Biodiversity impacts and conservation implications of urban land expansion projected to 2050

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As the global urban population is poised to grow by 2.5 billion over the next 30 y, urban land conversions are expected to be an increasingly prominent driver of habitat and biodiversity loss. Mitigating these impacts urgently requires an improved understanding of where and how these biodiversity losses might occur. Here, we use a recently developed suite of land-use projections to provide an assessment of projected habitat that will be lost to urban land expansion for 30,393 species of terrestrial vertebrates from 2015 to 2050 across three shared socioeconomic pathway (SSP) scenarios. We find that urban land expansion is a contributing driver of habitat loss (≥5% of total loss) for around one-third (26 to 39%) of the species assessed. For up to 855 species (2 to 3% of those assessed), urban land is a direct driver of species imperilment, driving at least one-quarter of a net habitat loss of 10% or more. Urban clusters with the greatest threats to species due to projected expansion are predominantly located in the developing tropical regions of sub-Saharan Africa, South America, Mesoamerica, and Southeast Asia. Our results suggest that strategies for minimizing the impacts of urban land could strengthen global biodiversity protection agreements. Collaborative, global action that focuses on vulnerable species and regions may represent an efficient strategy for avoiding the impacts forecast by our analysis.

urbanization | land-use change | biodiversity | conservation

Over the next 30 y, the global urban population is projected to increase by 2.5 billion people, making urbanization one of the defining transformations of the 21st century (1). Urban land will need to expand substantially in order to accommodate these new urban residents (2, 3), a process that often occurs at the expense of natural ecosystems (4). At a time when global biodiversity is seriously threatened (5), this represents a challenge for sustainable urban development.

Cities can support diverse communities of plants and animals, and access to nature is recognized as a key component of making cities functional and livable places for people (6–8). However, when urban land replaces natural habitat, it permanently alters the type of habitats available, along with their spatial configuration and level of interconnectedness, resulting in significant changes in the abundance and composition of species assemblages (9–11). Native species richness generally declines with urban land-use intensity (12–14). Urban areas tend to support more invasive species, with the proportion of invasive species typically increasing with the degree of urbanization (12). Urban land can also drive phenotypic adaptations, producing rapid ecoevolutionary change (15). These impacts to biota contribute to global biodiversity declines. For example, between 1992 and 2000, urban land expansion resulted in the loss of around 190,000 km^2 of habitat, equivalent to 16% of total habitat loss during this period (4). It is also estimated that around 8% of terrestrial vertebrate species on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species are primarily threatened due to urban expansion (16).

Despite the apparent importance of urban land expansion as a driver of habitat loss, the global response to this threat has been limited. Global agreements on biodiversity conservation, such as the Convention on Biological Diversity's (CBD's) now-expired Aichi Biodiversity Targets, have focused on broad-scale habitat loss caused by agriculture and forestry. However, the failure to address urban land expansion means that a potentially important source of habitat loss is being overlooked.

An important step in developing a societal response to urban impacts on biodiversity is understanding the magnitude and distribution of such impacts in the future. Forecasts of urban impacts on biodiversity can demonstrate the importance of urban land as a driver of habitat loss. They may also provide insights that facilitate implementation of targeted and effective policies by identifying particularly vulnerable species or regions where impacts will be most heavily concentrated.

Existing forecasts of global urban expansion demonstrate that 290,000 km^2 of natural habitat is likely to be lost to urban expansion between 2000 and 2030 (4). This includes a more than threefold increase in the extent of urban land near protected areas (17). Much of this urban expansion is predicted to occur in biodiversity hotspots, many of which contained relatively little urban land in 2000 (18). This is expected to drive declines in ecoregional endemic species, 13% of which occur within ecoregions that are predicted to experience a high threat from urban expansion (19).

Significance

Understanding the impacts of urbanization and the associated urban land expansion on species is vital for informed urban planning that minimizes biodiversity loss. Predicting habitat that will be lost to urban land expansion for over 30,000 species under three different future scenarios, we find that up to 855 species are directly threatened due to unmitigated urbanization. Our projections pinpoint rapidly urbanizing regions of sub-Saharan Africa, South America, Mesoamerica, and Southeast Asia where, without careful planning, urbanization is expected to cause particularly large biodiversity loss. Our findings highlight the urgent need for an increased focus on urban land in global conservation strategies and identify high-priority areas for this engagement.

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Although these assessments have provided important insights into the likely impacts of future urban land on biodiversity, they are limited in scope and utility in four key ways. First, they have coarse spatial resolution. They typically describe the impacts of urban land at an aggregated scale (countries or bioregions) that may span the jurisdiction of multiple authorities charged with conserving biodiversity, making identification of key actors and responsibilities difficult. Second, they have coarse taxonomic resolution. In many cases, they generalize across species that may respond to urban expansion in different ways. Third, they focus on the impact of urban land without quantifying habitat loss that may occur beyond the urban boundary. Combined habitat lost to urban and agricultural land expansion, for example, may drive species imperilment where individually these land uses do not. Finally, existing studies typically have forecast impacts over limited timeframes, typically to 2030. As we near this date, such forecasts become less useful and an updated set of forecasts is required.

We aim to address these shortcomings by providing a detailed set of projections of the impacts of urban land expansion on individual species. We identify species and regions that will undergo the greatest losses of habitat due to urban land expansion. We assess the impact of individual urban clusters as drivers of habitat loss and reveal urban impact hotspots. In undertaking this assessment, we highlight important implications of our study for global biodiversity conservation strategies and sustainable development agendas.

To do this, we utilize recently developed, spatially explicit projections of urban land to predict the extent of habitat lost to urban land expansion for 30,393 species of terrestrial vertebrates between 2015 and 2050. For each species, we also estimate the extent of habitat lost to nonurban land-use change in order to provide a more accurate indication of whether the observed urban-driven habitat losses are contributing to imperilment of each species. Together, urban and nonurban habitat loss relative to the 2015 baseline represent the projected species area scores of the Species Habitat Index (20, 21). To account for significant uncertainty in the likely extent of new urban land, we compare projections of land-use change under three shared socioeconomic pathways (SSPs), which describe plausible alternative trends in the evolution of society and natural systems over the 21st century (22).

We compare a sustainability scenario (SSP1), a regional rivalry scenario (SSP3), and a fossil-fueled development scenario (SSP5). Under SSP1, the world pursues a sustainable development pathway characterized by low population growth, low consumption, high agricultural productivity, and effective land-use regulation. In contrast, environmental pressures are much greater under SSP3, characterized by high population growth, high levels of material consumption, low agricultural productivity, and poor land-use regulation. Under SSP5, the world puts faith in markets and technological solutions. Strong economic growth, a population that peaks and declines in the 21st century, and incompletely regulated land use that slowly reduces the rates of tropical deforestation produce moderate levels of environmental pressure (23, 24). Under SSP1 and SSP5, 92% of the population is predicted to be urbanized by the end of the century, compared to 60% under SSP3 (23). We show that variation in both the degree of urbanization and predicted land-use pressures are predicted to have substantially different implications for biodiversity.

Results

Urban Land-Use Expansion. We find that the extent of global urban land is predicted to increase between 2015 and 2050 under all three evaluated scenarios (Fig. 1). Under the least urbanized scenario (SSP3), urban land is expected to double its 2015 extent, and it is expected to up to triple under the more urbanized scenarios (SSP1 and SSP5), resulting in 0.82–1.53 million km^2 of new urban land. Much of this expansion is projected to occur in Africa and Asia, but regions with currently already-large and mostly urbanized populations, such as North America and Europe, will also see substantial growth.

Under SSP3, the lower rates of urban land expansion are accompanied by relatively high rates of nonurban land-use expansion (crop, pasture, and forestry), resulting in the greatest net land-use change (i.e., combined urban and nonurban forms of land-use change) across the three scenarios (6.6 million km^2). Net land-use change under SSP1 and SSP5 is lower, despite the larger total expected area of urban land, reflecting the larger predicted urban populations, technological advancements in agriculture, and more regulated land use under these scenarios (2.3 million and 4.6 million km^2, respectively) (23) (Fig. 1*A*).

Our analysis shows that urban expansion is predicted to occur on land that is currently more modified by human land uses, including human settlement, agriculture, transportation, mining and energy production, and electrical infrastructure. However, there is variability among regions. In Asia, where the largest quantities of urban land expansion will occur, urban growth is strongly skewed toward more modified lands. A similar trend can be observed in Europe and, to a lesser extent, North America and Africa. In contrast, urban land expansion in Oceania and South America is predicted to occur more commonly on land that is less modified (Fig. 1*B*).

Species Impacts. These urban land changes are projected to cause substantial loss of habitat for some species. For example, the lionhead agama (*Calotes liocephalus*), a reptile restricted to the island of Sri Lanka, is expected to lose 22% of suitable habitat within its range—termed habitat-suitable range (HSR) (20)—between 2015 and 2050 under SSP1, i.e., an approximately −0.5 % average annual change in the global species area score of the Species Habitat Index (20). Almost half (47%) of this loss is due to urban land expansion (Fig. 2). A range of other species show similar trends (Fig. 2). Broadly, we find that urban land expansion is a contributing driver of HSR loss, defined as $\geq 5\%$ of the total loss, for around one-third (26–39% across the three SSPs) of the 30,393 species assessed. For 2–3% of the species assessed (459–855 species), urban land is a direct driver of species imperilment, driving at least one-quarter of a net HSR loss of 10% or more. We define these species as heavily impacted and use this terminology hereafter.

Species with limited HSR available in 2015 are inherently more vulnerable to habitat loss than species with larger areas of HSR available. The median 2015 HSR of non–heavily impacted species is at least 20 times larger than that of heavily impacted species across the scenarios (e.g., 48,200 km^2 compared to 2,400 km^2 under SSP1). Threatened species (IUCN Red List extinction risk vulnerable or higher) are disproportionately represented among these heavily impacted species, making up around one-third (32–36%) of the heavily impacted species compared to 18% of all species assessed (Fig. 3). Reptiles and amphibians were proportionally most represented among the heavily impacted species. Birds, which typically have larger ranges, were least likely to be heavily impacted (Fig. 3).

Urban Impact Hotspots. We assessed the impact of individual urban clusters—contiguous units of urban land, independent of administrative boundaries (2, 25)—estimated to be $\geq$400 km^2 in size in 2050. Together, these clusters represent up to 70% of predicted new urban land under the more urbanized scenarios SSP1 and SSP5 or around 60% of urban land under SSP3, where larger urban clusters are less common. Impacts on biodiversity differ among the clusters. We identify a set of urban

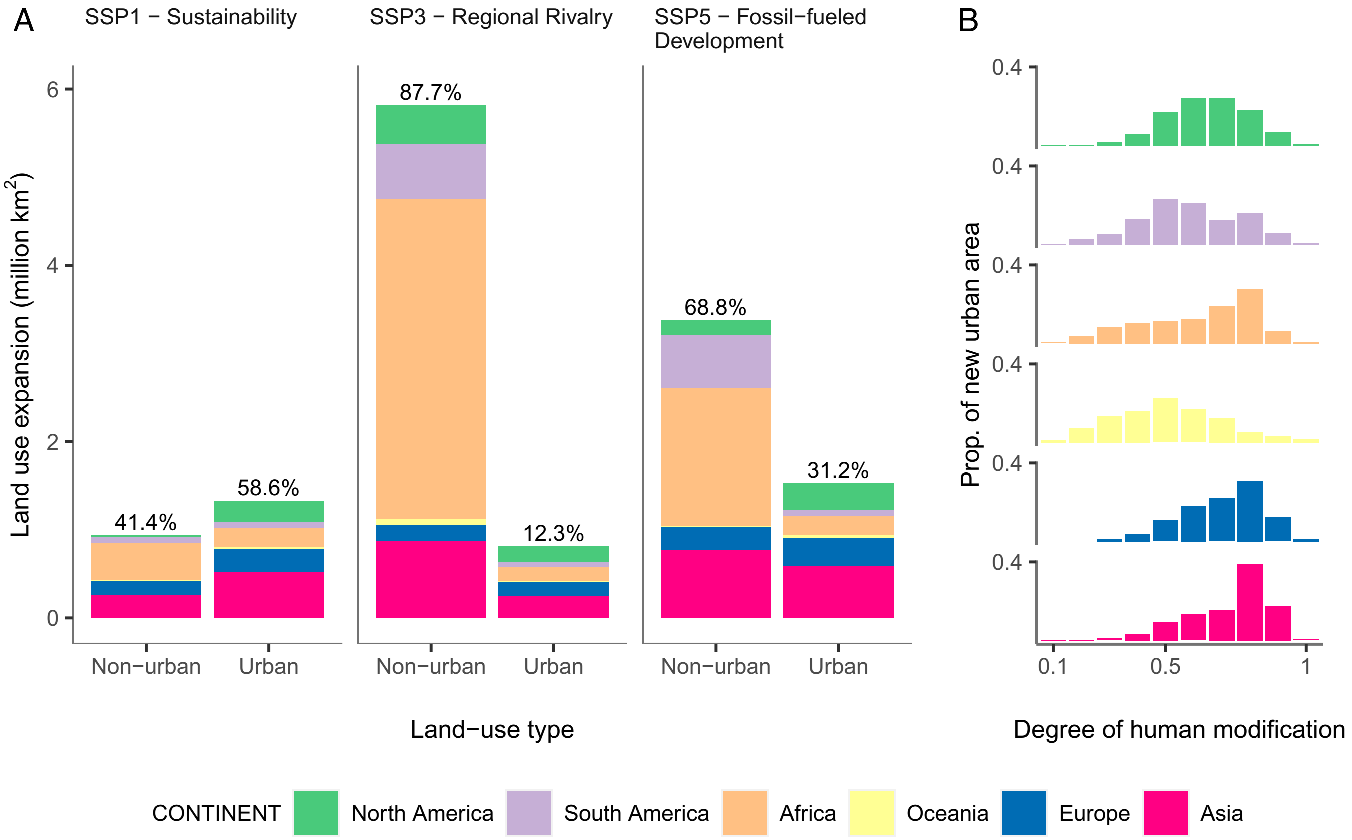

Fig. 1. (*A*) Quantities of new urban and nonurban (pasture, crop, and forestry) land projected between 2015 and 2050 under three SSP scenarios. Stacked segments indicate the distribution of new urban and nonurban land across continents. The urban and nonurban percentages of total land-use change under each SSP are shown above bars. (*B*) The distribution of new urban land across the range of present-day human modification levels from 0 (not modified) to 1 (entirely modified), in increments of 0.1, across continents. Values are the mean proportion across the three SSP scenarios.

impact hotspot clusters that are responsible for 70–75% of the predicted HSR lost to urban expansion among the heavily impacted species but collectively represent just 23–37% of predicted new urban land across the SSPs (Fig. 4).

Hotspot clusters are found in equatorial regions where urban growth coincides with biodiverse habitats. This includes clusters in Mesoamerica and the Caribbean, such as Guatemala City (Guatemala), Port-au-Prince (Haiti), and Mexico City (Mexico), along with clusters in Africa, particularly Lagos (Nigeria) and Bamenda (Cameroon); Southeast Asia, particularly Colombo (Sri Lanka), Jakarta and Kochi (Indonesia), Kuala Lumpur (Malaysia), and Bangkok (Thailand); and South America, such as Sao Paulo (Brazil) and Quito (Ecuador), among others (Fig. 4).

One common factor among these impact hotspots is their typically higher levels of species endemicity. We estimate levels of endemicity by comparing the median 2015 HSR of species impacted by each cluster. Across all scenarios, the median 2015 HSR of species affected by hotspot clusters is 25–40% smaller than that of species affected by the remaining clusters (e.g., 308,000 km^2, compared to 546,000 km^2 under SSP1). Lower species endemism in regions where large volumes of urban growth are expected, such as China, India, and some European countries, likely explains the lower numbers of heavily impacted species affected by these clusters. The tendency for urban land expansion to occur on modified land types in these regions (Fig. 1) might further contribute to this pattern.

For around 10% of the heavily impacted species, urban HSR loss is driven entirely by urban land outside of the clusters assessed here. The impact of urban land expansion outside of urban clusters is more prominent in countries that are less urbanized in 2015 and where large urban clusters are less common, such as in sub-Saharan Africa.

Variation among SSPs. There are systematic differences in the predicted extent of HSR loss among the scenarios, which reflect the narratives of the SSPs. Species are most impacted by urban land expansion under SSP1 and SSP5, reflective of the larger volumes of urban land forecast under these scenarios. Species lose more HSR to nonurban land-use change (pasture, crop, and forestry) under SSP3, reflecting the forecasted rapid agricultural land-use change under this scenario. The large volumes of agricultural land expansion under SSP3 produce the largest net HSR losses (driven by urban and nonurban land uses combined) for most species. Net HSR loss is greatest under SSP3 for 41% of all species impacted by urban land under at least one scenario, followed by SSP5 (34%) and SSP1 (25%) (Fig. 5). These patterns are reflected in the numbers of heavily impacted species across the scenarios. More species are predicted to lose at least 10% of 2015 HSR under SSP3, but the number of species for which urban land expansion drives at least one-quarter of this HSR loss is highest under SSP1, followed closely by SSP5 (Fig. 5).

Discussion

By forecasting global habitat losses, we aim to gain insights to guide future urban land expansion. Our findings demonstrate that although global habitat loss will primarily be driven by agricultural land-use change, the continued growth of urban land will drive habitat losses that directly imperil some species.

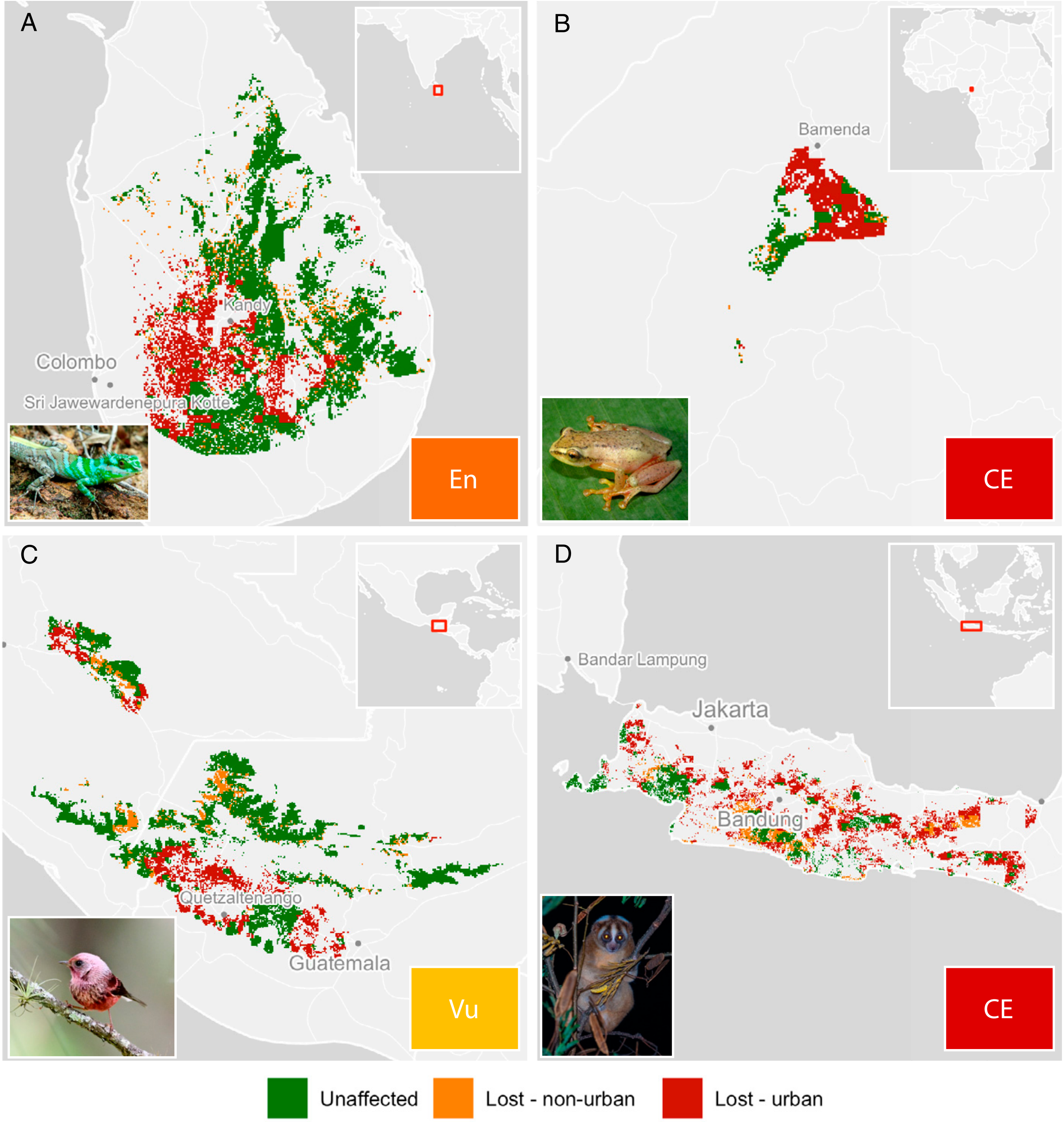

Fig. 2. Projected habitat loss expected from urban and nonurban land-use change under SSP1 by 2050. Projected range changes for four example species: (*A*) *Calotes liocephalus* (lionhead agama), 22% net HSR loss, 47% of which is caused by urban expansion; (*B*) *Hyperolius ademetzi* (Bamenda reed frog), 23% net HSR loss, 52% of which is caused by urban expansion; (*C*) *Ergaticus versicolor* (pink-headed warbler), 22% net HSR loss, 47% of which is driven by urban expansion; and (*D*) *Nycticebus javanicus* (Javan slow loris), 46% net HSR loss, 28% of which is driven by urban expansion. Red indicates all HSR loss where urban land expansion is a contributing driver. This may include HSR lost to a combination of urban and nonurban land-use change. To explore these and other species, see ref. 55. CE = critically endangered, En = endangered, Vu = vulnerable. The following attributions apply for images: (*A*) Image credit: Palinda Perera, licensed under CC BY-NC; (*B*) © 2013 Daniel Portik; (*C*) Image credit: Luis Guillermo, licensed under CC BY-NC; and (*D*) Image credit: Diki Muhamad Chaidir, licensed under CC BY-NC.

Our study highlights these species and the urban clusters that drive this imperilment. Here, we discuss our findings in the context of their implications for global conservation of biodiversity in the face of urban land expansion.

Urban Conservation Priorities. Our results show that at least 70% of the urban-driven HSR loss forecast for heavily impacted species is driven by a small subset of urban clusters representing around one-third of the total forecasted new urban land

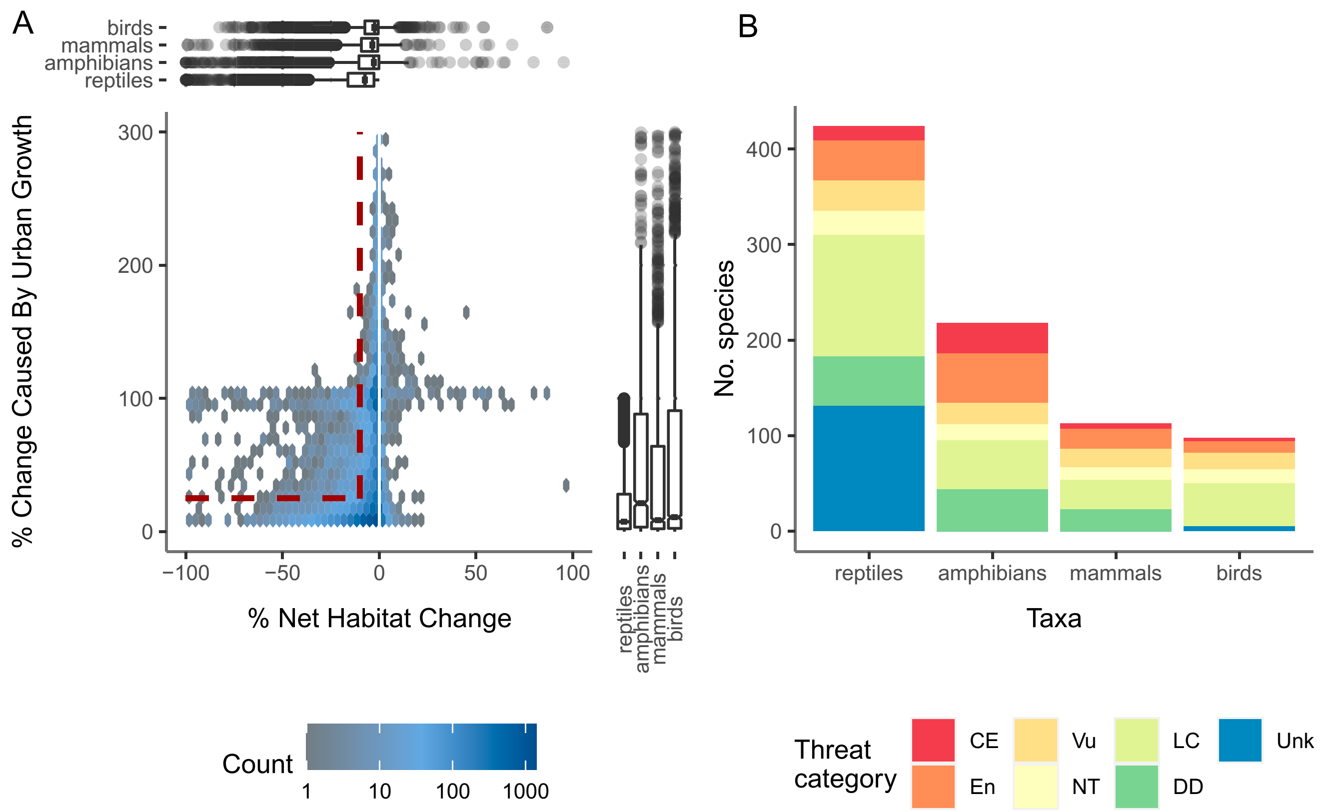

Fig. 3. (*A*) Relative range loss due to urban vs. all anthropogenic land-cover change summarized for all terrestrial vertebrate species affected by urban land expansion under SSP1 (n = 21,111). Hexagons colors indicate species count, and marginal boxplots display the distribution by class. Species with HSR expansion > 100% (<0.1% of all) are not shown. Species for which urban expansion drives > 300% of net HSR change are not shown for clarity (2.5% of all). Red dashed lines in *A* indicate the lower thresholds for considering species as heavily impacted by urban growth (n = 855). (*B*) Species are summarized by class and IUCN Red List conservation status. CE = critically endangered, En = endangered, Vu = vulnerable, NT = near threatened, LC = least concern, DD = data deficient, Unk = unknown.

(23–37% across the three SSPs). This concentration of impacts presents an opportunity for an efficient conservation strategy that prioritizes global urban conservation efforts toward species and regions that we predict are most at risk from urban expansion.

We provide a full list of species predicted to be heavily impacted by urban land expansion, and the urban clusters that drive this impact, in supplementary materials. Our analysis shows that these species have a restricted range size and limited habitat available within that range in 2015 (i.e., restricted HSR). This is reflected by the fact that close to one-third of the most heavily impacted species are already listed as threatened by the IUCN Red List. Urban clusters with the largest impacts are geographically concentrated in centers of endemism, where there is a greater proportion of species with restricted ranges. Island nations such as Sri Lanka and Indonesia, which often support proportionally more endemic and range-restricted species than continents (26), are particularly threatened by future urban expansion. Urban impact hotspots are concentrated in rapidly urbanizing equatorial regions, particularly the developing tropical regions of sub-Saharan Africa, South America, Mesoamerica, and Southeast Asia. These are regions that previous studies have identified as most at risk for future biodiversity declines more broadly (20, 27–29).

Our results suggest that targeted protection of the species predicted to be most vulnerable to urban land expansion may be facilitated by placing a focus on protecting the habitat of endemic and range-restricted species in these rapidly urbanizing regions. Such actions may take place at a global scale through integration of priority regions into global agreements on biodiversity conservation, such as the CBD's post-2020 agreement, or by targeted global conservation investment from sources such as the Global Environment Facility. Global strategies can facilitate targeted action at local scales, where national and subnational governments enact policies to guide conservation actions within their jurisdiction. A significant challenge for these localized efforts will be that many of the urban impact hotspots lie within regions with low institutional and fiscal capacity and weaker governance structures, which may reduce capacity to mitigate the impacts of urban land expansion on biodiversity (30, 31).

Urban Land in Global Conservation. Our findings show that urban land expansion is predicted to drive global habitat loss that imperils species under each of the three SSPs assessed. Approaches to global conservation that acknowledge the importance of urban land-use change as a driver of habitat loss can provide important protection for the species highlighted by our analysis. Protecting species from urban land expansion will be a substantial challenge. Global population densities have been declining in recent decades, meaning that urban land is growing faster than urban populations (32). This trend is predicted to continue in the coming decades (33), with implications for broader sustainable urban development (31). Unless these trends are reversed, more urban land will be required for a given urban population increase, with the potential for impacts on biodiversity, as predicted by our study.

Habitat loss for most of the species assessed is driven by urban clusters, which in many cases, span multiple city and/or national

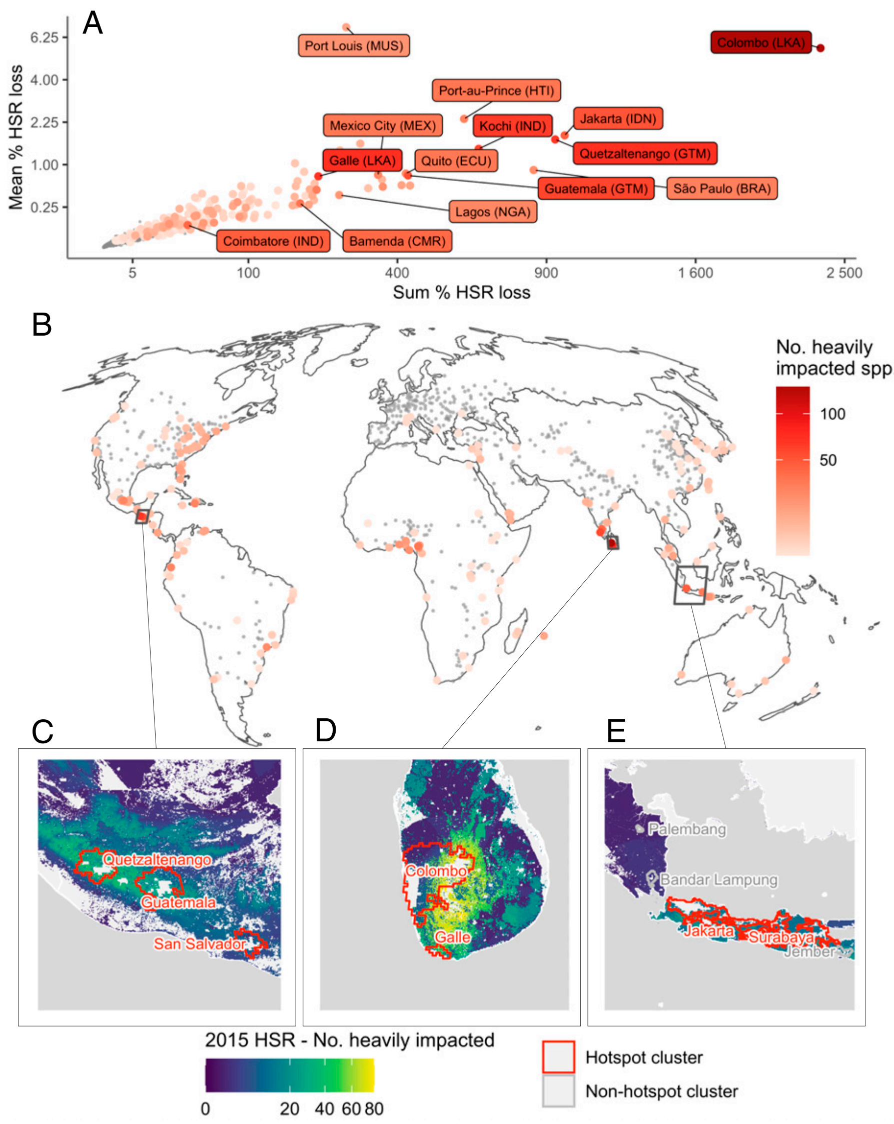

Fig. 4. Urban impact hotspot clusters under SSP1. In *A* and *B*, the color of points indicates the number of heavily impacted species affected by an urban cluster. (*A*) The summed percentage of individual species' 2015 HSR lost to urban expansion within each cluster (*x* axis) and the mean percentage of 2015 HSR lost to urban expansion across species affected by a cluster (*y* axis). (*B*) The geographic distribution of urban impact hotspot clusters. (*C*–*E*) Example regions. Background color shows the extent of 2015 HSR for species predicted to be heavily impacted in our analysis. Color represents species count. Boundaries of hotspot and nonhotspot urban clusters are shown. To explore urban impact hotspots, go to ref. 55. MUS = Mauritius; HTI = Haiti; LKA = Sri Lanka; MEX = Mexico; IND = India; IDN = Indonesia; ECU = Ecuador; GTM = Guatemala; BRA = Brazil; NGA = Nigeria; CMR = Cameroon.

governments. To protect these species, conservation actions implemented by cities, states, or countries may be most effective where coordinated to ensure that the impact of urban-driven habitat loss is mitigated across a species range. Global frameworks for conservation and sustainable urban development can facilitate this coordination. However, the impacts of urban land expansion on biodiversity have been poorly addressed by global agreements to date.

The United Nations Human Settlement Program's (UN-Habitat's) New Urban Agenda (NUA) sets a sustainable development agenda for cities in line with the Sustainable Development Goals (SDGs) (31). This includes goals aimed at reducing the impact of urban land on biodiversity through planning for biodiversity and reducing urban sprawl. However, despite the introduction of the NUA in 2016, the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services cites the ongoing loss of important habitats driven by urban expansion within global biodiversity hotspots as a substantial challenge for achieving sustainable urban development targets set out in the SDGs (5). Our results support UN-Habitat's call for a renewed commitment to the aims of the NUA as the world enters the Decade of Action to deliver the SDGs by 2030 (31).

International biodiversity agreements have also fallen short of recognizing the need to manage urban land. The threat posed by urban land has typically been overshadowed by the urgent need for reform among other more widespread forms of land use, such as agriculture and forestry. The CBD's Aichi Biodiversity Targets, which expired in 2020, did not directly recognize the role of urban land expansion as a driver of habitat loss, and the current draft of the post-2020 global biodiversity framework does not rectify this omission (34).

Incorporation of urban land management into the post-2020 agreement, and renewed focus on implementation of the NUA, may help to facilitate the global coordination of urban conservation efforts that guide national to local urban conservation strategies. Cooperation between cities may also be facilitated

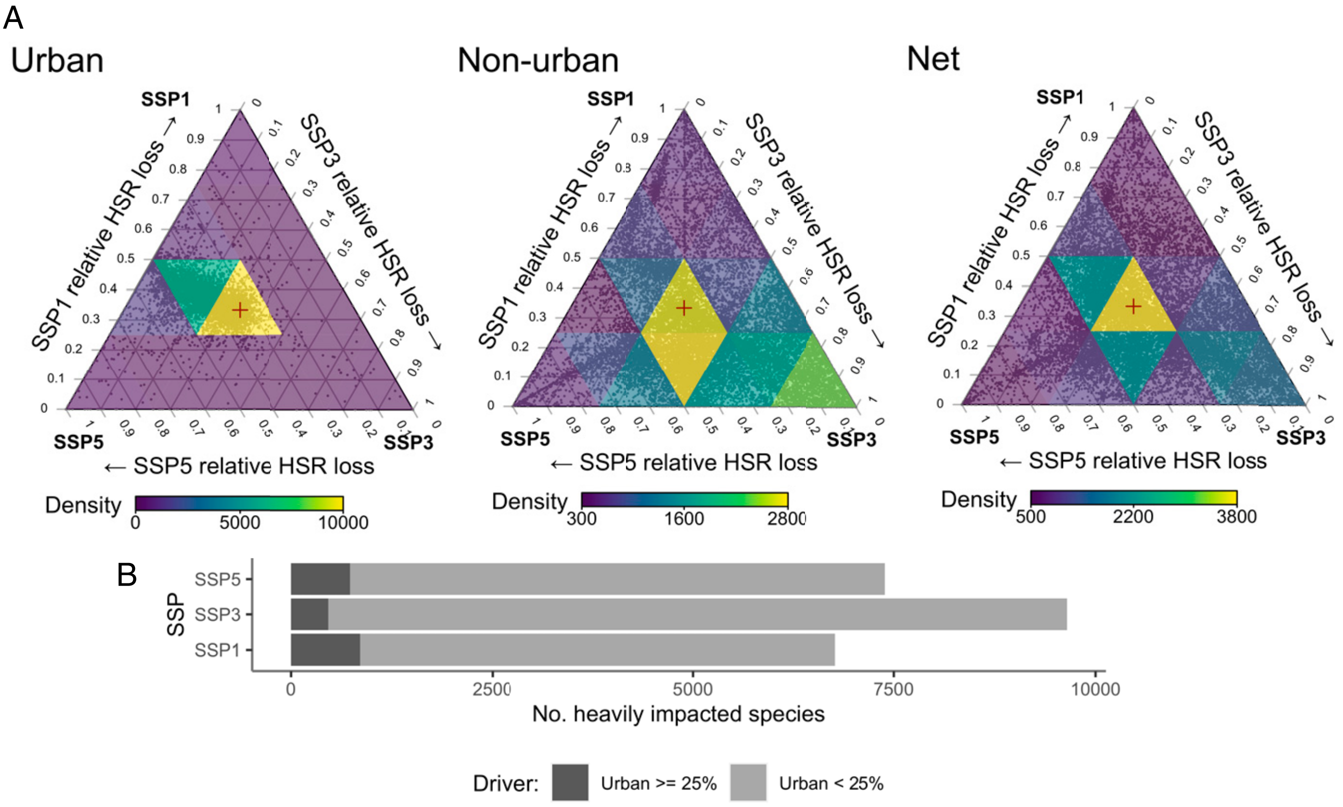

Fig. 5. (*A*) For all species impacted by urban land expansion under at least one SSP (gray background points, n = 19,837), the relative HSR loss is shown across the three SSP scenarios driven by urban (*Left*), nonurban (pasture, crop, and forestry, *Middle*), and net (urban and nonurban, *Right*) land-use change. For each species, the relative HSR loss under a given SSP (SSPX) is a value 0–1, given by the HSR loss under SSPX expressed as a fraction of the summed HSR losses under all SSPs. For each species, the relative HSR losses under the three SSPs sum to 1. Species with similar HSR losses under each SSP are located in the center of the plot, marked by a red cross. The greater the relative habitat loss under a given SSP, the closer a species is located to the corresponding corner. Species located at the far corners lose habitat under one SSP only. Colored shading indicates density of points to display general trends. (*B*) Number of heavily impacted species by scenario. Length of bars indicates the number of species that lose ≥10% of 2015 HSR by 2050. Darker stacked segments indicate the proportion of these species for which urban land expansion drives ≥25% of this habitat loss.

through voluntary multicity networks, such as Local Governments for Sustainability that enable cities to work together to pursue sustainable development agendas.

Remaining Questions and Research Priorities. Our analysis demonstrates the potential direct impacts of urban land as a driver of habitat loss over the next 30 y. However, while habitat loss is arguably the most important driver of biodiversity declines globally (5), cities contribute to biodiversity declines both directly and indirectly in ways not assessed by this study (35). Direct impacts of urban land beyond the loss of habitat include the introduction of invasive species (9) and fragmentation of habitat (36). Indirect impacts are those mediated by an intermediate process and can be driven by resources consumed by cities (e.g., food and building materials) and wastes they produce (e.g., greenhouse gas emissions or industrial waste) (8, 35, 37). These impacts may be felt well outside the boundaries of urban areas via teleconnections that link urban demand for resources to habitat loss in all parts of the globe (38).

Urbanization occurs alongside threats to biodiversity driven by climate change which are not addressed by our study. Changes in climate are likely to shift the geographic ranges for some species in our assessment over the forecast period. The urban heat island effect may influence the suitability of urban areas for some temperature-sensitive species (39). Climate change may also place pressures on wildlife populations that make them more susceptible to habitat loss, for example, via disruption to breeding cycles or availability of food (40). This will alter the outcomes of our assessment in ways that are difficult to predict.

Finally, our study is limited to a set of terrestrial vertebrate species for which we have enough data on distribution and habitat preferences to make an assessment. It is important to note that the species assessed here represent a very small proportion of the species on Earth. In particular, we do not assess impacts to plants or invertebrate species. Our study also uses a simplistic binary classification for species' ability to adapt to urban land that reflects a large knowledge gap concerning how species will be able to use the urban landscape.

Future research that addresses the broader direct and indirect impacts of urban land in a changing climate and across a broad suite of species will strengthen our understanding of urbanization's impacts on biodiversity.

Conclusion

Our results illustrate the impacts of projected urban land expansion on global biodiversity over the next 30 y under different scenarios. We show that urban land is likely to be a driver of habitat loss that deserves global attention alongside drivers such as agriculture and forestry. However, our results also demonstrate a way forward. Focusing global efforts on high-priority species and regions may represent an efficient strategy for minimizing impacts to biodiversity with limited conservation funding and effort. Our results demonstrate the importance of integrating strategies that mitigate the impact of urban land into biodiversity conservation actions, from global to local scales.

Materials and Methods

Data Sources.

Land-use and land-cover data. We construct land-use and land-cover (LULC) maps for 2015 and 2050 by combining global categorical LULC forecast maps at 10-arcsec (~300 m) resolution, developed for use in the GLOBIO 4 global biodiversity model for policy support (29), with URBANMOD-ZIPF, a probabilistic spatial urban land forecast at 5,000-m resolution developed by Huang et al. (2). GLOBIO LULC forecasts are available in ref. 41 and URBANMOD-ZIPF is available in ref. 42. Both datasets provide a baseline estimate of LULC extent in 2015, and forecast LULC to 2050, based on SSP scenarios. We use URBANMOD-ZIPF to define present and future urban land as we believe that it represents urban land more accurately than the GLOBIO model. URBANMOD-ZIPF includes minimum thresholds for population density, population size, and built-up area to distinguish urban from rural settlements, and it explicitly preserves the log-scale size distribution of future urban clusters known as Zipf's law (2, 43). Throughout this analysis, we multiply the URBANMOD-ZIPF probability values by pixel size to derive the expected area of new urban land.

To examine the level of human modification of land covers, we use the global human modification (gHM) layer, developed by Kennedy et al. (44). This global gridded dataset provides an estimate of the level of human modification of terrestrial land based on the modeled physical extent of five major categories of stressors, including human settlement, agriculture, transportation, mining and energy production, and electrical infrastructure, with a median year of 2016. The gHM is available for download via ref. 44.

As per Powers and Jetz (20), we map elevation using EarthEnv-DEM90 (45), a global digital elevation model at a 90-m spatial resolution and 5-m vertical resolution, resampled to 0.0083° or ~1-km resolution. EarthEnv-DEM90 is available to download via ref. 45.

Cultural vector data. Countries and continental regions are defined by the Natural Earth 1:50 Admin 0–Countries dataset (https://www.naturalearthdata.com/). We adjust the continent of French territories outside of the European continental region to reflect their geographic location. The location of cities is defined using the Natural Earth 1:10 Populated Places dataset (https://www.naturalearthdata.com/).

Throughout the analysis, we use country names as per the *ADM0NAME* field in the Natural Earth Populated Places dataset, with some minor alterations to facilitate joining of datasets.

Species data. We obtained distribution data collated by Powers and Jetz (20), and subsequently updated by the Map of Life (MOL) project (46), for terrestrial vertebrate species including birds (n = 9,740), mammals (n = 4,999), reptiles (n = 9,885), and amphibians (n = 5,769). Bird expert range maps were based on Jetz et al. (47) and can be viewed at https://www.mol.org. Amphibian and mammal expert range maps are obtained from IUCN (50) and are available at https://www.iucnredlist.org. Reptile expert range maps are obtained from Roll et al. (48) and are available to download via ref. 48. We obtained habitat preference data summarized by Powers and Jetz (20) from text descriptions in the literature for birds (49) and IUCN Red List threat assessments for amphibians and mammals . At the time of analyses, detailed habitat and elevation preferences were not available for reptile species. As such, we assign all "natural" land-cover classes as suitable habitat for reptile species and exclude all urban, crop, pasture, and forestry land. We do not clip expert range maps for reptiles to elevation (as described below for other taxa). We follow Powers and Jetz (20) to combine a generalized expert range map with data on habitat preferences and known elevational ranges to estimate species' HSR (see below).

The IUCN Red List conservation categorization for all assessed birds, mammals, reptiles, and amphibians was obtained from the IUCN (50). Species in the MOL database without a matching species name or synonym in the IUCN Red List database are assigned a conservation category of unknown.

Land-Cover Analysis. We sum the expected area of new urban land as defined in the URBANMOD-ZIPF forecasts for SSP1, SSP3, and SSP5 across six major continental regions using Google Earth Engine.

To understand the present-day level of modification of land predicted to become urban by 2050, we compare the URBANMOD-ZIPF urban land forecasts for SSP1, SSP3, and SSP5 to the 2015 gHM map. Within each continental region, we sum the area of new urban land predicted to occur on land within binned levels of modification ranging from 0 (entirely natural) to 1 (entirely modified) in increments of 0.1. Area calculations are conducted at the scale of the gHM map (1 km) in Google Earth Engine.

Species Analysis. Following an approach developed by Powers and Jetz (20), we estimate the change in each species' HSR between 2015 and 2050. This represents a forecast of the global species area component of the Species Habitat Index which relates the HSR of a reference period to that of later point in time (20, 21, 51). HSR is estimated for each species by refining expert range maps based on species preferences for LULC categories and elevation.

We first create a LULC map for 2015 that combines the extent of urban land in the GLOBIO and URBANMOD-ZIPF maps for 2015, with remaining nonurban areas assigned the values from the GLOBIO 2015 LULC map. Using this map as a base, we create a HSR map for each species in 2015 by masking any LULC classes that do not match the species' habitat preferences and clipping to the extent of the expert range map and known elevation range for the species. Species' habitat preferences obtained from MOL are classified using the International Geosphere-Biosphere Program land-cover classification scheme (52), and we match these to the LULC classes in our 2015 LULC map as described in detail in the *SI Appendix*.

In order to estimate change in species' HSR caused by urban land expansion by 2050, we superimpose the URBANMOD-ZIPF forecasts over the 2015 HSR map for each species. Urban land expansion may reduce a species' HSR where it is forecast to replace suitable habitat for the species. Urban land expansion may increase a species' HSR if the species has a habitat preference for urban land and the new urban land is predicted to occur, within the range defined by the expert range map and elevation preferences, on land that is not currently suitable habitat for the species. The area of HSR lost or gained is equivalent to the area of new urban land. Where a pixel has a probability of becoming urban > 0 but < 1, the forecasted urban land area is less than the total pixel area and habitat is considered only partially lost or gained.

The impact of nonurban land-use change is estimated by examining changes in nonurban LULC classes as defined by the GLOBIO 2050 LULC map. The process is similar to that used to estimate changes driven by urban land. Areas of HSR in 2015 that transition to LULC classes that are considered unsuitable for the species by 2050 are considered lost, and the resulting land use is considered the driver of that loss. A species may gain HSR where pixels within the bounds of the expert range map and elevation range for a species that were not identified as suitable in 2015 become suitable in 2050.

Where changes in HSR are driven by urban and nonurban land uses at the same pixel, we count the urban driver first, with any remaining change in HSR attributed to the nonurban driver. This approach follows the logic used in the GLOBIO 4 land-use allocation algorithm, which acknowledges that urban land expansion is typically prioritized at the expense of other land-use types (29, 53). All analyses are conducted in Google Earth Engine at the scale of the GLOBIO LULC maps (~300 m).

The net change in HSR for each species is the change in HSR between 2015 and 2050 caused by all forms of land-use change. The area of HSR may increase, decrease, or stay constant. We express this as a percentage of the species' 2015 HSR. We express the contribution of urban and nonurban land-use change drivers of HSR loss as a percentage of the net change in HSR, or as a percentage of the species' 2015 HSR. Frequently, species lose HSR due to expansion of a nonsuitable land cover in one area but gain HSR due to expansion of a suitable land cover in another area. In such circumstances, it is possible that the contribution of urban or nonurban land-use HSR change may exceed 100% of the net HSR change.

The GLOBIO LULC map includes areas of secondary habitat in 2050—land dedicated to urban, agriculture, or forestry in 2015 that is abandoned by 2050 (29). We assume that species do not recolonize secondary vegetation, but we assume that species present in the 2015 modified LULC category are able to persist as this land transitions to secondary vegetation. This is a source of uncertainty. To account for this uncertainty, we conduct a sensitivity analysis detailed in the *SI Appendix*.

Defining Urban Clusters. We delineate urban clusters based on the predicted extent of urban land in 2050. We define an urban cluster as a contiguous group of urban land pixels in URBANMOD-ZIPF with a probability of becoming urban > 0.25. Due to the disjointed nature of some urban land, this process creates a large number of clusters, including many small clusters. In order to focus on the contribution of major urban centers, we refine the full set of clusters to only include those with an area $\geq$400 km^2 that contain a city point as defined by the Natural Earth Populated Places dataset. Urban clusters are named based on the intersecting city with the largest present-day population (*POP_MAX* field in the Natural Earth Populated Places dataset) but may represent more than one metropolitan administrative unit. For example, the New York cluster encompasses an area of 29,834 km^2 under SSP1 and includes cities from Hartford, CT, through to Philadelphia, PA. Using these criteria, we identify 654 urban clusters under SSP3, 834 under SSP1, and 884 under SSP5.

Urban Impact Hotspot Identification. By identifying urban impact hotspots, we aim to identify the places where urban land is a driver of species imperilment. To this end, we classify a set of urban clusters as urban impact hotspots by focusing on the clusters that drive the largest proportion of the predicted HSR loss among heavily impacted species. To identify these clusters, we use the prioritizr package in R (54) to develop an optimized approach that allows us to identify the smallest set of urban clusters that are collectively responsible for ≥75% of the HSR lost to urban clusters for each heavily impacted species. To do this, we calculate the percentage of each species' 2015 HSR predicted to be lost to each urban cluster in Google Earth Engine and import the result into R. Using prioritizr, we define a minimum set problem using the urban clusters as planning units. We set a relative target of 75% of HSR loss and allocate each cluster an equal "cost."

Data Availability. Species range maps, land-use forecasts, the gHM, EarthEnv-DEM90 and cultural vector data are publicly available for download, with sources as described in *Materials and Methods*. Detailed results, range map, and habitat preference information are also available from Map of Life at https://mol.org/species/projection/urban, and for any further questions contact info@mol.org. Code for the analysis is available in GitHub at https://github.com/MapofLife/urban-species-projection.

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