nature sustainability

REVIEW ARTICLE

https://doi.org/10.1038/s41893-019-0436-6

Research gaps in knowledge of the impact of urban growth on biodiversity

Robert I. McDonald[1*], Andressa V. Mansur[2], Fernando Ascensão[3,4], M'lisa Colbert[5], Katie Crossman[1], Thomas Elmqvist[6], Andrew Gonzalez[7], Burak Güneralp[8], Dagmar Haase[9,10], Maike Hamann[11], Oliver Hillel[12], Kangning Huang[13], Belinda Kahnt[14], David Maddox[5], Andrea Pacheco[2], Henrique M. Pereira[2,3,15], Karen C. Seto[13], Rohan Simkin[13], Brenna Walsh[16], Alexandra S. Werner[2] and Carly Ziter[17]

By 2030, an additional 1.2 billion people are forecast in urban areas globally. We review the scientific literature (*n* = 922 studies) to assess direct and indirect impacts of urban growth on habitat and biodiversity. Direct impacts are cumulatively substantial, with 290,000 km² of natural habitat forecast to be converted to urban land uses between 2000 and 2030. Studies of direct impact are disproportionately from high-income countries. Indirect urban impacts on biodiversity, such as food consumption, affect a greater area than direct impacts, but comparatively few studies (34%) have quantified urban indirect impacts on biodiversity.

The next few decades will be the most rapid period of urban population growth in human history. In 2000, the United Nations Population Division (UNPD) estimated there were 2.9 billion people in urban areas, rising to 4.0 billion by 2015. By 2030, an additional 1.2 billion residents in urban areas globally are forecast, with much of this population growth happening in countries such as China (242 million), India (178 million), Nigeria (70 million), and Indonesia (48 million)[1]. Urban population growth, together with economic development, is forecast to expand urban areas by 1.2–1.8 million km² between 2000 and 2030[2–4]. The scale and speed of urban growth have multifaceted impacts on the global environment[5]. Studies have shown that urban population growth has had and will continue to have significant implications for land use[6], energy consumption and climate change[7,8], water security[9], food demand[10], and air pollution[11].

This Review focuses on the impacts of urban growth on biodiversity through 2030. We define 'urban growth' as the increase in the area of cities or towns, reserving the term 'urban population growth' when we want to refer specifically to the increase in urban population. Both of these terms are different from 'urbanization', which we use to refer to the change in the proportion of a population living in an urban area[12]. Different studies have different definitions of what is 'urban', often using population density[13], built-up area[14], or some composite definition[15]. In this Review, we cite studies using various definitions of urban, indicating their definition if it is relevant to the topic discussed.

We consider biodiversity in this Review as the variability among living organisms, from genes to species to ecosystems to biomes[16]. Human activity has impacted biodiversity across the planet, and the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) Global Assessment suggests that one million species may be at risk of extinction[17]. Human activity is consistently found to be the dominant contemporary driver of biodiversity change from local to global scales, and these impacts are projected to continue throughout the twenty-first century[18–20]. The role of urban growth in causing biodiversity change has been relatively less studied, even though urban growth contributes to the global trend of biodiversity loss in a myriad of ways[4,5].

One useful categorization of biodiversity impacts of urban area is as either direct or indirect[5]. Direct impacts are those where urban land expansion leads to land cover change such as the loss of natural habitat[21]. Also included in direct impacts are the alteration in abiotic and biotic conditions that occur as urban land use fragments natural habitat, increasing edge effects and decreasing habitat connectivity among remaining habitat patches. Indirect impacts are those mediated by an intermediate process. Indirect impacts include the impacts of resources consumed within a city (for example, energy and food), as well as the impacts of solid, liquid and gaseous wastes released from urban areas.

Despite the importance of historical and future urban growth as a driver of global change, the global impact on biodiversity remains unclear. Previous assessments[5,22,23] have assembled information on how urban growth impacts biodiversity in particular places, focusing on either direct or indirect impacts, but have not offered a comprehensive literature review of both direct and indirect impacts. As part of the *Nature in the Urban Century* assessment[4], we

[1]Global Cities Program, The Nature Conservancy, Arlington, VA, USA. [2]German Centre for Integrative Biodiversity Research Halle-Jena-Leipzig, Leipzig, Germany. [3]CIBIO/InBio, Universidade do Porto, Porto, Portugal. [4]Department of Conservation Biology, Estación Biológica de Doñana, Seville, Spain. [5]The Nature of Cities, New York, NY, USA. [6]Stockholm Resilience Center, Stockholm University, Stockholm, Sweden. [7]Department of Biology, Quebec Centre for Biodiversity Science, McGill University, Montreal, Quebec, Canada. [8]Department of Geography, Texas A&M University, College Station, TX, USA. [9]Humboldt Universität zu Berlin, Berlin, Germany. [10]Helmholtz Centre for Environmental Research, Leipzig, Germany. [11]Institute of the Environment and Humphrey School of Public Affairs, University of Minnesota, Minneapolis, MN, USA. [12]Secretariat of the Convention on Biological Diversity, Montreal, Quebec, Canada. [13]Yale School of Forestry & Environmental Studies, Yale University, New Haven, CT, USA. [14]General Zoology, Martin-Luther-University Halle-Wittenberg, Halle, Germany. [15]Institute of Biology, Martin-Luther-University Halle-Wittenberg, Halle, Germany. [16]Future Earth, Montreal, Quebec, Canada. [17]Biology Department, Concordia University, Montreal, Quebec, Canada. *e-mail: Rob_mcdonald@tnc.org

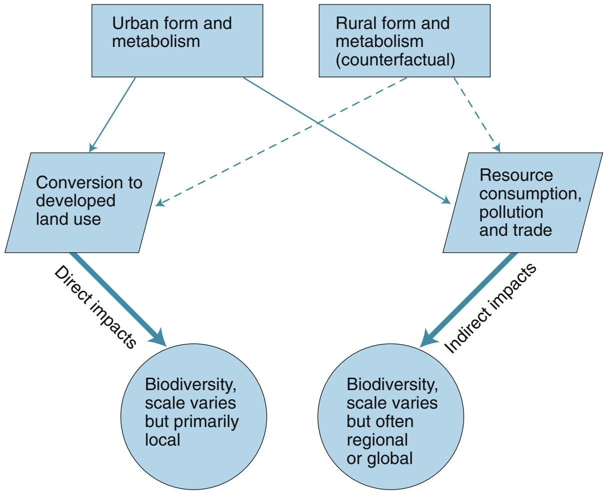

Fig. 1 | Conceptual diagram of direct and indirect impacts on urban areas. This Review evaluated the aggregate impact of urban form and metabolism on biodiversity, both directly and indirectly. One could compare this aggregate impact with what would occur in a counterfactual scenario, where people live in rural settlements instead. Solid arrows show effects of urban form and metabolism, while dotted arrows show effects of rural form and metabolism under the counterfactual of no urban development.

summarized what is known about the direct impact of urban areas on biodiversity. Here, we expand on that early report to also review research into indirect impacts.

We conducted a literature review of published urban biodiversity studies in this decade (2010–2018, $n = 922$) and identified major gaps in existing urban biodiversity research. To quantitatively map direct effects, we combine previously published scenarios of future urban growth[2,3] with land cover information to forecast future direct urban impacts on natural habitat. See Supplementary Methods for details. In this Review, we answer the following questions:

- What is known about the aggregate direct and indirect impact of urban population and area growth on biodiversity?
- Where is the impact of urban growth highest on biodiversity and natural habitat, and what are the likely trends over time?
- What are the existing gaps in scientific knowledge that prevent a more complete understanding of the potential impacts of urban growth, in both population and area, on biodiversity?

Framework of urban impacts on biodiversity

There is a great variety of analytical frameworks in the literature on urban biodiversity impacts, as well as a variety of terminology in use, which make comparisons among studies challenging. We thus structured our Review around a simple conceptual framework (Fig. 1) that clarifies many of the disagreements in the literature. This paper focuses on the aggregate direct and indirect impact of urban areas on biodiversity, where aggregate impact is defined as the total biodiversity impact that occurs either in urban areas or because of an activity that occurs in urban areas.

The majority of human population[1] and economic activity[24] is located in urban areas and so it is perhaps not surprising that urban areas are major sources of pollution emissions and resource demands. Urban form, the physical characteristics of urban areas such as the size, density and spatial configuration of built-up areas[25], modulates impacts on biodiversity[26]. Similarly, urban metabolism, the inflows and outflows of materials and energy in urban areas, also has a profound effect[27]. Urban form and metabolism are interrelated and are themselves controlled in complex ways by factors like income, available technology, infrastructure, behaviours, and cultural norms that evolve over time[6,28]. Importantly, urban form and metabolism are the outcomes of many human choices[29], they have changed substantially over time[30], and they could change substantially in the future if humans made different choices[31].

Urban form and metabolism jointly affect the pattern of local land use and human activity, which in turn leads to direct impacts on biodiversity (Fig. 1)[32]. The intensity and pattern of direct impacts are affected by urban form with, for instance, more compact and dense urban forms generally having spatial impacts over a smaller area[4,33]. Urban form and metabolism also affect an urban area's resource consumption, pollution and trade, which in turn lead to indirect impacts on biodiversity. The spatial scale of indirect impacts varies from local (for example, sewage impacts on a downstream coral reef) to regional (for example, movement of water for urban use) to global (for example, greenhouse gas (GHG) emissions)[21].

While some quantitative data exist that can be used to estimate the aggregate impact from urban areas, it is still unclear how much of that aggregate impact to attribute to urban population growth per se rather than the other processes that go along with urbanization, such as economic development and technological change. Some authors only attribute an environmental impact to urban areas if the environmental impact occurs as a consequence of urban form and metabolism. In this strict definition, an environmental impact is attributed to urban areas if it is worsened because of urban form or metabolism, relative to rural settlements. For instance, urban areas are major sources of GHG emissions, but there is evidence that the urban pattern of settlement, co-locating higher population and employment densities, reduces per capita emissions by creating efficiencies in transportation and building energy use[34,35]. If urban form reduces GHG emissions, relative to rural settlements, then under the strict definition of attribution, one would not attribute greater GHG emissions to urban areas per se.

Attribution of environmental impact to urban areas under the strict definition of attribution requires the evaluation of a counterfactual scenario[36,37] that answers the question: what would the environmental impact have been if people lived dispersed in rural areas rather than together in urban areas? The difference in impacts between the real-world and counterfactual scenarios would be what is attributable to urban areas (Fig. 1). This is a difficult counterfactual to analyse in a comprehensive way[38], since the process of urbanization has been shown to affect population growth rates, as well as rates of economic development, consumption, technology, social organization and human behaviour[39]. In this Review, we present aggregate data on the major direct and indirect impacts of urban areas and their likely trends over time, constructing only simple counterfactual scenarios based upon the differences in per capita urban and rural consumption of resources.

The growing direct impact of urban areas

In this section, we discuss trends of urban area growth, how that urban area growth has impacted natural habitat, and the relationship between natural habitat loss and biodiversity. We then turn to reviewing the empirical findings of studies that have investigated how direct impacts of urban areas have affected biodiversity in particular locations.

Forecasts of urban growth. According to the UNPD, urban population has grown dramatically in recent decades, from 2.3 billion in 1990 to 4 billion in 2015[1]. The UNPD bases its estimates on statistics reported by national governments and calculated that in 2018, 55% of total population was in urban areas, which is forecast to rise to 70% urban by 2050[1]. Jiang and O'Neill[40] projected urbanization would be between 60–92% by the end of the century, depending on government policy and social trends, and different futures lead to different forecasts of potential future urban population[41].

There is considerable uncertainty in urban population growth estimates, driven in part by uncertainty in how urban areas are defined[28]. It is important to note that the definition of urban used by national governments supplying data to the UNPD varies (see Table 1 in the UNPD's report[1]). Different studies with different definitions of urban may have quite different estimates of urban population. For instance, a study by the European Commission defined urban area as contiguous areas with more than 5,000 people and a density of more than 300 people per km^2 and estimated that 84% of the world's population was urban[42]. Some scholars have critiqued this density threshold as too low, encompassing areas that are primarily agricultural, and argue that different lines of evidence suggest that 52–56% of the world's population is in urban areas[43]. Regardless of how urban area is defined, there is broad consensus that urban populations have grown substantially in the last few decades and will continue to grow rapidly in the future. The UNPD projections, which we feature in this Review, include that urban population is expected to grow to 5.2 billion by 2030[1].

Urban population growth has led to a large increase in urban area, from 350,000 km^2 in 1992 to 740,000 km^2 in 2015[4] (Fig. 2a). The amount of urban area estimated globally varies depending on how urban area is defined, the spatial unit of analysis, and the types of demographic and remotely sensed data used to map urban areas. See Table 1 in Schneider et al.[44] for a review of the amount of urban area classified as urban by different analyses. In this Review, we follow the definition of urban area used by the Climate Change Initiative (CCI) Land Cover dataset, which used multiple sensors (Envisat MEdium Resolution Imaging Spectrometer (MERIS) Full Resolution and Reduced Resolution, and Spot Vegetation) to classify pixels into 22 land-cover classes to create a consistent time series of land cover. Pixels with the spectral signature of built-up surfaces such as asphalt and concrete are classified as urban[14].

It is projected that in 2030 there will be 1.9 million km^2 of urban area (Fig. 2a), according to one commonly used set of forecasts from Seto and colleagues[2–4,45,46]. While we use the Seto et al. forecasts[2] in this Review, we acknowledge that there are other published

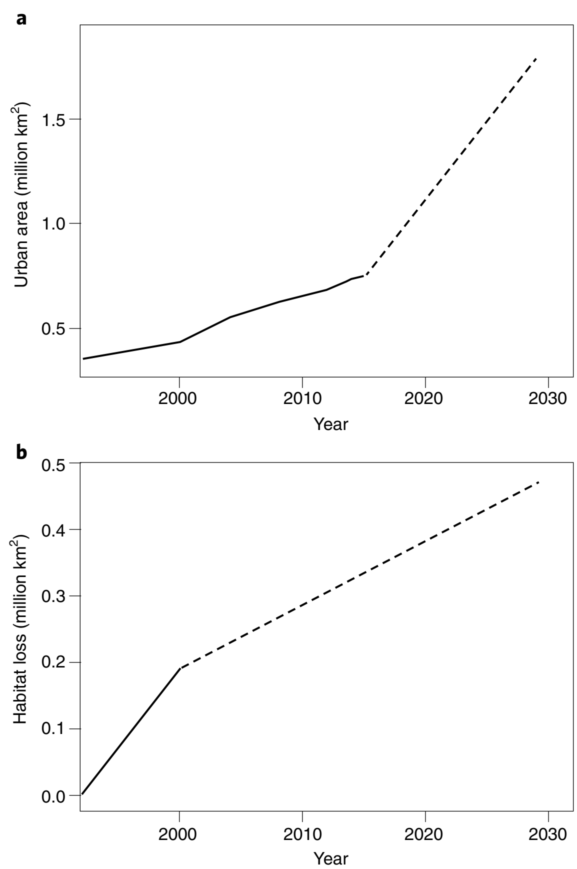

Fig. 2 | Direct impacts of urban growth on habitat over time. Historical data are shown with solid lines, forecasts with dashed lines. **a**, Direct impact on urban area from urban growth over time. **b**, Cumulative habitat loss caused by urban growth since 1992.

Table 1 | Estimated urban-caused habitat loss for the world's terrestrial biome types, 2000–2030

Biome name	Urban area in 2000 (% of biome area)	Urban-caused habitat loss, 2000–2030		Scientific studies	
		(km²)	(% of biome area)	Direct impacts (% of total, $n=687$)	Indirect impacts (% of total, $n=317$)
Temperate broadleaf forests	2.65	78,430	0.61	47.5	46.7
Tropical moist forests	0.67	63,439	0.32	13.1	15.5
Deserts	0.26	38,206	0.14	5.2	5.4
Tropical grasslands	0.22	26,636	0.13	1.9	3.5
Mediterranean habitat	1.87	20,515	0.64	13.8	11.4
Temperate grasslands	0.92	15,156	0.15	6.8	6.3
Temperate coniferous forests	0.82	11,135	0.27	3.6	3.8
Mangroves	1.73	10,091	2.90	1.5	0.6
Montane grasslands	0.21	8,036	0.15	1.7	1.6
Tropical dry forests	0.85	7,573	0.25	1.9	1.9
Tropical coniferous forests	0.86	3,356	0.47	0.3	0.3
Flooded grasslands	0.36	3,289	0.30	0.7	0.9
Boreal forests/taiga	0.08	1,430	0.01	1.3	1.3
Tundra	0.01	72	0.00	0.0	0.3

Data are shown for area lost between 2000 and 2030, as well as the proportion of the biome's total area that will be converted. Biomes are sorted in descending order by area (km²) converted. Also shown are the percentages of scientific studies of urban impact that occur within this biome.

forecasts that vary in their magnitude and pattern. For instance, Angel and colleagues[47] forecast there will be 1.3 million km^2 of urban area in 2030. Zhou and colleagues[48] estimated that urban areas will grow 1.7 million km^2 between 2020 and 2050.

Several studies have suggested that the amount of area used by urban populations would be much greater if people were not concentrated in urban areas[34]. One simple counterfactual scenario can be constructed using population density statistics for both rural and urban areas. According to the Gridded Population of the World[49], globally, the mean urban population density in 2000 for urban areas was 1,500 people per km^2. For rural inhabited areas (excluding barren areas that have little human inhabitation), the global mean population density in 2000 was 58 people per km^2. While average household size varies widely between countries, for a developing country with a household size of around five people per household[50], this rural population density implies 8.6 ha per house, which would be defined as exurban settlement by Theobald[51]. In exurban settlements, while some natural land cover can be maintained, there is likely to be considerable impacts upon biodiversity and ecosystem function from human infrastructure and activities[52]. Hypothetically, if all urban population growth between 1990 to 2030 had occurred instead as the global average rural density, it would have been spread out over 26 times more land, some 50 million km^2. Thus, urban population has greatly reduced the area over which human settlement has occurred, relative to the counterfactual.

Natural habitat loss. The most important direct impact of urban growth on biodiversity is the loss of natural habitat due to conversion to urban land uses[4,5]. In this Review, we combine previously published scenarios of future urban growth by Seto et al.[2,3] with land cover information from the CCI Land Cover dataset[14] to forecast future direct urban impacts on natural habitat (see Supplementary Methods for details). We estimate that globally, urban growth converted 190,000 km^2 of natural habitat to urban land cover between 1992 and 2000, 16% of the total natural habitat loss from all causes (for example, agriculture expansion and deforestation) during this period. We estimate that urban growth will convert an additional 290,000 km^2 of natural habitat to urban land cover between 2000 and 2030 (Fig. 2b). Note that there are only three time points measured in Fig. 2b, so differences in the shapes of the curves in Figs. 2a and 2b may not be statistically meaningful.

A number of factors affect the amount of habitat impacted by urban population growth. Urban population density and urban form affect the amount of built urban land per capita. Also important is where urban growth occurs. In some places such as the southern Chinese coast, substantial amounts of urban growth are occurring predominantly on natural habitat. In other places, urban growth occurs predominantly on agricultural land, such as in northern China[45,53]. Note that urban areas are disproportionately located in places like coastlines and floodplains that have above average productivity and biodiversity[54–57], so globally the direct impacts of urban growth are greater than if urban settlements were randomly located across the landscape.

In terms of the total area of natural habitat forecast to be lost to direct urban impacts (2000–2030), four countries exceed 10,000 km^2: the United States, Brazil, Nigeria and China (Fig. 3). However, several other countries on each continent (excluding Antarctica) are also forecast to have high levels of urban-caused habitat loss. Alternatively, one could look at the forecast amount of urban-caused habitat loss relative to a country's area, by which metric islands, such as Hong Kong S.A.R., Mauritius and Puerto Rico, have the greatest relative impact from urban growth (Supplementary Table 1).

A more ecologically meaningful way to quantify direct urban impacts is to examine which biomes will be impacted. We forecast that the temperate broadleaf forest biome will have the greatest amount of natural habitat converted to urban land uses, followed by the tropical moist forest biome (Table 1). The tropical moist forest biome is where some of the most rapidly expanding urban areas are located, such as those along the Brazilian coast, in West Africa and southeast Asia. This biome is predominately in middle- and low-income countries, where the majority of urban growth is occurring. Supplementary Table 2 lists forecast habitat loss by biome and the income of the country.

In proportional terms, urban growth (2000–2030) is forecasted to cover around 2.9% of the total area of the mangrove biome, more than any other biome type (Table 1). The Mediterranean biome is also forecast to be highly impacted in proportional terms, with 0.6% of this biome impacted by urban growth between 2000 and 2030. By contrast, the tundra and boreal forest/taiga biomes are forecast to be minimally impacted by urban growth, simply because there are so few urban areas located in these biomes.

Habitat loss and biodiversity impacts. At a local scale, when natural habitat is converted to urban land uses, there is often a subset of sensitive species that are lost[58]. Another set of tolerant native species can persist in urban areas, like Eastern grey squirrels (*Sciurus carolinensis)* in eastern North America. Finally, there are a set of synanthropic species that follow humans into new urban areas, such as the Norway rat (*Rattus norvegicus*) or the house sparrow (*Passer domesticus)*. Thus, depending on the relative size of these three subsets, urban growth may locally increase or decrease species richness[59].

Newbold and colleagues[60] statistically estimated within-sample (local) species richness and abundance as a function of human pressures, based upon data from 11,525 sites, including 613 urban sites. Urban sites were classified into three groups based upon intensity of human use: minimal use urban sites (extensive managed green spaces, villages), light use urban sites (suburban areas with gardens or small green spaces), and intense use urban sites (urban areas with no green spaces). Relative to primary vegetation, minimal use urban sites had on average 4% lower within-sample species richness (95% confidence interval (CI): 21% lower to 16% higher), while light use urban and intense use urban had 34% (95% CI: 19–47% lower) and 50% lower (95 CI: 34–62% lower) within-sample species richness, respectively. Similarly, minimal use urban sites had 17% lower within-sample species abundance than primary vegetation (95% CI: 48% lower to 29% higher), while light use urban and intense use urban had 45% (95% CI: 12–65% lower) and 62% lower (95 CI: 32–79% lower) within-sample species abundance, respectively. While some biodiversity persists after natural habitat is converted to urban uses, local species richness and abundance on average declines.

At a global scale, the conversion of natural habitat to urban decreases biodiversity as sensitive, endemic species are driven to extinction[5]. McDonald and colleagues[53] estimated that globally, 13% of terrestrial vertebrate ecoregional endemics are under high threat from urban expansion. The largest biodiversity loss occurs when a parcel of natural habitat that was converted to urban land use contained unique biodiversity at the level of genes, species or ecosystems that was unable to survive after conversion.

Bias in research on direct impacts. The scientific literature on direct impacts of urban growth on biodiversity is geographically biased. Studies of direct impacts are concentrated in particular geographic locations (Fig. 4a), including northeastern United States, Europe, coastal China, and around Sydney and Melbourne in Australia. In contrast, there are many urban areas with relatively few published urban biodiversity studies conducted nearby, including urban areas in West Africa and Central Asia. While some of these areas with few urban biodiversity studies may be due to the language in which we conducted our search (English), they may also reflect spatial areas where urban biodiversity impacts deserve more study.

We found that per capita income is related to the amount of urban biodiversity studies of direct impacts, compared to a null

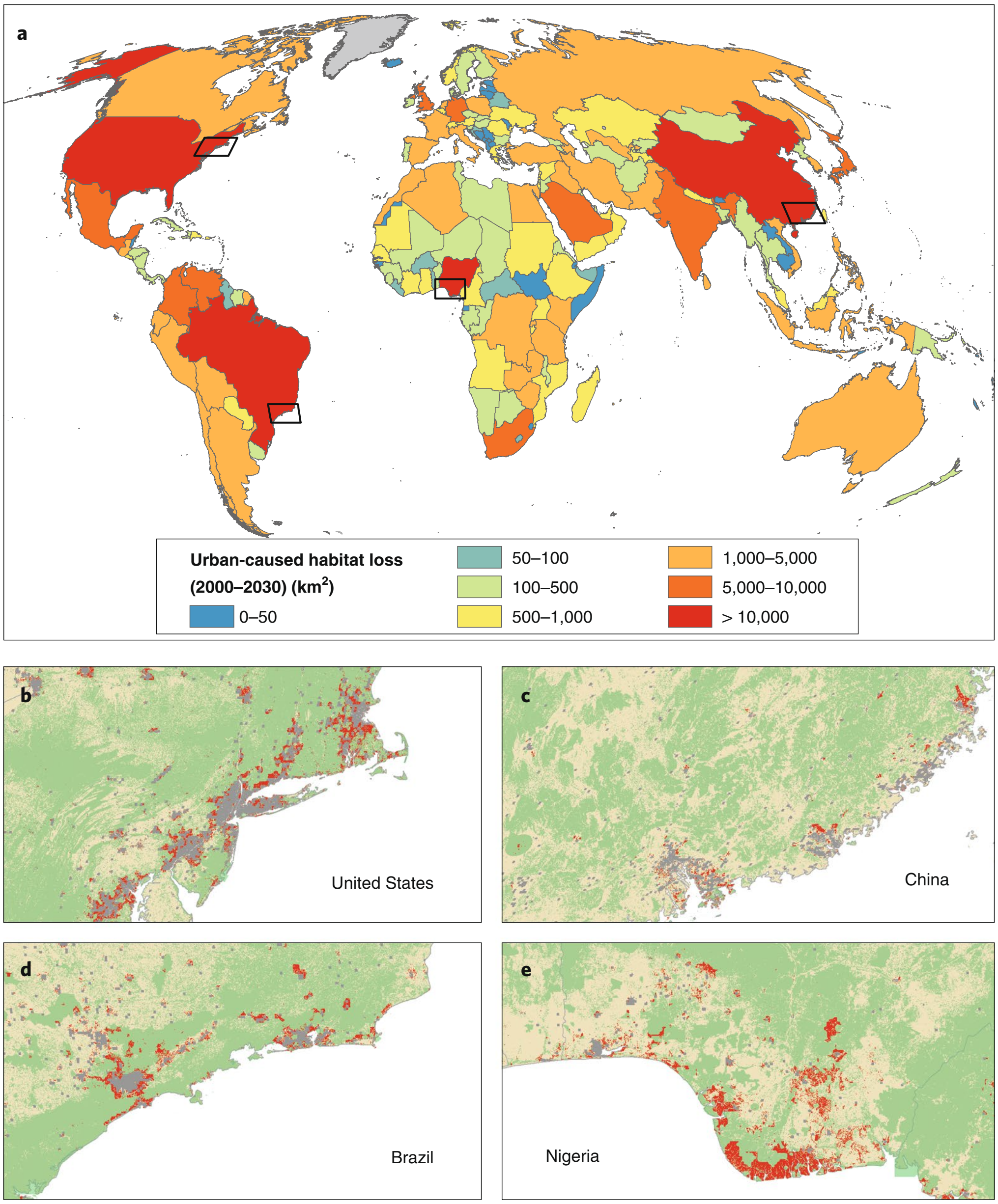

Fig. 3 | Forecast direct impacts of urban growth on habitat. a, Forecast direct natural habitat loss from urban growth (2000–2030), by country. **b**–**e**, The analysis was done at the pixel level, as shown for four example areas with fast urban growth: United States (**b**), China (**c**), Brazil (**d**), and Nigeria (**e**). Grey, urban in 2000; green, natural habitat; red, urban-caused habitat loss.

hypothesis where studies occurred proportional to the amount of people living in different income categories ($\chi^2 = 1{,}521$, d.f. $= 3$, $P < 0.001$). Of studies that looked at the direct impact of urban growth on biodiversity, 72% are from high-income countries (with a gross national income (GNI) per capita more than US$12,055), like the United States and countries in the European Union, even though these countries contain only around 17% of global population. Fewer studies of direct impacts (22% of the total) are from urban areas in upper middle-income countries (GNI per capita US$3,896–12,055), which contain 34% of the global population. Very few studies of direct impacts (7% of the total) are in lower middle-income and low-income countries, even though these countries contain 49% of the world's population. The relative lack of scientific studies from middle- and low-income countries is concerning, as it is these countries that we forecast to have the greatest urban-caused habitat loss.

The tendency of high-income countries to have a greater number of studies addressing direct urban biodiversity impacts has implications for which biomes are studied (Table 1). Temperate broadleaf forest is the most common biome in high-income countries, and 48% of all scientific studies of direct urban biodiversity impact occur in this biome. Tropical moist forest, a biome most commonly found in middle- and low-income countries, is forecast to lose a similar amount of land to urban conversion as temperate broadleaf forests but only 13% of all scientific studies of direct impact occurred there. In contrast, urban biodiversity impacts in Mediterranean habitat are more frequently studied (14% of all studies) despite the relatively small size of this biome, primarily due to studies in high-income countries in Europe (Supplementary Table 2).

Moreover, the tendency of high-income countries to have a greater number of studies means that relatively few studies focus on the places where global modelling studies suggest urban growth will

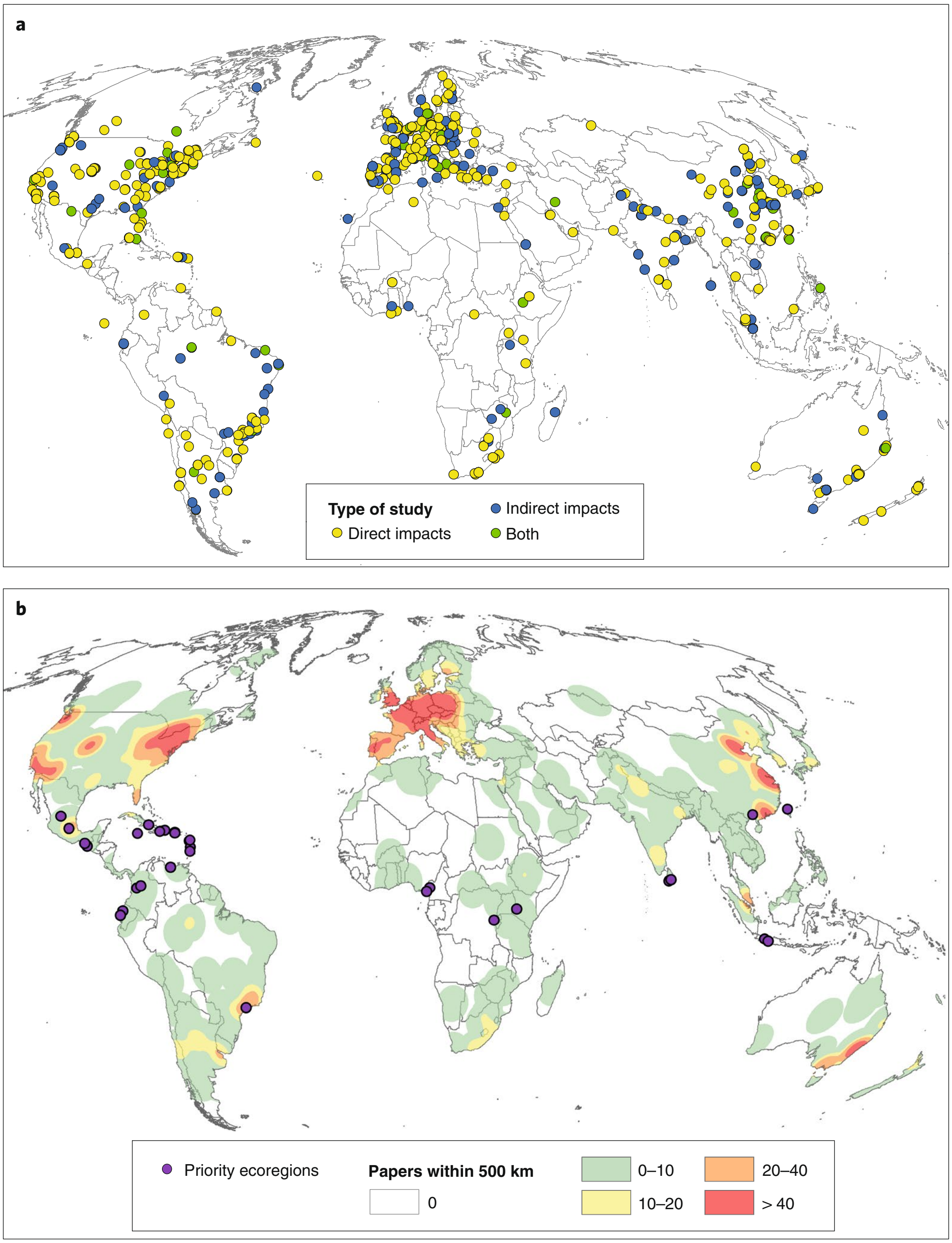

Fig. 4 | Locations of research studies into urban impacts on biodiversity. a, Location of urban biodiversity studies ($n = 922$). A disproportionately large number of research studies have looked at impacts in Europe and the United States. **b**, Urban biodiversity study intensity, measured as the number of studies (direct and indirect) within 500 km. For comparison, also shown are priority ecoregions[53] for urban biodiversity conservation, defined based upon vertebrate endemism and urban-caused natural habitat loss. These 30 priority ecoregions contain 78% of all vertebrate endemics threatened by the direct effects of urban growth (2000–2030).

have the greatest direct impact on biodiversity. A number of global analyses have compared scenarios of urban growth with biodiversity data in order to define key places where biodiversity is most at risk[2,4,46,53,61–63]. For instance, McDonald and colleagues[53] used spatially explicit scenarios to study how urban growth to 2030 would cause habitat conversion, then compared this habitat loss with levels of vertebrate endemism. They defined 30 priority ecoregions that collectively contain 78% of all vertebrate endemics threatened by the direct effects of urban growth (Fig. 4b).

Published urban biodiversity studies, however, are generally not near these priority ecoregions. Of the 30 priority ecoregions, only three (South China–Vietnam subtropical evergreen forests; Serra do Mar coastal forests in Brazil; and Trans-Mexican Volcanic Belt pine–oak forests) have more than 10 published urban research studies within 500 km. Indeed, some priority ecoregions have no nearby published studies on urban impacts on biodiversity (Western Java rain forests, Western Java montane rain forests, Cameroonian Highlands forests, Mount Cameroon and Bioko montane forests) and are potential places where future research is needed.

Our literature review also revealed taxonomic biases in the literature on urban biodiversity impacts. Of studies that examined direct impacts, three out of four (74%) focused on terrestrial taxa. Of these direct impact studies, about half (47%) are related to plants, most commonly focusing on trees or major plant habitat types. Birds are studied (19% of terrestrial studies) more than insects (8% of terrestrial studies), despite insect species richness far exceeding that of birds[64] and despite recent indications that insects may be at least as susceptible to global change[65]. Studies of urban direct impacts on freshwater taxa constitute 20% of all urban biodiversity studies, most commonly focused on macroinvertebrates (32% of freshwater studies). Studies of marine taxa are only 7% of all urban biodiversity studies and examine a broad variety of focal taxa.

Indirect impacts may be growing

In comparison to direct impacts, the indirect impacts of urban growth, in terms of population or area, on biodiversity are relatively little studied. Relatively few studies (34% of the total) explicitly looked at indirect impacts of urban areas on biodiversity. However, note that studies that do not explicitly mention urban areas were not surveyed in our literature review. For example, studies of increased logging or agricultural expansion that might plausibly be related to urban demand but do not mention urban areas are not included in this total.

As with studies of direct impacts, there is a clear geographic and income bias of studies of indirect impacts. Studies of indirect impacts are most common in the United States and Europe, most commonly in temperate forests (47% of all studies, Table 1). Per capita income is positively associated with the amount of urban biodiversity studies of indirect impacts ($\chi^2 = 501$, d.f. = 3, $P < 0.001$). Of studies that looked at the indirect impact of urban population or area growth on biodiversity, 62% are from high-income countries (GNI per capita more than US$12,055) while 28% are from urban areas in upper middle-income countries (GNI per capita US$3,896–12,055). Only 10% of studies are from lower middle-income and low-income countries.

Studies of indirect impacts have a few unique characteristics, compared with direct impacts. First, the majority of indirect studies (55%) look at freshwater systems. The directional flow of water through watersheds is the subject of many studies that look at the effect of urban water pollution on downstream freshwater ecosystems[66–69]. The most commonly studied taxa in freshwater ecosystems are macroinvertebrates (29% of all freshwater studies). Second, the scientific literature on indirect effects of urban areas sometimes explores long-distance teleconnections[70,71], where the resource demands of urban areas can affect far away landscapes[72].

The paucity of scientific studies of indirect impacts is concerning, as the available global data suggest that indirect impacts may be even more substantial for global biodiversity than direct impacts. To illustrate this, consider an issue identified as key in urban footprint analysis: food consumption[10]. Studies of urban environmental footprints in US urban areas[73], Vancouver[74] and others[75], have found that food consumption is one of largest components of a city's environmental footprint. The Food and Agriculture Organization (FAO) estimates that globally there was 48.7 million km^2 of agricultural land (arable land, permanent crops and permanent pasture) in 2016[76]. According to the UNPD, 54.4% of humans lived in urban areas in that year[1]. If we assume that per capita consumption of food is identical between urban and rural dwellers, then more than half of the world's agricultural land, 26.5 million km^2, is needed to support the food consumption of those in urban areas. This amount of agricultural land is 36-times greater than the estimated urban area in 2015 of 740,000 km^2, suggesting that the area impacted by indirect effects of food production for urban areas is far greater than the area impacted by direct effects.

However, the impact of urbanization on diet is a complex and multifaceted topic, and it is not reasonable to assume that per capita caloric consumption in urban and rural areas is identical. Economic development and urbanization are associated with one another, and both are associated with changes in patterns of work and leisure that lead to an increase in per capita caloric consumption[77]. Related dietary shifts from economic development and urbanization are associated with reduced consumption of cereals and increased consumption of animal products, fats and vegetables[78].

Note that the rise over time in caloric demand of urban populations does not necessarily result in agricultural expansion and habitat conversion. Some of the increased agricultural production necessitated by the growth in urban consumption may occur on existing cropland or rangeland, although there can still be biodiversity impacts from intensification[79]. The rest will occur on land newly converted to agriculture, leading to potentially considerable impacts on biodiversity[80]. It is beyond the scope of this Review to model the complex supply chains that supply urban areas with food, which vary among urban areas and countries, but it is apparent that urban caloric demand substantially affects agricultural land use in some regions[81].

Future research needs

Our assessment found that urban areas have had and will continue to have major impacts on biodiversity, both direct and indirect, through to at least 2030. However, we identified two major gaps in the literature on urban biodiversity impacts. In this section, we discuss the implications of these research gaps for policymaking and suggest potential ways to close these two research gaps. A discussion of possible policies and conservation strategies to reduce direct and indirect impacts of cities on biodiversity is beyond the scope of this Review, but we refer readers to other works on this subject[4,5,53,63,82–85].

First, our literature review shows that urban biodiversity research has focused on places that are different from where the most intense biodiversity impacts are forecast to occur, and there is a need for more research in middle- and low-income countries on the impacts of urban growth on biodiversity. One implication of this research gap is that a lack of data on the significance of urban biodiversity loss in middle- and low-income countries could lead policymakers to underestimate the importance of the issue. Another implication of this research gap is that we may lack understanding of unique types of urban biodiversity impacts that occur in middle- and low-income countries. We may lack information on socioeconomic processes, such as the unique role informal settlements play in urban areas in middle- and low-income countries. We may not fully understand ecological processes, such as how tropical forest biomes respond to urban perturbations. Finally, we may not have studied the unique policy and governance responses that urban areas in middle- and low-income countries are taking to protect their environment[86].

One way to close this research gap is for institutions that set science priorities and allocate science funding to focus efforts on research on this topic. International fora that encourage scientific collaboration also could play an important role. For instance, scientific networks like Future Earth or networks of urban areas like the International Council for Local Environmental Initiatives (ICLEI)—Local Governments for Sustainability can help connect researchers in the Global South with collaborators and funding from the Global North.

Second, our research shows the need for more studies of indirect impacts of urban areas on biodiversity. Only about one-third (34%) of the studies in our literature review focused on indirect impacts. Moreover, there are relatively few studies that attempt to quantify indirect impacts when the impacts are not simply additive (as with GHG emissions, where the well-mixed atmosphere and long residence time of major pollutants mean that the location of emission is unimportant for the magnitude of global climate change) but interact in complex ways (as with the way urban demand affects national and global commodity markets for food). Climate change bodies such as the United Nations Framework Convention on Climate Change (UNFCCC) has begun to develop standards for

GHG accounting, including dealing with the concept of 'leakage', where climate mitigation action in one place may increase emissions elsewhere[87]. This type of accounting framework is needed for other aspects of urban indirect impacts and would allow for a more comprehensive picture of indirect biodiversity impacts to be constructed.

In order to close this research gap, increased scientific study is needed of the indirect impacts of urban population and area growth, including the further conceptual and methodological development of attribution accounting frameworks. Science funding agencies and science institutions could promote research into the indirect environmental impacts of urban population and area growth, including studies of urban land teleconnections[71] and telecoupling[88], in order to increase scientific and policy-relevant understanding of indirect effects.

Data availability

The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Received: 19 April 2019; Accepted: 30 October 2019;
Published online: 09 December 2019

References

1. *World Urbanization Prospects: The 2018 Revision* (United Nations Population Division, 2018).
2. Seto, K., Guneralp, B. & Hutyra, L. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl Acad. Sci. USA* **109**, 16083–16088 (2012).
3. Güneralp, B. & Seto, K. Futures of global urban expansion: uncertainties and implications for biodiversity conservation. *Environ. Res. Lett.* **8**, 014025 (2013).
4. McDonald, R. et al. *Nature in the Urban Century: A Global Assessment of Where and How to Conserve Nature for Biodiversity and Human Wellbeing* (The Nature Conservancy, 2018).
5. Elmqvist, T. et al. *Urbanization, Biodiversity, and Ecosystem Services: Challenges and Opportunities, a Global Assessment* (Springer, 2013).
6. Angel, S., Blei, A. M., Civco, D. L. & Parent, J. *Atlas of Urban Expansion* (Lincoln Institute of Land Policy, 2012).
7. Satterthwaite, D. in *United Nations Expert Group Meeting on Population Distribution, Urbanization, Internal Migration and Development* ESA/P/WP.206 (ed. Department of Economic and Social Affairs, Population Division) 309–334 (United Nations, 2008).
8. Güneralp, B. et al. Global scenarios of urban density and its impacts on building energy use through 2050. *Proc. Natl Acad. Sci. USA* **114**, 8945–8950 (2017).
9. Flörke, M., Schneider, C. & McDonald, R. I. Water competition between cities and agriculture driven by climate change and urban growth. *Nat. Sustain.* **1**, 51–58 (2018).
10. Regmi, A. & Dyck, J. in *Changing Structure of Global Food Consumption and Trade* WRS-01-1 (ed. Regmi, A.) 23–30 (Market and Trade Economics Division, Economic Research Service, USDA, 2001).
11. Cole, M. A. & Neumayer, E. Examining the impact of demographic factors on air pollution. *Popul. Environ.* **26**, 5–21 (2004).
12. Dyson, T. The role of the demographic transition in the process of urbanization. *Popul. Dev. Rev.* **37**, 34–54 (2011).
13. *World Bank* (Oxford University Press, 2009).
14. *Land Cover CCI Product User Guide Version 2.0* (European Space Agency, 2017); www.esa-landcover-cci.org
15. *Redefining "Urban": A New Way to Measure Metropolitan Areas* (OECD, 2012).
16. CBD *Global Biodiversity Outlook 3* (Secretariat of the Convention on Biological Diversity, 2010).
17. Díaz, S. et al. *Summary for Policymakers of the Global Assessment Report on Biodiversity and Ecosystem Services of The Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services* 1–39 (United Nations, 2019).
18. Pereira, H. M. et al. Scenarios for global biodiversity in the 21st century. *Science* **330**, 1496–1501 (2010).
19. Pimm, S. L. et al. The biodiversity of species and their rates of extinction, distribution, and protection. *Science* **344**, 1246752 (2014).
20. Ceballos, G. et al. Accelerated modern human–induced species losses: entering the sixth mass extinction. *Sci. Adv.* **1**, e1400253 (2015).
21. McDonald, R. I. Ecosystem service demand and supply along the urban-to-rural gradient. *J. Conserv. Plan.* **5**, 1–14 (2009).
22. Aronson, M. F. et al. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc. R. Soc. B* **281**, 20133330 (2014).
23. Alberti, M. et al. Global urban signatures of phenotypic change in animal and plant populations. *Proc. Natl Acad. Sci. USA* **114**, 8951–8956 (2017).
24. UN Habitat *Cities and Climate Change: Global Report on Human Settlements 2011* (Earthscan, 2011).
25. Frey, H. *Designing the City: Towards a More Sustainable Urban Form* (Taylor & Francis, 2003).
26. Alberti, M. et al. The impact of urban patterns on aquatic ecosystems: an empirical analysis in Puget lowland sub-basins. *Landsc. Urban Plan.* **80**, 345–361 (2007).
27. Kennedy, C., Pincetl, S. & Bunje, P. The study of urban metabolism and its applications to urban planning and design. *Environ. Pollut.* **159**, 1965–1973 (2011).
28. Montgomery, M., Stren, R., Cohen, B. & Reed, H. E. *Cities Transformed: Demographic Change and its Implications in the Developing World* (National Academies Press, 2003).
29. Lynch, K. *Good City Form* (MIT Press, 1984).
30. Mumford, L. *The City in History: Its Origins, Its Transformations, and Its Prospects* (Harvest Books, 1968).
31. Gaspar, J. & Glaeser, E. L. Information technology and the future of cities. *J. Urban Econ.* **43**, 136–156 (1998).
32. Sanderson, E. W., Walston, J. & Robinson, J. G. From bottleneck to breakthrough: urbanization and the future of biodiversity conservation. *BioScience* **68**, 412–426 (2018).
33. Van Der Waals, J. The compact city and the environment: a review. *Tijdschr. Econ. Soc. Geogr.* **91**, 111–121 (2000).
34. McDonald, R. I. Global urbanization: can ecologists identify a sustainable way forward? *Front. Ecol. Environ.* **6**, 99–104 (2008).
35. Seto, K. et al. in *Climate Change 2014: Mitigation of Climate Change. Contribution of Working Group III to theFifth Assessment Report* (eds Edenhofer, O. et al.) 923–1000 (Intergovernmental Panel on Climate Change, 2014).
36. Meyer, S. B. & Lunnay, B. The application of abductive and retroductive inference for the design and analysis of theory-driven sociological research. *Sociol. Res. Online* **18**, 1–11 (2013).
37. Ferraro, P. J., Sanchirico, J. N. & Smith, M. D. Causal inference in coupled human and natural systems. *Proc. Natl Acad. Sci. USA* **116**, 5311–5318 (2019).
38. McDonald, R. I. in *Encyclopedia of Biodiversity* 2nd edn (ed. Levin, S.) (Academic Press, 2013).
39. NRC *Cities Transformed: Demographic Change and its Implication in the Developing World* (National Academies Press, 2003).
40. Jiang, L. & O'Neill, B. C. Global urbanization projections for the Shared Socioeconomic Pathways. *Global Environmental Change* **42**, 193–199 (2017).
41. Jones, B. & O'Neill, B. Spatially explicit global population scenarios consistent with the Shared Socioeconomic Pathways. *Environ. Res. Lett.* **11**, 084003 (2016).
42. Pesaresi, M., Melchiorri, M., Siragusa, A. & Kemper, T. *Atlas of the Human Planet 2016: Mapping Human Presence on Earth with the Global Human Settlement Layer* (European Commission, 2016).
43. Angel, S. et al. *Our Not-So-Urban World* Working Paper No. 42 (The Marron Institute of Urban Management, New York University, 2018); https://go.nature.com/2qnGrJ2
44. Schneider, A., Friedl, M. A. & Potere, D. A new map of global urban extent from MODIS satellite data. *Environ. Res. Lett.* **4**, 0044003 (2009).
45. d'Amour, C. B. et al. Future urban land expansion and implications for global croplands. *Proc. Natl Acad. Sci. USA* **114**, 8939–8944 (2017).
46. Güneralp, B., Lwasa, S., Masundire, H., Parnell, S. & Seto, K. Urbanization in Africa: challenges and opportunities for conservation. *Environ. Res. Lett.* **13**, 015002 (2017).
47. Angel, S., Parent, J., Civco, D. L., Blei, A. & Potere, D. The dimensions of global urban expansion: estimates and projections for all countries, 2000–2050. *Progress Plan.* **75**, 53–107 (2011).
48. Zhou, Y., Varquez, A. C. & Kanda, M. High-resolution global urban growth projection based on multiple applications of the SLEUtH urban growth model. *Sci. Data* **6**, 34 (2019).
49. Doxsey-Whitfield, E. et al. Taking advantage of the improved availability of census data: a first look at the gridded population of the world, version 4. *Papers Appl. Geogr.* **1**, 226–234 (2015).
50. UNPD *Household Size and Composition Around the World* (United Nations, Department of Economic and Social Affairs, Population Division, 2017).
51. Theobald, D. M. Landscape patterns of exurban growth in the USA from 1980 to 2020. *Ecol. Soc.* **10**, 32 (2005).
52. Theobald, D. M. Land-use dynamics beyond the American urban fringes. *Geogr. Rev.* **91**, 544–564 (2001).
53. McDonald, R. I., Güneralp, B., Huang, C.-W., Seto, K. & You, M. Conservation priorities to protect vertebrate endemics from global urban expansion. *Biol. Conserv.* **224**, 290–299 (2018).

54. Luck, G. W. A review of the relationships between human population density and biodiversity. *Biol. Rev.* **82**, 607–645 (2007).
55. Luck, G. W. The relationships between net primary productivity, human population density and species conservation. *J. Biogeogr.* **34**, 201–212 (2007).
56. Burgess, N. D. et al. Correlations among species distributions, human density and human infrastructure across the high biodiversity tropical mountains of Africa. *Biol. Conserv.* **134**, 164–177 (2007).
57. Polaina, E., González-Suárez, M. & Revilla, E. Socioeconomic correlates of global mammalian conservation status. *Ecosphere* **6**, 1–34 (2015).
58. Shochat, E. et al. Invasion, competition, and biodiversity loss in urban ecosystems. *BioScience* **60**, 199–208 (2010).
59. Faeth, S. H., Bang, C. & Saari, S. Urban biodiversity: patterns and mechanisms. *Ann. N. Y. Acad. Sci.* **1223**, 69–81 (2011).
60. Newbold, T. et al. Global effects of land use on local terrestrial biodiversity. *Nature* **520**, 45–50 (2015).
61. Weller, R., Hoch, C. & Huang, C. *Atlas for the End of the World* http://atlas-for-the-end-of-the-world.com (2017).
62. Conde, D. A. et al. Opportunities and costs for preventing vertebrate extinctions. *Curr. Biol.* **25**, R219–R221 (2015).
63. Güneralp, B., Perlstein, A. S. & Seto, K. C. Balancing urban growth and ecological conservation: a challenge for planning and governance in China. *Ambio* **44**, 532–543 (2015).
64. Baillie, J. E. M., Griffiths, J., Turvey, S., Loh, J. & Collen, B. *Evolution Lost Status & Trends of the World's Vertebrates* (Zoological Society of London, 2010).
65. Eisenhauer, N., Bonn, A. & Guerra, C. A. Recognizing the quiet extinction of invertebrates. *Nat. Commun* **10**, 50 (2019).
66. Girgin, S., Kazanci, N. & Dügel, M. Relationship between aquatic insects and heavy metals in an urban stream using multivariate techniques. *Int. J. Environ. Sci. Technol.* **7**, 653–664 (2010).
67. Carvalho, L., Cortes, R. & Bordalo, A. A. Evaluation of the ecological status of an impaired watershed by using a multi-index approach. *Environ. Monit. Assess.* **174**, 493–508 (2011).
68. Violin, C. R. et al. Effects of urbanization and urban stream restoration on the physical and biological structure of stream ecosystems. *Ecol. Appl.* **21**, 1932–1949 (2011).
69. Carew, M. E., Kellar, C. R., Pettigrove, V. J. & Hoffmann, A. A. Can high-throughput sequencing detect macroinvertebrate diversity for routine monitoring of an urban river? *Ecol. Indic.* **85**, 440–450 (2018).
70. Güneralp, B., Seto, K. C. & Ramachandran, M. Evidence of urban land teleconnections and impacts on hinterlands. *Curr. Opin. Environ. Sustain.* **5**, 445–451 (2013).
71. Seto, K. C. et al. Urban land teleconnections and sustainability. *Proc. Natl Acad. Sci. USA* **109**, 7687–7692 (2012).
72. Zimmerer, K., Lambin, E. & Vanek, S. Smallholder telecoupling and potential sustainability. *Ecol. Soc.* **23**, 30 (2018).
73. Luck, M. A., Jenerette, G. D., Wu, J. & Grimm, N. B. The urban funnel model and the spatially heterogeneous ecological footprint. *Ecosystems* **4**, 782–796 (2001).
74. Moore, J., Kissinger, M. & Rees, W. E. An urban metabolism and ecological footprint assessment of Metro Vancouver. *J. Environ. Manag.* **124**, 51–61 (2013).
75. Zhang, Y., Yang, Z. & Yu, X. Urban metabolism: a review of current knowledge and directions for future study. *Environ. Sci. Technol.* **49**, 11247–11263 (2015).
76. FAO *FAOSTAT Agri-Environmental Indicators* (Food and Agriculture Organization of the United Nations, 2016).
77. Popkin, B. M. Urbanization, lifestyle changes and the nutrition transition. *World Dev.* **27**, 1905–1916 (1999).
78. *Diet, Nutrition, and the Prevention of Chronic Diseases: Report of a Joint WHO/FAO Expert Consultation* Vol. 916 (World Health Organization, 2003).
79. Matson, P. A., Parton, W. J., Power, A. & Swift, M. Agricultural intensification and ecosystem properties. *Science* **277**, 504–509 (1997).
80. Chaplin-Kramer, R. et al. Spatial patterns of agricultural expansion determine impacts on biodiversity and carbon storage. *Proc. Natl Acad. Sci. USA* **112**, 7402–7407 (2015).
81. Seto, K. C. & Ramankutty, N. Hidden linkages between urbanization and food systems. *Science* **352**, 943–945 (2016).
82. Platt, R. H., Rowntree, R. A. & Muick, P. C. *The Ecological City: Preserving and Restoring Urban Biodiversity* (Univ. Massachusetts Press, 1994).
83. Muller, N., Werner, P. & Kelcey, J. G. *Urban Biodiversity and Design* (John Wiley & Sons, 2010).
84. Beatley, T. *Biophilic Cities: Integrating Nature into Urban Design and Planning* (Island Press, 2010).
85. Steiner, F., Thompson, G. & Carbonell, A. *Nature and Cities* (The Lincoln Institute for Land Policy, 2016).
86. Nagendra, H., Bai, X., Brondizio, E. S. & Lwasa, S. The urban south and the predicament of global sustainability. *Nat. Sustain.* **1**, 341–349 (2018).
87. Schwarze, R., Niles, J. O. & Olander, J. Understanding and managing leakage in forest–based greenhouse–gas–mitigation projects. *Philos. Trans. Royal Soc. A* **360**, 1685–1703 (2002).
88. Fang, C., Liu, H. & Li, G. International progress and evaluation on interactive coupling effects between urbanization and the eco-environment. *J. Geogr. Sci.* **26**, 1081–1116 (2016).

Acknowledgements

The authors thank the thousands of scientists whose data and papers have made this Review possible. This Review is a joint effort of the working group sUrbio2050 kindly supported by sDiv, the Synthesis Centre of the German Centre for Integrative Biodiversity Research (iDiv) Halle-Jena-Leipzig, funded by the German Research Foundation (FZT 118).

Author contributions

Authors co-designed the literature review during a working group meeting. A.V.M. led the literature review, which all authors contributed to. R.I.M. wrote the initial version of this manuscript, with significant feedback and guidance from H.M.P. and A.V.M. All authors made substantial contributions to the intellectual content, analysis and interpretation of the literature review, and editing of the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41893-019-0436-6.

Correspondence should be addressed to R.I.M.