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REVIEW PAPER

Biodiversity and human health: evidence for causality?

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Abstract The Millennium Ecosystem Assessment and other commentators have warned about the impacts that biodiversity decline will have on human health. There is no doubting that the natural world provides mankind with the majority of the resources required to sustain life and health. Many species provide food, fuel, medicines; with the potential for many more (as of yet) undiscovered uses for various species. Despite this, there have been very few attempts to actually investigate relationships between biodiversity (i.e. number of species, rather than the ability of specific species to provide health benefits) and human health. This paper reviews the available evidence and demonstrates that while the links between biodiversity and health seem intuitive, they are very difficult to prove. Socio-economics has a huge influence on health status and the exploitation of natural resources (leading to eventual biodiversity loss) tends to have a positive economic effects. More direct effects of biodiversity on health include the diversity of the internal microbiome, the effect of natural diversity on our mental health and well-being (although this has large social aspects with many people feeling fearful in very diverse environments). Still to be elucidated are the tipping points where the level of global biodiversity loss is such that human health can no longer be sustained.

Keywords Ecosystem services · Disease regulation · Dilution effect · Microbiome · Quality of life

Introduction

One of the challenges facing those who want to raise the profile of the relationship between the diversity of life and human health, is the requirement to cross the agenda of the environmental and health sectors. This agenda has been treated extensively by international

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Conventions—in particular the Ramsar Convention on Wetlands, and the Convention for Biological Diversity (CBD); from these conventions frameworks have been developed demonstrating the on-going nature of the MEA work. However, significant challenges remain to promoting the protection of biodiversity up the health policy agenda. Many commentators have indicated that causality is central to the derivation of health policy with policy makers familiar with the types of evidence provided by biomedical research (e.g. Petticrew et al. 2004). More weight is often given to individual-level studies, compared to ecological studies that look at broader trends over groupings of individuals (Hough 2007). Some commentators have argued that there is a significant disconnect at the core of the global environmental crisis—that health policy makers (and the public by and large) do not understand that health outcomes are ultimately dependent on other species and on the integrity of the planet's ecosystems, and, as a result, they do not appreciate the urgent need to protect the natural world (Chivian and Bernstein 2004). It could therefore be argued that for measures to reduce biodiversity loss in order to protect human health to be considered, direct causality between biodiversity and human health outcomes needs to be established.

According to the CBD, biodiversity is defined as 'the variability among living organisms from all sources including, *inter alia*, terrestrial, marine and other aquatic ecosystems and ecological complexes of which they are part; this includes diversity within species, between species and of ecosystems' (UNEP 1995). This is one of the most comprehensive definitions, but other definitions of biodiversity are also used. For example, Leemans (1999) defines biodiversity as 'the collection of genes, species, communities and ecosystems, which constitute the living component of the earth's system'.

Approximately 1.7×10^6 species have been identified on Earth and given Linnaean names (UNEP 1996), but there may be ten times that number and perhaps many more if microbial diversity is included (Pimm et al. 1995). Species interact with each other and with their physical and chemical environments to make up ecosystems such as forests and wetlands. Stratospheric ozone depletion, pollution, the introduction of alien species, the over-harvesting of species, and increasingly global climate change all threaten biodiversity and thus ecosystem function (Walther et al. 2002). The degradation, reduction, and fragmentation of habitats on land, in fresh water, and in the oceans are possibly the greatest threats (Pimm and Raven 2000). All of these factors are primarily the result of human activity and are driven by unsustainable consumption, especially in the industrialised world, and by rising human populations. These activities have increased the rate of species extinction. While no one knows how many species have disappeared, estimates range from tens to hundreds of thousands; the vast majority of which have never been catalogued, let alone investigated for their potential benefit to mankind (Herndon 2010).

Potential consequences of biodiversity loss are considered to be the loss of medical models, diminished supplies of raw materials for drug discovery and biotechnology, and threats to food production and water quality; and climate regulation (Grifo and Rosenthal 1997; NEA 2011). Maintaining a certain level of biodiversity is considered necessary for proper ecosystem functioning and the provisions of ecosystem services (i.e. the benefits provided to humankind from a multitude of resources and processes that are supplied by natural ecosystems) to mankind, although what the critical levels are is unclear (Schulze and Mooney 1994; Chapin et al. 2000; Sala et al. 2000; WRI 2000; De Groot et al. 2000). Biodiversity loss could therefore result in compromised ecosystem functions, which, in turn, could negatively influence human health. Several authors have addressed the links between biodiversity and ecosystem functioning (e.g. Schulze and Mooney 1994; UNEP 1995; Mooney 1996; Folke et al. 1996; Chapin et al. 2000; Schwartz et al. 2000), but it is still unclear which ecosystem functions are primarily important to sustain human health.

Huynen et al. (2004) described the following 'health functions' that ecosystems provide: (i) provision of basic needs like food, clean air, clean water and clean soils; (ii) prevention of the spread of diseases through biological control; (iii) medical and genetic resources necessary to prevent or cure diseases; and (iv) contributions to the maintenance of mental health by providing opportunities for recreation and cognitive development. The Millennium Ecosystem Assessment (MEA 2005) summarised these four areas as: ecosystem services, disease regulation, medical and genetic resources, and quality of life (it could be argued that the latter three are simply a subset of 'ecosystem services'). Paradoxically, the same report found that declines in the majority of ecosystem services assessed have been accompanied by steady gains in human well-being, at least at global scale (MEA 2005).

The majority of the discourse that relates biodiversity to human health is associated with provisioning services: the production of food and fibre, production of agents of biomedical value (e.g. sources of pharmaceutical agents), as a genetic resource. Clearly the more diverse the biology, the greater the likelihood of species existing which produce useful products for mankind. Similarly, the greater the likelihood of species existing that produce products detrimental to human health (e.g. poisons, diseases) and therefore it is difficult to argue from a statistical perspective that biodiversity per sé is vital for human health. However, the ability of the natural world to provide mankind with the building blocks to maintain its health and existence is fundamentally important. Much of the evidence presented in the scientific literature relates to the links between specific beneficial species and human health, rather than a reliance on biodiversity per sé. An example of this is the biomedical value (e.g. sources of pharmaceutical agents) of specific species. As scientists continue to discover new biological sources of pharmaceutical agents, both scientists and public health advocates have asserted that the preservation of biodiversity is crucial for present and future human health (Chivian 1997; Grifo et al. 1997). As most species have little or no biomedical value, this argument focuses more on preserving particular biomedically important organisms than on biodiversity per sé (Ostfeld and Keesing 2000a). This is an important distinction, as it is relatively easy to think of examples of species that are beneficial (in health terms) to humans; however, in many cases mankind has optimised exploitation of beneficial species by actually reducing biodiversity (e.g. monoculture cropping).

Therefore, this review does not consider the links between biodiversity, intermediate factors such as basic provisioning services and human health (Sect. 2 provides a more detailed explanation of this). These are implicit in how the world functions—mankind needs food, water, air, and also medicines. This review aims to move beyond this basic relationship to investigate whether there is any epidemiological evidence (including weight of evidence) to suggest that biodiversity per sé has a *direct* influence on human health and wellbeing.

Methodology

This was a purposive review of peer-reviewed literature related to biodiversity decline as a risk factor for disease. In a few cases, this was supplemented with literature from web-accessible documents and other *grey literature*. This review was interested in documented evidence for *direct* causality of biodiversity on human health outcomes. Therefore, studies that attempted to make statistical associations with biodiversity (i.e. number of species) with specific human health outcome(s) were sought. In all cases, these associations will be adjusted by modifying factors such as socioeconomic status, and confounding factors. Only studies that adjusted (either explicitly, or in commentary) any associations between biodiversity and human health outcomes for identified modifying and confounding factors were considered. Studies that looked at the direct association between biodiversity and 'intermediate factors' (Huynen et al. 2004), rather than human health outcomes, were discounted. While a study may show a strong association between e.g. biodiversity and yield, the knock-on impact on human health is merely implicit and does not help elucidate a causal link between biodiversity and health.

Computerized database searching of a range of international databases was carried out: MEDLINE (MEDLINE Database, National Library of Medicine, Bethesda, MD, USA www.biomednet.com), BIDS (Join Information Systems Committee, University of Bath, Bath, UK, www.bids.ac.uk), PubMed (National Library of Medicine, www.ncbi.nlm.nih.gov/PubMed) and ISI Web of Knowledge (Mimas, University of Manchester, UK, wok.mimas.ac.uk).

A systematic, staged search strategy was employed using the following search terms: 'biodiversity' or 'ecosystem services' and 'human health' or 'public health' or 'wellbeing' or 'infectious disease' or 'mental health' or 'cancer'. Almost 9,000 references were found. The search was further refined to 197 papers that explicitly investigated potential links between biodiversity and/or ecosystem services and health. Only papers written in English were fully included. Original full texts were obtained for all studies. Upon examination of the full texts, only 13 provided any form of quantitative statistical analysis of potential associations between biodiversity and health. Therefore, wider, more descriptive studies and accounts were also included while the following types of studies were excluded (except where a method was used that showed principles relevant to the context of this review): (i) studies focussed on intermediate factors (e.g. food production and water quality) as although biodiversity loss could result in negative effects on intermediate factors (due to compromised ecosystem functions), it is merely one of the many factors (e.g. land use, pollution) affecting intermediate factors. Therefore any relationship between human health and intermediate factors is impossible to de-tangle from any association between biodiversity and health. (ii) Studies looking at the (potential) health benefits from specific species or ecosystems (e.g. pharmaceuticals, traditional medicine, nutrition) as these do not look at biodiversity per sé, (iii) similarly, the effects of loss of raw materials for drug discovery and biotechnology and human health are difficult to determine by linking spatial differences in health to spatial differences in loss of raw materials due to globalisation of trade/markets, and (iv) other papers that only made passing inference to biodiversity decline as a risk factor for disease. The remaining 54 studies formed the basis of this review, although other papers within the database were used as background material.

The review itself is structured into three sections, based on how directly humans are exposed to biodiversity. A structure based on directness of exposure ties in with the aims of this review, as more direct exposures are more likely to provide the conditions necessary for elucidating causality. As such, this review starts with discussing the more indirect exposures to biodiversity "Indirect exposure to biodiversity" section, before working down to direct exposures (where individuals have direct contact with nature and diversity; "Direct exposure to biodiversity" section), and finally to internal exposures to diversity such as the gut micro-flora "Internal exposure to biodiversity" section).

Indirect exposure to biodiversity

Ecosystem function

There is growing concern that loss of biodiversity may affect ecosystem functioning and, therefore, may threaten the continued provision of various ecosystem services on which humans depend (Chapin et al. 2000). Recent syntheses have shown many positive effects of biodiversity on ecosystem properties (e.g. plant aboveground and root biomass, biomass of marine plants and algae) related to the provision of ecosystem services (e.g. carbon storage, erosion control, regulation of water quality; Balvanera et al. 2006; Worm et al. 2006). With care, such results, while based primarily on small-scale biodiversity manipulation experiments, can be extrapolated to estimate the contribution of different components of biodiversity to the provision of services at larger spatial and temporal scales (Schläpfer et al. 1999; Roscher et al. 2005; Duffy 2009). However, only a very limited number of studies have attempted to make explicit connections between biodiversity components, ecosystem properties and services, and human health (Quijas et al. 2010).

Huynen et al. (2004) explored the association between health and biodiversity loss by means of regression analysis, with controlling for socio-economic developments. Available country-level indicators were used in this analysis: for human health (life expectancy at birth (5-year average), disability adjusted life expectancy (DALE), infant mortality rate per 1,000 live births, percentage low-birthweight babies); biodiversity (percentage threatened species, percentage of land highly disturbed by human activities, current forest as a percentage of the land that would have been covered by closed forest about 8,000 years ago assuming current climatic conditions); socioeconomics (gross national product (GNP) per capita (Atlas method), development grade, adult (>15 years of age) illiteracy rate, total health expenditure as a percentage of gross domestic product (GDP), percentage of 1-year-olds immunised against measles, polio, tuberculosis and DTP (diphtheria, tetanus, poliomyelitis)). The authors chose not to include indicators of intermediate biodiversity factors, e.g. food production and water quality due to difficulties in statistical inference as described in "Methodology" section above.

The analysis by Huynen et al. (2004) showed that (as expected) all socio-economic indicators were significantly correlated with all health indicators in such a way that an increase in socio-economic development was positively correlated with better health. Crude associations between health and biodiversity indicators showed that life expectancy was significantly correlated with the percentage of threatened species and the percentage of highly disturbed land; DALE was significantly correlated with current forest as a percentage of 8,000-year-old forest and the percentage of highly disturbed land; infant mortality rate was significantly correlated with all indicators of biodiversity; and the percentage of low-birthweight babies was significantly correlated with the percentage of land highly disturbed by humans. However, adjusting the model for confounding by socio-economic factors revealed only two significant associations. An increase in the percentage of threatened species was significantly associated with an increase in life expectancy and an increase in DALE. These results suggest that *decreasing* biodiversity is in fact beneficial for human health. This is a similar finding as that reported by the MEA, again indicating a positive impact of ecosystem service loss on human well-being at a global scale (NEA 2011). In many respects, these findings are intuitive as economic/industrial development tends to threaten species whilst at the same time increasing human life expectancy.

It should be noted, however, that the study by Huynen (2004) did not control for climate (or a proxy for climate such as latitude). Climate is a key factor in biodiversity, with the most bio-diverse countries tending to be in equatorial and tropical regions and much less diversity towards the poles. The correlation between climate and socioeconomic indicators is non-linear with the wealthiest nations tending to be located in the world's temperate zones; hence adjustment for socioeconomic status alone is likely to be inadequate.

In a very similar study, Sieswerda et al. (2001) investigated the link between life expectancy and measures of ecological (dis)integrity (percentage of land highly disturbed by human activities, percentage of forest remaining, percentage of annual change in forest, percentage threatened species, percentage of totally protected land, percentage of partially protected land) with controlling for GDP per capita. While Sieswerda et al. (2001) also concluded that GDP per capita was the best predictor of health; they could not demonstrate any relationships between the selected measures of ecological integrity and life expectancy. This is unexpected, as increasing human economic activity usually increases life expectancy. It should be noted that the model of Huynen et al. (2004) contained more recent data and almost double the number of observations compared to the model of Sieswerda et al. (2001).

Large country-level assessments (e.g. MEA 2005; Huynen et al. 2004; Sieswerda et al. 2001) must be interpreted with some caution. Data measured at country-level are likely to mask regional and local-level effects. Apart from the fact that there are limitations to regression analysis in providing any proof of causality, least squares regression models assume linear relationships between reductions in biodiversity and human health and thus imply a linear relationship between loss of biodiversity and the provision of relevant ecosystem goods and services. A number of authors, however, have suggested that ecosystems can lose a proportion of their biodiversity without adverse consequences to their functioning (e.g. Schwartz et al. 2000). Only when a threshold in the losses of biodiversity is reached does the provision of ecosystem goods and services become compromised. These models also tend to assume a positive relationship between socio-economic development and loss of biodiversity. One problem with this expectation is that the loss in biodiversity in one country is not per definition the result of socio-economic developments in that particular country, but could also be the result of socio-economic developments in other parts of the world (Wackernagel and Rees 1996). Furthermore, the use of existing data means researchers can only make use of available indicators. Unlike for human health and socio-economic development, there are no broadly accepted core-set of indicators for biodiversity (Soberon et al. 2000). The lack of correlation between biodiversity indicators (Huynen et al. 2004) shows that the selected indicators do not measure the same thing, which hinders interpretation of results. Finally, there is likely to be some sort of latency period between ecosystem imbalance and any resulting health consequences. To date, this has not been investigated using regression approaches.

Finally, it is thought that provisioning services are more crucial for human health and well-being that other ecosystem services (Raudsepp-Hearne et al. 2010). Trends in measures of human well-being are clearly correlated with food provisioning services, and especially with meat consumption (Smil 2002). While $\sim$60 % of the ecosystem services assessed by the MEA were found to be in decline, most of these were regulating and supporting services, whereas the majority of expanding services were provisioning services such as crops, livestock and aquaculture (MEA 2005). Raudsepp-Hearne et al. (2010) investigated the impacts on human well-being from decreases in non-food ecosystem services using national-scale data in order to reveal human well-being trends at the global scale. At the global scale, forest cover, biodiversity, and fish stocks are all decreasing; while water crowding (a measure of how many people shared the same flow unit of water placing a clear emphasis on the social demands of water rather than physical stress

(Falkenmark and Rockström 2004)), soil degradation, natural disasters, global temperatures, and carbon dioxide levels are all on the rise, and land is becoming increasingly subject to salinization and desertification (Bennett and Balvanera 2007). However, across countries, Raudsepp-Hearne et al. (2010) found no correlation between measures of well-being and the available data for non-food ecosystem services, including forest cover and percentage of land under protected-area status (proxies for many cultural and regulating services), organic pollutants (a proxy for air and water quality), and water crowding index (a proxy for drinking water availability, Sieswerda et al. 2001; WRI 2009) This suggests there is no direct causal link between biodiversity decline and health, rather the relationship is a ‘knock-on’ effect. I.e. if biodiversity decline affects mankind’s ability to produce food, fuel and fibre, it will therefore impact on human health and well-being. As discussed in the introduction, the fact that humans need food, water and air to live is an obvious one. All these basic provisions *can* be produced in a diversity-poor environment. Therefore, to understand whether there is a potential causality relationship between biodiversity in its own right and human health, we need to move beyond the basic provisioning services.

Disease regulation

Well over 100 years ago, medical entomologists suggested a connection between species diversity and transmission of vector-borne diseases of humans (reviewed in Service 1991). Recently, there has been renewed interest in the potential effects of diversity on disease risk, primarily due to interest in identifying and evaluating utilitarian functions of biodiversity (Loreau et al. 2001). Despite the fact that hypothetical effects of diversity on disease transmission have now been described for multiple diseases including Hantavirus (e.g. Ruedas et al. 2004; Mills 2006; Susán et al.. 2009), Lyme disease (e.g. Van Buskirk and Ostfeld 1995; Norman et al. 1999; Gilbert et al. 2001; Allan et al. 2003; LoGiudice et al. 2003;), West Nile Virus (e.g. Quirun et al. 2004; Telfer et al. 2005; Ezenwa et al. 2006), Nipah Virus (Chua et al. 1999; Lam and Chua 2002), Yellow fever (Ribeiro and Antunes 2009), Ross River Virus (e.g. Carver et al. 2009), malaria (e.g. Molyneux et al. 2008; Yasuoka and Levins 2007), schistosomiasis (Evers et al. 2006), leptospirosis (Derne et al. 2011), and ciguatera fish poisoning (e.g. Bagnis 1981), the specific mechanisms underlying these effects are not well understood. For example, various empirical and modelling investigations have suggested that increased species diversity could reduce disease risk by regulating the abundance of an important host species (Burdon and Chilvers 1982; Rudolf and Antonovics 2005), or by redistributing vector meals in the case of vector-borne diseases (Van Buskirk and Ostfeld 1995; Norman et al. 1999; LoGiudice et al. 2003). However, other studies have suggested that increased diversity could increase disease risk if, for example, added species function as alternative sources of infection, or if they increase vector numbers or activity by providing additional sources of vector meals (Holt and Pickering 1985; Norman et al. 1999; Gilbert et al. 2001; Schmidt and Ostfeld 2001; Saul 2003; Dobson 2004).

Incidence of infectious disease has increased during the last decades (Jones et al. 2008). The explanatory factors reported are generally those associated with on-going global changes including loss of biodiversity, but also climate change and increased international trade. However, it is difficult to demonstrate a direct impact of biodiversity loss on infectious diseases because of non-linear complex interactions between biodiversity and climate, pathogens, disease vectors and hosts (Lafferty 2009). A reduction in biodiversity at the local-level may reduce human exposure to certain vector-borne diseases suggesting a novel function of biodiversity with quantifiable value for human health (Keesing et al.

2010; Ostfeld and Keesing 2000a,b). The majority of emerging infectious diseases seem to be localised in higher latitudes and in developed countries (North America, Europe and Japan; Jones et al. 2008). However, research investigating the explanatory factors for the variety (total number) of endemic diseases paints a very different picture. Their diversity seems to be greater in the tropical zones where bird and animal biodiversity is greatest (Guernier et al. 2004; Dunn et al. 2010). Overall, two principal mechanisms by which biodiversity can be protective of human health through regulation of infectious diseases are proposed in the literature: firstly, regulation of populations of pathogen hosts by direct predatory and competitive interactions, and secondly, reduction of pathogen success by the dilution effect (Derne et al. 2011). A biodiverse community has a greater probability of supporting predatory species that effectively regulate prey populations (Mills 2006; Ostfeld and Holt 2004), thereby reducing pathogen levels if the prey species is a host. Similarly, a larger number of species within a community makes the presence of competitors more likely (Hooper and Dukes 2010), which will lower a host population's growth or survival rates (Mills 2006).

Morand and Waret-Szkuta (2012) carried out a large epidemiologic analysis of European data from the GIDEON (Global Infectious Diseases and Epidemiology Network) database, which provided information on the presence and occurrence of possible epidemics of human infectious diseases between 1950 and 2010 by country. This included 114 epidemic infectious diseases identified in 36 different countries. Socioeconomic, demographic and environmental data provided by FAO and the World Bank were also incorporated into the analysis; these data included information on demography, GDP, forested surface area, average temperatures and rainfall, as well as annual variability of these latter two factors. Data for birds (Bird Life International) and mammals (International Union for Conservation of Nature) were also included. For the total number of infectious diseases, it was found that the best predictors included each country's surface area ($p = 0.02$) and the richness of birds and mammals therein ($p < 0.0001$). This suggested that a country with a large surface area and having large biodiversity would also have a greater variety of infectious diseases. Therefore, a decrease in biodiversity could actually be protective against incidence of epidemics. These results seem in line with other global indicator analyses such as that of Huynen et al. (2004).

'Dilution' and 'rescue' effects

A primary mechanism by which biodiversity may moderate disease risk, referred to as the 'dilution effect', has been described, *inter alia,* for Lyme disease (Ostfeld and Keesing 2000b; Schmidt and Ostfeld 2001; LoGiudice et al. 2003) and may also operate for a range of other vector-borne diseases (Ostfeld and Keesing 2000a; Holt et al. 2003; Telfer et al. 2005). The dilution effect predicts that infection rates among vectors, and ultimately human infection risk, will be lower in highly diverse host communities where incompetent reservoir hosts dilute rates of disease transmission between vectors and highly competent hosts (Ezenwa et al. 2006). Conversely, if species tend to be highly competent reservoirs, high species diversity may actually increase disease prevalence. This opposing effect, called a 'rescue effect' (Ostfeld and Keesing 2000b), describes the relationship between species diversity and disease prevalence if multiple species serve as competent virus hosts. While the dilution and rescue effects have been shown to apply to a limited number of pathogens spread by generalist vectors (Ostfeld and Keesing 2000a), it is unclear how broadly these models apply in natural disease systems, and our understanding of the extent to which patterns of biodiversity affect human disease is extremely limited (Ezenwa et al. 2006).

Lyme disease

One classic example of the dilution effect is the relationship between Lyme disease (caused by the spirochete bacterium *Borrelia burgdorferi*, which is transmitted through the bite of ticks of the genus *Ixodes* (*I. scapularis* and *I. pacificus* in North America; *I. ricinus* and *I. persulcatus* in Europe, Asia, and Africa). Between 10,000 and 17,000 cases of Lyme disease are reported each year in the Unites States alone (CDC 1998), with thousands of cases per annum across Europe and Asia (Lane et al. 1991; Barbour and Fish 1993).

The ticks of the genus *Ixodes* feed on a wide variety of host species, each with a different probability of infecting the ticks with the Lyme bacterium. The white-footed mouse (*Peromyscus leucopus*) is one of the most competent known reservoir species for the bacterium with >90 % of ticks feeding on wild mice becoming infected with the Lyme bacterium (Dobson et al. 2006). In contrast, fewer than 15 % of ticks feeding on grey squirrels (*Sciurus carolinensis*) become infected despite virtually all squirrels carrying the bacterium (LoGiudice et al. 2003). As a consequence, the lyme bacterium is much more prevalent in habitats dominated by white-footed mice than in habitats that harbour a diversity of species (LoGiudice et al. 2003). Several studies have shown that (anthropogenic) habitat fragmentation is associated with mice numbers in that small patches of woodland are unable to support the predators that would usually keep the mouse population in check (Allan et al. 2003; Van Buskirk and Ostfeld 1998, 1995). Thus there is an association between habitat fragmentation, diversity loss, and increased disease risk (Dobson et al. 2006).

Intuitively, this result can be understood as a 'dilution effect'. Any factor that decreases the representation by white-footed mice relative to other hosts in the vertebrate community would reduce the proportion of ticks infected with the Lyme disease spirochete. One mechanism of reducing the infection prevalence of ticks is therefore to reduce the abundance of white-footed mice while maintaining the presence of alternative host species. Another mechanism is to increase the number of alternative hosts, which typically are incompetent reservoirs (Matushka et al. 1991, 1993).

If higher diversity in the tick host community results in lower infection prevalence in the population of nymphal ticks, one would expect a negative correlation between species richness in the vertebrate community and the number of Lyme disease cases per capita. This was investigated in the Eastern seaboard of the United States by Ostfeld and Keesing (2000b) who tallied the species richness of terrestrial small mammals (orders Rodentia, Insectivora, Lagomorpha; Hamilton and Whitaker 1998), ground-nesting, shrub-nesting, and ground-foraging birds (Ehrlich et al. 1988), and lizards (Conant and Collins 1998) in each state. They found significant negative correlations between species richness of small mammals and lizards and incidence of Lyme disease cases. Interestingly, increasing species richness of ground dwelling birds was associated with increasing Lyme disease incidence. These results, however, were strongly confounded by latitude although the authors argue that it is the latitudinal gradient in species diversity that causes the apparent latitudinal gradient in Lyme disease incidence, i.e. consistent with a dilution effect. As with the analysis of Morand and Waret-Szkuta (2012), it seems almost impossible to disentangle the effects of climate from the effects of biodiversity.

West Nile Virus

Another classic example of the dilution effect is the potential associations between avian biodiversity and the prevalence of West Nile Virus (WNV); a mosquito-borne viral encephalitis for which wild birds serve as the primary reservoir hosts (Work et al. 1955;

Taylor et al. 1956; Hayes 1989). The virus first appeared in the United States in 1999 in New York City and soon afterwards the first human cases were reported along with several fatalities (CDC 1999; Campbell et al. 2002). By the end of 2004, WNV had spread to 48 states (CDC 2003; 2004), Canada (Lindsay et al. 2003), Mexico (Estrada-Franco et al. 2003), and the Caribbean (Dupuis et al. 2003; Komar et al. 2003a; Quirun et al. 2004). Evidence suggests that passerine birds tend to be the most competent avian WNV hosts, whereas non-passerines are much poorer hosts (Work et al. 1955; Komar et al. 2003b; Peterson et al. 2004). If non-passerine birds are relatively incompetent WNV hosts, then, according to the dilution effect, avian communities composed of high diversities of non-passerine birds may be less able to sustain WNV epizoonotics. Therefore, based on a dilution effect model, the rate at which vectors aquire and transmit virus should decline with increasing non-passerine diversity, resulting in reduced prevalence of both mosquito infections and human disease.

Ezenwa et al (2006) investigated possible associations between host diversity, vectors infection rates, and disease risk for WNV in humans. They found that virus amplification rates in mosquito vectors were significantly lower at locations with high diversity of non-passerine bird species. Similarly, significant negative associations were found between human disease incidence and non-passerine species richness in both 2002 and 2003. In contrast, there were no significant correlations between passerine species richness and either mosquito infection rates or human disease incidence. Since the dilution effect should only hold when individual species are poor virus hosts, the lack of an association between passerine species richness and virus infection rates supports the idea that passerines, as a group, are more competent virus hosts than non-passerines.

Zooprophylaxis

Many authors have put forward zoopropylaxis as being an example of biodiversity being protective of human health. A variety of historical papers have suggested that sleeping in close proximity to domestic livestock, particularly cattle, may reduce the rate at which mosquitoes bite humans, and thus reduce the likelihood of infection with malaria or other vector-borne pathogens (Zozaya 1943; Brumpt 1944/45; Downs and Pittendrigh 1946; Ejercito 1951; Issaris et al. 1953; Walton 1958; Al-Azawi and Chew 1959; all cited in Service 1991). Active zooprophylaxis is also known to have been undertaken where livestock are deliberately used as a barrier between mosquito breeding sites and human settlements (Dobson et al. 2006) and was most widely used in Soviet collective agriculture (WHO 1991). However, in many dry regions where malaria exhibits seasonal patterns of abundance, the by-products of cattle supply vital sources of moisture and nutrients that can contribute to the breeding success of mosquitoes. While cattle tend to divert mosquito bites in the short-term, they tend to increase mosquito abundance in the longer-term (Bouma and Rowland 1995).

In balance it is difficult to consider zooprophylaxis as an association between biodiversity and health. Rather it is the association between animal husbandry/management and infectious disease.

Direct exposure to biodiversity

Studies from around the world have found a link between how much green space a neighbourhood has and the health of the resident population. In some respects this link is expected because evidence from experimental studies in the laboratory and field suggests that being in natural environments may reduce stress, enable recovery from fatigue, lower blood pressure and promote healing. Green spaces may also encourage physical activity, and social contact, and there is also some evidence that suggests this relationship is synergistic. However, not all studies contained within this review found a link between green space and health; the relationship varied by country, gender, socio-economic position and, importantly, by the measure of health used. As with the preceding sections, the reasons for this variation are not yet clear.

Direct health indicators

While the majority of studies into the relationship between access to nature and health have focussed on indirect and psychological indicators, there is a limited literature that has investigated direct indicators of health. For example, a large (n=10,000) cross sectional study in the Netherlands investigated associations between diversity of environment (% greenspace, agricultural land, forestry, nature areas, gardens, urbanity) and self-reported symptoms, perceived general health and GHQ (12-point General Health Questionnaire) score (de Vries et al. 2003). They found that living in a green environment was positively related to all three health indicators, and more strongly than the degree of urbanity. The presence of a garden was also beneficial when measured against self-reported symptoms. These effects tended to be more significant in lower socioeconomic groups and in those who tend to spend more time at home. However, all types of greenspace were found to be equally effective, regardless of the diversity thus no explicit evidence was found linking biodiversity per sé to the three health indicators.

Takano et al. (2003) investigated the association between walkable green open space near the residence and longevity of senior citizens in a densely populated city. This longitudinal cohort study ($n = 3{,}144$) was conducted in Tokyo over a period of 5 years. Survival rates after 5 years were correlated with residential-environmental data gathered via a baseline assessment. It was found that living in a green neighbourhood, with accessible, walkable spaces positively influenced the longevity of urban senior citizens independent of age, gender, marital status, and socioeconomic status. Again, this study suggests that it is access to greenspace, rather than biodiversity per sé, that is associated with positive human health outcomes.

Ulrich (1984) undertook a retrospective study to try to ascertain whether greenspace accelerates the healing process. Ulrich used medical data over 9 years ($n = 46$) looked at a number of direct health measures: discharge date from hospital, comments from nursing staff, number of painkillers administered. It was found that patients with a window view of trees had less need for painkillers, had a reduced stay in hospital, and also had less behaviour-related issues. At best this study suggests that there is an association with looking at trees and more positive patient outcomes. Also, the indicators used in this study have been criticised as being unreliable measures of health effects (Schimmack et al. 2010).

Synergistic benefits of exercising whilst being exposed to nature

A number of researchers have investigated the possible synergistic relationship between rates of exercise, access to greenspace, and associated positive health effects. While it can be argued that the benefits described can be simply attributed to exercise, a number of published studies do suggest that the level of benefit associated with exercising is relatively greater if that exercise is conducted in a more natural, more biodiverse environment. For example, Pretty et al. (2005) studied 5 × 20 individuals exposed to a sequence of 30 different scenes whilst exercising on a treadmill. Four different category of scene were tested: rural pleasant, rural unpleasant, urban pleasant and urban unpleasant. A control group running with no images was also included. The images themselves were categorised by an independent panel of 50 in order to minimise subjectivity. Measures taken included blood pressure, self-esteem and mood (measured using the Profile of Mood States tool, POMS). It was found that exercise alone significantly reduce blood pressure, increased self-esteem and had a positive effect on four of the six different moods covered by the POMS tool. Pleasant rural and pleasant urban scenes produced a significantly positive effect on self-esteem compared to the exercise only control. The pleasant rural scene also significantly reduced blood pressure. The unpleasant rural scene had the most dramatic effect, depressing three measures of mood. Overall, there seems to be a synergistic benefit to exercising in pleasant rural and urban scenes; however it was unclear from this study as to whether biodiversity per sé actually played any role in these effects especially as the indicators measured were in response to viewing pictures of environments, rather than experiencing those environments first hand. There was also no evidence to suggest that an unpleasant rural or urban scene would have any less diversity than their pleasant counterparts.

Quality of life and wellbeing

Discerning the linkages between human well-being and ecosystem change is difficult because of the complexity of interactions between ecological and social systems, or linked social-ecological systems (Kittinger et al. 2009). The complex dynamics of social-ecological systems have been described as nonlinear and cross-scale, exhibiting multiple stable states between which abrupt and potentially irreversible changes can occur (Gunderson and Holling 2002; Berkes et al. 2003; Liu et al. 2007).

In 1948, the World Health Organisation (WHO) defined human health as: *a state of complete physical, mental and social well-being and not merely the absence of disease or infirmity* (cited in WHO 2009). Western ideas about the benefits of nature to human health and well-being go back at least two centuries, but until the emergence of landscape perception and assessment research in the 1960s these benefits were considered too subjective to measure (Jorgensen and Gobster 2010). Kaplan et al. (1972) were among the first to measure people's preferences for natural over urban scenes. Since then, investigators have developed models to predict green space preferences based on biophysical, psychological, and artistic properties of vegetation and other landscape elements (Daniel 2001). These included psycho-evolutionary models that suggested that humans prefer savannah-like landscapes characterised by open glades with smooth ground texture, framed by clumps of mature trees (e.g. Ulrich 1986); and that vegetation types associated with more biodiverse landscapes such as rough ground cover, woodland edge, or scrub were generally lower in preference (Parsons 1995). Nassauer's (1995) work, suggesting that preferences for "messy ecosystems" could be enhanced by placing landscapes within "orderly frames", helped to move the discussion beyond the relative merits of scenic as opposed to ecological aesthetics. In terms of studies looking at biodiversity, a recent review (Jorgensen and Gobster 2010) identified a total of 29 studies which looked at the relationships between biodiversity and preference or attitudes, meanings and values. In these studies, biodiversity included measures of actual animal and plant biodiversity (Asakawa et al. 2004; Lindemann-Matthies and Bose 2007; Nassauer 2004a), as well as surrogate measures used in remote sensing, such as net primary productivity (NPP) as an indicator of species diversity and biological productivity (Alessa et al. 2008), and the normalised differential vegetation index (NDVI) as an indicator of the percentage of vegetated area per location (Hur et al. 2009). Other proxies for biodiversity included structural complexity, evaluated at a site level by Home et al. (2010) to study preferences for green spaces around social housing; and landscape heterogeneity, mapped by Dramstad et al. (2001) to study aesthetic appreciation/experience and cultural heritage values. Another approach was to contrast preferences or attitudes toward various scenarios for the enhancement of biodiversity in different contexts, such as the design of residential subdivisions in the United States (Nassauer 2004b) or business sites in the Netherlands (Snep et al. 2009). A further approach was to assess the impact of levels of structural alteration in naturally-occurring vegetation communities on viewer preference (Purcell and Lamb 1998) and judgements of naturalness (Lamb and Purcell 1990).

On a coarse spatial scale, human presence is positively related to biodiversity, suggesting that people contribute to biodiversity through species introductions and habitat diversification (Di Giulio et al. 2009). Apparently, people also tend to preferentially settle in areas of high biodiversity (Kühn et al. 2004; Luck et al. 2004; Pautasso 2007). The latter process poses a threat to global biodiversity and stresses the importance of human demographic and socioeconomic dynamics in biodiversity conservation (Cincotta et al. 2000; Liu et al. 2003). On a smaller spatial scale, urbanisation destroys, alters and dissects natural and semi-natural habitats, and at the same time, also creates new habitats (Blair 1999). In a study looking at the relationships between species richness in 34 riparian green spaces and self-reported well-being across a large urban conurbation in the UK, Dallimer et al. (2012) noted that although well-being increased with higher levels of bird species (a finding supported by Fuller et al. 2007), it actually declined with greater diversity of plant life. Three different measures of well-being were used: reflection (derived from attention restoration theory, Kaplan and Kaplan 1989; Hawkes et al. 1995; Hood Morris 1996; Engel 1977; McKee and Chapel 1992); attachment (derived from the theory and research on place, Proshansky et al. 1983; Altman and Low 1992; Twigger-Ross and Uzzell 1996; Manzo 2003; Patterson and Williams 2005); and continuity with the past (e.g. Fuller et al. 2007). All measures of well-being were derived from a self-reported questionnaire that contained a series of closed-ended questions with responses made on a five-point Linkert scale from strongly disagree to strongly agree based on the stem question “Please indicate how much you agree with each statement about this park”.

The final analysis indicated that park area was positively correlated with the number of habitat types ($r = 0.65$, $n = 15$, $p = 0.009$), but unrelated to plant richness ($r = 0.29$, $n = 15$, $p = 0.296$). The number of habitat types was positively correlated with plant richness ($r = 0.70$, $n = 15$, $p = 0.003$); although the level of correlation will be dependent on the habitat classification used. Reflection and continuity with the past increased with green space area. Plant richness was positively associated with reflection and this effect was stronger than that seen with area. Butterfly richness was not associated with any of the well-being measures. Bird richness was positively associated to continuity with the past, although this effect was weaker than that of area. The number of habitat types was positively associated with reflection and continuity with the past, although tree cover was unrelated to any measure of well-being.

While the studies of Dallimer et al. (2012) and Fuller et al. (2007) demonstrated that certain aspects of psychological well-being of users of urban green space increase as species richness of plants or birds in the green space increases, Luck et al. (2011) examined the issue in places where people live, where, arguably, the majority of human-nature interactions occur. Luck et al. (2011) conducted a series of surveys across 9 towns and cities (population sizes ranged from 16,845 to 78,221) in Victoria and New South Wales, Australia. They measured demographic variables and resident's well-being and connection to nature in four neighbourhoods in each town (total of 36 neighbourhoods) where each neighbourhood boundaries were defined by census collection district (the smallest sampling unit used by the Australian Bureau of Statistics in its census of the Australian population and equates to roughly 200 households). The neighbourhoods were selected using a stratified random sampling approach to ensure a cross-section of housing density, income levels, and vegetation cover (Luck et al. 2009). Personal well-being was found to be positively associated with species richness and abundance and vegetation cover and density and negatively associated with urban development. The strength of the association was strongest for vegetation cover and density and urban development. The odds that a householder had a high level of personal well-being increased by 55 % (26–90 % confidence limits based on 1 SE) as vegetation cover increased across the range of the data and increased by 48 % (22–79 %) as vegetation density increased. The odds that a household had a higher level of personal well-being increased by 20 % (1–45 %) as species richness increased across the range of the data. Similarly to the large-scale assessments already discussed in previous sections (e.g. Huynen et al. 2004; Sieswerda et al. 2001), socio-economic factors were found to be significantly more important predictors of personal well-being compared to biodiversity (Luck et al. 2009).

Over the years, biodiversity research has focused almost entirely on the environment with little to do with human well-being. A number of researchers, however, have expressed relatively strong opinions that this needs to change in order to maintain this area of research (Mlambo 2012). They argue that failure to adequately and actively incorporate human well-being elements in biodiversity research has limited the ability of this field to capture the public's attention to issues concerning biodiversity conservation. Watson (2005) stated that politicians are elected primarily to sustain and look after the well-being of humans, so if the discourse about biodiversity conservation has little to do with humans, then it is not hard to imagine why it will continue to be a non-priority issue to many people including politicians and the public alike. These arguments, to some extent, undermine the findings of the studies described above as the suggestion is that the move towards linking biodiversity to human health and well-being is primarily one of propaganda.

Internal exposure to biodiversity

The human-microbial ecosystem is thought to play a variety of important roles in human health and disease (Costello et al. 2012). Babies are born essentially sterile and acquire their microbiome (the community of microbes and collection of genomes found in and on the human body; Relman 2012) from their surroundings (Costello et al. 2012). The postnatal assembly of the human microbiota plays an important role in infant health, providing resistance to pathogen invasion, immune stimulation, and other important developmental cues early in life (Mackie et al. 1999). Acute and chronic disorders, such as necrotising enterocolitis, antibiotic-associated diarrhoea, malnutrition, inflammatory bowel disease, and asthma have been linked to inadequate, inappropriate, or disrupted postnatal microbiome acquisition and development (Torrazza and Neu 2011). Therefore, the microbial diversity of the environment from which the infant is exposed is of key importance to health. In 1989 the hygiene hypothesis (Strachan 1989) was proposed as an explanation for the well-documented increase in asthma and atopic disease reported in westernised countries in the latter decades of the 20th century. Humans have evolved in a pathogen rich environment and the hygiene hypothesis proposed that a modern westernised, non-traditional lifestyle no longer exposes people to the diverse microbe-rich environment in response to which the human immune system has evolved and most probably is required for 'normal' maturation. This concept is supported by the observation that within westernised countries children brought up on farms and exposed to a heavy load and wide variety of micro-organisms are less likely to develop asthma and atopic disease (Braun-Fahrlander et al. 1999; Ege et al. 2006, 2011; Riedler et al. 2001). In particular early life exposure to, and diversity of such a micro-organism rich environment appear to be especially important in reducing the risk of asthma and atopic disease.

The diversity of human microbiome has been found to play a larger role in adult human health and disease than previously recognised (Dethlefsen et al. 2007; Turnbaugh et al. 2007). Among the benefits to human health, the microbiota contributes to food digestion and nutrition (Arumugam et al. 2011; Muegge et al. 2011; Qin et al. 2010; Wu et al 2011; Turnbaugh and Gordon 2009); processing, and, in some cases, detoxification of xenobiotics; regulation of human metabolism; development and terminal differentiation of host mucosa; 'education' and regulation of immune system target recognition and responses (Lee and Mazmanian 2010); integrity of the barrier function of the skin and mucosa (Grice et al. 2009; Charlson et al. 2010); and prevention of colonisation and invasion of the host by pathogens (Relman 2012). Important insights have been gained from analysis of large-scale human microbiome data, including the discovery of enterotypes (Arumugam et al. 2011) and discovery of the link between diet and these enterotypes (Wu et al. 2011).

Two central themes in human microbiome studies are to identify potential biological and environmental factors that are associated with microbiome composition, and to define the relationship between microbiome features and biological or clinical outcomes (Chen et al. 2012; Spor et al. 2011; Virgin and Todd 2011). A variety of human diseases and other forms of pathology are associated with alterations to the diversity of the microbiome. These pathologies include chronic periodontitis, Chron's disease and other forms of inflammatory bowel disease, irritable bowel syndrome, tropical enteropathy, antibiotic-associated diarrhoea, and bacterial vaginosis. For each of these forms of host pathology, the concept of 'microbial community as a pathogen' has been proposed and a distinction drawn between this type of scenario and more traditional medical paradigms for infectious disease (e.g. Koch's postulates) in which a single ethiological agent can be identified (Lepp et al. 2004; Vianna et al. 2008). In general, well-documented differences in the microbiomes of specific individuals reflect a combination of multiple factors: genetics, various aspects of life history including antigen, diet, chemical, human, and other animal exposures, and health status (Turnbaugh et al. 2009).

The diversity of the human microbiome and how this relates to health is a topic in its infancy. At this stage it is impossible to say what aspects of diversity are required to maintain health. Having said this, there is good evidence for the Hygiene Hypothesis (Strachan 1989) thus suggesting that where the microbiome is concerned, there is a direct link between microbial biodiversity and human health.

Concluding remarks

Intuitively, one would presume biodiversity loss to have negative impacts on human health; the extant evidence is however, less clear cut. In terms of provisioning services, the ecosystem is essential for life. While the planet is still able to provide, it seems that socioeconomic factors primarily govern human health and well-being. This has been demonstrated time and time again regardless of whether the study is focussed on indirect exposure to biodiversity (e.g. ecosystem services or disease regulation), or on more direct exposures to biodiversity (such as psychological aspects of well-being associated with experiencing nature). Many approaches to improving socioeconomic status involve exploitation of natural resources, and so we have seen that improved health seems to be related to a decrease in biodiversity. This is not a direct relationship, as it is the ability of people to pay for better housing, nutrition, medicines, etc. that is causing the improved health status that is observed. It would be naïve to say that decreasing biodiversity has a positive impact on human health as ultimately, the sources of wealth, i.e. natural resources, will be expired resulting in decreases in socioeconomic status. Unless it is possible to decouple the positive benefits of improved socioeconomic status from biodiversity, it is unlikely that a causal relationship between biodiversity loss and health will be found. The hygiene hypothesis and diversity of the human microbiome is probably the most convincing direct/causal relationship of biodiversity on health. However, it is important to remember that this relationship takes place at a very different scale than e.g. the relationships between natural spaces and well-being. Much more research is required in order to understand the influences of the human microbiome on health status.

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