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1	Unpacking the People-Biodiversity Paradox: A Conceptual
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26 Abstract

27 Global phenomena, including urbanization, agricultural intensification and biotic 28 homogenization, have led to extensive ecosystem degradation and species extinctions, and, 29 consequently, a reduction in biodiversity. Yet, while it is now widely asserted in the research, 30 policy and practice arenas that interacting with nature is fundamental to human health/well-31 being, there is a paucity of nuanced evidence characterizing how the living components of nature, biodiversity, play a role in this accepted truth. Understanding these human-32 33 biodiversity relationships is essential if the conservation agenda is to be aligned successfully 34 with that of public health by policy-makers and practitioners. Here we show that an apparent 35 'people-biodiversity paradox' is emerging from the literature, comprising a mismatch 36 between: (a) people's biodiversity preferences and how these inclinations relate to personal 37 subjective well-being; and, (b) the limited ability of individuals to accurately perceive the 38 biodiversity surrounding them. Additionally, we present a conceptual framework for 39 understanding the complexity underpinning human-biodiversity interactions.

40

Keywords: conservation biology, cultural ecosystem services, green space, human well-being,
nature

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44 Introduction

Despite considerable effort on the part of conservationists, the biodiversity (box 1) extinction crisis shows no sign of abating with human activities driving species losses worldwide (Cardinale et al. 2012). Solutions to stemming biodiversity loss will thus depend on changing people's attitudes and behavior (Fuller and Irvine 2010, Duraiappah et al. 2013). Yet, the same global changes that threaten species and ecosystems, such as urbanization, agricultural intensification and biotic homogenization, also modify the ways in which humans interact

51 with nature in their day-to-day lives (Turner et al. 2004, Pilgrim et al. 2008). Human-nature 52 interactions can be intentional (e.g. going to a park to feed birds, drawing trees in-situ within 53 a woodland), incidental (e.g. running across a beach and suddenly realising you have been 54 hearing birds calling, kicking up dead leaves as you walk although you are not cognisant of 55 what you are doing at the time) or indirect (e.g. looking at images of butterflies in a book, 56 watching a television documentary on brown bears, looking through a window to view a fox 57 in the garden) (Keniger et al. 2013). In the highly urbanized societies which predominate in 58 the developed, and increasingly developing, world, the human-nature interactions that occur 59 are often restricted to green spaces (e.g. public parks and woodlands, riparian areas, private 60 gardens; box 1) within towns and cities (Fuller and Irvine 2010). Consequently, a number of 61 authors have argued that people are becoming progressively 'disconnected' from nature (e.g. 62 Pyle 1978, Miller 2005).

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64 The erosion of human-nature/biodiversity interactions is concerning for two reasons. Firstly, 65 such interactions are known to provide people with multiple benefits for health/well-being 66 (Irvine and Warber 2002, Keniger et al. 2013, Hartig et al. 2014, Lovell et al. 2014; box 1). 67 Secondly, some authors posit that an absence of contact with nature/biodiversity could 68 contribute towards a lack of public interest and involvement in conservation (Miller 2005). 69 Nonetheless, the first of these points may present an important opportunity for 70 conservationists to leverage more support for policy and management interventions to protect 71 and enhance biodiversity, thereby improving the frequency and/or quality of people's 72 interactions with nature (Clark et al. 2014, Shwartz et al. 2014a). If these opportunities can be 73 capitalized on they might bestow additional positive co-benefits by increasing public 74 engagement in conservation.

75

76 The prevalence and costs associated with treating poor mental health and non-communicable 77 diseases (e.g. diabetes, cardiovascular disease, depression) are expanding worldwide, 78 particularly in developed nations (WHO 2014). As such, the beneficial outcomes associated 79 with human-nature/biodiversity interactions (e.g. stress reduction, Peschardt and Stigsdotter, 80 2013; improved physical exercise, Pretty et al. 2005; lower depression, Marselle et al. 2014) 81 which can help in combatting these issues are of interest to the health sector (Coutts et al. 82 2014). Through carefully targeted interventions, such as strategically optimizing access to 83 urban green spaces of high ecological quality across heavily populated landscapes, relatively 84 small gains at an individual level could scale-up to substantial cost-effective benefits across entire populations, even in comparison to approaches focused specifically on people with 85 higher health risks (Dean et al. 2011). Investment in biodiversity could therefore be 86 87 considered a worthwhile societal prophylactic, reducing the economic and human costs of ill 88 health (Sandifer et al. 2015).

89

90 Given that practitioners and policy-makers tasked with managing human-dominated 91 landscapes have to deliver, and trade-off between, multiple biodiversity, individual and 92 societal benefits (Reyers et al. 2012), environmental interventions that deliver mutually 93 reinforcing outcomes for both biodiversity conservation and people are highly desirable. 94 Before such scenarios can be pushed forwards, it is vital to understand the role played by 95 biodiversity per se, rather than the more nebulously defined nature, in producing measurable 96 health/well-being benefits for individuals and, in turn, the wider population. In this paper, we 97 discuss the complex relationship between biodiversity and human health/well-being, which is 98 emerging from a growing international literature (e.g. Lovell et al. 2014), highlighting the 99 'people-biodiversity paradox' (Fuller and Irvine 2010, Shwartz et al. 2014b pg. 87). 100 Additionally, we present a conceptual framework that, like others in the ecological public

health paradigm (Coutts et al. 2014), can be a useful tool in communicating these concepts across the different research disciplines required to unpack this paradox. The peoplebiodiversity paradox differs conceptually from the 'environmentalists' paradox' (Raudsepp-Hearne et al. 2010) in terms of both scale (the former is at the level of the individual, whereas the latter is global) and what is being measured (individual perceptions/subjective well-being in response to personal interactions with biodiversity versus objective well-being and the state of ecosystem service provision).

108

109 How does biodiversity underpin human well-being?

Despite ecosystem assessments being the prominent lens through which nature is valued and incorporated into decision-making (MA 2005, UKNEA 2011), our knowledge of how biodiversity underpins ecosystem functioning and services remains limited (Mace et al. 2012). This is especially true for non-material cultural ecosystem services (e.g. aesthetics, spiritual enrichment, recreation, reflection), where the relationships have rarely been investigated (Cardinale et al. 2012). How biodiversity underpins mental and physical health is less clear still and has proven harder to quantify reliably (Clark et al. 2014).

117

118 Few studies directly consider how variation in the 'quality' of environmental spaces, as 119 measured by ecologists, impacts upon human well-being and individual preferences for 120 certain elements of biodiversity (see Lovell et al. 2014 for a review). For example, 121 epidemiological research has typically considered the size and distribution of green space 122 surrounding properties, and the influence this has on the health/well-being of an individual 123 (e.g. de Vries et al. 2003, Mitchell and Popham 2008). While this work provides valuable 124 insights regarding green space accessibility/proximity across a population and the associated 125 health/well-being benefits this might confer, it assumes that the spaces are homogenous

126 entities and does not tease apart ecological complexity in terms of, for instance, species 127 richness (box 1), community assemblages or land cover diversity (Wheeler et al. 2015). 128 Indeed, we know little about which aspects of biodiversity trigger the positive human well-129 being benefits reported in studies to-date. Furthermore, it is highly improbable that all species 130 and ecological traits, and different compositions of these various attributes, will be 131 advantageous or deleterious for health/well-being, particularly as responses are likely to be 132 moderated by an array of contextual, social and cultural filters. Future research should thus 133 explicitly consider measures of ecological quality alongside individual health/well-being 134 outcomes.

135

Studies that have examined objective metrics of biodiversity (e.g. species richness and abundance) are inconclusive, identifying an inconsistent and complex relationship between biodiversity and self-reported human health/well-being. They reveal a 'people-biodiversity paradox' (Fuller and Irvine 2010, Shwartz et al. 2014b pg. 87), comprising a mismatch between: (a) people's biodiversity preferences and how these inclinations relate to personal subjective well-being; and, (b) the limited ability of individuals to accurately perceive the biodiversity surrounding them.

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Several papers highlight people's preferences for greater species richness, a finding that has been repeated across a range of habitats including urban gardens (Lindemann-Matthies and Marty 2013), grasslands (Lindemann-Matthies et al. 2010a), green roofs (Fernandez-Cañero et al. 2013) and in bird song (Hedblom et al. 2014). Fuller et al. (2007) found that selfreported psychological well-being was associated positively with plant species richness, and that people could perceive accurately levels of diversity for this taxon, although this relationship was less evident for birds and not found for butterflies. Dallimer et al. (2012)

151 found no consistent relationship between plant or butterfly species richness and self-reported 152 psychological well-being within in urban riparian environmental spaces, although a positive 153 trend was apparent for avian diversity. Intriguingly, however, well-being was positively 154 related to the perceived richness of all three taxonomic groups. A similar inconsistency was 155 noted by Shwartz et al. (2014b) who discovered that people could not detect increases in 156 flowering plant, bird or pollinator richness after experimental manipulations within public 157 gardens, and underestimated considerably levels of diversity. Nonetheless, individuals 158 expressed a strong preference for species richness in these green spaces and related the 159 presence of diversity to their well-being. At a neighborhood scale, Luck et al. (2011) found a 160 strong positive relationship between vegetation cover and self-reported well-being. However, 161 the authors found demographic characteristics explained a greater proportion of the variation 162 in well-being.

163

164 The people-biodiversity paradox is also evident within the literature examining individual's 165 landscape preferences and attitudes towards biodiversity. For example, when investigating 166 attitudes towards field margins in Swiss agricultural landscapes, Junge et al. (2009) found that 167 people expressed a greater appreciation for margins where they estimated plant species 168 richness was higher. Yet, actual plant richness of the field margins did not influence 169 appreciation. Thus, as was true of the urban green space studies highlighted above, people's 170 predilections appear to be driven by the biodiversity they perceive to be present. However, 171 there are exceptions. Qiu et al. (2013) discovered that people could correctly estimate the 172 differences in plant diversity across habitats, and that the species richness of this taxon was 173 not related to preference, with open park locations rated more highly than areas of more 174 complex vegetation. Likewise, Shanahan et al. (2015a) found that people do not preferentially

visit parks with higher tree and vegetation cover, despite these areas having the potential forenhanced experiences of biodiversity.

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178 The disparities outlined above may be a consequence of ecological factors such as spatial 179 scale, taxonomic group and the metrics used to measure biodiversity. Findings at a broad 180 scale (i.e. asking people to rank images of landscapes by the level of human disturbance) 181 indicate that people can reliably identify differences in landscape intactness (Bayne et al. 182 2012), but fail to estimate the objective level of greenness of their neighborhood (Leslie et al. 183 2010). While Lindemann-Matthies et al. (2010b) reported a positive relationship between 184 plant species richness and individual aesthetic preferences, the effect was modified by the 185 spatial distribution of the plants. Additionally, plant communities consisting of the same 186 number of species were perceived to be more species-rich when evenness (the relative 187 abundance of different species) was higher (Lindemann-Matthies et al. 2010b). This suggests 188 that species richness alone may not be the best measure of biodiversity when considering 189 human responses to, and appreciation of, biodiversity. Indeed, this is understandable, as many 190 species cannot be detected without specialist training (e.g. because they are difficult to 191 identify) or without a great deal of effort (e.g. because of their elusive behavior). When 192 unpicking the people-biodiversity paradox, researchers should consider using a suite of more 193 resolved biodiversity metrics (e.g. abundance, evenness, functional diversity) to determine the 194 ecological quality of environmental green spaces (Lovell et al. 2014).

195

196 Explicit consideration of the complexity associated with human well-being and 197 biodiversity

198 It is possible that the emerging people-biodiversity paradox is a result of the multi-199 dimensionality of both biodiversity and human well-being, making it difficult to account for

200 and measure the complex social and ecological characteristics that may influence the outcome 201 of interactions (Hartig et al. 2014, Lovell et al. 2014). The concepts of health and well-being 202 are just as multifarious as that of ecological quality, incorporating a wealth of different 203 aspects of human physiological, cognitive, emotional, social and spiritual wellness, and 204 studies have explored these facets from several disciplinary perspectives (Irvine and Warber 205 2002, Keniger et al. 2013, Irvine et al. 2013). Heterogeneity in research design, and the use of 206 different ecological and well-being measures, thus reflects the complexity that social and 207 natural scientists are grappling with in trying to understand how people derive benefits from 208 interacting with nature/biodiversity. Our conceptual framework (figure 1) illustrates that such 209 interactions could generate outcomes for an individual's health/well-being and, in turn, this 210 might relate to human perceptions of, and behaviors towards, biodiversity.

211

212 The type and intent of the human-biodiversity interaction are likely to influence the outcome 213 (Church et al. 2014), which might be positive, neutral or negative (figure 1). Additionally, 214 experiences of biodiversity can be influenced by physical/environmental characteristics 215 associated with the point of interaction, such as the season and prevailing weather conditions 216 (figure 1, table 1). These filters are often ignored in research projects, but are potentially 217 important determinants of outcomes (White et al. 2014). While the majority of studies 218 conducted on human-nature/biodiversity interactions thus far have concentrated on benefits 219 gained by people, disservices also require research attention (Dunn 2010), as practitioners and 220 policy-makers need to be able to make fully informed decisions in a land-use planning and 221 management context (Lyytimäki and Sipilä 2009). At the most extreme, interactions with 222 biodiversity can lead to death and injury, for instance, through attacks from predators or via 223 the contraction of pathogens. Human-wildlife conflict can also lead to diminished health/well-224 being in addition to physical injury or pathology (Barua et al. 2013) and, in an urban context, close contact with nature has been associated with fear, disgust and discomfort (Bixler andFloyd 1997).

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228 The outcome of an interaction with biodiversity can feedback to the individual (figure 1), 229 changing aspects of their ecological knowledge, values, and underlying health/well-being. 230 Indeed, a particular interaction might be perceived as positive or negative, depending on the 231 individual making the evaluation (Buchel and Frantzeskaki 2015). In turn, this could 232 contribute to the likelihood that the individual will subsequently interact with biodiversity and 233 may influence future outcomes (e.g. positive interactions might predispose future outcomes to 234 being more positive and vice versa). A suite of individual characteristics can moderate both 235 the magnitude and direction of an outcome, as well as the probability that an interaction will 236 take place (figure 1, table 2). To illustrate, a review of fear of crime experienced in urban 237 green spaces found variability in responses according to factors such as age, gender, socio-238 economic status, frequency of visits and familiarity with the site, as well as the bio-physical 239 attributes of the areas (Maruthaveeran and van den Bosch 2014). Cultural factors are also 240 likely to be important. A recent paper by Lindemann-Matthies et al. (2014) demonstrated that 241 a cohort of Chinese people did not show a preference for biodiverse forest, whereas the 242 comparative Swiss participants favored species rich forest over monoculture. Similarly, a 243 study in Singapore found that neither access to, nor use of, green spaces influenced measures 244 of well-being (Saw et al. 2015). There is a paucity of such cross-cultural studies, with most 245 work on human-nature/biodiversity interactions being geographically biased towards 246 industrialized regions of the Global North (Keniger et al. 2013). This hinders our 247 understanding, and there is a need for greater focus on biodiversity rich countries where urban 248 development is accelerating rapidly (Lindemann-Matthies et al. 2014).

250 How frequently people choose to visit green spaces, if at all, can be influenced by both the 251 characteristics of individuals (table 2), as well as the accessibility/proximity of the green 252 space (table 1). The contribution of these different sets of attributes appears to be variable, 253 with contradictory results reported in studies. For example, people's nature orientation, that 254 is, the affective, cognitive and experiential relationship they have with the natural world, has 255 been shown by some to be more important in determining time spent in urban green spaces 256 than the availability of nearby green space (Lin et al. 2014). Conversely, others report that 257 proximity and the time it takes individuals to reach a site are stronger predictors of visit 258 frequency (Dallimer et al. 2014). The visit duration can also influence the outcome of 259 interactions (a dose-response relationship), with research typically finding a positive 260 relationship between the time spent in a green space and the response (White et al. 2013). 261 However, others have found less straightforward dose-response relationships. For instance, 262 Barton and Pretty (2010) found diminishing, but still positive, mental health returns from 263 higher intensity and duration green exercise, while Shanahan et al. (2015b) suggests several 264 potential dose-response relationships.

265

A further complexity that requires careful consideration is that spending time in green spaces can be beneficial to individuals, not necessarily because of interaction with biodiversity, but by virtue of the fact it encourages and facilitates behaviors that are known to be mentally and physical favorable, such as exercise and social interaction. It is therefore important to evaluate the extent to which human-biodiversity interactions provide added value. Research into green exercise, for example, has shown that there are synergistic benefits associated with taking part in physical activities while viewing nature (Pretty et al. 2005).

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274 What are the consequences of the people-biodiversity paradox for conservation?

275 If, as recent studies suggest, human-biodiversity interaction outcomes are influenced by 276 people's perceptions of biodiversity, rather than objective measures, the role of ecological 277 knowledge in influencing the relationship is a key dimension worthy of consideration. The 278 lack of ecological knowledge in developed world citizens (Pilgrim et al. 2008, Dallimer et al. 279 2012) might support authors' assertions that there is a growing 'disconnection' between 280 people and nature (Pyle 1978, Turner et al. 2004, Miller 2005). They propose that an 281 'extinction of experience' is occurring because individuals are isolated increasingly from 282 nature in their everyday lives and, as such, they have less impetus to protect and experience 283 nature, leading to a vicious deleterious cycle. Social or education interventions have been 284 advocated as a means to reverse this negative feedback. For instance, research has shown that 285 people with more taxonomic knowledge express preferences for more species rich flower 286 meadows (Lindemann-Matthies and Bose 2007), and children who participated in an 287 educational program had an increased appreciation of local nature (Lindemann-Matthies 288 2005). However, questions remain as to whether such interventions have a long-term impact 289 on levels of interest and engagement with biodiversity (Shwartz et al. 2012).

290

291 If people are only responding positively to certain traits and assemblages of species, it is 292 possible that these might not be the biodiversity elements that conservationists would wish to 293 support. Urban areas are highly susceptible to biotic homogenization and harbor many non-294 native species (McKinney 2002). As yet, it is still unclear whether the nativeness of species 295 makes a difference to the well-being response an individual receives from an interaction. 296 People may value species that they know to be native more (Lundhede et al. 2014), although 297 non-native species may possess traits (e.g. larger body size, more colorful or behaviorally 298 distinct) which people prefer (Frynta et al. 2010). This could present a potential challenge and 299 conflict for conservationists and practitioners, who may seek to promote native taxa through the management of non-native species, but also need to encourage the health/well-being benefits that may gained from interacting with charismatic non-native species. A better understanding of the public perception of non-native species could feed usefully into the ongoing debates on the legitimacy of the novel ecosystem (box 1) concept (Hobbs et al. 2006, Kowarik 2011), as well as providing an evidence-base for land-use planning, management and decision-making.

307 Even if future research continues to corroborate the advantages people can gain from 308 interacting with biodiversity, individuals might not consciously relate these benefits to 309 biodiversity per se. If this is the case, there is no reason to expect an individual's perception 310 of biodiversity to alter as a consequence human-biodiversity interactions and, subsequently, to 311 presume a shift towards more pro-biodiversity behavior. Indeed, positive attitudes towards 312 biodiversity alone do not translate into pro-biodiversity behaviors (Waylen et al. 2009) (figure 313 1), being modified by numerous external as well as internal factors, including subjective 314 norms, facilitating factors and moral obligations (Clayton and Myers 2009). Much more 315 research is needed to discern the links between exposure to biodiversity and how this might, 316 ultimately, lead to shifts in underlying attitudes and behavior. Beyond education, 317 understanding what individual's perceive as constituting a preferable biodiverse environment 318 will allow for human-modified landscapes to be designed in a manner which delivers benefits 319 to both people and biodiversity.

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321 Conclusion

The examples presented here of the people-biodiversity paradox illustrate the need for careful consideration before a straightforward relationship between increased biodiversity and improved human well-being can be implied. If we wish to align the agendas of public health

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and biodiversity conservation, we first need to understand the mechanisms behind the peoplebiodiversity paradox, and the added value that enhanced people-biodiversity interactions can
deliver for conservation. Well-designed and carefully conducted interdisciplinary research,
which genuinely bridges traditional disciplinary boundaries, will be the key to effectively
unpacking this paradox.

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Figure 1: Conceptual framework of human-biodiversity interactions and potential outcomes for health and well-being, perceptions of biodiversity and pro-biodiversity behavior. Humanbiodiversity interactions can lead to a cascade of potential outcomes. The question marks represent less well-understood relationships. The dotted lines represent feedbacks from outcomes back to biodiversity or the individual.

Box 1: Key terminology

Biodiversity	The variability among living organisms from	Convention on Biological Diversity
	all sources including, inter alia, terrestrial,	(www.cbd.int/convention/articles/default.shtml?a=cbd-02)
	marine and other aquatic ecosystems and the	
	ecological complexes of which they are part;	
	this includes diversity within species,	
	between species and of ecosystems	
Green space	Open, undeveloped land with natural	Centers for Disease Control and Prevention
	vegetation	(www.cdc.gov/healthyplaces/terminology.htm)
Novel ecosystem	Ecosystems which have been heavily	Hobbs et al. 2009
	modified by humans, and differ in	
	composition and/or function from present and	
	past systems	
Human health	Health is 'a complete state of physical,	World Health Organization
	mental and social well-being, and not merely	WHO 1948
	the absence of disease or infirmity	
Human well-being	(Subjective) well-being encompasses	Stiglitz et al. 2009
	different aspects - cognitive evaluations of	
	one's life, happiness, satisfaction, positive	
	emotions such as joy and pride and negative	
	emotions such as pain and worry	
Species richness	The number of species observed in a defined	Begon et al. 2006
	geographic location	

 Table 1: Illustrative physical/environmental characteristics which could influence the

 likelihood that people will interact with nature/biodiversity, and the outcome of such

 interactions.

Characteristic	Description and supporting examples
Season	Seasonal changes affect the well-being of office workers (Hitchings 2010)
Weather	Landscape preferences are influenced by climatic conditions (White et al. 2014)
Accessibility	People who report that they have easy access to green spaces use green spaces more regularly
	(Hillsdon et al. 2011)
Proximity	People with less green space in close proximity to their home reported greater loneliness and a
	perceived shortage of social support (Maas et al. 2009). Populations exposed to the greenest
	environments have the lowest levels of health inequalities (Mitchell and Popham 2008). People
	visit more frequently when it takes less time to reach a green space (Dallimer et al. 2014)

Table 2: Illustrative individual characteristics which could influence the likelihood that people will interact with nature/biodiversity, and the outcome of such interactions.

Characteristic	Description and supporting examples
Gender	Gender differences have been observed in associations between urban green space and health outcomes (Richardson and Mitchell 2010). Women demonstrate a
	preference for higher plant species richness than men (Lindemann-Matthies and Bose 2007, Lindemann-Matthies et al. 2010a)
Age	Proximity to green space has a greater influence on the health of the elderly than other age groups (de Vries et al. 2003). Older people prefer species rich field margins
	(Junge et al. 2009) and meadows (Lindemann-Matthies and Bose 2007)
Education	Health benefits from proximity to green space are greater for people with a lower level of completed formal education (de Vries et al. 2003)
Socio-demographic/	There are racial and economic inequalities regarding access to biodiversity, for example fewer native birds have been found in neighborhoods comprising of
economic factors	predominantly Hispanic and lower-income people (Lerman and Warren 2012)
Home location	People who identify themselves as 'urban' report lower levels of restoration from images of nature than 'rural' individuals (Wilkie and Stavridou 2013)
Culture	Chinese study participants demonstrate no strong preferences for biodiversity when compared to Swiss participants, who favored species-rich forests over monocultures
	(Lindemann-Matties et al. 2014). The wellbeing of residents in Singapore was not affected by access to, or the use of, green spaces (Saw et al. 2015)
Childhood experience	People who spent their childhood in a more natural environment show a greater preference for green roofs over gravel (Fernandez-Cañero et al. 2013)
Connectedness to nature	Residents living in neighborhoods with greater richness and abundance of bird species and density of plants had a higher connection to nature (Luck et al. 2011)
Ecological knowledge	Children who participated in an educational program had increased appreciation of local nature (Lindemann-Matthies 2005). People with better wildlife identification
	skills were able to more accurately estimate the species richness of surrounding vegetation, birds and butterflies (Dallimer et al. 2012)
Intention	Although interacting with nature is beneficial to urban park visitors, it was not a main motivation for visiting (Irvine et al. 2013). Frequent users of urban green spaces
	state motivations relating to physical activities, whereas infrequent users motivations are more associated to the quality of the space (Dallimer et al. 2014)
Social interaction	Individuals who visited natural areas accompanied by children experienced less restoration than those who were alone (White et al. 2013). Fear of crime influences
	some individuals to avoid urban green spaces (Maruthaveeran and van den Bosch 2014)

State of mind Urban green spaces which are perceived to contain more nature are also perceived to be more restorative by stressed individuals (Peschardt and Stigsdotter 2013)