nature sustainability

ARTICLES

https://doi.org/10.1038/s41893-022-00930-8

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Impacts of urban expansion on natural habitats in global drylands

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Urban regions across the world have expanded rapidly in recent decades, affecting fragile natural habitats, including in drylands, and threatening the achievement of the UN Sustainable Development Goal 15, 'life on land'. Yet, few studies have comprehensively investigated impacts of urban expansion on natural dryland habitats globally even though these cover 40% of global land area and provide habitats for 28% of endangered species. Here, we quantify at multiple scales the loss of habitat quality directly and indirectly caused by dryland urban expansion. Direct impacts are conversions of natural habitats to urban land. We define indirect impacts as proximate impacts within 10 km around the expanded urban land footprint. We found that although urban expansion from 1992 to 2016 resulted in an average 0.8% loss of dryland habitat quality, the indirect impacts were 10–15 times greater. By considering the coincidence of habitat-quality loss and threatened species ranges, we found that, globally, nearly 60% of threatened species were affected by such indirect impacts of dryland urban expansion. Our findings suggest that strategic management is imperative to mitigate the substantial impacts of dryland urban expansion on biodiversity.

Covering 40% of the world's land and inhabited by more than 30% of the world population, drylands are critically important for global sustainability[1,2]. Natural habitats in drylands are fragile and easily affected by human activities such as urban expansion, which can threaten the integrity of ecosystems[1,3]. Over the past decades, global drylands have experienced rapid urban expansion[4]. Therefore, it is of great importance to effectively evaluate the impacts of urban expansion on natural habitats in global drylands.

Urban expansion can directly impact natural habitats through direct conversion of habitats to urban uses[5]. It can also have indirect impacts on natural habitats through disturbances emanating from expanding urban land, such as noise, air and water pollution[6]. The impacts of urban expansion on natural habitats at the global scale have been evaluated in several studies. For example, approximately 12% and 9% of urban expansion have been found to occur at the expense of grasslands and forests, respectively, from 1985 to 2015[7]. Global urban land within 50 km of protected areas was predicted to increase nearly three times from 2000 to 2030[8]. The mean distance between the protected areas and nearest city was estimated to decrease from 44 km to 38 km from 2000 to 2030[9]. The area of natural habitats, area of urban land around the protected areas and distance between the protected areas and nearest city are indicators commonly used in evaluating impacts of urban expansion on natural habitats[10]. However, these studies typically focus only on the direct impact of urban expansion on natural habitats. Exceptions exist; for instance, a particular form of indirect impact of global urban expansion was investigated through cropland displacement without accounting for other forms of indirect impact of urban expansion[11].

In our study, we use habitat quality index to evaluate and compare the direct and indirect impacts of urban expansion on natural habitats in global drylands[12,13]. The index was initially developed to estimate the ability of the habitat to support species persistence, with the hypothesis that higher habitat quality supports higher species richness, and decreases lead to reductions in species persistence[14]. Specifically, urban expansion leads to the loss of habitat quality through the conversion of natural habitat to urban land, which is defined as direct impacts. Urban expansion can, on the other hand, decrease the habitat quality by increasing disturbances across surrounding natural habitats, which is defined as indirect impacts. Here, we assumed that indirect impacts are caused by proximate disturbances (for example, trampling) and limited by the maximum effective distance of the urban land (10 km) because the indirect impacts are commonly greater close to urban areas and mainly concentrated at the regional scale[8,15]. Our consideration of 'indirect impacts' is intentionally conservative to facilitate a straightforward comparison to the direct impact and hence do not include such long-distance impacts as telecoupling of the food system or global-scale air pollution[16–18]. Using the habitat quality index, the impacts of urban expansion on natural habitats have previously been evaluated comprehensively for various regions, including the Mediterranean region[13], West Africa[19] and Beijing[20]. However, thus far, there has not been a global analysis of the impacts of urban expansion on natural habitats that differentiated between its direct and indirect impacts using a well-defined quantitative criterion.

In this study, we analysed the impacts of urban expansion on natural habitats from 1992 to 2016 in global drylands. To achieve this goal, we first estimated the habitat quality index in 1992 for all dryland habitats at multiple scales, that is, global drylands, 4 subtypes of dryland, 14 biomes and 467 ecoregions. It is worth mentioning that we analysed and presented results pertaining only to those parts of the biomes and ecoregions that are drylands. We divided

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ecoregions into five levels according to the average habitat quality using the equal interval method and reported the area of natural habitats at each scale of the analysis. We then analysed the dynamics of dryland urban expansion from 1992 to 2016 by calculating a normalized indicator, that is, the percentage of the urban area relative to the total area in a region. Then, we estimated both the direct and indirect impacts of dryland urban expansion on natural habitats. Details can be found in Methods. We also discuss the implications of the loss of habitat quality for threatened species, as well as potential ways to mitigate these adverse biodiversity impacts of dryland urban expansion.

Results

Quality of dryland natural habitats in 1992. Low-quality ecoregions had the largest area of natural habitats (nearly 17 million km^2), accounting for 34% of natural habitats in global drylands in 1992. Of all the dryland subtypes, hyper-arid drylands had the largest low-quality natural habitats extent (10 million km^2, corresponding to 61% of natural habitats in global low-quality ecoregions). This, however, mainly reflects the fact that even in the absence of anthropogenic disturbances, hyper-arid drylands are characterized by harsh environmental conditions that make them suitable only for a relatively small number of endemic and specialist species uniquely adapted to such conditions[21–23]. In the absence of an objective indicator to quantify the value of such unique biota, what we evaluated as habitat quality in this study then is the extent to which various dryland habitats support species persistence. That is, low-quality natural habitats usually have less species richness under the environmental limitations (harsh environment) instead of suffering high degradation or having less value of biodiversity conservation. Among biomes, low-quality dryland habitats were dominant in desert and xeric shrubland biome (15 million km^2, accounting for nearly 90% of low-quality habitat in global drylands). In contrast, total low-quality dryland habitat was less than 2 million km^2 in the 10 biomes (Fig. 1a, Supplementary Fig. 1a and Table 1).

In desert and xeric shrubland biome, ten low-quality ecoregions (for example, Sahara Desert ecoregion, Arabian Desert ecoregion, and North Saharan Steppe and Woodland ecoregion) accounted for 80% of natural-habitat extent in low-quality ecoregions. Each of these ten ecoregions had over 500 thousand km^2 of natural habitats, reaching a total area of 13 million km^2. Among them, the Sahara Desert ecoregion had the largest natural-habitat extent, which was 5 million km^2, accounting for approximately 30% of natural habitats in low-quality ecoregions in desert and xeric shrubland biome (Supplementary Fig. 1b).

Dynamics of dryland urban expansion from 1992 to 2016. Drylands experienced urban expansion at a slightly higher rate than the global average. Dryland urban land increased from 95 thousand km^2 in 1992 to 230 thousand km^2 in 2016, corresponding to an average annual growth rate of 3.8%. In comparison, the global average annual growth rate was 3.5% over 1992–2016[4]. We used a normalized indicator, that is, the percentage of the urban area relative to the total area in the corresponding region (hereafter referred to as the percentage of the urban area), to analyse the dynamics of dryland urban expansion. We found that the percentage of the urban area increased by 0.2% in global drylands. Dry sub-humid drylands underwent the most rapid urban land expansion, where the percentage of the urban area increased by 0.35% (Fig. 1b and Supplementary Table 2).

Among the biomes, urban areas in the drylands of the mangrove biome expanded the fastest. The percentage of these urban areas increased from 1.5% in 1992 to 3.3% in 2016, an eightfold faster increase than that of the urban areas across the entire global drylands. The growth in urban land percentage in this biome was also twice as fast as that within temperate broadleaf and mixed forest biome that had the second fastest urban expansion. In drylands in the other biomes, growth of the percentage of the urban area was less than 1.0%, with the slowest growth having taken place on habitats within the tundra biome (Supplementary Fig. 2a and Table 3).

Among the ecoregions in the mangrove biome, the urban area across the drylands of the Indus River Delta-Arabian Sea mangrove ecoregion increased the most rapidly. The percentage of the urban area in this ecoregion increased 5.3%, that is, almost triple the average growth across the entire mangrove biome. In addition, 4.4% and 3.9% of the land area in drylands of the Southern Atlantic mangrove ecoregion and Goadavari-Krishna mangrove ecoregion, respectively, were converted to urban land from 1992 to 2016 (Supplementary Fig. 2b).

Impacts of urban expansion on natural habitats. At the global scale, the influence of urban expansion on dryland habitats was small. The average habitat quality in global drylands decreased from 0.3981 in 1992 to 0.3951 in 2016, a decrease of only 0.76% (Fig. 2a). Meanwhile, urban expansion led to a 0.10% (or 0.05 million km^2) decrease in the area of natural habitats, which was substantially lower than the loss in natural habitat quality. Urban expansion had the greatest impacts on natural habitats in dry sub-humid drylands (0.93%), which also experienced the fastest urban expansion among the four dryland subtypes (Fig. 2b and Supplementary Table 2).

There was clear disparity among biomes in terms of the impacts of urban expansion on dryland habitats. Urban expansion had the greatest impacts on the dryland habitats within the mangrove biome (5.5%), followed by those in the temperate broadleaf and mixed forest biome (2.8%) and Mediterranean forest, woodland and scrub biome (2.7%). The loss in dryland habitat quality within the mangrove biome was 6.6 times the mean loss across global drylands. In addition, the losses in dryland habitat quality in other biomes were less than 1.4%, with the smallest decrease in the tropical and subtropical grassland, savanna and shrubland biome (0.28%) (Fig. 2c and Supplementary Table 3).

We identified eight hotspots (which may span across several ecoregions, hereafter referred to as dryland hotspots) where dryland natural habitats were severely affected by urban expansion using spatial autocorrelation analysis. In these dryland hotspots, the losses in habitat quality were significantly more severe than in other ecoregions (95% confidence). Habitat quality in dryland hotspots decreased by 6.8% on average, which was 9 times the mean loss across global drylands. Natural habitats in the Malabar coast had the greatest loss in habitat quality, with a decrease of 14%, corresponding to 18 times the mean loss in global drylands. In the dryland hotspots of East of Deccan Plateau, Californian coast, North of Mediterranean and Loess Plateau-Huanghe Plain, urban expansion resulted in a 5% to 10% reduction in habitat quality. In the Tamaulipas-Texas, West of Ecuador and East of Brazil, the dryland habitat quality declined by 2.7% to 4.9%, which represented 3.6 to 6.4 times the mean habitat quality loss in global drylands (Fig. 3 and Supplementary Table 4).

Indirect impacts far exceeded direct impacts. The indirect impacts of urban expansion in the drylands resulted in a loss of habitat quality 14.2 times greater than that caused by its direct impacts (0.71% vs 0.05%, respectively). Across the dryland subtypes, the largest difference between indirect and direct impacts occurred in semi-arid drylands (0.84% vs 0.05%, respectively) and the smallest occurred in hyper-arid drylands (0.07%, vs 0.70%, respectively) (Fig. 4a and Supplementary Table 2).

The indirect impacts in each biome were also greater than the corresponding direct impacts. We estimated the largest difference between the two in the tropical and subtropical coniferous forest biome. In this biome, indirect impacts decreased the habitat quality by 0.47%, which was 47 times the decrease in habitat quality due to

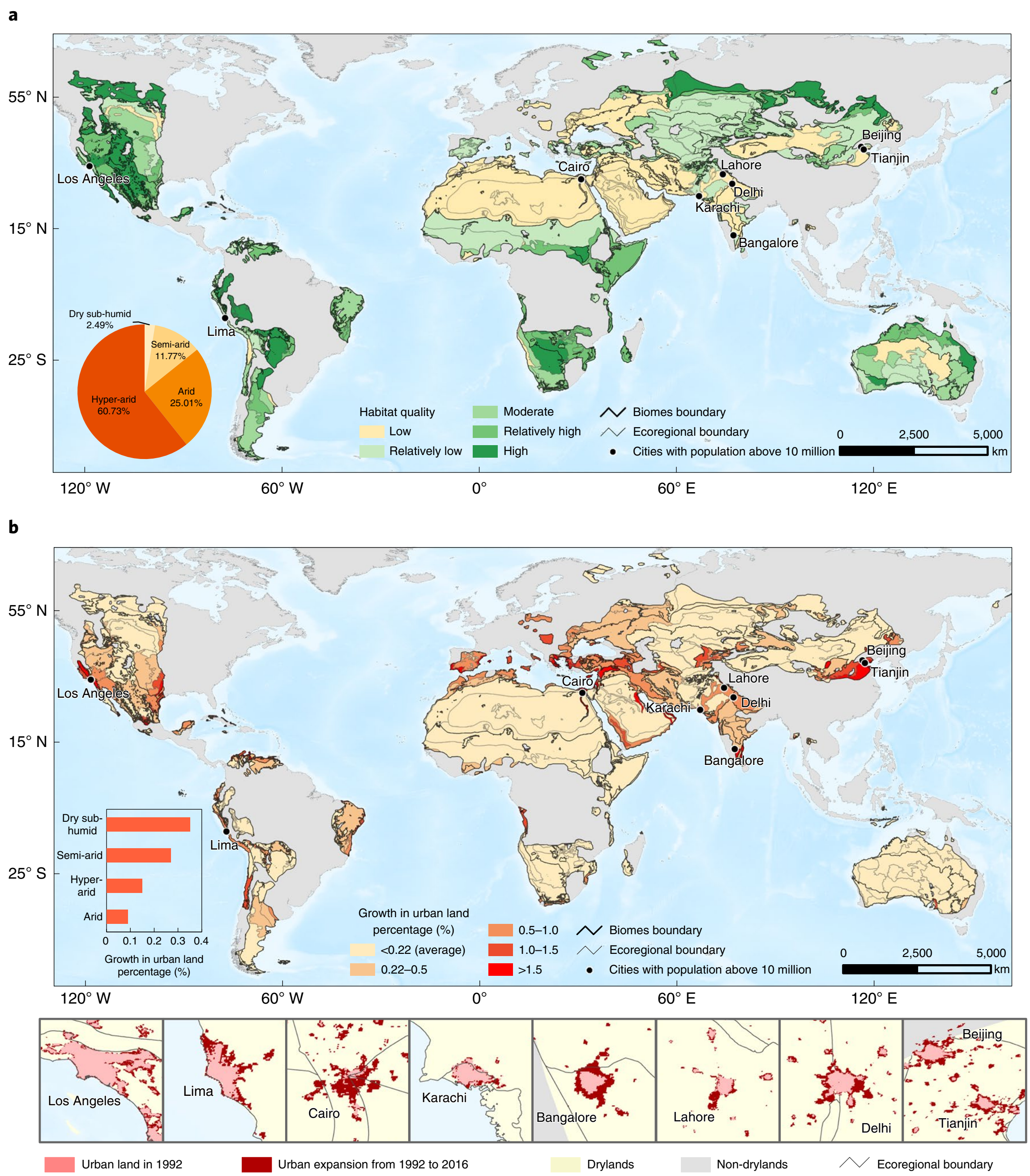

Fig. 1 | Patterns of natural habitats and dynamics of urban expansion in global drylands. a, Patterns of dryland natural habitats in 1992. The pie chart represents the percentage of natural habitats in low-quality ecoregions across all drylands that fall in each of the four dryland subtypes. **b**, Dynamics of urban expansion from 1992 to 2016. Inset bars represent the percentage of the urban expansion area relative to the total area in the corresponding region. Cities with a population above 10 million in drylands are also shown.

direct impacts (0.01%). In other biomes, the indirect impacts were over 7 times larger than the direct impacts, with the smallest difference between the two being found in the flooded grassland and savanna biome (7.7 times) (Fig. 4b and Supplementary Table 3).

Likewise, in the identified dryland hotspots, urban expansion led to on average 6.26% indirect loss in habitat quality, which is 11.5 times more than the direct loss in habitat quality (0.55%). The largest difference in the habitat quality loss between indirect and direct urban impacts was in the North of Mediterranean hotspots, followed by the East of Brazil and Californian coast hotspots. In the North of Mediterranean hotspots, indirect impacts of urban expansion led to a decrease in habitat quality 27 times more than that caused by direct impacts (6.43% and 0.27%, respectively) (Fig. 4c and Supplementary Table 4).

Discussion

Indirect impacts jeopardize threatened species. Natural habitat is the foundation for maintaining biodiversity[24,25]. The loss of habitat quality could reduce the ability of natural habitats to provide living space for species, which in turn could cause species extinctions[26,27]. Following Seto et al.[28], we estimated the impacts of urban expansion on threatened species by overlapping the range of habitat loss and the distribution of threatened species. We found that although urban expansion has led to only a small decline in the value of

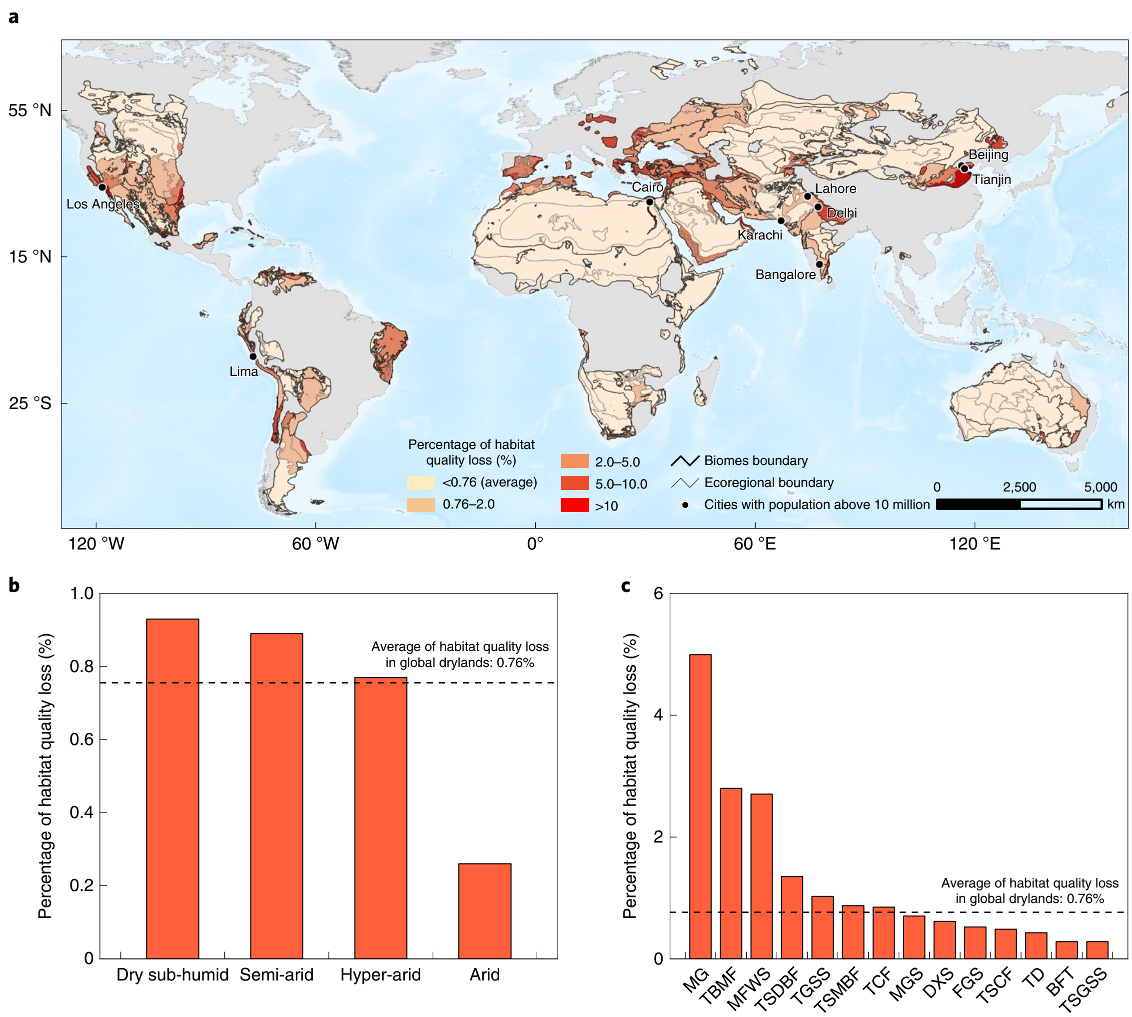

Fig. 2 | Impacts of urban expansion on natural habitats from 1992 to 2016 at the global and biome scale. a–c, Impacts in global drylands (**a**), in different subtypes of drylands (**b**) and in different biomes (**c**). TSMBF, tropical and subtropical moist broadleaf forests; TSDBF, tropical and subtropical dry broadleaf forests; TSCF, tropical and subtropical coniferous forests; TBMF, temperate broadleaf and mixed forests; TCF, temperate conifer forests; BFT, boreal forests/taiga; TSGSS, tropical and subtropical grasslands, savannas and shrublands; TGSS, temperate grasslands, savannas and shrublands; FGS, flooded grasslands and savannas; MGS, montane grasslands and shrublands; TD, tundra; MFWS, Mediterranean forests, woodlands and scrub; DXS, deserts and xeric shrublands; and MG, mangroves.

habitat quality (0.78%), it nevertheless overlapped with the range maps of 1,595 threatened species, or 57.6% of the threatened species in global drylands. We focus on the indirect impacts of urban expansion on the threatened species because indirect impacts were much greater than the direct impacts. We found that the indirect impacts of urban expansion affected the range maps of 1,463 threatened species, which represent 52.9% of endangered species across the global drylands. In the four subtypes of dryland, urban expansion encroached on the ranges of 49.3%–58.4% of threatened species indirectly (Fig. 5a). At the biome scale, urban expansion indirectly affected 52.2% of threatened species on average, with the largest percentage in flooded grassland and savanna biome (Fig. 5b). Across the eight identified hotspots, 68.4% of threatened species were affected by urban expansion. In the northern Mediterranean hotspot, this percentage was as high as 82.3% (Fig. 5c). The spatial overlap between urban expansion and the range map of threatened species was mainly due to their reliance on and competition for freshwater resources in dryland[29,30]. Existing studies also showed that human activities (for example, urban expansion) in drylands greatly affected the life and reproduction of threatened species. For example, urban expansion in the Ecuadorian dry forest ecoregion was estimated to have affected terrestrial vertebrate endemism by occupying the natural habitat[31]. Field surveys by the International Union for Conservation of Nature (IUCN)[32] also showed that threatened species, such as the Merriam kangaroo rat, went nearly extinct because of urban expansion in the California coastal sage and chaparral ecoregion, one of the dryland hotspots we identified in this study.

We then further analysed the indirect impacts of urban expansion on different taxonomic groups of threatened species in the hotspots. We found that urban expansion had the largest indirect impacts on threatened mammals. There were 117 threatened mammals indirectly affected by urban expansion, accounting for 90% of the total threatened mammals in the hotspots. The percentages for endangered reptiles, amphibians and birds were 80.4%, 73.9% and 57.9%, respectively (Fig. 5d). Existing studies have also confirmed that the indirect impacts of urban expansion could affect the survival of threatened mammals. For example, urban expansion was found to have possibly reduced mammalian movements indirectly through habitat change and fragmentation[33]. Urban expansion was also found to have possibly affected threatened mammals indirectly by increasing human activities and invasive alien species[34].

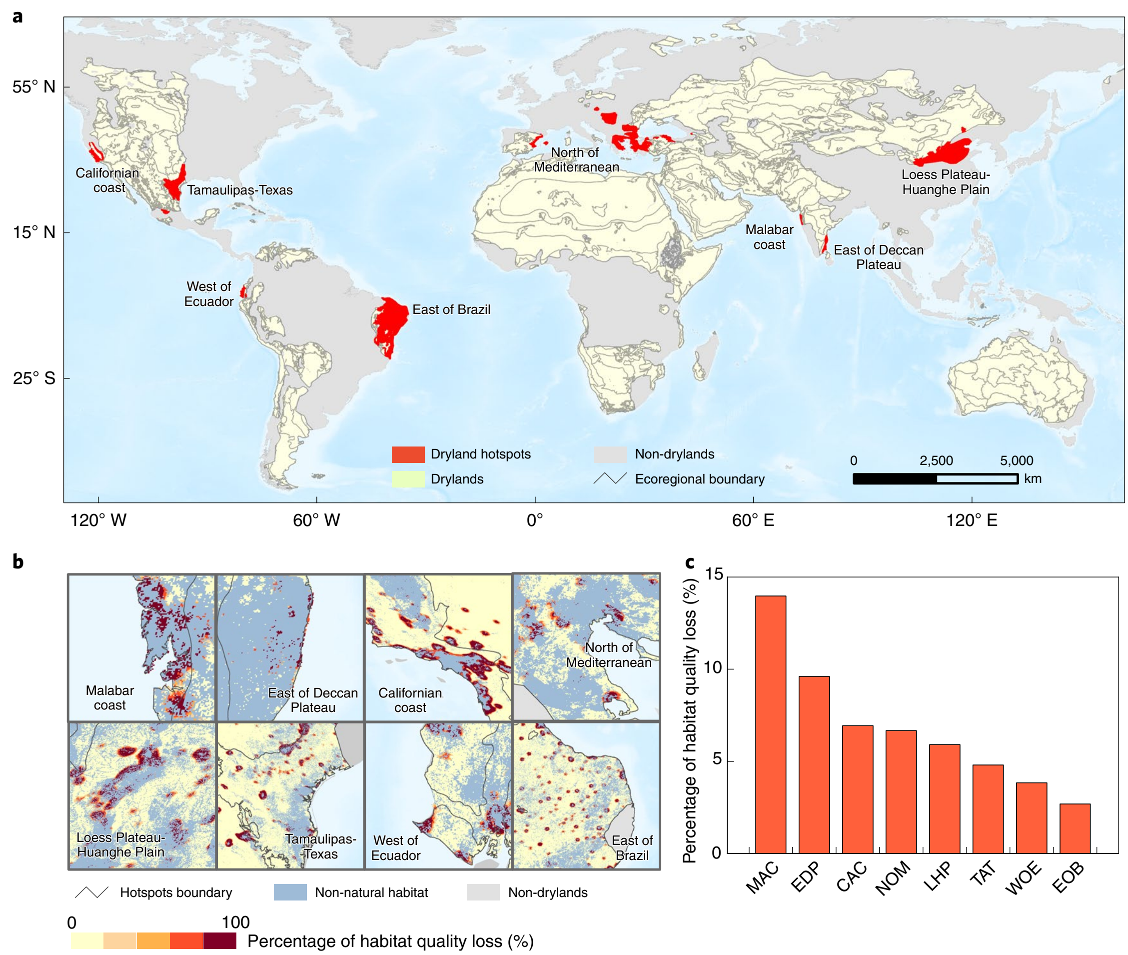

Fig. 3 | Impacts of urban expansion on natural habitats from 1992 to 2016 at the ecoregion scale. a, Patterns of the hotspots in drylands. **b**, Changes of habitat quality in eight hotspots. **c**, Percentage of habitat quality loss at the hotspot scale. Dryland hotspots: MAC, Malabar coast; EDP, East of Deccan Plateau; CAC, Californian coast; NOM, North of Mediterranean; LHP, Loess Plateau-Huanghe Plain; TAT, Tamaulipas-Texas; WOE, West of Ecuador; and EOB, East of Brazil.

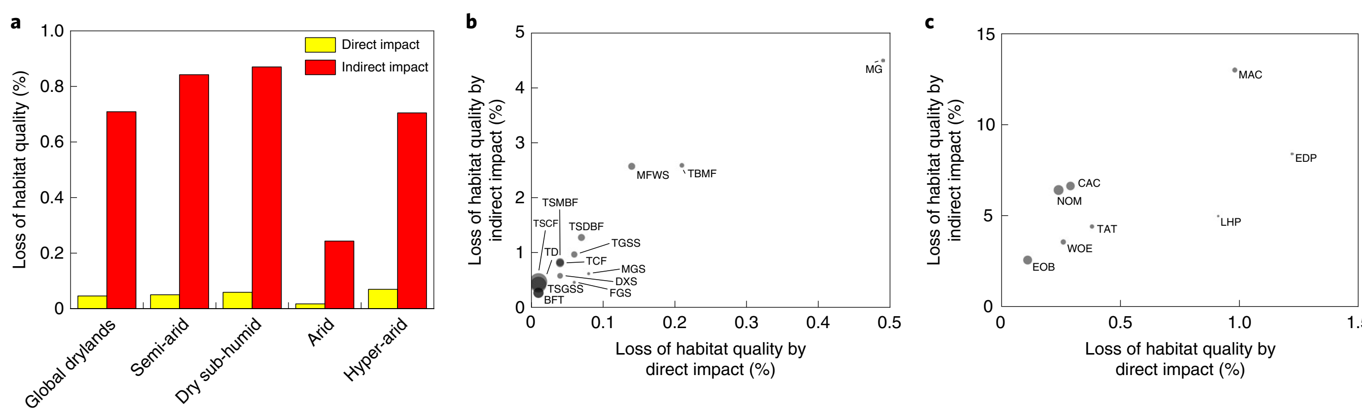

Fig. 4 | Direct and indirect impacts of urban expansion. a–c, Impacts at the global scale (**a**), at the biome scale (**b**) and in eight hotspots (**c**). In **b** and **c**, the size of the dot represents the difference between direct and indirect impacts. Abbreviations of biomes and hotspots can be found in Figs. 2 and 3, respectively.

Special attention should be given to indirect impacts. Currently, conservation planning mainly focuses on the direct impacts of urban expansion. For example, the conservation policies for protected areas proposed by the World Commission on Protected Areas (WCPA) and the IUCN mainly limit urban expansion within the protected areas[35]. China, in an effort to protect its natural habitats, has been implementing the Ecological Conservation Red Line policy since 2011, which forbids urban expansion within the

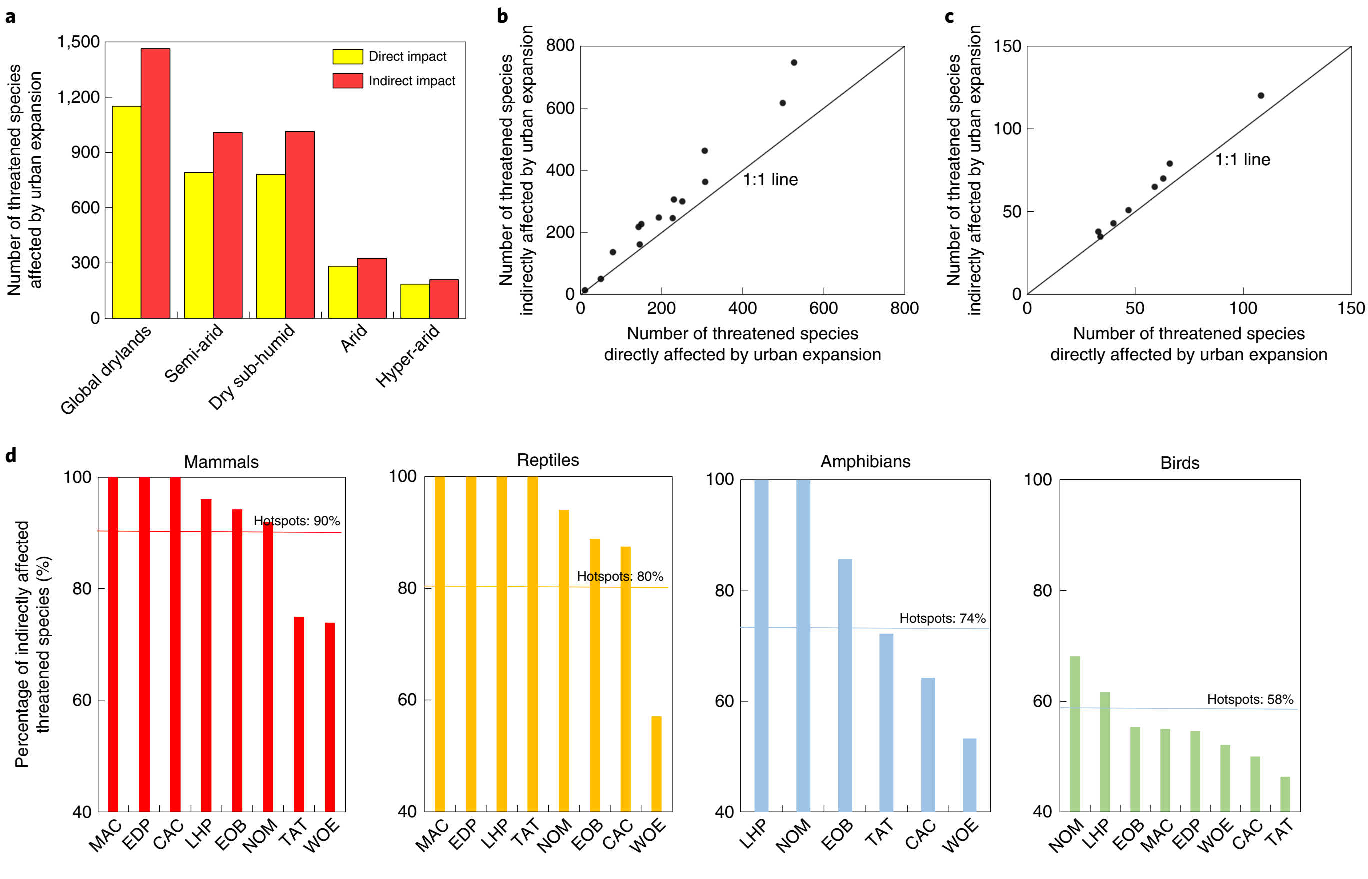

Fig. 5 | Indirect impacts of urban expansion on threatened species. a–d, Indirect impacts at the global scale (**a**), at the biome scale (**b**), in eight hotspots (**c**) and on different threatened species taxa in the hotspots (**d**). Abbreviations of biomes and hotspots can be found in Figs. 2 and 3, respectively. There are no threatened amphibians in two hotspots (MAC and EDP); hence, only six bars are shown in the corresponding plot.

designated red line areas[36,37]. Several studies identified conservation priorities only in consideration of the direct conversion of natural habitats to urban land[3126]. Indeed, scientific studies also mainly focused on the direct impacts of urban expansion on natural habitats. A review of studies on the impacts of urbanization on biodiversity found that only a few studies focused on the indirect impacts of urban expansion at the global scale[6].

Here, we provide presumably the first quantitative estimation of the scale of the indirect impacts of urban land expansion in comparison to its direct impacts in dryland habitats around the world. We find that indirect impacts of urban expansion, even with the conservative definition that we adopted in this study, far exceed its direct impacts in drylands. This is primarily because the indirect impacts of urban expansion could reach far more extensively in terms of areal cover than its direct impacts[15]. Furthermore, urban expansion usually converts cropland where habitat suitability is low[11], while the indirect impacts of urban expansion can affect nearby high-suitability habitats depending on their proximity to the urban lands. For example, among the identified hotspots, the North of Mediterranean hotspot had the largest gap between indirect and direct impacts on natural habitats and biodiversity. In this hotspot, the urban area expanded by 5,380 km^2 and over 80% of the urban expansion occurred over croplands and rural settlements. Yet, we estimated that urban expansion in this area disturbed 32.4 thousand km^2 of natural habitats indirectly, of which nearly 60% were high-quality habitats.

Therefore, urban growth policies and conservation planning need to account for both direct and indirect impacts of urban expansion. Low-density urban land expansion may prove especially damaging to natural habitats, as such expansion will spread the indirect impacts a lot farther than more compact urban expansion patterns[38,39]. Moreover, urban expansion can impact food security; for example, urbanization is predicted to cause the loss of 1.6–3.3 million hectares per year of prime agricultural land from 2000 to 2030[40]. It is also not sufficient to prevent urban expansion only within critical habitats and croplands but also in the vicinity of these habitats to minimize indirect impacts. Certain environmental protection projects, such as green belts, should be developed with proper accounting of the indirect impacts of urban expansion in drylands[41]. It should be noted that the loss of habitat quality per unit area caused by direct impacts was larger than that caused by indirect impacts. Therefore, although we urged that indirect impacts of urban expansion should not be overlooked, direct impacts should also not be ignored because even though the area of direct impacts may be relatively small, they also tend to be irreversible. To this end, measures such as the habitat quality index can serve as effective first-order indicators at large regional scales.

Effectiveness of the habitat quality index. The impacts of urban expansion on natural habitats often alter by species richness[26]. Thus, current studies usually verify the effectiveness of indicators for assessing the impacts of urban expansion on natural habitats by investigating their relationships with species richness[13]. Here, we assessed the effectiveness of the habitat quality index in drylands at the site and ecoregion scale. We found that in the absence of any information on how species richness in dryland habitats may have changed due to urban expansion, the habitat quality index serves as a useful proxy to estimate the change in the capacity of dryland habitats to host species due to urban expansion (Supplementary Material 1 and Fig. 3). In addition, we also assessed the effectiveness of the two commonly used indicators, that is, the area of natural habitats and area of urban land. The results also suggest that the habitat quality index is more informative in capturing the impacts of urban expansion on natural habitats than the two commonly used indicators (Supplementary Material 1 and Fig. 4). The difference in the magnitude of the number of species in Supplementary Figs. 3 and 4 is due to the former considering the site scale while the latter considers the ecoregion scale. It should be noted that areas with low habitat quality can still have a high biodiversity conservation value because of unique biota with many endemic and specialist species. In this study, we mainly assessed the impacts of urban expansion on natural habitats from the perspective of habitat quality (species richness) rather than the conservation value of special species.

We determined the parameters required in calculating habitat quality through literature survey and expert knowledge and assumed that they were invariant across all dryland subtypes, which would introduce uncertainty to our quantitative estimates. Therefore, we assessed this uncertainty in our results using an exploratory ensemble modelling approach[42] (Supplementary Material 2). We found that the results of different parameter combinations were consistent with the main findings of this study and that the indirect impacts of urban expansion on natural habitats far exceed direct impacts in global drylands (Supplementary Fig. 5). Notably, we only considered a specific form of indirect impact of urban expansion, that is, proximate impacts. We assumed that the maximum effective distance of urban area was 10 km on the basis of an extensive review of indirect impacts of urban expansion[15]. How far an indirect impact extends depends on the type of impact[43,44]. To account for this variability in the range of indirect impacts, we conducted a sensitivity analysis using different distances (Supplementary Fig. 6). The radius of influence was calculated at the pixel level, and the maximum effective distance was measured for each urban pixel rather than from the edge or the centre of the city. We found that habitat quality and direct loss of habitat quality had a negative relationship with the maximum effective distance of urban area, whereas total loss and indirect loss of habitat quality had a positive relationship. We also recognize that there are other forms of indirect impact, which were not considered in this study[16–18]. For example, urbanization can lead to higher consumption of soya-based feed and consequently lead to the deforestation and grassland conversion in the exporting countries through soybean trade[45,46]. Therefore, in light of our conservative approach, the indirect impacts of urban expansion are far larger than the direct impacts of urban land expansion.

Our findings are consistent with existing studies at different scales. At the global scale, indirect impacts of urban expansion on natural habitats were found to be more substantial than direct impacts[11,6]. At the biome scale, existing studies found that mangrove biomes experienced rapid urban expansion because of their large shallow-sloping intertidal areas, which are suitable for infrastructure and urban development, resulting in massive degradation of natural habitats[47–49]. At the ecoregion scale, some ecoregions in drylands, such as the Ecuadorian dry forest ecoregion, have been found to have a relatively greater fraction of urban expansion and large impacts on natural habitats[31]. Our study also identified these ecoregions as dryland hotspots. Importantly, by accounting for the indirect impacts of urban expansion, we identified additional ecoregions that were not previously identified as conservation priorities[31] (for example, the northern Mediterranean and east of Brazil). Moreover, using the PREDICTS database, no significant differences were observed in species richness across land uses in dryland between primary vegetation and urban lands[50]. However, using the same database, we found that habitat quality had a constraining relationship with species richness (Supplementary Fig. 3a). This may be because the primary vegetation used in ref. [50] includes barren and sparsely vegetated land[50] with low habitat suitability, which is similar to urban land. The habitat quality index, however, allows for distinguishing species richness between primary vegetation and urban lands. Moreover, our proposed approach can potentially be used to assess the impact of other threats on natural habitats. Cropland expansion is one example, the direct and indirect impacts of which on natural habitats can be comparatively estimated by employing the habitat quality index, instead of only focusing on direct loss of habitats to cropland[11].

Methods

Study area description. Our study area is the global dryland, where the ratio of mean annual precipitation to mean annual potential evapotranspiration is below 0.65[1,51]. Global drylands are characterized by the lack of water, which limits primary production and nutrient cycling[52]. We used the drylands map from the United Nations Environment Programme World Conservation Monitoring Centre (UNEP-WCMC) datasets, which was developed to define the Millennium Ecosystem Assessment dryland system boundary[53]. Covering western and central Asia, northern Africa, and central and western North America, global drylands have a total area of 60.9 million km^2, which account for about 40% of the global land area (Supplementary Fig. 7). On the basis of precipitation and evaporation dynamics, drylands can be classified into four subtypes: hyper-arid, arid, semi-arid and dry sub-humid drylands[1]. Among these subtypes, the semi-arid dryland is the largest with 22.6 million km^2, corresponding to about 37% of global drylands. The areas of the arid, dry sub-humid and hyper-arid drylands were 15.7 million, 12.8 million and 9.8 million km^2 (26%, 21% and 16% of the global drylands), respectively. With varying assemblages of natural communities and species, drylands are distributed across 14 biomes and 467 ecoregions[54]. The largest dryland extent is found in desert and xeric shrubland biomes (26.4 million km^2, accounting for 43% of global dryland area), and the Sahara Desert is the largest dryland ecoregion (4.5 million km^2, accounting for 7% of drylands). Over 2.2 billion people live in drylands, accounting for 30% of the global population[55]. The number of people living in dryland urban areas is 1 billion, corresponding to 45% of the total population in drylands. Approximately 200 cities with a population above 1 million can be found in drylands, and nine of them have a population of more than 10 million[56].

Data. Land use/cover data in 1992 were used to extract the natural habitats in 1992 and were obtained from the European Space Agency (ESA) with a spatial resolution of 300 m and an overall accuracy of 71% [57]. The ESA land use/land cover data are one of the most accurate land use/cover data and are commonly used in global long-term assessment studies[58–60]. For estimating the impacts of urban expansion from 1992 to 2016, we used the 1992 land use/cover data. Thus, we assumed urban land expansion as the only land change dynamic during the study period. Considering the rapidity of global urban expansion, this is a useful assumption that allowed us to focus only on those changes in the direct and indirect habitat impacts due to urban land expansion, rather than in combination with other land changes. Following the habitat classification scheme of the IUCN, natural habitats refer to any non-artificial vegetation, including forest, grassland, scrubland, wetland and unused land[24]. Urban land data in 1992 and 2016 were used to analyse the dynamics and assess the impacts of urban expansion. The data were obtained from a recent global urban land dataset, with a spatial resolution of 1 km[4]. We chose this dataset instead of urban land in the ESA dataset because of its higher accuracy in depicting urban areas[4] (Kappa = 0.47, overall accuracy = 90.89% vs Kappa = 0.19, overall accuracy = 90.47%). Existing studies also use a similar method to assess the impact of urban expansion[61]. Road data were used to calculate the habitat quality in 1992 and were obtained from the global roads open access datasets published by the Center for International Earth Science Information Network. We excluded road segments that are shorter than 1 km, which is the spatial resolution of our analysis. The global drylands boundaries were obtained from the UNEP-WCMC datasets, which followed the definition of the Millennium Ecosystem Assessment[53] (data downloaded on 8 January 2020). Biome and ecoregion boundaries were used to make a multiscale analysis and were obtained from the World Wildlife Fund's terrestrial ecoregions database[54]. Threatened species data were used to analyse impacts of habitat quality loss on biodiversity and were obtained from the IUCN Red List Database[32] (accessed on 6 January 2019). Following He et al.[62], we selected near-threatened, vulnerable, endangered and critically endangered species (collectively termed threatened species) and excluded the data-deficient, least concern, extinct in the wild and extinct species. For raster data with a spatial resolution finer than 1 km, we resampled them to 1 km resolution using a nearest-neighbour approach for consistency with other data.

Evaluating habitat quality. The methodological flow chart for assessing the impacts of urban expansion on natural habitats is illustrated in Supplementary Fig. 8. First, an indicator called 'habitat quality' was used to estimate the ability of the habitat to provide an environment for species persistence, on the basis of the type of the natural habitat and the intensity of degradation[12]. The indicator can be expressed as:

$$\mathrm{HQ}_x = H_x\left(1 - \frac{D_x^z}{D_x^z + k^z}\right) \tag{1}$$

where HQ_x is the habitat quality of natural habitats at the pixel x, which varies from 0 to 1. A higher score indicates a higher habitat quality, which assumes a higher species richness. H_x refers to the habitat suitability of the pixel x. A higher habitat suitability value suggests that such natural habitat type has a higher potential ability of providing an environment for species persistence. D_x represents the degradation of the pixel x caused by surrounding threats. k and z are the half-saturation constant and the scaling parameter, which are set to 2.5 and 0.5 by default, respectively[12]. From the formula, we can see that a lower habitat quality pixel does not necessarily represent a higher level of degradation, but it may have low habitat suitability. D_x can be calculated as:

$$D_x = \sum_{r=1}^{R}\left(\frac{\omega_r}{\sum_{r=1}^{R}\omega_r}\right) i_{rx} S_{xr} \tag{2}$$

where ω_r is the relative importance of the threat r. Here, the threats are represented by specific land use/cover types that lead to a degradation of the surrounding natural habitats[12]. Thus, the threats are not the particular disturbance on natural habitats such as trampling, firewood collection and water pollution; rather, referring to Bai et al.[14], we took urban, cropland and road as proxies for threats. i_{rx} is the impact of the threat r on the habitat pixel x. S_{xr} is the sensitivity of the habitat pixel x to threat r. A higher value of the sensitivity of the habitat to a threat indicates that the habitat is more probably affected by that threat. R is the number of threat types, which is 3 in this study. i_{rx} can be calculated as:

$$i_{rx} = \sum_{y=1}^{Y}\left(1 - \left(\frac{d_{yx}}{d_{r\max}}\right)\right) \text{ if linear} \tag{3}$$

$$i_{rx} = \sum_{y=1}^{Y}\left(\exp\left(-\left(\frac{2.99}{d_{r\max}}\right) d_{yx}\right)\right) \text{ if exponential} \tag{4}$$

where d_{yx} is the linear distance between the habitat pixel x and the threat pixel y. $d_{r\max}$ is the maximum effective distance of the threat pixel r. It should be noted that the radius of influence is calculated at the pixel level. The maximum effective distance is measured for each urban pixel, rather than from the edge or the centre of the city. Y is the pixel number of the threat r. If the influence of a threat has a linear decline with the distance, we choose equation (3). If the distance-decay function is exponential, we use equation (4). The conceptual diagram for calculating the habitat quality index can be found in Supplementary Fig. 9. The method of determining the parameters can be found in Supplementary Material 2. Considering the uncertainty of parameters, we randomly selected 100 parameter combinations (uniform distribution) on the basis of the range of parameters obtained through literature review and analysing the uncertainty of results (Supplementary Tables 5–13). Finally, we conducted the reliability analysis of our result by investigating the correlations between the habitat quality and the number of species following Terrado et al.[13] and Febbraro et al.[63] (Supplementary Material 1).

Following McDonald et al.[31], we used the ecoregion as the basic unit to evaluate the habitat quality in 1992. First, we calculated the average habitat quality in each ecoregion as:

$$\mathrm{AHQ}_e = \frac{\sum_{x=1}^{n} \mathrm{HQ}_{e,x}}{n_e} \tag{5}$$

where AHQ_e is the average habitat quality in ecoregion e, which varies from 0 to 1. A higher value of AHQ_e indicates a better habitat quality in this ecoregion. $\mathrm{HQ}_{e,x}$ represents the habitat quality of the pixel x in ecoregion e. n_e represents the number of pixels in ecoregion e. To facilitate comparisons of the impacts of urban expansion across dryland habitats of varying quality, we divided ecoregions into five levels according to the average habitat quality, which can be expressed as:

$$\mathrm{Class}_e = \begin{cases} 1 & 0 \le \mathrm{AHQ}_e < 0.2 \\ 2 & 0.2 \le \mathrm{AHQ}_e < 0.4 \\ 3 & 0.4 \le \mathrm{AHQ}_e < 0.6 \\ 4 & 0.6 \le \mathrm{AHQ}_e < 0.8 \\ 5 & 0.8 \le \mathrm{AHQ}_e \le 1 \end{cases} \tag{6}$$

where Class_e represents the level of the ecoregion e, with 1–5 indicating low, relatively low, moderate, relatively high and high habitat quality ecoregion, respectively. Similar to the concept of habitat quality, an ecoregion with a lower habitat quality may have lower species richness due to the harsh environmental conditions rather than suffering high degradation or having lesser value for biodiversity conservation. Then, we calculated and reported the area of natural habitats at the global, dryland subtype, biome and ecoregion scales.

Analysing the dynamics of urban expansion. We used a normalized indicator to compare the changes in urban areas among different regions in drylands[62]. This indicator can be expressed as:

$$\mathrm{PU}_r = \frac{U_r}{S_r} \tag{7}$$

where PU_r represents the percentage of the urban area relative to the total area in the region r. U_r and S_r are the urban area and total area in the region r, respectively. We calculated the percentage at the global, dryland subtype, biome and ecoregion scales and then analysed the dynamics of urban expansion from 1992 to 2016.

Assessing impacts of urban expansion on natural habitats. The impacts of urban expansion on natural habitats include the direct and indirect impacts[6]. In this study, direct impacts refer to the changes in habitat quality caused by the conversion of natural habitats to urban land, whereas indirect impacts refer to the changes in the quality of nearby habitats caused by the expanding urban land (Supplementary Figs. 10 and 11). Thus, the impact of urban expansion on natural habitats can be divided into the direct and indirect impacts as:

$$\mathrm{UTI}_r = \mathrm{UDI}_r + \mathrm{UII}_r \tag{8}$$

where UTI_r is the total impact of urban expansion on natural habitats in the region r. UDI_r and UII_r are the direct and indirect impacts of urban expansion, respectively. UDI_r can be calculated as:

$$\mathrm{UDI}_r = \sum_{i=1}^{m} \mathrm{HQ}_i \tag{9}$$

where HQ_i refers to the habitat quality at pixel i before the urban expansion. If the habitat was occupied by urban expansion, the value of habitat quality will become 0; that is, the loss of habitat quality equals the value of habitat quality of pixel i before the urban expansion. m is the number of pixels that became urban between 1992 and 2016. UII_r can be calculated as:

$$\mathrm{UII}_r = \sum_{j=1}^{n} H_j\left(\frac{(D_j + \mathrm{UD}_j)^z}{(D_j + \mathrm{UD}_j)^z + k^z} - \frac{D_j^z}{D_j^z + k^z}\right) \tag{10}$$

where n is the pixel influenced by urban expansion indirectly, which is limited by the maximum effective distance of the urban land. We determined the maximum effective distance of the urban land as 10 km on the basis of an extensive review of indirect impacts of urban expansion[15]. We also conducted a sensitivity analysis using different maximum effective distances to better judge the suitability of the habitat quality index (Supplementary Fig. 6). It should be noted that the indirect impacts evaluated in this study are mainly the proximate impacts of urban expansion, and other forms of indirect impact, such as telecoupling impacts at the global scale, were excluded[16–18]; hence, the indirect impacts evaluated are conservative. H_j is the habitat suitability at pixel j. D_j represents the degradation of the pixel j caused by surrounding threats before urban expansion. UD_j is the degradation of the pixel j caused by expanded urban areas, which can be calculated as:

$$\mathrm{UD}_j = \sum_{y=1}^{y} \omega_u S_j \exp\left(-\left(\frac{2.99}{d_{u\max}}\right) d_{yj}\right) \tag{11}$$

where y is the pixel of expanded urban area. ω_u is the relative weight of urban land among all threats. S_j represents the sensitivity of pixel j to urban land. $d_{u\max}$ refers to the maximum effective range of urban land as disturbance, and d_{yj} represents the distance between pixel y and pixel j. The values of parameters used in this study were introduced above.

It should be noted that the results (dependent variable) in equations (9), (10) and (11) are only affected by the expanded urban land (independent variables). In fact, there were other land use/cover changes within the 10 km strip around the expanded urban land. Among them, the area of bare land decreased the most, whereas the area of croplands increased the most (Supplementary Table 14). We did not consider these other land use/cover changes in our calculation to ensure the changes in habitat quality were exclusively due to urban expansion. Taking the ecoregion as the basic unit, we identified the hotspots of natural habitats that were severely affected by urban expansion, using spatial autocorrelation analysis (that is, hotspot analysis) based on the loss of habitat quality[64]. We analysed the changes in habitat quality caused by urban expansion at the global, dryland subtype, biome and ecoregion scales from 1992 to 2016.

Ethics. This study was approved by the Faculty of Geographical Science at Beijing Normal University for the ethical conduct of research with human participants (Supplementary Material 3). The study was performed in accordance with the Declaration of Helsinki and with the laws and regulations of China, as well as applicable international norms and standards. All interviewees of this research consented to participate in the research and to the use of the information they provided in the paper. This information is used only for scientific research and is confidentially protected.

Reporting summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The datasets generated during and/or analysed in this study are publicly available as referenced within the article. All data and scripts are also available from the corresponding author on request.

Code availability

Code used is available at https://github.com/Qiang-Ren/habitat-quality.git.

Received: 22 December 2020; Accepted: 15 June 2022;
Published online: 25 July 2022

References

1. *Ecosystems and Human Well-being: Synthesis* (Millennium Ecosystem Assessment, 2005).
2. Huang, J. et al. Dryland climate change: recent progress and challenges. *Rev. Geophys.* **55**, 719–778 (2017).
3. Fu, B. et al. The Global-DEP conceptual framework — research on dryland ecosystems to promote sustainability. *Curr. Opin. Environ. Sustain.* **48**, 17–28 (2021).
4. He, C. et al. Detecting global urban expansion over the last three decades using a fully convolutional network. *Environ. Res. Lett.* **14**, 034008 (2019).
5. Güneralp, B., Reba, M., Hales, B. U., Wentz, E. A. & Seto, K. C. Trends in urban land expansion, density, and land transitions from 1970 to 2010: a global synthesis. *Environ. Res. Lett.* **15**, 044015 (2020).
6. McDonald, R. I. et al. Research gaps in knowledge of the impact of urban growth on biodiversity. *Nat. Sustain.* **3**, 16–24 (2019).
7. Liu, X. et al. High-spatiotemporal-resolution mapping of global urban change from 1985 to 2015. *Nat. Sustain.* **3**, 564–570 (2020).
8. Güneralp, B. & Seto, K. C. Futures of global urban expansion: uncertainties and implications for biodiversity conservation. *Environ. Res. Lett.* **8**, 014025 (2013).
9. McDonald, R. I., Kareiva, P. & Forman, R. T. T. The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biol. Conserv.* **141**, 1695–1703 (2008).
10. McDonald, R. I., Marcotullio, P. J. & Güneralp, B. *Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities* (Springer, 2013).
11. van Vliet, J. Direct and indirect loss of natural area from urban expansion. *Nat. Sustain.* **2**, 755–763 (2019).
12. Sharp, R. et al. *InVEST 3.2.0 User's Guide* (The Natural Capital Project, Stanford Univ., Univ. Minnesota, The Nature Conservancy and World Wildlife Fund, 2015).
13. Terrado, M. et al. Model development for the assessment of terrestrial and aquatic habitat quality in conservation planning. *Sci. Total Environ.* **540**, 63–70 (2016).
14. Bai, Y. et al. Developing China's Ecological Redline Policy using ecosystem services assessments for land use planning. *Nat. Commun.* **9**, 3034 (2018).
15. McDonald, R. I. et al. Urban effects, distance, and protected areas in an urbanizing world. *Landsc. Urban Plan.* **93**, 63–75 (2009).
16. Mirzabaev, A. et al. in *Climate Change and Land* (eds Shukla, P. R. et al.) 249–343 (IPCC, 2019).
17. Friis, C. & Nielsen, J. *Telecoupling. Exploring Land-use Change in a Globalised World* (Palgrave Macmillan, 2019).
18. Maestre, F. et al. Structure and functioning of dryland ecosystems in a changing world. *Annu. Rev. Ecol. Evol. Syst.* **47**, 215–237 (2016).
19. Leh, M. D. K., Matlock, M. D., Cummings, E. C. & Nalley, L. L. Quantifying and mapping multiple ecosystem services change in West Africa. *Agric. Ecosyst. Environ.* **165**, 6–18 (2013).
20. Xie, W., Huang, Q., He, C. & Zhao, X. Projecting the impacts of urban expansion on simultaneous losses of ecosystem services: a case study in Beijing, China. *Ecol. Indic.* **84**, 183–193 (2018).
21. Whitford, W. & Wade, E. L. *Ecology of Desert Systems* (Academic Press, 2002).
22. Brito, J. C. et al. Conservation biogeography of the Sahara-Sahel: additional protected areas are needed to secure unique biodiversity. *Divers. Distrib.* **22**, 371–384 (2016).
23. Jenkins, C. N., Pimm, S. L. & Joppa, L. N. Global patterns of terrestrial vertebrate diversity and conservation. *Proc. Natl Acad. Sci. USA* **110**, E2602–E2610 (2013).
24. Salafsky, N. et al. A standard lexicon for biodiversity conservation: unified classifications of threats and actions. *Conserv. Biol.* **22**, 897–911 (2008).
25. Oliver, T. H. et al. Declining resilience of ecosystem functions under biodiversity loss. *Nat. Commun.* **6**, 10122 (2015).
26. Powers, R. P. & Jetz, W. Global habitat loss and extinction risk of terrestrial vertebrates under future land-use-change scenarios. *Nat. Clim. Change* **9**, 323–329 (2019).
27. Díaz, S. M. et al. *The Global Assessment Report on Biodiversity and Ecosystem Services: Summary for Policy Makers* (IPBES, 2019).
28. Seto, K. C., Guneralp, B. & Hutyra, L. R. Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proc. Natl Acad. Sci. USA* **109**, 16083–16088 (2012).
29. Pautasso, M. Scale dependence of the correlation between human population presence and vertebrate and plant species richness. *Ecol. Lett.* **10**, 16–24 (2007).
30. Luck, G. W. A review of the relationships between human population density and biodiversity. *Biol. Rev. Camb. Phil. Soc.* **82**, 607–645 (2007).
31. McDonald, R. I., Güneralp, B., Huang, C.-W., Seto, K. C. & You, M. Conservation priorities to protect vertebrate endemics from global urban expansion. *Biol. Conserv.* **224**, 290–299 (2018).
32. *The IUCN Red List of Threatened Species* Version 2017-3 (IUCN, 2017); https://www.iucnredlist.org/resources/spatial-data-download
33. Tucker, M. A. et al. Moving in the Anthropocene: global reductions in terrestrial mammalian movements. *Science* **359**, 466–469 (2018).
34. Howard, C., Flather, C. H. & Stephens, P. A. A global assessment of the drivers of threatened terrestrial species richness. *Nat. Commun.* **11**, 993 (2020).
35. *Guidelines for Geoconservation in Protected and Conserved Areas* (IUCN, 2020).
36. Gao, J. How China will protect one-quarter of its land. *Nature* **569**, 457 (2019).
37. Chen, C. et al. China and India lead in greening of the world through land-use management. *Nat. Sustain.* **2**, 122–129 (2019).
38. Gao, B., Huang, Q., He, C., Sun, Z. & Zhang, D. How does sprawl differ across cities in China? A multi-scale investigation using nighttime light and census data. *Landsc. Urban Plan.* **148**, 89–98 (2016).
39. Mace, G. M. et al. Aiming higher to bend the curve of biodiversity loss. *Nat. Sustain.* **1**, 448–451 (2018).
40. Lambin, E. A. & Meyfroidt, P. Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl Acad. Sci. USA* **108**, 3465–3472 (2011).
41. Arlidge, W. et al. A global mitigation hierarchy for nature conservation. *Bioscience* **68**, 336–347 (2018).
42. Moallemi, E. A., Kwakkel, J., de Haan, F. J. & Bryan, B. A. Exploratory modeling for analyzing coupled human-natural systems under uncertainty. *Glob. Environ. Change* **65**, 102186 (2020).
43. 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).
44. Ramaswami, A. et al. A social-ecological-infrastructural systems framework for interdisciplinary study of sustainable city systems. *J. Ind. Ecol.* **16**, 801–813 (2012).
45. Boerema, A. et al. Soybean trade: balancing environmental and socio-economic impacts of an intercontinental market. *PLoS ONE* **11**, e0155222 (2016).
46. Garrett, R. D., Lambin, E. F. & Naylor, R. L. Land institutions and supply chain configurations as determinants of soybean planted area and yields in Brazil. *Land Use Policy* **31**, 385–396 (2013).
47. Friess, D. A., Rogers, K., Lovelock, C. E., Krauss, K. W. & Shi, S. The state of the world's mangrove forests: past, present, and future. *Annu. Rev. Environ. Resour.* **44**, 89–115 (2019).
48. Ferreira, A. C. & Lacerda, L. D. Degradation and conservation of Brazilian mangroves, status and perspectives. *Ocean Coast. Manage.* **125**, 38–46 (2016).
49. Richards, D. R. & Friess, D. A. Rates and drivers of mangrove deforestation in Southeast Asia, 2000–2012. *Proc. Natl Acad. Sci. USA* **113**, 201510272 (2016).
50. García-Vega, D. & Newbold, T. Assessing the effects of land use on biodiversity in the world's drylands and Mediterranean environments. *Biodivers. Conserv.* **29**, 393–408 (2020).
51. Martínez-Valderrama, J., Guirado, E. & Maestre, F. Desertifying deserts. *Nat. Sustain.* **3**, 572–575 (2020).
52. Maestre, F. et al. Biogeography of global drylands. *New Phytol.* **231**, 540–558 (2021).
53. United Nations Environment World Conservation Monitoring Centre. World dryland areas according to UNCCD and CBD definitions. https://resources.unep-wcmc.org/products/789fcac8959943ab9ed7a225e5316f08 (2022).
54. Olson, D. M. et al. Terrestrial ecoregions of the world: a new map of life on Earth. *Bioscience* **51**, 933–938 (2001).
55. Goldewijk, K. K., Beusen, A., Doelman, J. & Stehfest, E. Anthropogenic land use estimates for the Holocene – HYDE 3.2. *Earth Syst. Sci. Data* **9**, 927–953 (2017).
56. *Revision of World Urbanization Prospects* (United Nations, 2018); https://esa.un.org/unpd/wup
57. *Land Cover CCI—Product User Guide* Version 2.0. (European Space Agency, 2017); http://maps.elie.ucl.ac.be/CCI/viewer/index.php

58. Grekousis, G., Mountrakis, G. & Kavouras, M. An overview of 21 global and 43 regional land-cover mapping products. *Int. J. Remote Sens.* **36**, 5309–5335 (2015).
59. Xu, X., Jain, A. K. & Calvin, K. V. Quantifying the biophysical and socioeconomic drivers of changes in forest and agricultural land in South and Southeast Asia. *Glob. Change Biol.* **25**, 2137–2151 (2019).
60. Gong, P. et al. Annual maps of global artificial impervious area (GAIA) between 1985 and 2018. *Remote Sens. Environ.* **236**, 111510 (2020).
61. Huang, Q. et al. The occupation of cropland by global urban expansion from 1992 to 2016 and its implications. *Environ. Res. Lett.* **15**, 084037 (2020).
62. He, C., Liu, Z., Tian, J. & Ma, Q. Urban expansion dynamics and natural habitat loss in China: a multiscale landscape perspective. *Glob. Change Biol.* **20**, 2886–2902 (2014).
63. Di Febbraro, M. et al. Expert-based and correlative models to map habitat quality: which gives better support to conservation planning? *Glob. Ecol. Conserv.* **16**, e00513 (2018).
64. Anselin, L. Local Indicators of Spatial Association—LISA. *Geogr. Anal.* **27**, 93–115 (2010).

Acknowledgements

We thank R. McDonald (The Nature Conservancy, Arlington, VA, USA) for his insightful comments, which have improved the quality of the manuscript. This work was supported by the National Natural Science Foundation of China (Grant No. 41971270, 41971225 & 41801184) and the 111 project (BP0820003).

Author contributions

C.H., Q.H. and Q.R. designed the study and planned the analysis. Q.R. performed the experiments and analysed the data. Q.R. and Q.H. drafted the manuscript. P.S., D.Z. and B.G. contributed to revising the manuscript. All authors contributed to the interpretation of findings, provided revisions to the manuscript and approved the final manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at https://doi.org/10.1038/s41893-022-00930-8.

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Peer review information *Nature Sustainability* thanks Mark Goddard, Stefanie Herrmann, Fernando Maestre and the other, anonymous, reviewer(s) for their contribution to the peer review of this work.

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Last updated by author(s): Jun 4, 2022

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Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	No code or software was used in data collection.
Data analysis	We wrote code to calculate the habitat quality in 1992 and the impacts of urban expansion on natural habitats from 1992 to 2016 using IDL 8.5. The code is available at https://github.com/Qiang-Ren/habitat-quality.git. Other data processing in this study are conducted at ArcGIS 10.3 and Microsoft Excel 2016.

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Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Based on the habitat quality index, we quantified the loss of habitat quality caused by urban expansion both directly and indirectly in global drylands (1km spatial resolution), as well as at the scale of dryland-subtypes, biomes and ecoregions.
Research sample	We ran the model based on pixels. All pixels in global drylands were involved in the calculation. We analyzed the results at the scale of global drylands, dryland-subtypes, biomes and ecoregions based on the full samples.
Sampling strategy	We resampled the raster data to 1 km resolution using a nearest neighbor approach following the common global urban expansion research.
Data collection	The land use/cover data, urban land data, road data, boundary data and threatened species data can be download directly. Qiang Ren did this procedure. Detailed links were supported in the Method section.
Timing and spatial scale	Land use/cover data in 1992 were obtained from the European Space Agency (ESA) with a spatial resolution of 300 m and an overall accuracy of 71%. Urban land data in 1992 and 2016 were obtained from a recent global urban land dataset, with a spatial resolution of 1 km. Road data were obtained from the global roads open access datasets published by Center for International Earth Science Information Network. Threatened species data were obtained from the IUCN Red List Database, accessed on 6 January 2019.
Data exclusions	We excluded the road segments that are shorter than 1 km to keep the resolution consistent.
Reproducibility	All attempts to repeat the experiment were successful.
Randomization	This is not applicable in this study
Blinding	Blinding is not applicable in this study

Did the study involve field work? ☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
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☒	☐	Animals and other organisms
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Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging

Human research participants

Policy information about studies involving human research participants

Population characteristics	See above.
Recruitment	We designed a questionnaire about the habitat suitability and sensitivity to threats based on the expert scoring method (5-point scale). The invited experts were divided into four types to minimize biases in experts' assessment. Type 1 expert was the professor or associate professor with ecological backgrounds. These experts (6 experts) engaged in the research of urban expansion and its impact on the environment and biodiversity. Their research areas include urban ecology, urban ecology,

geography and ecosystem service. These experts were consulted through the face-to-face interview to ensure their responses addressed the questions adequately since January 2019. Type 2 expert was the scientific researcher who was familiar with the habitat quality index, and 28 researchers were included in this class. Type 3 expert was the postgraduate student (75 students) who majored in geography or ecology. Type 4 expert was the postgraduate student in other majors, and 91 students participated in the survey. Type 2, 3 and 4 experts completed the questionnaire in an anonymous manner since December 2021 and agreed us to use the information they provided in the paper.

Ethics oversight	This study was approved by the Faculty of Geographical Science in Beijing Normal University for the ethical conduct of research with human participants. The study is performed in accordance with the Declaration of Helsinki and takes into consideration the laws and regulations in China as well as applicable international norms and standards. All interviewees of this research were consented to participate in the research, including using the information they provided in the paper. Their information is only used for scientific research and protected confidentially.

Note that full information on the approval of the study protocol must also be provided in the manuscript.