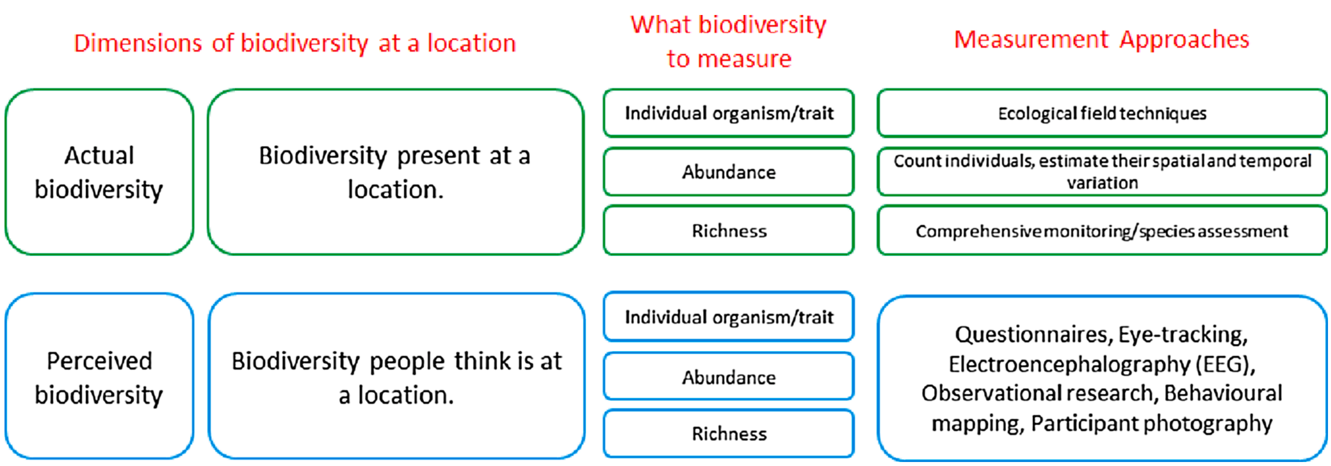

Fig. 2. Measurement of actual and perceived biodiversity.

forest) (Fig. 2). Perceived biodiversity is measured by asking people for their individual assessment of the species identity or richness in an environment through self-report questionnaires (e.g. Cameron et al., 2020; Dallimer et al., 2012; Fuller et al., 2007; Marselle et al., 2016; Southon et al., 2018). Perceived biodiversity can have stronger correlations with well-being than actual biodiversity (Cameron et al., 2020; Dallimer et al., 2012; Meyer-Grandbastien et al., 2020). However, the proxy measure of perceived biodiversity cannot replace a measure of actual biodiversity (Hoyle, 2020). While perceived biodiversity assessments have been shown to be correlated with actual biodiversity measures (Cameron et al., 2020; Fuller et al., 2007; Meyer-Grandbastien et al., 2020; Southon et al., 2018), other studies have found no relationship between the two measures (Dallimer et al., 2012; Shwartz et al., 2014). Perceived biodiversity assessments may over or underestimate the amount of actual biodiversity in a location (Shwartz et al., 2014).

As implied in Fig. 1, the measurement of biodiversity (Component 1) has a reciprocal relationship with contact with biodiversity (Component 2). That this is so is most apparent with the measurement of perceived biodiversity, which assumes some contact with actual biodiversity, whether contact is framed solely in terms of exposure or in terms of both exposure and experience. We will return to this issue after elaborating on Component 2.

2.4. Contact with biodiversity (Component 2)

Component 2 of the biodiversity-health framework describes a person's contact with the elements of biodiversity identified in Component 1. Here, contact with biodiversity is defined by two different aspects: exposure and experience. Exposure refers to a person's amount of contact with biodiversity. Experience refers to how a person experiences and interacts with biodiversity. Nevertheless, our conceptual model (Fig. 1) also acknowledges that elements of biodiversity may affect health without an individual or group having contact with biodiversity, through the 'reducing harm' domain (Section 2.5.1).

2.4.1. Exposure to biodiversity (Component 2.1)

To a greater or lesser extent, people are exposed to biodiversity throughout their daily lives. Here, exposure refers to the amount of contact that an individual or population has with biodiversity (cf. Bratman et al., 2019; Frumkin et al., 2017). How exposure is measured is important for determining which causal pathways and health outcomes can be inferred (Nieuwenhuijsen, 2015). Exposure can be measured in one of two ways. The first is actual exposure to biodiversity, based on the frequency (how often) and duration (how long) a person or population has had contact with biodiversity (Frumkin et al., 2017; Shanahan et al., 2016a; Shanahan et al., 2015). For example, two people live on the same street which contains a certain number and diversity of street trees (actual biodiversity, Component 1), but one person walks every day along the street while the other person only walks along the street once a week. The two people have different exposure profiles (Frumkin et al., 2017), and this difference is not captured solely in the measurement of the number and diversity of tree species (from Component 1). Exposure may also differ markedly in environments with different elements of biodiversity and with the behavior (Methorst et al., 2020) or occupation of individuals (e.g. farmers in rural areas or in the tropics may be exposed to more potentially dangerous wildlife than city dwellers in the Global North) (Covert and Langley, 2002; Fontoura-Junior and Guimarães, 2019). Data on frequency and duration of exposure can be obtained with smartphone apps that use ecological momentary assessment with location tracking (e.g. Beute et al., 2016; Cameron et al., 2020; de Vries et al., 2021; MacKerron and Mourato, 2013; Tost et al., 2019) or self-report questionnaires (e.g. Marselle et al., 2015, 2016). Exposure to biodiversity can also be manipulated as a research design choice (e.g. Lindemann-Matthies and Matthies, 2018).

When data on actual exposure are not available, proxy measures are used (Bratman et al., 2019). These proxy measures for assessing exposure to biodiversity are based on the amount of the elements of biodiversity identified in Component 1 (Bratman et al., 2019; Ekkel and de Vries, 2017). The first proxy measure is cumulative opportunity, which is the total amount of biodiversity surrounding a person's location (e.g. residence, workplace, neighborhood) (Ekkel and de Vries, 2017). Data used to map actual biodiversity, such as from remote sensing and metagenomics, can be used to determine the proportion or number of specific habitats, species or genes within the geographical area of interest (Dennis et al., 2018; Donovan et al., 2018). The second proxy measure is proximity, comprising metrics that estimate exposure as a function of the distance from one's location to the nearest environment with a specified minimum level of biodiversity (e.g. park) (Bratman et al., 2019; Ekkel and de Vries, 2017; Frumkin et al., 2017). Walking distance from a residence to the nearest environment satisfying the minimally required level of biodiversity has also been used as a measure of proximity (Ekkel and de Vries, 2017).

The frequency and duration of exposure will have differential influences on the mediating pathways (Component 3, e.g. stress of the 'restoring capacities' domain) as well as the health outcomes (Component 4) (Shanahan et al., 2015). For example, short time periods of exposure (e.g. 2–5 min) to fish species richness (Cracknell et al., 2016) and plant species richness (Lindemann-Matthies and Matthies, 2018) have been shown to reduce stress. Two hours of nature interaction per week might be beneficial for health and well-being (White et al., 2019), but a single occurrence spent in long grass might be sufficient to become infected with Lyme Disease.

2.4.2. Experience of biodiversity (Component 2.2)

Approaches to exposure measurement in Component 2.1 (e.g. frequency, cumulative opportunity) do not capture the experiential aspects of contact with biodiversity—what we term as the experience of biodiversity. It is important to recognize that people may experience biodiversity differently (Gaston, 2020), and these experiential characteristics of contact with biodiversity may be highly relevant for any health effects (Frumkin et al., 2017). In this component of the framework, we consider how biodiversity can be experienced by people.

Firstly, humans experience biodiversity through the five senses. The majority of the literature assumes vision as the primary sensory modality for biodiversity interaction (Conniff and Craig, 2016). The auditory (Hedblom et al., 2017; Ratcliffe et al., 2013), olfactory, somatosensory and gustatory senses may also be important to consider for their differential impacts on health outcomes (Franco et al., 2017).

Secondly, experience includes an individual's interactions with elements of biodiversity. While there are many ways to characterize human-nature interactions (e.g. Clayton et al., 2017; Kahn et al., 2010), the approach we adopt is a typology specifically focused on the impact of nature interactions on human health (Keniger et al., 2013; Pretty et al., 2005; Soga and Gaston, 2020). Using this typology, the experience of biodiversity is classified into four different experience types clearly delineated by: (i) whether the physical proximity with biodiversity is indirect or direct; and (ii) whether the type of interaction is incidental or intentional (see Table 1).

To determine which of the four experience types a person or population is experiencing, one must measure both the physical proximity to biodiversity and the intention behind the interaction. The degree of physical proximity (indirect or direct) can be specified in the research design. Researchers can design a study which determines whether and how participants experience biodiversity through indirect contact (e.g. photographs, videos, Virtual Reality) (e.g. Chiang et al., 2017; White et al., 2017; Wolf et al., 2017), through direct contact (e.g. visits to a greenspace type with a certain level of biodiversity) (e.g. Carrus et al., 2015; Chang et al., 2016; Dallimer et al., 2012; Fuller et al., 2007) or through both indirect and direct contact, in a within-subjects design (e.g. Browning et al., 2020). It is difficult to measure intentions objectively (Soga and Gaston, 2020). Thus, measuring intentions is best done by asking people (e.g. via interviews or questionnaires) about whether their interaction with biodiversity was intentional or incidental, or through a research design which manipulates the type of interaction (e.g. instructing participants to smell flowers, Colléony et al., 2020). As a proxy measure, intentions could be assumed through human behavior. For example, incidental interactions can be assumed when a person is running, walking with others, or playing with children outdoors. In these examples experiencing biodiversity is a by-product of these activities. Similarly, intentional interactions can be assumed when a person is gardening, birdwatching, hunting or conservation volunteering. It is important to note that intentional interactions with biodiversity may be triggered by prior experience or knowledge, such as when a person intentionally visits a particular ecosystem at a particular time of year because they know they can observe the migration of a rare species of bird at that time/place.

Table 1
Typology of people's experiences with biodiversity.

Degree of physical proximity	Type of interaction: Incidental	Type of interaction: Intentional
	Experiencing biodiversity as a by-product of another activity	Experiencing biodiversity through direct intention
Indirect Experiencing biodiversity without being physically present in it	A person has no physical contact with biodiversity, and interaction is a by-product of another activity, e.g. video of an aquarium in the dentist waiting room (Clements et al., 2019).	A person has no physical contact with biodiversity but interaction is intentional, e.g. viewing fish in an aquarium (Cracknell et al., 2016), or trees through a window (Cox et al., 2019, 2017a) or bird watching through a hide (Keniger et al., 2013).
Direct Experiencing biodiversity by being physically present in it	A person is physically exposed to biodiversity, but the interaction is incidental to another activity, e.g., walking with others outdoors (Marselle et al., 2016, 2015), driving along vegetated roadsides (Parsons et al., 1998) encountering vegetation indoors (Bringslimark et al., 2009) or working on a farm (Fontoura-Junior and Guimarães, 2019) or in a forest (Covert and Langley, 2002).	A person is physically exposed to biodiversity through direct intention (e.g. gardening, camping, diving, hunting, citizen science activities or conservation volunteering (Currie et al., 2016)).

The interaction type (Table 1) influences what a person experiences and the amount of biodiversity they 'absorb' (Frumkin et al., 2017), which in turn may influence outcomes relating to the mediating pathways and health. For example, Carrus et al. (2015) looked at the types of activities in which people were engaged in an urban green space, and how these activities affected well-being and restorative quality perceptions, a mediator in the 'restoring capacities' domain (Section 2.5.2). People who were contemplating the setting, walking or exercising in urban greenspaces of varying biodiversity reported better well-being and experienced more restorative quality in the environment than people who were reading, talking, or socializing with others (Carrus et al., 2015). This suggests that perhaps a person whose interaction with biodiversity is incidental (e.g. socializing with a friend in a biodiverse greenspace) experienced less well-being benefits because they were more distracted and less observant of the environment than a person, in the same location, whose interaction with biodiversity is intentional (e.g. contemplating the biodiverse setting). However, incidental contact with nature, such as everyday contact with street trees around the home, may still be very important for mental health (Dzhambov et al., 2020b; Marselle et al., 2020). As such, awareness might be an important aspect for interaction with biodiversity (Lin et al., 2014; Soga and Gaston, 2020). This awareness can be tested through, for example, eye-tracking methods (Franěk et al., 2019), neuroscience (Berman et al., 2019; Norwood et al., 2019), participant photography or citizen science apps (Frumkin et al., 2017).

Experiences of micro-biodiversity, however, are limited in this classification system. Direct contact with microorganisms is ubiquitous in all human environments, and humans are host to a diverse microbiome (Gilbert et al., 2018; Grice and Segre, 2012). However, the type of interaction with microbial biodiversity is usually incidental, as humans have limited abilities to experience microorganisms (Patel et al., 2018; Rieder et al., 2017). A notable exception is the intentional interaction with microorganisms when a person consumes microbial metabolic products (Liu et al., 2018) or views soil microorganisms through a microscope (Puig de la Bellacasa, 2019).

The human health effects from exposure to and experience of biodiversity may occur through four domains of pathways. In moving from contact with biodiversity to human health effects, we need to consider these mediating pathways. This consideration is the focus of Component 3.

2.5. Domains of pathways (Component 3)

The third component in the biodiversity-health framework describes the causal pathways linking biodiversity and human health. In Sections 2.5.1–2.5.4, we provide an overview of the four domains of pathways linking biodiversity to human health.

2.5.1. Reducing harm

Biodiversity can influence health and well-being by mitigating or reducing ill health. In this domain, we discuss the ways biodiversity contributes to the determinants of health—for example, access to essential provisioning services, such as medicines, food and clean drinking water—as well as reducing harm caused by environmental stressors through regulating services (e.g. regulation of air and noise pollution or extreme heat) (Coutts and Hahn, 2015). Some pathways in this particular domain may not always require exposure to or interaction with biodiversity by the benefitting person or population (Fig. 1). The consumption or benefit of a specific element of biodiversity might be completely spatially distant from the origin of service (for example where the medicinal plant is grown, or air quality is improved).

2.5.1.1. Medicinal drugs. Medicinal drugs derived from natural sources are one of the clearest examples of the importance of biodiversity for human health. Biodiverse environments provide natural products and genetic resources, which form the basis for both traditional medicine and modern pharmaceuticals (van Wyk and Wink, 2017). Medicinal plants are the primary source of natural product drugs for a majority of the human population (Romanelli et al., 2015), and an estimated 70–80% of the global population depend on some form of traditional medicine for their primary health care (Ekor, 2014). Seventy-five percent of all antibacterial, antiviral and antiparasitic drugs approved by the United States have natural product origins (Newman and Cragg, 2012). Consequently, the prospective extinction of one million species (IPBES, 2019) may harm human health through the loss of medicinal plants and opportunity costs of forgone biomedical discovery (Chivian and Bernstein, 2008).

2.5.1.2. Food provision. Good nutrition is fundamental for our physical well-being (World Health Organization, 2017b). Genetic and species diversity—both above and belowground—are essential for food production (Bernstein, 2014; FAO et al., 2020) and a well-balanced, nutritious diet. Maintaining biodiversity is important for the development of potential food crops of the future, which may help ensure food security under threats of climate change (Bernstein, 2014) or intensive land use (Fahrig et al., 2015). However, intensive agro-chemical based food and agricultural production systems are also big drivers of global environmental change and biodiversity loss (Wyckhuys et al., 2020). Biodiversity-based interventions — like organic farming, maintenance of a high biodiversity of crops and surrounding habitats, as well as invertebrate-based natural pest control — can also reduce pest infestation and pesticide use (Petit et al., 2015; Wyckhuys et al., 2020) and to support the health of pollinators (IPBES, 2016) and people (Kim et al., 2017).

2.5.1.3. Reducing exposure to water health risks. Access to clean water is a necessity for human health (World Health Organization, 2019). Biodiversity plays a fundamental role in the provision and regulation of water quantity and quality. Much of the world's freshwater is provided downstream from mountains through river networks, and forests play an important role in flow regulation (Zhang et al., 2017). Biodiversity is central to the health of these ecosystems, as it supports ecosystem functions that provide, regulate and purify freshwater (Dudley and Stolton, 2003). The ability of wetland plants to remove heavy metals from water differs between species (Schück and Greger, 2020). A proxy indicator of good water quality and ecosystem health is the diversity and composition of aquatic organisms, as they are sensitive to nutrient pollutants in the water, such as nitrate (Cardinale, 2011), pesticides (Liess and Beketov, 2011) and pharmaceuticals (Binelli et al., 2015). For example, freshwater mollusks (Ostroumov, 2005) or reed beds can contribute to clean freshwater by filtering water and controlling phytoplankton densities. In addition to the provision of freshwater, biodiverse environments can provide regulating ecosystem services that regulate severe flooding (Carter et al., 2018), buffering of water scarcity (Ellison et al., 2017) or landslides (Miura et al., 2015).

2.5.1.4. Reducing exposure to air and noise pollution. Air and noise pollution are well known causes of negative human health outcomes (Basner et al., 2014; Lelieveld et al., 2019; Zivin and Neidell, 2018), particularly for urban dwellers. In locations where health-related standards are exceeded, the potential of tree and other plant species to regulate air pollutant concentrations and to mitigate noise can be especially important (Cohen et al., 2014; Haase et al., 2014; Salmond et al., 2016). There is also evidence that tree diversity has a significant impact on the potential to mitigate air pollution in cities (Churkina et al., 2015; Grote et al., 2016). Similarly, vegetation with higher structural complexity and density has been found to be an effective barrier to ultrafine particles from roads (Hagler et al., 2012). Nevertheless, in the case of air quality, the tangible effect of urban vegetation is still under debate due to its complex chemical and physical interaction with the surrounding air depending on vegetation structure (e.g. planting density) and specific functional traits (e.g. leaf area, water-use strategy, pollen production) (Hewitt et al., 2020; Salmond et al., 2016; Xing and Brimblecombe, 2019). Some traits, such as allergenic pollen or volatile organic compounds may also negatively impact on health (see 2.5.4.4). While air and noise pollution have been investigated as mediators linking nature to human health (e.g. Bloemsma et al., 2019; Crouse et al., 2019; Triguero-Mas et al., 2017a), to date, no study has investigated whether reduction of air and noise pollution mediates the relationship between specific elements of biodiversity and human health.

2.5.1.5. Reducing exposure to extreme heat. Human health is inevitably linked to the ambient temperatures to which populations are acclimatized, therefore deviations from non-optimum temperatures will lead to impacts on morbidity and mortality (Gasparrini et al., 2015). Temperature extremes are one aspect of this health burden. Heatwaves already have the highest cumulative death rates of any extreme weather-related event in Europe (European Environment Agency, 2017)—disproportionately affecting older people, people with pre-existing health problems and people living in urban areas (Grize et al., 2005; Johnson et al., 2004; Poumadere et al., 2005). Although extreme cold has been estimated to be more important than extreme heat, extreme heat is a particular concern for the future due to climate change, more people living in urban areas, and higher vulnerability (e.g. ageing populations) (European Environment Agency, 2017; United Nations Department of Economic and Social Affairs, 2019a; United Nations Department of Economic and Social Affairs, 2019b).

The design of cities can influence human exposure to extreme heat. Elevated land and air temperatures in urban areas are primarily due to the replacement of natural land covers with impervious cover with different thermal and structural properties (Gunawardena et al., 2017; Oke, 1982). The cooling properties of vegetation and water (from evapotranspiration and/or shading) mean that even modest amounts play an important role in temperature moderation and therefore influence human thermal comfort and the reduction of heat stress (Bowler et al., 2010a). Vegetation abundance, structural characteristics, taxonomic diversity, species composition, functional diversity and functional identity are all known to affect the extent of cooling provided (Lindley et al., 2019; Schwarz et al., 2017; Ziter, 2016). For instance, tree traits (e.g. leaf area, pigmentation and canopy structure) influence how incoming solar radiation is intercepted (Speak et al., 2020). Furthermore, evapotranspiration rates are determined by a range of species-dependent characteristics such as leaf area, canopy height and stomatal and hydraulic resistances, moderated by factors such as water availability (Gunawardena et al., 2017). Some of the shading properties important for cooling may also influence health impacts from other harmful exposures, such as non-melanoma skin cancers from excess UV exposure (Datzmann et al., 2018). Despite evidence of the role of biodiversity for temperature regulation, to our knowledge, no epidemiological study has used mediation analysis to investigate whether the beneficial effects of biodiversity on human health can be explained by reducing exposure to extreme heat.

2.5.2. Restoring capacities

The restoring capacities domain of pathways refers to the recovery of adaptive capabilities that have been diminished through the demands of dealing with everyday life (Hartig, 2017). Over time, lack of restoration of these resources can lead to mental and physical ill health (von Lindern et al., 2017). Environments that support the restoration of these depleted resources are called restorative environments. While recent theorizing considers how experiences in natural settings might figure in the renewal of relational and social resources (Hartig, 2021), the current conventional narrative about how the experience of specific elements of biodiversity produces restorative benefits centers on theories about the renewal of psychophysiological and cognitive resources used to mobilize and direct action (Marselle, 2019).

2.5.2.1. Stress recovery theory. Stress recovery theory (SRT) considers that natural environments benefit health by facilitating recovery from stress (Ulrich, 1983; Ulrich et al., 1991). Environments that facilitate stress recovery are those that evoke interest, pleasantness and calmness in a person. Evidence of stress recovery is seen in, for example, reduced physiological arousal and negative emotions, together with enhanced positive emotions (Ulrich et al., 1991). Qualities of the natural environment that facilitate stress recovery are: moderate to high complexity; a focal point; moderate to high level of depth; a ground surface that is conducive for movement; a lack of threat; a deflected vista; and water (Ulrich, 1983). Qualities of biodiverse environments that are considered a threat (e.g. large predators, snakes, spiders or stinging insects) could contribute to stress because they can cause a negative affective reaction (e.g. dislike, fear) and behavioral responses to avoid or escape the environment for personal safety (Ulrich, 1993).

In terms of SRT, biodiversity can be considered as an aspect of an environment's complexity (Ulrich, 1983, p.96). Reduced physiological stress has been related to greater plant species richness (Lindemann-Matthies and Matthies, 2018). Greater afternoon bird abundances (Cox et al., 2017b), and perceived plant species richness (Schebella et al., 2019) have been related to reduced psychological stress. Greater positive emotions have been associated with increases in the diversity of forests (Johansson et al., 2014), abundance of fish/crustaceans (Cracknell et al., 2017), species richness of trees and birds (Wolf et al., 2017), and perceived species richness of various taxa (Schebella et al., 2019; White et al., 2017). While stress has been investigated as a mediator linking greenspace to mental health (e.g. Triguero-Mas et al., 2017a), to our knowledge, no study has tested whether stress, or negative or positive emotions mediate the relationship between biodiversity and human health.

2.5.2.2. Attention restoration theory. Attention restoration theory (ART) focuses on the aspects of environmental experience that allow for the restoration of the ability to direct attention (Kaplan and Kaplan, 1989; Kaplan, 1995; Kaplan and Berman, 2017). According to ART, a person can restore a depleted ability to direct attention when they experience four restorative qualities of an environment: (i) *fascination,* when observation and exploration of an environment attracts and hold a person's attention without cognitive effort; *(ii) being away* from everyday tasks or demands that draw upon directed attention; (iii) *extent,* with the environment perceived as coherently organized and with sufficient scope to sustain exploration; and (iv) *compatibility* between the environmental setting and one's purposes and inclinations (Kaplan and Kaplan, 1989; Kaplan, 1995). Changes in cognitive tests after exposure to an environment are used as evidence of attention restoration in ART (Ohly et al., 2016; Stevenson et al., 2018).

Biodiversity is not systematically addressed in the theoretical writings of the ART (Marselle, 2019). However, natural environments providing specific elements of biodiversity (e.g., greater species richness) may better serve attention restoration as they are more likely to support the experience of *all* four restorative qualities (Korpela et al., 2018; Marselle, 2019). One study found restoration from directed attention fatigue was greatest for people who looked at images of urban greenspaces with high vegetation density compared to those who looked at urban greenspaces with medium- or low- density vegetation (Chiang et al., 2017). This suggests that the effect of high vegetation density was most likely linked to abundance of plant species or their species composition. Perceived restoration—where people self-report changes indicative of restoration (e.g. feeling relaxed, refreshed after a long day) (Hartig, 2011)—has been found to be positively associated with actual and perceived landscape heterogeneity of urban greenspace (Meyer-Grandbastien et al., 2020), vegetation structure and plant species of gardens (Hoyle et al., 2017), and actual (Wood et al., 2018) and perceived (White et al., 2017) species diversity of various taxa. The four restorative qualities have shown positive associations with structural complexity of urban greenspace (Carrus et al., 2015; Scopelliti et al., 2012) and perceived species richness of birds (Marselle et al., 2016). To date, no study has tested the ability to direct attention as a mediator; only restorative qualities (separately or in aggregate) have been tested as mediators of the relationship between biodiversity and health (Dahlkvist et al., 2016; Marselle et al., 2019a). Restorative quality has been found to mediate the relationship between biodiversity of urban greenspace and general well-being (Carrus et al., 2015). The restorative qualities *being away*, *fascination* and *compatibility* have been shown to mediate the relationship between perceived bird species richness and positive affect, and the *compatibility* quality to mediate the inverse associations between perceived bird species richness and negative affect (Marselle et al., 2016).

2.5.3. Building capacities

The building capacities domain of pathways refers to the deepening or strengthening of capabilities for meeting everyday demands, rather than the restoration of a depleted resource (Hartig, 2007). As with regard to restoring capacities, we discuss here how biodiversity can contribute to health human via capacity building primarily on an individual level, though we also acknowledge how it can be approached on a neighborhood, community or other higher level of analysis.

2.5.3.1. Encouraging physical activity. Physical activity is important for physical and mental well-being (Biddle and Mutrie, 2008; World Health Organization, 2018). Research suggests that physical activity in nature may produce greater physiological and psychological benefits than physical activity indoors (Bowler et al., 2010b; Thompson Coon et al., 2011) or in urban areas (Bowler et al., 2010b). It has been shown that enhancing streetscapes by increasing biodiversity may promote physical activity (Säumel et al., 2016). Biodiversity loss of ash trees is associated with people spending less time on outdoor recreation (e.g. sport, exercise, walking) (Jones, 2016). Björk et al. (2008) and de Jong et al. (2012) found a positive association between environments that were 'lush', i.e. rich in species, and greater self-reported physical activity, although others (Annerstedt et al., 2012; Foo, 2016) could not find an association. While physical activity has been investigated as a mediator linking nature to mental health (e.g. Triguero-Mas et al., 2017a), to our knowledge no study has investigated physical activity as a mediator of biodiversity-human health relationships.

2.5.3.2. Facilitating social interaction and social cohesion. Social interaction, and social cohesion within neighborhoods, are related to health and well-being (Fone et al., 2014; Holt-Lunstad, 2017). Social cohesion refers to "shared norms and values, the existence of positive and friendly relationships, and feelings of being accepted and belonging" (Hartig et al., 2014, p.215); as social cohesion is more a characteristic of neighborhoods than of individuals it is more susceptible to changes in the physical characteristics of the neighborhood (Baum et al., 2009). Biodiverse neighborhoods with more trees may provide a setting for social interaction with others, which is likely to increase social cohesion (Sugiyama et al., 2008; Sullivan et al., 2004). However, Shanahan et al. (2016b) found no relationship between vegetation complexity of a visited green space – a measure that often correlates with plant and animal diversity – and social cohesion. While previous studies have investigated social interaction and social cohesion as a mediator of greenspace and health (de Vries et al., 2013; Ruijsbroek et al., 2017; Sugiyama et al., 2008; Triguero-Mas et al., 2017a), only one study to date tested social interaction as a mediator of the association between parks with different levels of plant, bird and animal species richness and human health, and it did not find evidence for mediation (Foo, 2016).

2.5.3.3. Transcendent experiences (awe, humility, reflection). Transcendent experiences—such as humility, awe (strong emotions of amazement and wonder; Ballew and Omoto, 2018), and reflection (thinking about one's life, goals and priorities; Kaplan and Kaplan, 1989)—contribute to well-being (Capaldi et al., 2015; Davis and Gatersleben, 2013). Sights and sounds of nature, both mundane and awesome, have been found to elicit transcendent experiences (Capaldi et al., 2015; Irvine et al., 2019). Scientists report a "controlled sense of wonder before the universal mystery" (Schroeder, 1996, p.93) and sense of humility (Goodenough, 1998) when making great advances in modern biology. Qualitative research has shown that viewing some types of wildlife can contribute to a sense of humility and awe (Curtin, 2009). Quantitative research shows that the number of habitat types (Fuller et al., 2007), and actual species richness of plants (Fuller et al., 2007) and birds (Dallimer et al., 2012) were positively associated with reflection. Perceived species richness of birds, butterflies and plants were also found to be positively associated with reflection (Dallimer et al., 2012). To date, no study has tested whether transcendent experiences mediate the associations between biodiversity and health.

2.5.3.4. Promote place attachment and place identity. People may form emotional bonds, or place attachments, to biodiverse environments (Ives et al., 2017; Manzo and Devine-Wright, 2019; Raymond et al., 2010). These emotional connections mean that these biodiverse environments could also form part of one's place identity (Manzo and Devine-Wright, 2019). Both place attachment and place identity are associated with psychological well-being (Manzo and Devine-Wright, 2019). Previous research has found that both place attachment and place identity were positively associated with the abundance of tree cover (Dallimer et al., 2012), actual and perceived species richness of birds (Dallimer et al., 2012; Fuller et al., 2007), as well as perceived species richness of butterflies and plants (Dallimer et al., 2012). Place identity was also found to be positively related to the number of habitat types and actual plant species richness (Fuller et al., 2007). While, place attachment or place identity have been tested as mediators of the relationship between nature and health (e.g. Knez et al., 2018), to our knowledge, no study has investigated the degree to which a beneficial health effect of some feature of biodiversity can be explained by place attachment or place identity using mediation analysis.

2.5.4. Causing harm

In this section, we illustrate some of the adverse effects that biodiversity can have for human health.

2.5.4.1. Contact with wildlife that cause harm. Research on contact with wildlife has traditionally focused on negative aspects, such as injuries through encounters with poisonous plants, mushrooms or berries, and large mammalian predators or reptiles (Methorst et al., 2020). This includes, for example, attacks by large cats, bears or alligators, snake bites or skin irritation when in contact with amphibia. Injuries can also be induced by plants and fungi, through skin contact (e.g. stinging nettles, algae; for allergens see 2.5.4.4) or poisoning through consumption. Dangerous interaction with wildlife may also cause mental and emotional harm, in addition to physical harm due to injury. This mental or emotional harm may also be invoked through fear, even in the absence of actual contact with wildlife, or as a constraint to the restoring and building capacities pathways (Sections 2.5.2 and 2.5.3) by avoiding particular biodiverse settings out of fear of contact with potentially harmful wildlife. Nevertheless, interactions with wildlife may also engage pathways in the restoring and building capacities domains with beneficial effects of wildlife on health (Methorst et al., 2020).

2.5.4.2. Exposure to infectious agents causing human diseases. Serious infectious human diseases such as the recently emerged COVID-19 (pandemic), Ebola (West Africa), Borna (Germany) and the vector-borne diseases (VBDs)—such as malaria, dengue, zika, schistosomiasis, visceral leishmaniasis or tick-borne encephalitis—all stem from animals (Ahmad et al., 2020; Müller et al., 2019; Niller et al., 2020; World Health Organization, 2017c). Human actions (e.g. agro-chemical pesticide application, habitat loss, agricultural intensification and urbanization) can increase interactions with such animals (Barouki et al., 2021). Unsustainable resource exploitation can thus also increase the risk of interactions between humans and animals that potentially distribute infectious diseases. Thus, in exploiting nature, we ourselves promote these conflicts (IPBES 2020).

VBDs relate to very important aspects of biodiversity as they comprise an inter-relationship between pathogens (arboviruses, bacteria, protozoa), invertebrate vectors (i.e. mosquito, sand fly, tsetse fly, tick, snail, lice, flea) and host species (i.e. human, livestock, rodents, birds). The interactions of these three VBD components attribute to qualitative and quantitative biodiversity, for instance: genotype-specific replication in the vector (Riehle et al., 2006); pathogen transmission to the host (Heitmann et al., 2018); context-dependent host preference (Simpson et al., 2012); differential responses in phenology and distribution (Elyazar et al., 2013; Hasyim et al., 2018); and dynamic pathogen spreading in social networks of host species (Ezenwa et al., 2016).

Numerous studies have investigated whether there is a causal pathway between infectious disease agents and the level of biodiversity (genetic, phenotypic and species diversity of vectors/hosts, functional diversity for vector and reservoir competence) (Ostfeld, 2009; Roberts and Heesterbeek, 2018; Vadell et al., 2020). Evidence has been found for both the dilution hypothesis (increased biodiversity causes a decreased VBD prevalence; zooprophylaxis; e.g. Schmidt and Ostfeld, 2001) and amplification hypothesis (increased biodiversity causes an increased VBD prevalence, zoopotentation; e.g. Roiz et al., 2019). But very often, no or weak relationships between biodiversity measures and VBD prevalence were detected (e.g. Ruyts et al., 2018; Stensgaard et al., 2016; Vadell et al., 2020). Certainly, the enormous complexity in biodiversity-health-environment interactions at local to global level is a major challenge when designing VBD prevention and vector control strategies. Nevertheless, biodiversity can also be part of the solution to combat VBDs by providing inspiration for new chemical and biological pesticides and pharmaceuticals and innovative genetic vector control tools (Famakinde, 2020; Kendie, 2020; Wooding et al., 2020).

2.5.4.3. Exposure to microorganisms beyond infectious disease. Due to the potentially fatal effect of human-pathogenic microbes, the dominant public health objective is to limit contact with harmful microbes, through infrastructural and socio-cultural practices (e.g. sanitation and hygiene measures), or the use of pharmaceutical drugs targeting infectious microorganisms (Armstrong et al., 1999). However, the human microbiome may also mediate positive effects of biodiversity on human health, as negative correlations between microbial or environmental diversity and the incidence of non-communicable, and in particular auto-immune, disease have been observed (Aerts et al., 2018; Mosca et al., 2016; Ruokolainen et al., 2015). Overall biodiversity decline can decrease microbiome diversity (Blum et al., 2019; Heiman and Greenway, 2016; Johnson et al., 2019; Ng et al., 2019). In addition, some microbiota, such as Wolbachia sp., can be employed for pest control and thereby limit biodiversity-inflicted harm, e.g. the spread of VBD through mosquitoes (Hoffmann et al., 2011). To fully understand pathways mediating biodiversity effects on health, rigorous investigations of microbial exposure are required (Porras and Brito, 2019), as well as of the mechanisms of microbial protective diversity, e.g. dilution of pathogens (Libertucci and Young, 2019), improvements in metabolism (Adar et al., 2016; Visconti et al., 2019) and regulation of the immune system (Al Nabhani et al., 2019; Belkaid and Hand, 2014; Kamada et al., 2013; Mezouar et al., 2018; Zhang et al., 2019).

2.5.4.4. Increasing exposure to airborne allergens and volatile organic compounds. Allergies have a major impact on people's health and quality of life (Baiardini et al., 2006) and the loss of exposure to biodiversity may increase susceptibility to allergies (Prescott, 2020). The emission of biogenic particulate matter (spores and pollen) and volatile organic compounds (e.g. isoprene, a critical substance in O_3 formation) is species-specific (Grote et al., 2016; Peñuelas and Staudt, 2010). Studies investigating whether allergenic pollen mediates the effect of biodiversity on health have found two different pathways. First, the biodiversity in an allergic person's microbiome is suspected to influence whether or not they will experience an allergic reaction (Haahtela et al., 2013). Second, the abundance and species richness of allergenic plants can influence the opportunity for an individual to come into contact with allergenic pollen. While a large abundance of allergenic plants may affect allergic people negatively, a more biodiverse environment can protect through the dilution effect from exposure to allergenic pollen. However, a more biodiverse environment may also mean that a person is potentially exposed to a greater variability of allergens. Whether this leads to more allergies or protection from allergic sensitization is still a matter of debate. For example, Hanski et al. (2012) showed that neighborhood environmental biodiversity affects the composition of bacterial classes on people's skin, thus affecting allergy. The biodiversity hypothesis states that "contact with natural environments enriches the human microbiome, promotes immune balance and protects from allergy and inflammatory disorders" (Haahtela, 2019). Previous studies support the biodiversity hypothesis finding a more diverse environment is correlated with a healthy microbiome (Hanski et al., 2012), and fewer allergic people (Haahtela et al., 2013). Moreover, a highly biodiverse environment was found to be more protective against allergens, than the exposure to specific environmental allergens in early life (Von Mutius and Vercelli, 2010). This suggests that biodiversity in the environment may be protective against allergic response.

In terms of currently rising levels of atmospheric pollutants, new challenges for allergic people will rise as the composition and allergenicity of pollen can be altered (Beck et al., 2013; Gilles et al., 2018) and the skin barrier that is needed to protect from allergy development can be damaged by the influence of pollutants (e.g. O3 or NO2; Heuson and Traidl-Hoffmann, 2018). A higher biodiversity can also show a protective effect as it is shown that different tree species mitigate ozone levels at different seasons of the year and therefore guarantee a protection against high ozone levels for a considerable lapse of time (Manes et al., 2012).

2.6. Health effects (Component 4)

The fourth and final step in the biodiversity-health framework involves the assessment of human health and well-being effects that follow from the mediating pathways in the different domains.

2.6.1. Measurement of health

Health (Box 2) is operationalized across three dimensions of well-being—physical, mental and social—in keeping with the bio-psychosocial model of health (Engel, 1977; Fava and Sonino, 2008). Biodiversity has been shown to affect all three dimensions of well-being (Aerts et al., 2018; Lovell et al., 2014; Marselle et al., 2019b). Quantification of each dimension of well-being can be arrayed upon a spectrum from externally observable and measurable to internally experienced and self-reported (Table 2). Regarding self-report measurements of health, it is important to use existing valid, reliable questionnaires to assess well-defined clinical outcomes (Aerts et al., 2018), and ensure comparability with previous health research (Linton et al., 2016). To improve relevance to the participants and end users, the specific approaches and measurements selected may need to be adapted to or emerge from the specific cultural context of the research (Datta, 2018; Krusz et al., 2020; Smith, 2012).

3. Considerations for statistical analyses

The causal pathways in the biodiversity-health framework can be tested through mediation models. Statistically, mediation models consist of a sequence of regression models in which the predictor variable, in this case biodiversity or contact with biodiversity, affects one or more intervening variables—a mediator within one of the four domains of pathways—which in turn affects human health. Investigation of interrelationships between mediators of the four different domains involves multiple mediator models in which mediators are working in parallel or serial—rather than single mediators (Dzhambov et al., 2020a; Hayes, 2009). Analytical approaches recommended to test for mediation are the

Table 2
Definitions of the three dimensions of health and well-being and examples of their objective and subjective measurement.

Health and Well-Being Dimension[1]	Measurement	
	Observable Measures	Self-report Measures
Physical well-being refers to the quality and performance of bodily functioning. This includes having the energy to live well, the capacity to sense the external environment and the capacity to experience pain and comfort.	e.g. mortality and morbidity; prevalence of a disease (or allergenic potential) within the population (e.g. COVID-19, malaria, dengue fever, plant allergies); criterion measures of disease processes, e.g. Hemoglobin A1C for diabetes	Self-report questionnaires on physical health
Mental well-being refers to dimensions such as the psychological, cognitive and emotional quality of a person's life. This includes the thoughts and feelings that individuals have about the state of their life, and a their experience of happiness.	e.g. antidepressant prescriptions; criteria-based diagnosis (e.g., use of the International Classification of Diseases as suggested by the World Health Organization)	Self-report questionnaires on quality of life, depression, anxiety, emotional state
Social well-being concerns how well an individual is connected to others in their local and wider social community. This includes social interactions, the depth of key relationships and the availability of social support.	e.g. number of people who volunteer in their local community; crime rates; observational research on social interactions	Self-report questionnaires on social well-being, e.g. the social well-being scale (Keyes, 1998) or UCLA loneliness scale (Russell, 1996)

[1] All definitions from Linton et al. (2016, p.12).

product-of-coefficients approach using ordinary least squares regression and bootstrapping, and structural equation modelling (for more information, see Dzhambov et al., 2020a).

3.1. Confounding variables

In a mediation analysis, confounding is a threat to validity, undermining the relationships between the predictor and outcome variables (Valente et al., 2017). A confounding variable is a 'third' variable that is related to two (or more) variables in the mediation model that partially explains the relationship between the variables (Valente et al., 2017). Thus, confounding variables may influence the predictor-outcome relation, the predictor-mediator relation, or the mediator-outcome relation (Valente et al., 2017). Identifying the potential confounders of the association between biodiversity, health and its mediating pathways is paramount to establishing the studied links clearly without biasing the study results or leading to erroneous conclusions. If no adjustment is made for these confounders, for example by including them as covariates in a regression analysis, then incorrect conclusions may be drawn about the plausibility of causal effects in the mediation model.

Biodiversity-health-pathways studies should consider the following confounders: gender, age, being part of a socially marginalized/privileged group (such as being from a certain ethnic group, race or socioeconomic group), alcohol and tobacco use, or taking care of elderly, children or pets. Additional confounders in biodiversity-mental health studies are perceived naturalness, visual complexity and amount of nature in general (de Vries and Snep, 2019). Moreover, specific study contexts may require consideration of other confounders such as area socioeconomic status, degree of urbanization, area deprivation or neighborhood gentrification stage (Cole et al., 2019), livestock rearing (Hasyim et al., 2018), weather, or study design factors like sampling order in experimental study designs (Triguero-Mas et al., 2017b). Statistical methods such as Bayesian network modelling can be a reasonable way to select a minimum sufficient set of confounders.

3.2. Modifying variables

The strength or direction of the relationship between biodiversity and human health via any of the four domains of pathways is subject to modification by the environmental/socio-cultural context and/or individual characteristics (Fig. 1). As detailed in Fig. 1, these moderating factors can influence the relationships between: i) biodiversity (Component 1) and contact with biodiversity (Component 2); ii) contact with biodiversity (Component 2) and each of the four domains of pathways (Component 3); and iii) the influence of pathways within each domain (Component 3) on health and well-being (Component 4). At any of these points in the conceptual model, depending on specific research aims and research questions, researchers may explore variables relating to the environmental/socio-cultural context and/or individual characteristics.

Measurements of both actual and perceived biodiversity (Component 1) are influenced by knowledge and experience. Actual biodiversity measurements are dependent on the knowledge of highly trained experts to identify species and count abundances with specialized technologies or prior experience of particular sites (Kelling et al., 2019). People who have better biodiversity knowledge also tend to be more accurate in their perceived biodiversity assessments (Dallimer et al., 2012; Southon et al., 2018).

Factors relating to the environmental/socio-cultural context and individual characteristics may influence whether a person is exposed to specific elements of biodiversity (Component 2.1). Exposure to biodiversity may be encouraged or discouraged through aspects of the environmental context, for example amenities (e.g. public toilets), park programming (Hunter et al., 2019; Vierikko et al., 2020), accessibility and maintenance status of the space where biodiversity is found, perceived safety in the space where biodiversity is, and other space-related variables such as size, type, land ownership (that can also be considered confounders) (Bratman et al., 2019). The socio-cultural context, in particular the cultural values and practices around specific elements of biodiversity will also influence exposure to biodiversity (e.g. indigenous and contemporary spiritual beliefs and practices regarding sacred natural sites, Irvine et al., 2019). Individual characteristics, such as personal time demands, transport corridors or income disparities may also influence exposure (Bratman et al., 2019).

Factors relating to the environmental/socio-cultural context as well as individual characteristics may also influence the ways in which people experience biodiversity (Component 2.2; Fig. 1) (Frumkin et al., 2017). Experience of specific elements of biodiversity will be influenced by the socio-cultural context, such as cultural practices and values around biodiversity (Bell et al., 2018; Chan et al., 2018, 2012; King et al., 2017). Moreover, individual characteristics such as connectedness to nature, and preference about, knowledge of, perception of (including fear of certain species), attitudes towards, receptivity towards, or childhood experiences of biodiversity (Bratman et al., 2019; Wells and Lekies, 2006) might influence the biodiversity a person 'absorbs' (Frumkin et al., 2017), which in turn may influence outcomes relating to the mediating pathways and health.

4. Data sources available to assess biodiversity, health and the mediators in the four domains

To help operationalize the model and support testing and application of the biodiversity-health framework, in this section we identify available data sources. Supplementary Table 2 details these possible data sources.

4.1. Biodiversity (Component 1)

Data on actual biodiversity (Component 1) exist on local to global geographical scales. These data can be in the public domain but are often "hidden" within administrative agencies, museums, research institutes, etc. (Beck et al., 2012). An increasing number of initiatives now combine biodiversity data from across the globe into (partly) open databases (e.g. GBIF: The Global Biodiversity Information Facility, 2020) or at the national scale in Atlases (e.g. German Atlas for Flowering Plants and Ferns, Bundesamt für Naturschutz, 2013). These data repositories are highly heterogeneous in structure or quality, and often biased both taxonomically and geographically, such as towards the Global North, charismatic species and aboveground terrestrial biodiversity (e.g. Cameron et al., 2018; Titley et al., 2017; Troudet et al., 2017). This bias might limit our understanding of biodiversity-health pathways. Local and indigenous knowledge is pivotal to place-based biodiversity knowledge (Wilder et al., 2016), especially in the Global South, also with regards to conservation and restoration practices. Remote sensing provides opportunities for reducing bias by assessing, for example, land cover, plant structural diversity or plant functional traits (Dennis et al., 2018; Lausch et al., 2016). The use of eDNA and meta-barcoding (Ji et al., 2013) can also help to support field biodiversity assessments.

4.2. Contact with biodiversity (Component 2)

Investigation of exposure (Component 2.1) to actual biodiversity can be assessed using measures to determine a person's frequency and duration of contact with these habitats. Proxy measures of cumulative opportunity or proximity to these habitats can be applied. To obtain data on actual exposure new data might need to be collected, for example with a study design in which participants are randomly assigned to spend a certain amount of time in different sample plots in which an ecological survey has been conducted (e.g. Chang et al., 2016; Lindemann-Matthies and Matthies, 2018). Assessment of experience of actual biodiversity (Component 2.2) would require self-report data, observational research or a research design in which participants are assigned different degrees of physical proximity and intention.

4.3. Assessment of mediators in the four domains (Component 3)

Many data sources on the four domains (Component 3) exist, which can support the analysis of mediating pathways linking biodiversity to human health. For the 'reducing harm' domain, open-access environmental data comprise, for example, local noise exposure information in European metropolitan areas, provided by the European Environment Agency, or Local Climate Zones (LCZs) for urban climatology (Demuzere et al., 2019; Stewart and Oke, 2012). Remote sensing can deliver information on land surface temperatures (e.g. Kremer et al., 2018; Zheng et al., 2014) and air quality (Gupta et al., 2006).

Datasets for the 'building capacities' and 'restoring capacities' domains range from the local scale in city-wide health studies (e.g. Nieuwenhuijsen et al., 2014), to the district-level in national surveys (e.g. the Monitor of Engagement with the Natural Environment survey in England), and the regional scale in medicinal plants databases (Babu et al., 2006). Access to local scale datasets will need to be requested; while data at coarser spatial resolution are often publicly available. However, depending on the specific mediators investigated (e.g. attention restoration, place attachment), researchers may need to collect new empirical data.

Data for the 'causing harm' domain may be available—usually upon request—at the local scale in health cohorts for the human microbiome, regional and national scale for allergenic pollen, or at the international scale for distribution of ticks and mosquitos (see Supplementary Table 2). Ground observation, remote sensing and genetic biodiversity monitoring can be used to determine the presence, abundance, density and functional traits of invasive, pest and allergenic biodiversity (Skjøth et al., 2013).

4.4. Human health effects (Component 4)

Human health data (Component 4) exists on local to global scales. As health data contain highly sensitive, personal information, strict ethical rules apply regarding confidentiality and anonymity. Consequently, individual-level data at the local level are not in the public domain. However, for research purposes, it is often possible to request access to these existing health datasets, for instance doctor or hospital records. In these cases, researchers must submit an official request to the data holder. Publicly available health data are aggregated at larger geographical scales, such as at county or state level (e.g. German Socio-Economic Panel (SOEP), Goebel et al., 2019; US CDC Behavioral Risk Factor Surveillance System, Jones, 2017). Global human health data are often open-access (see Supplementary Table 2).

5. Recommendations for policy, practice and future research

5.1. Policy implications

The increasing relevance of biodiversity for health and well-being is reflected both in the scientific arena with increasing work on EcoHealth, Planetary Health or One Health, and in the policy arena (IPBES, 2020, 2019; Korn et al., 2019). Human health already figured prominently in the 2005 Millennium Ecosystem Assessment (Corvalan et al., 2005), and an increasing range of UN actors have adopted respective resolutions addressing human consequences of biodiversity loss—specifically the UN Decade on Biodiversity (2011–2020), and the Sustainable Development Goals. The EU Green Deal has a specific objective to preserve and restore ecosystems and biodiversity (European Commission, 2019). Since 2015, the WHO has collaborated with the CBD to foster the work on health impacts of biodiversity (Romanelli et al., 2015). The IPBES is presently scoping a global nexus assessment on the links between biodiversity, water, food and human health. While progress is being made to link the biodiversity and public health sectors (Keune et al., 2019), "silo-thinking" is still common. To implement actions, policy frameworks are needed to assure that health and well-being is included as integral to biodiversity conservation policies (Korn et al., 2019). Likewise, biodiversity should be considered in public health, and spatial and urban planning policies (Cook et al., 2019; Heiland et al., 2019). The current discussions on the CBD post-2020 global biodiversity framework, the forthcoming IPBES nexus assessment and the EU Green Deal provide pertinent leverage points to strengthen the biodiversity-health policy agenda. Biodiversity-related public health threats can only be solved by integrating health and environmental perspectives. The provided biodiversity-health framework may provide clear guidance for this multisectoral and multidisciplinary dialogue.

5.2. Practice implications

The concept of nature to promote public health is longstanding, championed by Florence Nightingale, and the creation of hospital gardens, public parks (Hickman, 2013; Ward Thompson, 2011; Wheater et al., 2007), and allotment gardens (van den Berg et al., 2010). Presently, the use of natural environments is considered as a health promotion intervention (Frumkin et al., 2017; Irvine and Warber, 2002; Maller et al., 2005; Shanahan et al., 2019; World Health Organization, 2016). The asset-based approach to health has led to the development of a person- and asset-based 'social prescribing' movement, whereby non-medical interventions are provided to promote health and alleviate the pressure on acute medical care facilities (Polley et al., 2017). Social prescriptions can include nature-based interventions (Cook et al., 2019), such as outdoor walking groups (Irvine et al., 2020; Marselle et al., 2016, 2015), forest-bathing or horticulture-based therapies (e.g. https://www.adoseofnature.net/). We suggest that physicians and public health authorities may consider prescribing biodiversity-based interventions to bring humans into contact with biodiverse environments, such as nature conservation activities (Pillemer et al., 2010). In turn, these interventions might lead to a greater contact with and appreciation of biodiversity, that may then in turn foster environmental stewardship to engage in policy and practice to support further biodiversity conservation and biodiversity-based health measures (Clayton et al., 2017).

The provided biodiversity-health framework can help inform natural resource managers in developing and maintaining their protected areas or urban parks for both people and biodiversity conservation (Davies et al., 2019; MacKinnon et al., 2019). Public health implications of biodiversity-health relationships can foster the application of nature-based solutions as public health infrastructure by urban planners and landscape architects (Heiland et al., 2019; Hunter et al., 2019).

5.3. Recommendations for future research

Fundamentally, the functionality of the biodiversity-health framework lies in its capacity to orient attention to considerations of importance for understanding relations between biodiversity and health. These include but are not limited to the following: the need to consider (i) biodiversity in its complexity including the diversity, identity, abundance of species, genes and ecosystems; (ii) the distinction between actual and perceived biodiversity; (iii) how biodiversity can influence health via multiple pathways, many of them necessitating contact with biodiversity; (iv) how pathways can intertwine, on one level and across levels; and (v) how environmental/socio-cultural contextual factors and individual characteristics can modify the links between components of the biodiversity-health framework.

The presented conceptual framework provides a causal understanding of biodiversity-health linkages. Naturally, like its precursors (Bratman et al., 2019; Hartig et al., 2014; Markevych et al., 2017), the biodiversity-health framework does not aim to represent all the complexity of real-world situations. We have tried to strike a balance between representation of complexity and the utility of the framework as a guide to research, practice and communication. Some research questions might not appear in the visual and textual presentation of our biodiversity-health framework due to brevity, which does not mean that we consider them unimportant. For example, we represent the possibility of reciprocal relations and feedback between components of the biodiversity-health framework, but not as comprehensively due to space limitations. Yet, the framework is not simplistic, as we represent the multiple levels on which intertwined processes can run between biodiversity and health and the sets of moderators of those pathways. Future researchers may wish to build on our biodiversity-health conceptual model to account for complexity, such as creating more detailed frameworks for each of the four domains of pathways separately.

We need to understand the shape of the relationships between specific elements of biodiversity (i.e. the richness and abundance of species, their identity, their behavior, and their functional traits, as well as their structural, genetic and ecosystem diversity) and human health outcomes. The next steps for research are to operationalize this biodiversity-health framework. Using the biodiversity-health framework, we hope to inspire future researchers to specifically investigate these mediating relationships. By providing a causal understanding of biodiversity-health linkages moving from biodiversity (Component 1) to contact with biodiversity (Component 2) to the four domains of pathways (Component 3) to human health (Component 4), we show avenues to test the framework, with available data resources and analytic approaches. Data-driven experimental research approaches employing longitudinal, intervention and randomized controlled trial research designs from human health research are needed to test these conceptual pathways and their synergistic interaction to understand biodiversity-health linkages (Aerts et al., 2018; Marselle et al., 2019c; Müller et al., 2019). In order to assess the effects of compositional, functional and structural biodiversity, we need a rigorous design of ecological studies, both in the field and the lab, with gradients of biodiversity that are not confounded by other environmental variables. The biodiversity-health framework thus supports further collaboration by researchers trained in different disciplines who have already begun to study processes as depicted here and who can enlist other researchers to join their efforts.

When analyzing pathway mechanisms, it is crucial to assess how the environmental/socio-cultural context as well as individual characteristics may moderate the outcomes. Moderating factors relating to the environmental/socio-cultural context and individual characteristics have all been found to influence nature-health relationships (Cole et al., 2019; Jones, 2016; Lindley et al., 2018; Triguero-Mas et al., 2017a, 2015; Van den Berg et al., 2016; White et al., 2017; Zijlema et al., 2017). Such variables may also moderate the biodiversity-health pathways, but as yet there is little research on these moderating factors in biodiversity-health studies (see Carrus et al., 2015; Wheeler et al., 2015). Not least, we note the need to consider the particular cultural values and practices through which the different specific pathways may become manifest.

More research is needed on people's contact with biodiversity (Component 2) (Gaston, 2020). Future researchers could usefully investigate how differential exposures to biodiversity (Component 2.1) influence human health, in order to unravel 'dose-response' relationships. An important research frontier is to further our understanding of how we experience the elements of biodiversity (Gaston et al., 2018), and how this experience might be fostered as a proactive health intervention. Future studies could investigate whether the four different types of experience with biodiversity (Component 2.2) influence the mediating pathways in the four domains. This understanding will then inform how to better promote or—in the case of the 'causing harm' domain—possibly avoid harmful contact with biodiversity for human health. This future research into contact with biodiversity may then influence how we ultimately value biodiversity (Chan et al., 2018) both for developing conservation and enhancing human health. Importantly, research could usefully investigate the health consequences of biodiversity that is not consciously perceived or experienced at all, such as microbiota or soil organisms, and resulting value systems.

Future studies can investigate how to implement these findings in urban and rural landscape planning, considering synergies and potential trade-offs as well as nature-based solutions for public health interventions and conservation action. Public health and conservation interventions need to be evaluated in real-world situations to develop and share best practice. This includes cost-benefit and other economic analyses of the effectiveness of different interventions, since (complementary) nature-based health interventions may significantly contribute to reducing health care costs for non-communicable diseases, such as depression. The benefits then need to be publicized and well communicated to decision makers to flow into policy design as well as into individual behavioral choices. Scenario building and statistical modelling can assist in forecasting the effects of further biodiversity losses or gains for human health and thereby inform management priorities. Here, joint working should be sought with ongoing efforts of IPBES in scenario modelling and develop pandemic prevention measures. This will help foster informed decision making as well as appropriate indicator development to monitor trends to adapt management and policy accordingly.

5.4. Conclusion

We present a new conceptual framework to serve as the basis for strategic discussions and better alignment of biodiversity-health research, policy and practice with respect to public health, environmental psychology, landscape and urban planning as well as biodiversity conservation. The biodiversity-health framework draws on diverse forms of knowledge to elucidate a range of causal pathways linking biodiversity and health and, importantly, depicts the biodiversity that people can experience in their everyday lives. As such, the awareness of the breadth of effects biodiversity has on human health necessitates a large range of approaches to protect and restore biodiversity to promote health—starting in gardens and parks, over biodiverse agricultural areas to tropical forest, wilderness and nature reserves. Here, we provide a tool to explore explicit management options in a standardized and comprehensive manner and a given geographical context. Our biodiversity-health framework should therefore serve a broad range of purposes, including identification of health indicators and interventions, formulation of policy, and communication among diverse groups of audiences.

The COVID-19 pandemic brought biodiversity into the limelight. It showed how harming biodiversity through wildlife trade or habitat destruction can lead to severe health impacts, globally. At the same time, enjoying urban nature was important for many people's health and well-being during COVID-19 lockdowns. We now urgently need to further our understanding of salutogenic benefits and pathogenetic burden of biodiversity. At a policy level, the IPBES work (IPBES, 2020) has identified how appreciation of biodiversity-people linkages can provide opportunities for pandemic prevention, control and response measures. Now the current joint working of WHO and CBD needs to be supported and enshrined in the up-coming post-2020 global biodiversity framework and respective targets for policy and management to reach both the UN 2030 Agenda for Sustainable Development and the 2050 Vision for Biodiversity. Fundamentally, working across sectors and fostering biodiversity conservation and restoration needs to be viewed as an active investment into all our human health.

6. Disclaimer

The authors alone are responsible for the views expressed in this article and they do not necessarily represent the views, decisions or policies of the institutions with which they are affiliated.

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Appendix A. Supplementary material

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