

1 Pathways linking biodiversity to human health: A 2 conceptual framework

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65 **Highlights**

- 66 • Biodiversity underpins human health as an essential life-support system
- 67 • We developed an integrated biodiversity-health framework
- 68 • Biodiversity influences health via pathways in four broad domains: reducing harm, restoring
69 capacities, building capacities, and causing harm
- 70 • Both beneficial as well as harmful pathways link biodiversity with human health
- 71 • Understanding biodiversity-health pathways can inform nature-based solutions to public health

72

73 **Abstract**

74 Biodiversity is a cornerstone of human health and well-being. However, while evidence of the
75 contributions of nature to human health is rapidly building, understanding of how biodiversity relates to
76 human health remains limited in important respects. In particular, we need a better grasp on the range
77 of pathways through which biodiversity can influence human health, including those that run through
78 psychological and social processes as well as through biochemical and biophysical processes. Building on
79 evidence from across the natural, social and health sciences, we present a conceptual framework
80 organising the pathways linking biodiversity to human health. Four domains of pathways—both
81 beneficial as well as harmful—link biodiversity with human health: (i) reducing harm (e.g. provision of
82 medicines, decreasing exposure to air and noise pollution); (ii) restoring capacities (e.g. attention
83 restoration and stress reduction); (iii) building capacities (e.g. promoting physical activity,
84 transcendental experiences), and (iv) causing harm (e.g. dangerous wildlife, zoonotic diseases or
85 allergens). We discuss how to test components of the biodiversity-health framework with analytical
86 approaches and existing datasets. In a world with accelerating declines in biodiversity, profound land-
87 use change, and an increase in non-communicable and zoonotic diseases globally, greater understanding
88 of these pathways can reinforce biodiversity conservation as a strategy for the promotion of health for
89 both people and nature. We conclude by identifying research avenues and recommendations for policy
90 and practice to foster biodiversity-focused public health actions.

91 **Keywords (6 max):**

92 Biodiversity; Ecosystem services; Nature; Mediation; Public health; Human well-being

93

94 1. Introduction

95 Biodiversity comprises the diversity, abundance and identity of species, their genes and ecosystems, and
96 underpins ecosystem services that are essential for human health and well-being (Cardinale *et al.*, 2012;
97 Mace, Norris and Fitter, 2012; IPBES, 2019). However, biodiversity is declining at an unprecedented rate
98 (IPBES, 2019), threatening the quality of life of all humans, rich and poor. Understanding of the specific
99 aspects of biodiversity that are most relevant to human health and wellbeing, however, remains limited.
100 Of the large body of research on nature and human health, in particular those that focus on health
101 aspects derived through directly experiencing nature (e.g. Hartig *et al.*, 2014; Frumkin *et al.*, 2017), the
102 majority of studies focus on the amount of nature, without distinction of ecological characteristics or
103 quality (van den Berg *et al.*, 2015; Schwarz *et al.*, 2017; Collins *et al.*, 2020). We also acknowledge
104 extensive research on how nature affects human health and well-being in ways that do not involve
105 behavioural pathways, e.g. through provisioning or regulating ecosystem services, but these also often
106 lack specifics on the biodiversity involved (Cardinale *et al.*, 2012; Sandifer et al 2015). Accordingly, we
107 need to develop knowledge of whether and how biodiversity matters for human health (Marselle,
108 Stadler, *et al.*, 2019b). A simplistic approach to measuring nature, for example the amount of
109 greenspace, can serve as an important indicator for urban health planning goals, but it limits a clear
110 understanding of how human health is influenced by the presence of, contact with, or change in
111 biodiversity.

112 The importance of the fundamental linkages between biodiversity and human health, i.e. physical,
113 mental and social well-being, is increasingly recognized by global and regional policy development
114 (Corvalan *et al.*, 2005; Romanelli *et al.*, 2015; Ten Brink *et al.*, 2016; Korn, Stadler and Bonn, 2019). For
115 example, the Convention on Biological Diversity (CBD) and the World Health Organisation (WHO) are
116 collaborating to promote awareness of the influence of biodiversity on human health and well-being
117 (Convention on Biological Diversity, 2016). In recent years, evidence has emerged that biodiversity is
118 associated with physical health (Lovell *et al.*, 2014; Romanelli *et al.*, 2015; Aerts, Honnay and
119 Nieuwenhuyse, 2018) and mental health (Lovell *et al.*, 2014; Korpela, Pasanen and Ratcliffe, 2018;
120 Marselle, Martens, *et al.*, 2019). These studies show a direct relationship between biodiversity and
121 human health outcomes. However, it is more likely that biodiversity will influence on human health
122 indirectly, through causal pathways (Hough, 2014; Aerts, Honnay and Nieuwenhuyse, 2018).

123 A key research gap is, therefore, to unravel the specific causal pathways through which biodiversity
124 affects human health (Clark *et al.*, 2014; Sandifer, Sutton-Grier and Ward, 2015; Aerts, Honnay and

125 Nieuwenhuysse, 2018). Some causal pathways are better understood (e.g. nutrition, infectious diseases,
126 microbiota; Sandifer, Sutton-Grier and Ward, 2015; Aerts, Honnay and Nieuwenhuysse, 2018), than
127 others (e.g. cultural goods and values; Clark *et al.*, 2014). This lack of a causal understanding of pathways
128 linking biodiversity to human health limits application of nature-based solutions in public health, and
129 subsequent influence on policy (Hough, 2014). In order to facilitate cross-sector policy and research
130 integration on biodiversity conservation and public health (Korn, Stadler and Bonn, 2019), it is necessary
131 to better identify and characterise the linkages between biodiversity and human health. A conceptual
132 framework indicating the causal pathways through which biodiversity influences human health is
133 needed for organising and guiding epidemiological and experimental health research. It should help to
134 inform public health interventions, including nature-based solutions of biodiversity management for
135 public health.

136 In this paper, we summarize the evidence linking biodiversity to human health and discuss the
137 implications of this evidence for underlying causal pathways (for a detailed review of the literature, see
138 Marselle, Stadler, *et al.*, 2019b). After defining biodiversity and health, we develop a conceptual
139 framework for an understanding of biodiversity-health pathways, and then describe the four steps of
140 our framework. We discuss how to test each step of the framework with analytical approaches and
141 existing datasets. Finally, we identify applications in policy and practice and outline future research
142 frontiers.

143 This conceptual framework relating biodiversity to human health, and the research it aims to organise
144 and inspire, is intended to support the work of environmental and health researchers and professionals,
145 including landscape architects and urban planners, natural resource managers, and the planned nexus
146 assessment of the Intergovernmental Platform on Biodiversity and Ecosystem Services (IPBES) on the
147 interlinkages of biodiversity, water, food and health (<https://ipbes.net/nexus>). Importantly, we hope it
148 can support implementation of the Agenda 2030 Sustainable Development Goals, the EU Green Deal,
149 the WHO-CBD partnership, and the development of the CBD post-2020 global biodiversity framework
150 and its translation into regional and national policies and associated measures.

151 *Definitions*

152 'Biodiversity' and 'health' mean different things to different people (IPBES, 2019). The definitions
153 adopted here (Box 1 and Box 2, respectively) serve the identification of pathways linking biodiversity to

154 human health. The definitions offer a platform for collaboration between different disciplines and
155 professions for developing and applying knowledge about them.

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 here biodiversity 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, colours, sounds, contagious properties), and the genetic composition, and identity of particular species (e.g. lion, robin, ticks, oak).

In addition, there are two other broad and widely used, but different, 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 *Urban Greenspace* is defined as “all urban land covered by vegetation of any kind. This covers vegetation on private and public grounds, irrespective of size and function, and can also include small water bodies such as ponds, lakes or streams (“bluespaces”)” (World Health Organization, 2017c, p.2).

These broad terms can limit understanding of how variation in the ecological characteristics of the *Nature* or *Urban Greenspace* relates to health. *Biodiversity*, importantly, is more than just the amount of the *Nature* or *Urban Greenspace*, and refers more specifically to the details and qualities of living organisms and ecosystems.

156

Box 2. Health and Well-being

Health is defined by the World Health Organisation (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 not only the focus on factors that cause disease (pathogenesis), but also those 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 experiences of pain and comfort (Linton, Dieppe and Medina-Lara, 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 a person’s experience of happiness (ibid).

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 (ibid).

157

158 **2. Conceptual Framework Relating Biodiversity to Health**

159 **2.1. Framework Precursors, Features and Functions: A User's Guide**

160 The proposed biodiversity-health framework was generated during a three-day workshop in September
161 2019 with international experts from different disciplines, including biology, biomedical sciences,
162 ecology, environmental epidemiology, environmental psychology, geography, medicine, modern
163 literature, public health, and statistics, as well as experts from conservation agencies and health
164 authorities. This Review article summarizes the discussions that consider the evidence linking
165 biodiversity to human health from an interdisciplinary standpoint, focusing on the mediating pathways.
166 In addition, we discuss the analytical approaches (Section 5) and data sets (Section 6) available to test
167 the biodiversity-health framework, as well as recommendations for policy, practice and future research
168 (Section 7). It is not intended to be an exhaustive review of the literature.

169 *Consideration of other models, frameworks and approaches*

170 We developed the biodiversity-health framework drawing from other published models. Three broad
171 approaches linking the ecological environment and health are Planetary Health, One Health, and
172 EcoHealth (Lerner and Berg, 2017; Buse *et al.*, 2018; Assmuth *et al.*, 2020). The simplest definition of
173 Planetary Health is “the health of human civilisation and the state of the natural systems on which it
174 depends” (Whitmee *et al.*, 2015). One Health and EcoHealth focus on a wider spatial scale and
175 environmental determinants of health beyond biodiversity e.g. fossil fuel emissions (Whitmee *et al.*,
176 2015). This makes Planetary Health more suitable for the assessment of threats to health than
177 understanding the mechanisms of the wider relationships between biodiversity and health (Lerner and
178 Berg, 2017). One Health and EcoHealth are similar, both considering the interconnections between the
179 health of humans, animals and ecosystems. One Health focuses on human and animal health (often
180 domestic animals), with an emphasis on attaining optimal health through risk prevention (e.g. of
181 zoonosis). EcoHealth concentrates on sustainability and achieving better human health through better
182 ecosystem health (Lerner and Berg, 2017; Buse *et al.*, 2018). Whilst One Health and EcoHealth both
183 consider biodiversity, it is not their primary focus, as it is in our framework.

184 Our approach differs from One Health and EcoHealth in that we conceptualise the type of contact
185 between the individual and specific components of biodiversity, and the pathways leading to human
186 health within the broader relationship. This enables us to place more emphasis on understanding how
187 the different facets of this relationship work and their respective positive and negative aspects.

188 Further, biodiversity is considered in a number of existing conceptualizations of the relationship
189 between the environment and health. As our focus was to ensure the biodiversity-health framework
190 could be used to facilitate research on human health, the framework we put forward here builds upon
191 previous conceptual models that identified causal pathways linking nature to human health (i.e. Hartig
192 *et al.*, 2014; Frumkin *et al.*, 2017; Markevych *et al.*, 2017; Bratman *et al.*, 2019).

193 We also considered other models linking biodiversity to human well-being or quality of life, especially
194 through the lens of ecosystem services (e.g. Millennium Ecosystem Assessment, 2005; Potschin and
195 Haines-Young, 2011; Haines-Young and Potschin, 2012; Mace, Norris and Fitter, 2012; Díaz *et al.*, 2015).
196 These models, however, were designed to serve a broad range of functions and audiences and to guide
197 policy development, and – interestingly – human health is rarely considered explicitly as an outcome
198 (Ford, Graham and White, 2015). As the specific pathways linking biodiversity to human health,
199 however, are not directly identified in these models in such a way to facilitate health research, these
200 models were not utilized.

201 *Relationship to previous nature-health models*

202 The Hartig *et al.* (2014) model of nature-health relationships identified groups of mediators through
203 which the natural environment, and contact with nature, influences human health. The model
204 distinguishes between nature and contact with nature to acknowledge the importance of peoples'
205 encounters with nature and how they conceive of and experience it. Contact with nature is linked to
206 four mediating pathways: air quality; physical activity; social contacts; and stress reduction. The model
207 also acknowledges that the strength and direction of associations between nature and health may
208 depend on individual characteristics (e.g. age, gender, genetics, socioeconomic position) and features of
209 the broader context in which a person encounters nature (e.g. culture that may for instance lead visitors
210 to a park to assign a particular meaning to some species observed there). The model put forward by
211 Hartig *et al.* (2014) served as a review of extant research on already relatively well-described pathways,
212 noting that although they had been addressed separately in different scientific and professional fields,
213 they were likely to be intertwined and work together in various ways. However, the pathways were

214 limited to only four groups of mediators, and the review did not seek to cover as-yet little-explored
215 pathways.

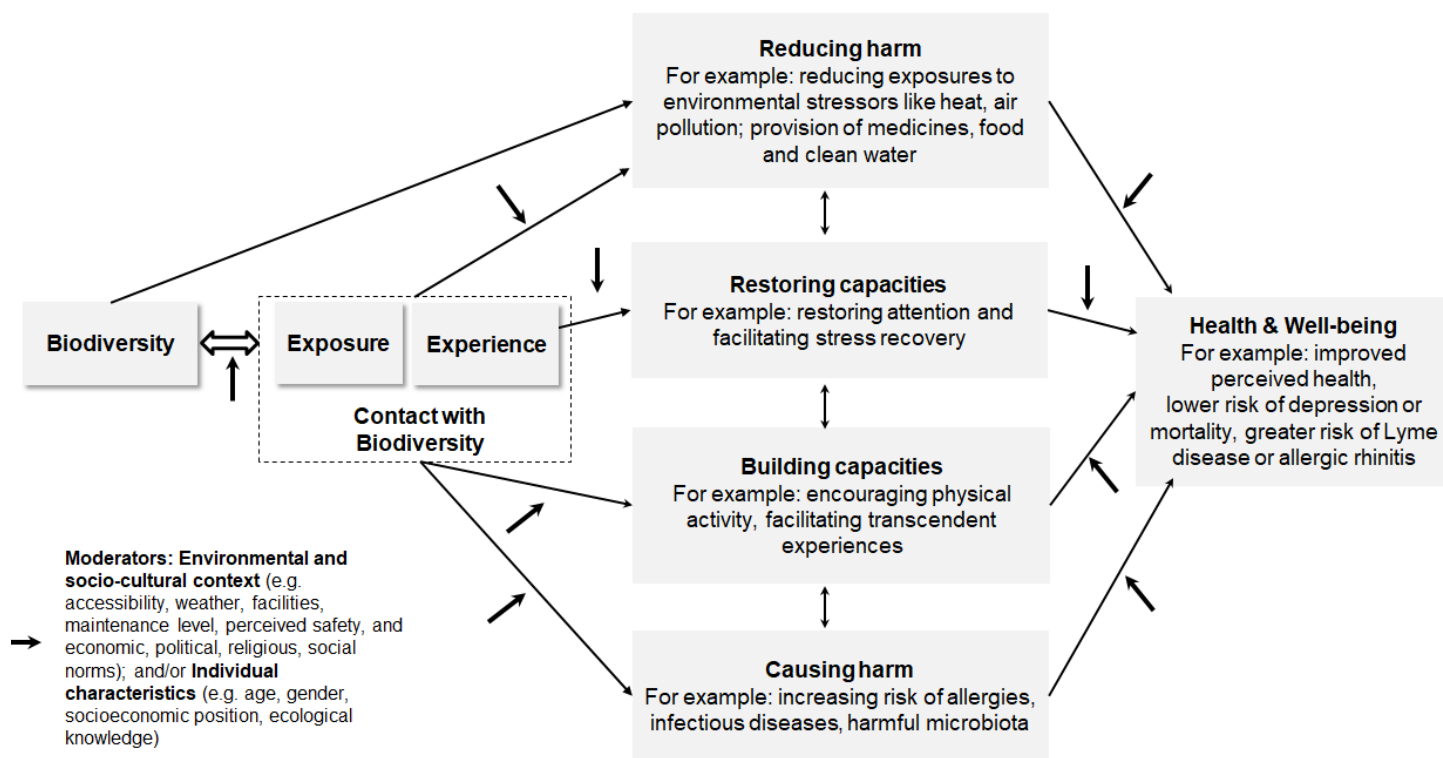
216 To extend the representation of possible mediators, the Markevych et al. (2017) model of greenspace-
217 health relationships details pathways in three broad domains by which greenspace could engender
218 human health benefits. The three domains match to the three general functions of greenspace that
219 relate to human adaptation: the ‘reducing harm’ domain relates to greenspace’s ability to mitigate
220 stressor exposures; the ‘restoring capacities’ domain relates to the ability of greenspace to restore
221 resources that have been depleted in efforts to cope with stressors; and the ‘building capacities’ domain
222 relates to the use of greenspace for instoration of resources (or capacity-building) to better support
223 coping. These three domains include Hartig et al.’s (2014) previously described pathways while also
224 providing a means to organise them with novel pathways that might serve adaptation in similar ways.
225 The Markevych et al. (2017) model did not distinguish nature from contact with nature.

226 The recently published Bratman et al. (2019) model specifically considers the effects of natural features,
227 exposure and experience of nature have an impact on mental health. None of these existing models
228 specifically addressed the different elements of biodiversity, or included the adverse influences of
229 nature on human health.

230 **2.2. Biodiversity and Health conceptual framework**

231 Our biodiversity-health framework (Fig. 1) builds on the respective strengths of the models by Hartig et
232 al. (2014), Markevych et al. (2017) and Bratman et al. (2019), while maintaining a focus on utility in
233 health research. In this way, we draw on a wide array of methodological approaches and sources of data
234 in order to address specific research questions and explore distinct pathways involving biodiversity.

235 Our conceptual framework shows how biodiversity, and contact with biodiversity, indirectly influences
236 human health through four domains of pathways: (i) reducing harm (e.g. provision of medicines,
237 decreasing exposure to air and noise pollution); (ii) restoring capacities (e.g. attention restoration and
238 stress recovery); (iii) building capacities (e.g. facilitating physical activity, transcendental experiences);
239 and (iv) causing harm (e.g. exposure to dangerous wildlife, infectious diseases or allergens).



241

242 **Fig. 1.** The conceptual framework identifies pathways linking biodiversity to human health and well-being. The first
 243 pathway is contact with biodiversity, which considers exposure to and experience of biodiversity. Four domains of
 244 pathways linking biodiversity and health necessitate contact with biodiversity. An additional pathway links biodiversity
 245 directly to the reducing harm domain, which implies that biodiversity features may affect health without an individual or
 246 group having contact with biodiversity (e.g. biodiversity improving upstream water quality through bioremediation).
 247 Each domain may be related with all others (for ease of presentation, only adjacent relationships are shown). Two-
 248 headed arrows between the domains speak to reciprocal relationships. Associations between variables at the different
 249 steps are subject to modification by the environmental and socio-cultural context or individual characteristics as
 250 moderators.

251 Several novel features of our biodiversity-health framework warrant mention here. First, our framework
252 focuses on the health effects of biodiversity rather than more general environmental entities (i.e.
253 “nature” and “urban greenspace”, Box 1). Biodiversity is considered with its different components and
254 hence with all its complexity (Box 1). Each step of the biodiversity-health framework has a critical focus
255 on these specific components of biodiversity which goes beyond previously conceptualized nature-
256 health relationships. Second, the framework distinguishes between biodiversity and contact with
257 biodiversity to acknowledge the importance of a person’s exposure to and their experience of
258 biodiversity. In addition, we also identify instances where biodiversity may influence human health
259 without contact with biodiversity, particularly through the ‘reducing harm’ domain (see Step 3.1 below).
260 Third, we include the domain ‘causing harm’ to represent the ways through which biodiversity can have
261 a negative influence on human health. Representation of both beneficial and harmful effects gives a
262 more complete picture of human relationships with biodiversity. Finally, the biodiversity-health
263 framework references both the environmental and socio-cultural context and individual characteristics
264 that can moderate relations at every step.

265 The present biodiversity-health framework refers to four intertwined domains of pathways that relate to
266 human adaptation. Multiple pathways may work together simultaneously, with synergies and trade-offs.
267 As such, it is important to consider how the effects realized through different pathways might stand in
268 relation to one another, rather than treating them as independent (c.f. Zhao, Lynch and Chen, 2010;
269 Dzhambov *et al.*, 2018, 2020). Consider the interrelationship between the two domains of pathways
270 ‘causing harm’ and ‘restoring capacities’. The COVID-19 coronavirus (SARS-CoV-2) is a dangerous,
271 communicable zoonotic virus, most likely a result of contact with wildlife due to habitat loss
272 (deforestation, agriculture, urbanization) (Taylor, Latham and Woolhouse, 2001; Yasuoka and Levins,
273 2007; Carrington, 2020). Consequences for individual and public health are severe, as COVID-19 can lead
274 to death and collateral health damages by disrupting public health interventions such as vaccination and
275 vector control programmes. During the COVID-19 pandemic lockdowns, in many countries people were
276 still allowed to visit parks and other nature areas and did so more than before the lockdown (Venter *et*
277 *al.*, 2020), indicating it fulfilled a need for psychological restoration. This intertwining of domains
278 necessitates interdisciplinary research. Researchers in different disciplines have already begun to study
279 processes as depicted here and can encourage other researchers to join their efforts.

280 Below we describe each step in the biodiversity-health framework. In Step 1, we discuss how to
281 characterize and measure biodiversity. In Step 2, we define our first pathway, contact with biodiversity,

282 as both exposure (Step 2.1) and experience (Step 2.2) of biodiversity. In Step 3, we describe the four
283 domains of pathways through which biodiversity influences human health, namely: (i) reducing harm, (ii)
284 restoring capacities, (iii) building capacities, and (iv) causing harm. In Step 4, we account for the human
285 health effects of biodiversity.

286 **Step 1. Biodiversity**

287 This step characterizes the specific components of biodiversity that potentially influence human health
288 and well-being (see Box 1). Depending on the health outcome studied (e.g. allergic rhinitis, depression),
289 researchers may measure the appropriate tiers of biodiversity, genes, species or ecosystems (Box 1). For
290 example, genetic diversity may be important for investigating allergic rhinitis, while species richness may
291 be important for investigating depression.

292 *Measurement of biodiversity*

293 Biodiversity is currently measured in two ways: actual and perceived biodiversity (Fig. 2). Measurements
294 of the actual biodiversity present at a location refer to the identity and number of species and
295 individuals present and their functional characteristics, for example, the species richness, identity and
296 abundance of street trees in a city district (see Supplementary Table 1). The amount of actual
297 biodiversity that is present at a location will vary depending on the spatial extent of an area under
298 observation (e.g. local, national, international) and the time of day and season of sampling (Kelling *et al.*,
299 2019). Accuracy will depend on sampling intensity (spatial and temporal extent), and previous
300 knowledge and experience of the observer (Kelling *et al.*, 2019). Data on actual biodiversity can be
301 gathered from a variety of sources (e.g. fieldwork, remote sensing) and operationalised in different ways
302 (e.g. databases; for more information see Section 6).

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

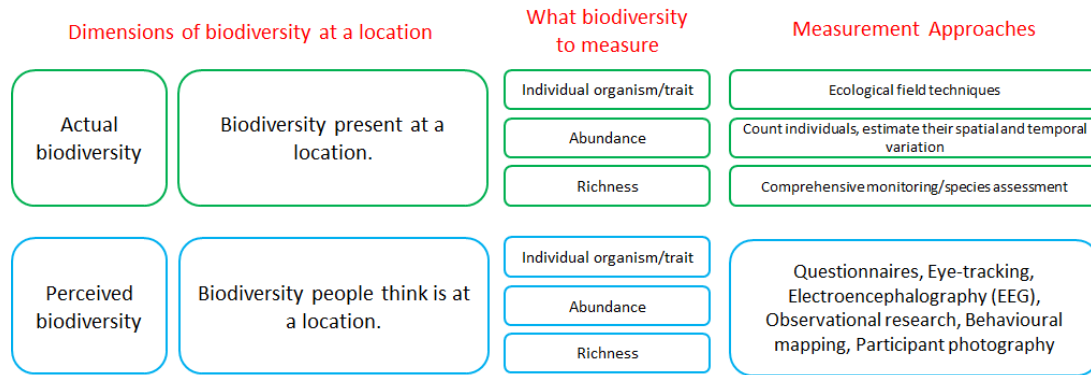


Fig. 2. Measurement of actual and perceived biodiversity.

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 (Fuller *et al.*, 2007; Dallimer *et al.*, 2012). Similar to actual biodiversity, perceived biodiversity may also refer to the identity and number of species (species richness) and individuals present (abundance) and their functional characteristics (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 (Fuller *et al.*, 2007; Dallimer *et al.*, 2012; Marselle *et al.*, 2016; Southon *et al.*, 2018; Cameron *et al.*, 2020). Perceived biodiversity has stronger correlations with well-being than actual biodiversity (Dallimer *et al.*, 2012; Cameron *et al.*, 2020; 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 (Fuller *et al.*, 2007; Southon *et al.*, 2018; Cameron *et al.*, 2020; Meyer-Grandbastien *et al.*, 2020), 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).

Irrespective of how biodiversity is measured, we must also consider how these specific components of biodiversity result in various amounts of exposure to individuals or populations, and how people experience these measured biodiversity components. This is addressed in Step 2.

Step 2. Contact with biodiversity

Step 2 describes a person’s contact with the components of biodiversity identified in Step 1. Here, contact with biodiversity is defined by two different aspects: exposure and experience. Exposure refers

333 to a person's amount of contact with biodiversity. Experience refers to how a person experiences and
334 interact with biodiversity.

335 ***Step 2.1 Exposure to biodiversity***

336 To a greater or lesser extent, people are exposed to biodiversity throughout their daily lives. Here,
337 exposure refers to the amount of contact that an individual or population has with biodiversity (Frumkin
338 *et al.*, 2017; Bratman *et al.*, 2019). How exposure is measured is important for determining which causal
339 pathways and health outcomes can be inferred (Nieuwenhuijsen, 2015). Exposure can be measured in
340 one of two ways. The first is actual exposure to biodiversity, based on the frequency (how often) and
341 duration (how long) a person or population has had contact with biodiversity (Shanahan *et al.*, 2015,
342 2016; Frumkin *et al.*, 2017). For example, two people live on the same street which contains a certain
343 number and diversity of street trees (actual biodiversity, Step 1), but one person walks every day along
344 the street while the other person only walks along the street once a week. The two persons have
345 different exposure profiles (Frumkin *et al.*, 2017), and this difference is not captured solely in the
346 measurement of the number and diversity of tree species (from Step 1). Data on frequency and duration
347 of exposure can be obtained with smartphone apps that use ecological momentary assessment with
348 location tracking (e.g. de Vries *et al.*, no date; MacKerron and Mourato, 2013; Beute, de Kort and
349 IJsselsteijn, 2016; Tost *et al.*, 2019; Cameron *et al.*, 2020) or self-report questionnaires (e.g. Marselle *et al.*,
350 2015, 2016). Exposure to biodiversity can also be manipulated as a research design choice (e.g.
351 Lindemann-Matthies and Matthies, 2018).

352 When data on actual exposure are not available, proxy measures are used (Bratman *et al.*, 2019). These
353 proxy measures for assessing exposure to biodiversity are based on the amount of the components of
354 biodiversity identified in Step 1 (Ekkel and de Vries, 2017; Bratman *et al.*, 2019). The first proxy measure
355 is cumulative opportunity, which is the total amount of biodiversity surrounding a person's location (e.g.
356 residence, workplace, neighbourhood) (Ekkel and de Vries, 2017). Data used to map actual biodiversity,
357 such as from remote sensing and meta-genomics, can be used to determine the proportion or number
358 of specific habitats, species or genes within the geographical area of interest (Dennis *et al.*, 2018;
359 Donovan *et al.*, 2018). The second proxy measure is proximity, comprising metrics that estimate
360 exposure as a function of the distance from one's location to the nearest environment with a specified
361 minimum level of biodiversity (e.g. park; Ekkel and de Vries, 2017; Frumkin *et al.*, 2017; Bratman *et al.*,
362 2019). Walking distance from a residence to the nearest environment satisfying the minimally required
363 level of biodiversity has also been used as a measure of proximity (Ekkel and de Vries, 2017).

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

371 ***Step 2.2. Experience of biodiversity***

372 Approaches to exposure measurement in Step 2.1 (e.g. frequency, cumulative opportunity) do not
373 capture the experiential aspects of biodiversity exposure—what we term as the experience of
374 biodiversity. It is important to recognise that people may experience biodiversity differently (Gaston,
375 2020), and these experiential characteristics of contact with biodiversity may be highly relevant for any
376 health effects (Frumkin *et al.*, 2017). In this step, we consider the how biodiversity is experienced by
377 people.

378 Firstly, humans experience biodiversity through the five senses (Frumkin *et al.*, 2017; Bratman *et al.*,
379 2019). The majority of the literature assumes vision as the primary sensory modality for biodiversity
380 interaction (Conniff and Craig, 2016). The auditory (Hedblom, Knez and Gunnarsson, 2017), olfactory,
381 somatosensory and gustatory senses may also be important to consider for their differential impacts on
382 health outcomes (Franco, Shanahan and Fuller, 2017).

383 Secondly, experience includes an individual's interactions with biodiversity stimuli. One approach to
384 classification of experience refers to degree of physical proximity with biodiversity is indirect or direct,
385 and whether the type of interaction is incidental or intentional (Pretty *et al.*, 2005; Keniger *et al.*, 2013;
386 Soga and Gaston, 2020). This classification results in four different experience types (see Table 1).

387 Experiences of micro-biodiversity are limited in this classification system. Direct contact with
388 microorganisms is ubiquitous in all human environments, and humans are associated with a diverse
389 microbiome (Grice and Segre, 2012; Gilbert *et al.*, 2018). However, the type of interaction with microbial
390 biodiversity is usually incidental, as humans have limited abilities to experience microorganisms (Rieder
391 *et al.*, 2017; Patel, Workman and Cohen, 2018). A notable exception is the direct, intentional interaction
392 with micro-organisms when a person consumes microbial metabolic products (Liu *et al.*, 2018).

393 **Table 1. Typology of people’s experiences with biodiversity**

Degree of physical proximity	Type of interaction	
	Incidental Experiencing biodiversity as a by-product of another activity	Intentional 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 <i>et al.</i> , 2019).	A person has no physical contact with biodiversity but interaction is intentional, e.g. viewing fish in an aquarium (Cracknell <i>et al.</i> , 2016), or trees through a window (Cox, Hudson, <i>et al.</i> , 2017; Cox <i>et al.</i> , 2019) or bird watching through a hide (Keniger <i>et al.</i> , 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 <i>et al.</i> , 2015, 2016), driving along vegetated roadsides (Parsons <i>et al.</i> , 1998) encountering vegetation indoors (Bringslimark, Hartig and Patil, 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, birdwatching, conservation volunteering (Currie, Lackova and Dinnie, 2016).

394
 395
 396 To determine which of the four experience types a person or population is experiencing, one must
 397 measure both the physical proximity to biodiversity and the intention behind the behaviour. The degree
 398 of physical proximity (indirect or direct) can be specified in the research design. Researchers can design
 399 a study in which determines whether participants experience biodiversity through indirect contact (e.g.
 400 photographs, videos, Virtual Reality) (e.g. Chiang, Li and Jane, 2017; White *et al.*, 2017; Wolf *et al.*,
 401 2017), or through direct contact (e.g. visits to a greenspace type with a certain level of biodiversity) (e.g.
 402 Fuller *et al.*, 2007; Dallimer *et al.*, 2012; Carrus *et al.*, 2015; Chang *et al.*, 2016). It is difficult to measure

403 intentions objectively (Soga and Gaston, 2020). Thus, measuring intentions is best done by asking people
404 about whether their intention to interact with biodiversity was intentional or incidental, or through a
405 research design which manipulates the type of interaction (e.g. walking alone or with a friend,
406 Johansson, Hartig and Staats, 2011; e.g. instructing participants to smell flowers, Colléony, Levontin and
407 Shwartz, 2020). As a proxy measure, intentions could be assumed through human behaviour. For
408 example, incidental interactions can be assumed when a person is running, walking with others, or
409 playing with children outdoors, as experiencing biodiversity is a by-product of these activities. Similarly,
410 intentional interactions can be assumed when a person is gardening, birdwatching, or conservation
411 volunteering.

412
413 The experience type (Table 1) influences what a person experiences and the amount of biodiversity they
414 'absorb' (Frumkin *et al.*, 2017), which in turn may influence outcomes relating to the mediating
415 pathways and health. For example, Carrus *et al.* (2015) looked at the types of activities people were
416 engaged, and how these activities affected restorative qualities, a mediator in the Restoring Capacities
417 domain (section 3.2), and well-being. People who were contemplating the setting, walking or exercising
418 in urban greenspaces of varying biodiversity had better well-being and experienced more restorative
419 qualities than people who were reading, talking, or socializing with others (Carrus *et al.*, 2015). This
420 suggests that perhaps a person whose interaction with biodiversity is direct-incidental (e.g. socializing
421 with a friend in a biodiverse greenspace) experienced less well-being benefits because they were more
422 distracted and less observant of the environment than a person, in the same location, whose interaction
423 with biodiversity is intentional (e.g. contemplating the setting). As such, awareness might be an
424 important aspect for interaction with biodiversity (Lin *et al.*, 2014; Soga and Gaston, 2020). This
425 awareness can be tested through eye-tracking methods (Franěk, Petružálek and Šefara, 2019),
426 neuroscience (Berman, Stier and Akcelik, 2019; Norwood *et al.*, 2019), participant photography or
427 citizen science apps (Frumkin *et al.*, 2017).

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

431 **Step 3. Domains of pathways**

432 The third step in the biodiversity-health framework describes the causal pathways linking biodiversity
433 and human health. In Sections 3.1 through 3.4, we overview the four domains of pathways linking
434 biodiversity to human health.

435 **3.1 Reducing harm**

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

444 **3.1.1 Medicinal drugs**

445 Medicinal drugs derived from natural sources are one of the clearest examples of the importance of
446 biodiversity for human health. Biodiverse environments provide natural products and genetic resources,
447 which form the basis for both traditional medicine and modern pharmaceuticals (van Wyk and Wink,
448 2017). Medicinal plants are the primary source of natural product drugs for a majority of the human
449 population (Romanelli *et al.*, 2015), and an estimated 70-80% of the global population depend on some
450 form of traditional medicine for their primary health care (Ekor, 2014). Seventy-five percent of all
451 antibacterial, antiviral and antiparasitic drugs approved by the United States have natural product
452 origins (Newman and Cragg, 2012). Consequently, the prospective extinction of one million species
453 (IPBES, 2019) may harm human health through the loss of medicinal plants and opportunity costs of
454 forgone biomedical discovery (Chivian and Bernstein, 2008). To the best of our knowledge, no study has
455 used mediation analysis to investigate whether the beneficial effects of biodiversity on human health
456 can be explained by medicinal drugs.

457 **3.1.2. Food provision**

458 Good nutrition is fundamental for our physical well-being (World Health Organization, 2017a). Genetic
459 and species diversity is essential for food production (e.g. Bernstein, 2014) and a well-balanced,
460 nutritious diet. Ensuring biodiversity of foods is important for the development of potential food crops

461 of the future, which may help ensure food security under threats of climate change (Bernstein, 2014) or
462 intensive land use (Fahrig *et al.*, 2015). Biodiversity of crops and surrounding habitats can also reduce
463 pest infestation, which in turn can reduce pesticide use (Petit *et al.*, 2015) to support the health of
464 pollinators (IPBES, 2016) and people (Kim, Kabir and Jahan, 2017). Whilst food is a determinant of
465 human health, to date, no study has explicitly tested whether nutrition mediates the associations
466 between biodiversity and human health.

467 **3.1.2 Reducing exposure to water health risks**

468 Access to clean water is a necessity for human health (World Health Organization, 2019). Biodiversity
469 plays a fundamental role in the provision and regulation of water quantity and quality. Much of the
470 world's freshwater is provided downstream from mountains through river networks, and forests play an
471 important role in flow regulation (Zhang *et al.*, 2017). Biodiversity is central to the health of these
472 ecosystems, as it supports ecosystem functioning that provide, regulate and purify freshwater (Dudley
473 and Stolton, 2003). The ability of wetland plants to remove heavy metals from water differs between
474 species (Schück and Greger, 2020). A proxy indicator of good water quality and ecosystem health is the
475 diversity and composition of aquatic organisms, as they are sensitive to nutrient pollutants in the water,
476 such as nitrate (Cardinale, 2011), pesticides (Liess and Beketov, 2011) and pharmaceuticals (Binelli *et al.*,
477 2015). For example, freshwater molluscs (Ostroumov, 2005) or reed beds can contribute to clean
478 freshwater by filtering water and controlling phytoplankton densities. In addition to the provision of
479 freshwater, biodiverse environments can provide regulating ecosystem services that regulate severe
480 flooding (Carter *et al.*, 2018), buffering of water scarcity (Ellison *et al.*, 2017) or landslides (Miura *et al.*,
481 2015).

482 **3.1.3 Reducing exposure to air and noise pollution**

483 Air and noise pollution are well known causes of negative human health outcomes (Basner *et al.*, 2014;
484 Zivin and Neidell, 2018; Lelieveld *et al.*, 2019), particularly for urban dwellers. In locations where health-
485 related standards are exceeded, the potential of tree and other plant species to regulate air pollutant
486 concentrations and to mitigate noise can be especially important (Cohen, Potchter and Schnell, 2014;
487 Haase *et al.*, 2014; Salmond *et al.*, 2016). There is also evidence that tree diversity has a significant
488 impact on the potential to mitigate air pollution in cities (Churkina *et al.*, 2015; Grote *et al.*, 2016).
489 Similarly, vegetation with higher structural complexity and density has been found to be an effective
490 barrier to ultrafine particles from roads (Hagler *et al.*, 2012). Nevertheless, in the case of air quality, the
491 tangible effect of urban vegetation is still under debate due to its complex chemical and physical

492 interaction with the surrounding air depending on vegetation structure (e.g. planting density) and
493 specific functional traits (e.g. leaf area, water-use strategy, pollen production) (Salmond *et al.*, 2016;
494 Xing and Brimblecombe, 2019; Hewitt, Ashworth and MacKenzie, 2020). Some traits, such as allergenic
495 pollen or volatile organic compounds may also negatively impact on health (see section 3.4.3).
496 Regarding mediation, while air and noise pollution have been investigated as mediators linking nature to
497 human health (e.g. Triguero-Mas, Donaire-Gonzalez, *et al.*, 2017; Bloemsma *et al.*, 2019; Crouse *et al.*,
498 2019), to date, no study has investigated whether air and noise pollution mediates the relationship
499 between biodiversity and human health.

500 **3.1.4 Reducing exposure to extreme heat**

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

511 The design of cities can influence human exposure to extreme heat. Elevated land and air temperatures
512 in urban areas are primarily due to the replacement of natural land covers with impervious cover with
513 different thermal and structural properties (Oke, 1982; Gunawardena, Wells and Kershaw, 2017). The
514 cooling properties of vegetation and water (from evapotranspiration and/or shading) mean that even
515 modest amounts play an important role in temperature moderation and therefore influence human
516 thermal comfort and the reduction of heat stress (Bowler *et al.*, 2010b). Vegetation abundance,
517 structural characteristics, taxonomic diversity, species composition, functional diversity and functional
518 identity are all known to affect the extent of cooling provided (Ziter, 2016; Schwarz *et al.*, 2017; Lindley
519 *et al.*, 2019). For instance, tree traits (e.g. leaf area, pigmentation and canopy structure) influence how
520 incoming solar radiation is intercepted (Speak *et al.*, 2020). Furthermore, evapotranspiration rates are
521 determined by a range of species-dependent characteristics such as leaf area, canopy height and
522 stomatal and hydraulic resistances, moderated by factors such as water availability (Gunawardena,

523 Wells and Kershaw, 2017). Some of the shading properties important for cooling may also influence
524 health impacts from other harmful exposures, such as non-melanoma skin cancers from excess UV
525 exposure (Datzmann *et al.*, 2018). Despite evidence of the role of biodiversity for temperature
526 regulation, to our knowledge, no study has used mediation analysis to investigate whether the beneficial
527 effects of biodiversity on human health can be explained by reducing exposure to extreme heat.

528 **3.2 Restoring capacities**

529 The restoring capacities pathway refers to the recovery of adaptive capabilities that have been
530 diminished through the demands of dealing with everyday life (Hartig, 2017). Over time, lack of
531 restoration of these resources can lead to mental and physical ill health (von Lindern, Lymeus and
532 Hartig, 2016). Environments that facilitate the restoration of these depleted resources are called
533 restorative environments. Recent theorizing considers how experiences in natural settings, including
534 contact with biodiversity, might figure in the renewal of relational and social resources (Hartig, 2020),
535 but the currently conventional narrative about how nature experience produces restorative benefits
536 centres on theories about the renewal of psychophysiological and cognitive resources used to mobilize
537 and direct action.

538 **3.2.1 Stress Recovery Theory**

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

549 In SRT, biodiversity is considered as a measure of an environment's complexity (Ulrich, 1983, p.96).
550 Reduced physiological stress has been related to greater plant species richness (Lindemann-Matthies
551 and Matthies, 2018). Greater afternoon bird abundances (Cox, Shanahan, *et al.*, 2017), and perceived
552 plant species richness (Schebella *et al.*, 2019) have been related to reduced psychological stress. Positive

553 emotions have been found to increase with increases in the diversity of forests (Johansson *et al.*, 2014),
554 abundance of fish/crustaceans (Cracknell *et al.*, 2017), species richness of trees and birds (Wolf *et al.*,
555 2017), and perceived species richness of various taxa (White *et al.*, 2017; Schebella *et al.*, 2019). While
556 stress has been investigated as a mediator linking nature to mental health (e.g. Triguero-Mas, Donaire-
557 Gonzalez, *et al.*, 2017), to our knowledge, no study has tested whether stress, or negative or positive
558 emotions mediate the relationship between biodiversity and health.

559 **3.2.2 Attention Restoration Theory**

560 Attention restoration theory (ART) focuses on components of environmental experience that allow for
561 the restoration of the ability to direct attention (Kaplan and Kaplan, 1989; Kaplan, 1995; Kaplan and
562 Berman, 2017). A person can restore their depleted ability to direct attention, when they experience
563 four restorative qualities in an environment: (i) *fascination*, with stimuli in the environment that
564 involuntarily attract and hold a person's attention without cognitive effort; (ii) experience of *being away*
565 from everyday tasks or demands that draw upon directed attention; (iii) *extent*, with stimuli in the
566 environment perceived as coherently organised and with sufficient scope to sustain exploration; and (iv)
567 the experience of *compatibility* between the environmental setting and one's purposes and inclinations
568 (Kaplan and Kaplan, 1989; Kaplan, 1995). Changes in cognitive tests after exposure to an environment
569 are used as evidence of attention restoration in ART (Ohly *et al.*, 2016; Stevenson, Schilhab and Bentsen,
570 2018).

571 Biodiversity is not addressed in the theoretical writings of the ART (Marselle, 2019). However, natural
572 environments providing specific components of biodiversity may be beneficial for attention restoration
573 as they are likely to contain stimuli that facilitate the experience of *all* four restorative qualities (Korpela,
574 Pasanen and Ratcliffe, 2018; Marselle, 2019). One study found restoration from directed attention
575 fatigue was greatest for people who looked at images of urban greenspaces with high vegetation density
576 compared to those who looked at urban greenspaces with medium- or low- density vegetation (Chiang,
577 Li and Jane, 2017). This suggests that the effect of high vegetation density was most likely linked to
578 abundance of plant species or their species composition. Perceived restoration—where people self-
579 report changes indicative of restoration (e.g. feeling relaxed, refreshed after a long day) (Hartig, 2011)—
580 has been found to be positively associated with actual and perceived landscape heterogeneity of urban
581 greenspace (Meyer-Grandbastien *et al.*, 2020), vegetation structure and plant species of gardens (Hoyle,
582 Hitchmough and Jorgensen, 2017), and actual (Wood *et al.*, 2018) and perceived species diversity (White
583 *et al.*, 2017) of various taxa. The four restorative qualities have shown positive associations with

584 structural complexity of urban greenspace (Scopelliti *et al.*, 2012; Carrus *et al.*, 2015) and perceived
585 species richness of birds (Marselle *et al.*, 2016). To date, no study has tested the ability to direct
586 attention as a mediator; only restorative qualities have been tested as a mediator of the relationship
587 between biodiversity and health (Marselle, Martens, *et al.*, 2019). Restorative quality has been found to
588 mediate the relationship between biodiversity of urban greenspace and general well-being (Carrus *et al.*,
589 2015). Restorative qualities *being away*, *fascination* and *compatibility* have been shown to mediate the
590 relationship between perceived bird species richness and positive affect, and *compatibility* to mediate
591 the inverse associations between perceived bird species richness and negative affect (Marselle *et al.*,
592 2016).

593 **3.3 Building capacities**

594 The building capacities pathway refers to the deepening or strengthening of capabilities for meeting
595 everyday demands, rather than the restoration of a depleted resource (Hartig, 2007). In this domain we
596 discuss how biodiversity can contribute to human via capacity building.

597 **3.3.1 Encouraging physical activity**

598 Physical activity is important for physical and mental well-being (Biddle and Mutrie, 2008; World Health
599 Organization, 2018). Research suggests that physical activity in nature may produce greater
600 physiological and psychological benefits than physical activity indoors (Bowler *et al.*, 2010a; Coon *et al.*,
601 2011) or in urban areas (Bowler *et al.*, 2010a). It has been shown that enhancing streetscapes by
602 increasing biodiversity may promote physical activity (Säumel, Weber and Kowarik, 2016). Biodiversity
603 loss of ash trees is associated with people spending less time on outdoor recreation (e.g. sport, exercise,
604 walking)(Jones, 2016). Bjork *et al.* (2008) and de Jong *et al.* (2012) found a positive association between
605 environments that were 'lush', i.e. rich in species, and greater self-reported physical activity, although
606 others (Annerstedt *et al.*, 2012; Foo, 2016) could not find an association. While physical activity has
607 been investigated as a mediator linking nature to mental health (e.g. Triguero-Mas, Donaire-Gonzalez, *et*
608 *al.*, 2017), to our knowledge no study has investigated physical activity as a mediator of biodiversity-
609 health relationships.

610 **3.3.2 Facilitating social interaction**

611 Social interaction is related to health and well-being (Holt-Lunstad, 2017). Biodiverse environments may
612 provide a setting for social interaction with others, such as in neighbourhoods with more trees (Sullivan,
613 Kuo and Depooter, 2004), or through conservation volunteering, where participants not only enjoy

614 social interaction but also greater personal equality (Currie, Lackova and Dinnie, 2016). While previous
615 studies have investigated social interaction as a mediator of nature and health (Ruijsbroek *et al.*, 2017;
616 Triguero-Mas, Donaire-Gonzalez, *et al.*, 2017), only one study to date tested social interaction as a
617 mediator of the association between parks with different levels of plant, bird and animal species
618 richness and human health, and it did not find evidence for mediation (Foo, 2016).

619 **3.3.3 Transcendent experiences (awe, humility, reflection)**

620 Transcendent experiences—such as humility, awe (strong emotions of amazement and wonder; Ballew
621 and Omoto, 2018), and reflection (thinking about one’s life, goals and priorities; Kaplan and Kaplan,
622 1989)—contribute to well-being (Davis and Gatersleben, 2013; Capaldi *et al.*, 2015). Sights and sounds
623 of nature, both mundane and awesome, have been found to elicit transcendental experiences (Capaldi
624 *et al.*, 2015; Irvine *et al.*, 2019). Considering wilderness as a proxy for a biodiverse environment, studies
625 have found that wilderness-based recreation can contribute to the ability to reflect about one’s purpose
626 and meaning in life, and the spiritual experiences of humility and awe (Irvine *et al.*, 2019). Qualitative
627 research has shown that viewing some types of wildlife can contribute to a sense of humility and awe
628 (Curtin, 2009). Quantitative research shows that the number of habitat types (Fuller *et al.*, 2007), and
629 actual species richness of plants (Fuller *et al.*, 2007) and birds (Dallimer *et al.*, 2012) were positively
630 associated with reflection. Perceived species richness of birds, butterflies and plants were also found to
631 be positively associated with reflection (Dallimer *et al.*, 2012). To date, no study has tested whether
632 transcendent experiences mediate the associations between biodiversity and health.

633 **3.3.4 Promote place attachment and place identity**

634 People may form emotional bonds, or place attachments, to biodiverse environments (Raymond, Brown
635 and Weber, 2010; Ives *et al.*, 2017; Manzo and Devine-Wright, 2019). These emotional connections
636 mean that these biodiverse environments could also form part of one’s place identity (Manzo and
637 Devine-Wright, 2019). Both place attachment and place identity are associated with psychological well-
638 being (Manzo and Devine-Wright, 2019). Previous research has found that both place attachment and
639 place identity were positively associated with the abundance of tree cover (Dallimer *et al.*, 2012), actual
640 and perceived species richness of birds (Fuller *et al.*, 2007; Dallimer *et al.*, 2012), as well as perceived
641 species richness of butterflies and plants (Dallimer *et al.*, 2012). Place identity was also found to be
642 positively related to the number of habitat types and actual plant species richness (Fuller *et al.*, 2007).
643 While, place attachment or place identity have been tested as mediators of the relationship between
644 nature-health (e.g. Knez *et al.*, 2018), to our knowledge, no study has investigated whether the

645 beneficial effect of biodiversity on health can be explained by place attachment or place identity using
646 mediation analysis.

647 **3.4 Causing harm**

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

649 **3.4.1 Contact with wildlife that cause harm**

650 Research on contact with wildlife has traditionally focussed on negative aspects, such as injuries through
651 contact with poisonous plants, mushrooms or berries, and large mammalian predators or reptiles
652 (Methorst *et al.*, 2020). This includes e.g. attacks by large cats, bears or alligators, snake bites or skin
653 irritation, when in contact with amphibia. Injuries can also be induced by plants, through skin contact
654 (stinging nettles, algae; for allergens see 3.4.3) or poisoning through consumption, e.g. mushrooms.
655 Dangerous interaction with wildlife may also cause mental and emotional harm, in addition to physical
656 harm due to injury. Nevertheless, interactions with wildlife may also impact the restoring and building
657 capacities domains with beneficial effects of wildlife on health (Methorst *et al.*, 2020).

658 **3.4.2 Exposure to infectious agents causing human diseases**

659 Serious infectious human diseases such as the recently emerged COVID-19 (pandemic), Ebola (West
660 Africa), Borna (Germany) and the vector-borne diseases (VBDs)—such as malaria, dengue, zika,
661 schistosomiasis, visceral leishmaniasis or tick-borne encephalitis—all stem from animals (World Health
662 Organization, 2017b; Müller *et al.*, 2019; Ahmad *et al.*, 2020; Niller *et al.*, 2020). VBDs relate to very
663 important aspects of biodiversity as they comprise an inter-relationship between pathogens (arboviruses,
664 bacteria, protozoa), invertebrate vectors (i.e. mosquito, sand fly, tsetse fly, tick, snail, lice, flea) and host
665 species (i.e. human, livestock, rodents, birds). The interactions of these three VBD components attribute
666 to qualitative and quantitative biodiversity, for instance: genotype-specific replication in the vector
667 (Riehle *et al.*, 2006); pathogen transmission to the host (Heitmann *et al.*, 2018); context-dependent host
668 preference (Simpson *et al.*, 2012); differential responses in phenology and distribution (Elyazar *et al.*,
669 2013; Hasyim *et al.*, 2018); and dynamic pathogen spreading in social networks of host species (Ezenwa
670 *et al.*, 2016).

671 Numerous studies have used mediation analysis to investigate whether there is a causal pathway between
672 infectious disease agents and the level of biodiversity (genetic, phenotypic and species diversity of
673 vectors/hosts, functional diversity for vector and reservoir competence)(Ostfeld, 2009; Roberts and
674 Heesterbeek, 2018; Vadell, Gómez Villafañe and Carbajo, 2020). Evidence has been found for both the

675 dilution hypothesis (increased biodiversity causes a decreased VBD prevalence; zooprophylaxis; e.g.
676 Schmidt and Ostfeld, 2001) and amplification hypothesis (increased biodiversity causes an increased VBD
677 prevalence, zoopotential; e.g. Roiz *et al.*, 2019). But very often, no or weak relationships between
678 biodiversity measures and VBD prevalence were detected (e.g. Stensgaard *et al.*, 2016; Ruyts *et al.*, 2018;
679 Vadell, Gómez Villafañe and Carbajo, 2020). Certainly, the enormous complexity in biodiversity-health-
680 environment interactions at local to global level is a major challenge when designing VBD prevention and
681 vector control strategies. Nevertheless, biodiversity can also be part of the solution to combat VBDs by
682 providing inspiration for new chemical and biological pesticides and pharmaceuticals and innovative
683 genetic vector control tools (Famakinde, 2020; Kendie, 2020; Wooding *et al.*, 2020).

684 **3.4.2 Exposure to microorganisms beyond infectious disease**

685 Due to the potentially fatal effect of human-pathogenic microbes, the dominant public health objective
686 is to limit contact with harmful microbes, through infrastructural and socio-cultural practices (e.g.
687 sanitation and hygiene measures), or the use of pharmaceutical drugs targeting infectious
688 microorganisms (Armstrong, Conn and Pinner, 1999). However, the human microbiome may also
689 mediate positive effects of biodiversity on human health, as negative correlations between microbial or
690 environmental diversity and the incidence of non-communicable, and in particular auto-immune,
691 disease have been observed (Ruokolainen *et al.*, 2015; Mosca, Leclerc and Hugot, 2016; Aerts, Honnay
692 and Nieuwenhuysse, 2018). Overall biodiversity decline can decrease microbiome diversity (Heiman and
693 Greenway, 2016; Blum, Zechmeister-Boltenstern and Keiblinger, 2019; Johnson *et al.*, 2019; Ng *et al.*,
694 2019). To fully understand pathways mediating biodiversity effects on health, rigorous investigations of
695 microbial exposure are required (Porrás and Brito, 2019), as well as of the mechanisms of microbial
696 protective diversity, e.g. dilution of pathogens (Libertucci and Young, 2019), improvements in
697 metabolism (Adar, Huffnagle and Curtis, 2016; Visconti *et al.*, 2019) and regulation of the immune
698 system (Kamada *et al.*, 2013; Belkaid and Hand, 2014; Mezouar *et al.*, 2018; Al Nabhani *et al.*, 2019;
699 Zhang *et al.*, 2019).

700 **3.4.3 Increasing exposure to airborne allergens and volatile organic compounds**

701 Allergies have a major impact on people's health and quality of life (Baiardini *et al.*, 2006) and the loss of
702 exposure to biodiversity may increase susceptibility to allergies (Prescott, 2020). The emission of
703 biogenic particulate matter (spores and pollen) and volatile organic compounds (e.g. isoprene, a critical
704 substance in O₃ formation) is species-specific (Peñuelas and Staudt, 2010; Grote *et al.*, 2016). Studies
705 investigating whether allergenic pollen mediates the effect of biodiversity and health have found two

706 different pathways. First, the biodiversity in an allergic person’s microbiome is suspected to influence
707 whether or not they will experience an allergic reaction (Haahtela *et al.*, 2013). Second, the abundance
708 and species richness of allergenic plants can influence the opportunity for an individual to come into
709 contact with allergenic pollen. While a large abundance of allergenic plants may affect allergic people
710 negatively, a more biodiverse environment can protect through the dilution effect from exposure to
711 allergenic pollen. However, a more biodiverse environment may also mean that a person is potentially
712 exposed to a greater variability of allergens. Whether this leads to more allergies or protection from
713 allergic sensitisation is still a matter of debate. For example, Hanski *et al.* (2012) showed that
714 neighbourhood environmental biodiversity affects the composition of bacterial classes on people’s skin,
715 thus affecting allergy. The biodiversity hypothesis states that “contact with natural environments
716 enriches the human microbiome, promotes immune balance and protects from allergy and
717 inflammatory disorders” (Haahtela, 2019). Previous studies support the biodiversity hypothesis finding a
718 more diverse environment is correlated with a healthy microbiome (Hanski *et al.*, 2012), and fewer
719 allergic people (Haahtela *et al.*, 2013). Moreover, a highly biodiverse environment was found to be more
720 protective against allergens, than the exposure to specific environmental allergens in early life (Von
721 Mutius and Vercelli, 2010). This suggests that biodiversity in the environment may be protective against
722 allergic response.

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

730 **Step 4. Health effects**

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

733 *Measurement of health*

734 Health (Box 2) is operationalised across three dimensions of well-being—physical, mental and social—to
735 acknowledge the holistic biopsychosocial model of health (Engel, 1977; Fava and Sonino, 2008).

736 Biodiversity has been shown to affect all three dimensions of well-being (Irvine and Warber, 2002; Lovell
 737 *et al.*, 2014; Aerts, Honnay and Nieuwenhuysse, 2018; Marselle, Stadler, *et al.*, 2019b). Each dimension of
 738 well-being can be measured both objectively and subjectively (Table 2). Regarding subjective
 739 measurement of health, it is important to use existing valid, reliable questionnaires to assess well-
 740 defined clinical outcomes (Aerts, Honnay and Nieuwenhuysse, 2018), and ensure comparability with
 741 previous health research (Linton, Dieppe and Medina-Lara, 2016).

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

	Measurement	
Health and Well-Being Dimension ¹	Objective	Subjective
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 experiences of 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); medical doctor diagnosis of diabetes or hypertension	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 person's experience of happiness.	e.g. antidepressant prescriptions; psychiatrist diagnosis of depression or anxiety	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, 1998)

744 *Note.* ¹ = All definitions from Linton, Dieppe & Medina-Lara (2016, p.12).

745

746 **5. Considerations for statistical analyses**

747 The causal pathways in the biodiversity-health framework can be tested through mediation models.
748 Statistically, mediation models consist of a sequence of regression models in which the predictor
749 variable, in this case biodiversity or contact with biodiversity, affects one or more intervening
750 variables—a mediator within one of the four domains of pathways—which in turn affects human health.
751 Investigation of inter-relationships between mediators of the four different domains involves multiple
752 mediator models in which mediators are working in parallel or serial—rather than single mediators
753 (Hayes, 2009; Dzhambov *et al.*, 2020). Analytical approaches recommended to test for mediation are the
754 product-of-coefficients approach using ordinary least squares regression and bootstrapping, and
755 structural equation modelling (for more information, see Dzhambov *et al.*, 2020).

756 **Confounding variables**

757 In a mediation analysis, confounding is a threat to validity, undermining the relationships between the
758 predictor and outcome variables (Valente *et al.*, 2017). A confounding variable is a ‘third’ variable that is
759 related to two (or more) variables in the mediation model that partially explains the relationship between
760 these two variables (Valente *et al.*, 2017). Thus, confounding variables may influence the predictor-
761 outcome relation, the predictor-mediator relation, or the mediator-outcome relations (Valente *et al.*,
762 2017). Identifying the potential confounders of the association between biodiversity, health and its
763 mediating pathways is paramount to establishing the studied links clearly without biasing the study results
764 or leading to erroneous conclusions. If no adjustment is made for these confounders, for example by
765 including them as covariates in a regression analysis, then incorrect conclusions may be drawn about the
766 plausibility of causal effects in the mediation model.

767 Biodiversity-health-pathways studies should consider the following confounders: gender, age, being part
768 of a socially marginalized/privileged group (such as being from a certain ethnic group, race or
769 socioeconomic group), or taking care of elderly, children or pets. Additional confounders in biodiversity-
770 mental health studies are perceived naturalness, visual complexity and amount of nature in general (de
771 Vries and Snep, 2019). Moreover, specific study contexts may require consideration of other confounders
772 such as area socioeconomic status, degree of urbanization, area deprivation or neighbourhood
773 gentrification stage (Cole *et al.*, 2019), livestock rearing (Hasyim *et al.*, 2018), weather, or study design
774 factors like sampling order in experimental study designs (Triguero-Mas, Gidlow, *et al.*, 2017). Statistical

775 methods such as Bayesian network modelling can be a reasonable way to select a minimum sufficient set
776 of confounders.

777 **Modifying variables**

778 The strength or direction of the relationship between biodiversity and human health via any of the four
779 domains of pathways is subject to modification by the environmental/socio-cultural context and
780 individual characteristics (Fig. 1). As detailed in Figure 1, moderating factors can influence the
781 relationships between biodiversity (Step 1) and contact with biodiversity (Step 2), and between contact
782 with biodiversity (Step 2) and each of the four domains of pathways (Step 3), and the influence of
783 pathways within each domain (Step 3) on health and well-being (Step 4).

784 At any steps in the conceptual model, and depending on specific research aims and research questions,
785 researchers may explore variables relating to the environmental/socio-cultural context and individual
786 characteristics. For example, individual characteristics such as age, gender or socioeconomic position may
787 be of interest. These moderator analyses ensure that potential differential effects and pathways by
788 population subgroups are understood and that any intervention is socially just. Moderating factors
789 relating to the environmental/socio-cultural context and individual characteristics have all been found to
790 influence nature-health (Triguero-Mas *et al.*, 2015; Jones, 2016; Van den Berg *et al.*, 2016; Triguero-Mas,
791 Donaire-Gonzalez, *et al.*, 2017; White *et al.*, 2017; Zijlema *et al.*, 2017; Cole *et al.*, 2019) and biodiversity-
792 health relationships (Carrus *et al.*, 2015; Wheeler *et al.*, 2015). These same personal and environmental
793 context variables may also moderate the biodiversity-health pathways.

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

799
800 Factors relating to the environmental/socio-cultural context and individual characteristics may influence
801 whether a person is exposed to specific components of biodiversity (Step 2.1), and the ways in which
802 people experience biodiversity—the relationship between biodiversity and contact with biodiversity (Step
803 2.2; Fig. 1)(Frumkin *et al.*, 2017). Exposure to biodiversity may be encouraged or discouraged through
804 aspects of the environmental/socio-cultural context, for example amenities (e.g. public toilets), park

805 programming (Hunter, Cleary and Braubach, 2019; Vierikko *et al.*, 2020), accessibility and maintenance
806 status of the space where biodiversity is found, perceived safety in the space where biodiversity is, and
807 other space-related variables such as size, type, land ownership (that can also be considered
808 confounders)(Bratman *et al.*, 2019). Individual characteristics, such as personal time demands, transport
809 corridors, may also influence exposure (Bratman *et al.*, 2019). Experience of the specific components of
810 biodiversity will be influenced by individual characteristics such as connectedness to nature, and
811 preference about, knowledge of, perception of (including fear of certain species), attitudes towards,
812 receptivity towards, or childhood experiences of biodiversity (Wells and Lekies, 2006; Bratman *et al.*,
813 2019). Moreover, the socio-cultural context, such as values around biodiversity (King *et al.*, 2017; Bell *et*
814 *al.*, 2018; Chan, Gould and Pascual, 2018) can also affect the experience of biodiversity (Bratman *et al.*,
815 2019).

816 **6. Data sources available to assess biodiversity, health and the mediators in the four** 817 **domains**

818 To operationalise the model and allow for application in testing of the biodiversity-health framework in
819 health research and application, in this section, we identify available data sources. Supplementary Table
820 2 details these possible data sources.

821 **6.1. Step 1: Biodiversity**

822 Data on actual biodiversity (Step 1) exist on local to global geographical scales. These data can be in the
823 public domain but are often “hidden” within administrative agencies, museums, research institutes, etc.
824 (Beck *et al.*, 2012). An increasing number of initiatives now combine biodiversity data from across the
825 globe into (partly) open databases (e.g. GBIF: The Global Biodiversity Information Facility, 2020) or at
826 the national scale in Atlases (e.g. German Atlas for Flowering Plants and Ferns, Bundesamt für
827 Naturschutz, 2013)(see Supplementary Table 2). These data repositories are highly heterogeneous in
828 structure or quality, and often biased both taxonomically and geographically, such as towards the Global
829 North, charismatic species and aboveground terrestrial biodiversity (e.g. Titley, Snaddon and Turner,
830 2017; Troudet *et al.*, 2017; Cameron *et al.*, 2018). This bias might limit or even misguide our
831 understanding of biodiversity-health pathways. Remote sensing provides opportunities for reducing bias
832 by assessing, for example, e.g. land cover, plant structural diversity or plant functional traits (Lausch *et*
833 *al.*, 2016; Dennis *et al.*, 2018). The use of eDNA and meta-barcoding (Ji *et al.*, 2013) can also help to
834 support field biodiversity assessments.

835 **6.2 Step 2: Contact with biodiversity**

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

844 **6.3. Step 3: Assessment of mediators in the four domains**

845 Many data sources on the four domains (Step 3) exist, which can support the analysis of biodiversity-
846 health relationships and mediating pathways. For the ‘Reducing Harm’ domain, open-access
847 environmental data comprise, for example, local noise exposure information in European metropolitan
848 areas, provided by the European Environment Agency, or Local Climate Zones (LCZs) for urban
849 climatology (Stewart and Oke, 2012; Demuzere *et al.*, 2019). Remote sensing can deliver information on
850 land surface temperatures (e.g. Zheng, Myint and Fan, 2014; Kremer *et al.*, 2018) and air quality (Gupta
851 *et al.*, 2006).

852
853 Datasets for the ‘Building Capacities’ and ‘Restoring Capacities’ domains range from the local scale in
854 city-wide health studies (e.g. Nieuwenhuijsen *et al.*, 2014), to the district-level in national surveys (e.g.
855 the Monitor of Engagement with the Natural Environment), and the regional scale in medicinal plants
856 databases (Babu *et al.*, 2006). Access to local scale datasets will need to be requested; while data at
857 coarser spatial resolution are often publicly available. However, depending on the specific mediators
858 investigated (e.g. attention restoration, place attachment), researchers may need to collect new
859 empirical data.

860
861 Data for the ‘Causing Harm’ domain may be available—usually upon request—at the local scale in health
862 cohorts for the human microbiome, regional and national scale for allergenic pollen, or at the
863 international scale for distribution of ticks and mosquitos (see Supplementary Table 2). Ground
864 observation, remote sensing and genetic biodiversity monitoring can be used to determine the
865 presence, abundance, density and functional traits of invasive, pest and allergenic biodiversity (Skjøth *et al.*, 2013).

867 **6.4. Step 4: Human health effects**

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

876 **7. Recommendations for policy, practice and future research**

877 **7.1 Policy implications**

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

897 **7.2 Practice implications**

898 The concept of nature to promote public health is longstanding, championed by Florence Nightingale,
899 and the creation of hospital gardens, public parks (Wheater *et al.*, 2007; Ward Thompson, 2011;
900 Hickman, 2013), and allotment gardens (van den Berg *et al.*, 2010). Presently, the use of natural
901 environments is considered as a health promotion intervention (Irvine and Warber, 2002; Maller *et al.*,
902 2005; World Health Organization, 2016; Frumkin *et al.*, 2017). The asset-based approach to health has
903 led to the development of a person- and asset-based ‘social prescribing’ movement, whereby non-
904 medical interventions are provided to promote health and alleviate the pressure on acute medical care
905 facilities (Polley *et al.*, 2017). Social prescriptions can include nature-based interventions (Cook, Howarth
906 and Wheeler, 2019), such as outdoor walking groups (Marselle *et al.*, 2015, 2016; Irvine *et al.*, 2020),
907 forest-bathing or horticulture-based therapies (e.g. <https://www.adoseofnature.net/>). We suggest that
908 physicians and public health authorities may consider prescribing biodiversity-based interventions to
909 bring humans into contact with biodiverse environments, such as nature conservation activities
910 (Pillemer *et al.*, 2010).

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

917 **7.3 Recommendations for future research**

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

927 The presented conceptual framework provides a causal understanding of biodiversity-health linkages.
928 Naturally, like its precursors (Hartig *et al.*, 2014; Markevych *et al.*, 2017; Bratman *et al.*, 2019), the
929 biodiversity-health framework does not aim to represent all the complexity of real-world situations. We
930 have tried to strike a balance between representation of complexity and the utility of the framework as
931 a guide to communication, research, and practice. For example, we represent the possibility of
932 reciprocal relations and feedback between components of the biodiversity-health framework, but not as
933 comprehensively due to space limitations. And yet, the framework is not simplistic, as we represent the
934 multiple levels on which intertwined processes can run between biodiversity and health and the sets of
935 moderators of those pathways.

936 By providing a causal understanding of biodiversity-health linkages moving from biodiversity (Step 1) to
937 contact with biodiversity (Step 2) to the four domains of pathways (Step 3) to human health (Step 4), we
938 show avenues to operationalise research to test the framework, with available data resources and
939 analytic approaches. The biodiversity-health framework thus supports further collaboration by
940 researchers trained in different disciplines who have already begun to study processes as depicted here
941 and who can enlist other researchers to join their efforts. Some research questions might not appear in
942 the visual and textual presentation of our biodiversity-health framework due to brevity, which does not
943 mean that we consider them unimportant.

944 The next steps for research are to operationalise this biodiversity-health framework. Using the
945 biodiversity-health framework, we hope to inspire future researchers to specifically investigate these
946 mediating relationships. In the short-term, the fields of biodiversity and public health could be fostered
947 by focussing on testing the two sides of the biodiversity-health framework separately: assessing the
948 relationship between biodiversity (Step 1) or contact with biodiversity (Step 2) and a specific mediating
949 variable (e.g. physical activity, Step 3); and assessing the relationship between the same mediating
950 variable (e.g. physical activity) and human health (Step 4). Most importantly, data-driven experimental
951 research approaches employing longitudinal, intervention and randomized controlled trial experimental
952 studies in the field and the lab are needed to test these conceptual pathways and their synergistic
953 interaction to understand biodiversity-health linkages (Aerts, Honnay and Nieuwenhuys, 2018;
954 Marselle, Stadler, *et al.*, 2019a; Müller *et al.*, 2019).

955 An important research frontier is to further our understanding of how we experience biodiversity
956 (Gaston *et al.*, 2018). This may then influence how we ultimately value (Chan, Gould and Pascual, 2018)
957 and shape our interaction with biodiversity—both for developing conservation and enhancing human

958 health. We need to understand the shape of the relationships between specific elements of biodiversity
959 (i.e. the richness and abundance of species, their identity, their behaviour, and their traits, as well as
960 genetic and ecosystem diversity) and human health outcomes. When analysing pathway mechanisms, it
961 is crucial to assess how the environmental and socio-cultural context and individual characteristics may
962 moderate the outcomes. Overall, more research is needed on people's contact with biodiversity (step
963 2)(Gaston, 2020). More research is needed on how differential exposures to biodiversity (Step 2.1)
964 influence human health, in order to unravel 'dose-response' relationships. Future research into the
965 biodiversity-health framework could usefully investigate whether the four different types of experience
966 with biodiversity (Step 2.2) influence the mediating pathways in the four domains. This understanding
967 will then inform how to better promote or—in case of the 'causing harm' domain—possibly avoid
968 harmful contact with biodiversity for human health.

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

982 **Conclusion**

983 We present a new conceptual framework to serve as the basis for strategic discussions and better
984 alignment of biodiversity-health research, policy and practice with respect to public health,
985 environmental psychology, landscape and urban planning as well as biodiversity conservation. The
986 biodiversity-health framework draws on diverse forms of knowledge to elucidate a range of causal
987 pathways linking biodiversity and health and, importantly, depicts the biodiversity that people can
988 experience in their everyday lives. As such, the awareness of the breadth of effects biodiversity has on

989 human health necessitates a large range of approaches to protect and restore biodiversity to promote
990 health—starting in gardens and parks, over biodiverse agricultural areas to tropical forest, wilderness
991 and nature reserves. Here, we provide a tool in order to explore explicit management options in a
992 standardized and comprehensive manner and a given geographical context. Our biodiversity-health
993 framework should therefore serve a broad range of purposes, including identification of health
994 indicators and interventions, formulation of policy, and communication among diverse groups of
995 audiences.

996 The COVID-19 pandemic brought biodiversity into the limelight. It showed how harming biodiversity
997 through illegal trade or habitat destruction can lead to severe health impacts, and how enjoying urban
998 nature was important for people’s health and well-being in lockdown. We now urgently need to further
999 our understanding of salutogenic benefits and pathogenetic burden of biodiversity. The current joint
1000 working of WHO and CBD needs to be supported and enshrined in the up-coming post-2020 global
1001 biodiversity framework and respective targets for policy and management. Fundamentally, investment
1002 into biodiversity conservation and restoration needs to be viewed as investment into our human health.
1003

1004 **Author contributions**

1005 Conceptualization: Marselle and Bonn developed the idea for the work and organised the workshop
1006 where the concepts and biodiversity-health framework were created with all authors.

1007 Project administration: Marselle and Bonn led management and coordination of writing with support
1008 from Cox, de Bell, Hartig, Knapp, Lindley & Triguero-Mas.

1009 Writing - original draft: Marselle, Braubach, Cook, Cox, de Bell, Hartig, Heintz-Buschart, Irvine, Kabisch,
1010 Knapp, Kolek, Krämer, Lindley, Martens, Müller, Potts, Stadler, Warber & Bonn.

1011 Writing - review & editing: All authors.

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