



Compact or Sprawling Cities: Has the Sparing-Sharing Framework Yielded an Ecological Verdict?

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Abstract

Purpose of Review Global urban land area is growing faster than the urban population, raising concerns that sprawling, low-density development will reduce biodiversity and human wellbeing. The sparing-sharing framework, adapted from agroecology, provides one approach to assessing alternative urban growth patterns. It compares ecological outcomes in landscapes matched for total population and land area, but differing in configuration: land sparing (partitioned between densely urbanized and undeveloped areas) or land sharing (low-density development throughout). We reviewed the urban sparing-sharing literature since 2010 and recovered 15 studies conducted in 22 cities on four continents.

Recent Findings Collectively, studies assessed effects of alternative development patterns on 296 species, 21 community metrics (such as species richness), and 26 indicators of ecosystem services or processes (such as carbon sequestration). Sparing was the best option for 51% of individual species; 43% of community metrics; and 27% of ecosystem service indicators.

Summary Existing ecological research does not clearly favor one pattern or the other, and new approaches are needed to facilitate decision making and ecological insight. Specifically, future work could (1) explicitly evaluate optimized urban development patterns across multiple competing priorities (such as providing housing, delivering ecosystem services, and protecting priority species), (2) tackle issues of spatial scale and connectivity that are often ambiguous in sparing-sharing research, and (3) improve geographical representation. These advances can be made while preserving the key insight of the framework—that choices between alternative landscape configurations are only meaningful when those landscapes are matched for total area and the level of human needs met.

Keywords Urbanization · Biodiversity · Ecosystem services · Landscape configuration · Housing density

Introduction

Future human population growth and settlement patterns will be overwhelmingly urban. At a global scale, rural population growth has ceased, while the urban population will increase from 4.4 to 6.7 billion in just 30 years (2020 to 2050) [1]. Meanwhile, urban land area is growing even faster than urban

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population [2–4]. Under a middle-of-the-road scenario for the year 2100, global urban land will equal 4.5 times the land area of Germany [2]. Although the area of urban land is still less than 5% of that used for agriculture [5, 6], the highly intensive nature of this land use can alter the trajectories of biodiversity and human wellbeing. The densest human populations are located non-randomly with respect to biodiversity; more people and more species tend to live in the same regions, such that urban growth threatens a disproportionate number of species and biodiversity hotspots [7–11]. In turn, the loss of species and “nature” from urban areas threatens the health of the growing number of humans in cities who need contact with biodiversity for wellbeing, including for mental health and immune development [12–14]. These concerns have motivated the growing disciplines of urban ecology and urban conservation biology, in the interest of both human wellbeing and species conservation [15–17].

For a given population size, some forms of urban growth may be better than others for the livability and conservation potential of a city. Urban form, extent, and rate of change are fundamental characteristics of urbanization [18], and global urban trends mask variation in spatial patterns of urban growth, which range from dense, high-rise development to sprawling automobile-dependent suburban and exurban land uses [19, 20]. In many regions worldwide, urban land expansion has outpaced population growth, such that sprawl—defined as relatively low-density and decentralized urban growth [21]—challenges sustainability goals of urban and regional planning [22–24]. Through landscape fragmentation and conversion to impervious surface, rapid spatial expansion of urban areas exacerbate regional and global climate change [25], water quantity and quality [26], food security, and public health [27]. In the USA, for example, rapid sprawl development throughout the twentieth century led to some of the largest increases in total urban extent among developed nations [18] and placed the USA among top countries worldwide for per capita impervious surface area [28].

Although many studies document the detriments of urban sprawl [29–31], far fewer make direct comparisons between compact and sprawling scenarios that are matched for total population and landscape area. Meaningful comparisons can only be made, and intensity-area tradeoffs clearly documented, by evaluating alternative arrangements of comparable numbers of people within a given landscape. The so-called “sparing-sharing” framework offers one way to conceptualize and quantify the ecological outcomes of intensity-area tradeoffs in alternative forms of development.

The sparing-sharing framework was first developed—albeit under different names—to assess the biodiversity outcomes of alternative forms of agricultural production [32, 33]. Briefly, in the agricultural context, the “sparing” form of land use concentrates production into high-yield patches, leaving the maximum amount of undisturbed habitat. The

“sharing” form attempts to make agricultural land more hospitable to other species by incorporating habitat elements or low-impact management practices—thereby increasing biodiversity within agricultural areas, but also increasing the total amount of land required to produce the same yield. The sparing-sharing framework provides a mathematical and graphical model to determine which species are best served (or least damaged) by each pattern of development. The approach was widely adopted after its elaboration in a 2005 *Science* paper [32], which has been cited 70 times per year on average since its publication; the concept acquired its catchy name in 2009 [34].

The classical assessment of sparing-sharing generates density-yield curves for as many individual species as possible, by sampling across a continuum of agricultural intensities from zero yield (in “baseline habitats” representing spared land) to maximum yield [32, 35]. The shape of the functional relationship between density and yield for each species then indicates which landscape configuration maximizes the total population (and minimizes extinction risk) for each species (Fig. 1). Many assessments use these density-yield curves to simulate the communities that would occur in landscapes composed of different farming intensities, but matched for total yield (Fig. 1). The contrast between sparing and sharing is typically simulated in simple

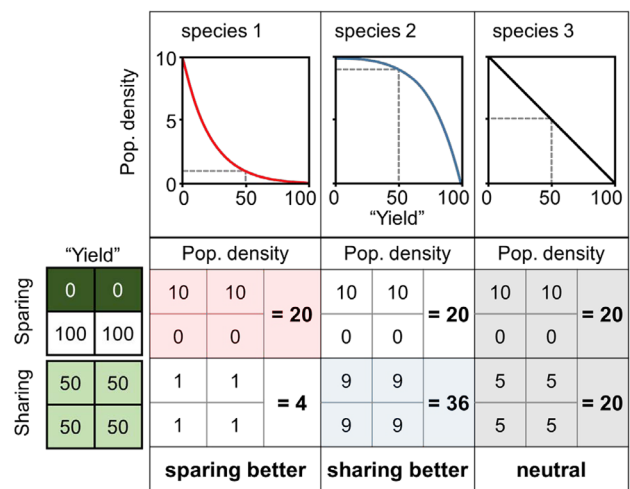


Fig. 1 Illustration of the basic sparing-sharing framework. The top three panels show functional relationships between population density and “yield,” where yield could refer to agricultural production, number of humans housed, or provision of other area-based human needs. Curves are shown for three hypothetical species—all urban “losers.” The panels on the lower left show two landscapes that accommodate the same yield in sparing (top) or sharing (bottom) configurations; each landscape cell is labeled with its “yield.” Finally, the table shows simple computations for the population size of each species in each landscape. Although all three species decline with urbanization, extinction risks are minimized by sparing for species 1 and sharing for species 2. Species 3, with a linear relationship, fares the same under either configuration

landscapes: Either the entire landscape is shared (with the same low level of yield throughout), or the landscape is segregated into two compartments (one high-yield compartment and one untouched compartment of baseline habitat).

The results, strengths, and weaknesses of the sparing-sharing framework in an agricultural context have been frequently and thoroughly reviewed [35, 36•, 37–40]. Despite all the attention, by 2021, Balmford [36•] was able to compile only eight empirical studies on four continents that followed all elements of the original framework. These studies assessed a total of 1591 species and found that 77% of them were agricultural “losers” whose densities declined as yield increased. Among the losers, 84% declined less severely under sparing than sharing [36•] – suggesting that agricultural land sparing would minimize the number of extinctions.

Even as evidence accumulates in favor of sparing in agriculture, the framework has been dogged by several critiques, one of the most persistent of which has been an ambiguity in spatial scale [38–40]. A 100 km² landscape that is shared might contain smaller landscapes that would be classified as spared on the scale of, say 1 km². Each focal species likely responds to landscape configuration at a particular scale, yet most applications of the framework are ambiguous about the scale at which agriculture is segregated from spared land. Balmford et al. [36•, 41] simply recommend that sparing-sharing should be evaluated at scales relevant to land use decisions—typically individual properties or regions of 1–10 km²—i.e., not hedgerows or individual trees, and not entire states or countries. Another ongoing debate concerns the extent to which spared areas, isolated in a sea of inhospitable intensified agriculture, can actually meet conservation goals [42, 43•]. Indeed, the relative contributions of land management practices versus fragmentation remain unclear in the sparing-sharing framework. General reviews of the effects of fragmentation on biodiversity point to positive effects more often than negative effects, suggesting that sharing—to the extent that it represents a more fragmented landscape—may be more favorable than sparing if effects were due to configuration alone [44]. This expectation is not met in agricultural sparing-sharing studies, emphasizing the need to define the land management practices that also characterize sharing.

Despite critiques in agriculture, the sparing-sharing framework has been adapted more recently to address similar tradeoffs between the intensity and extent of urban development [36•]. In 2013, Lin and Fuller [45] introduced the sparing-sharing lens to urban development, with the immediate benefit of exposing several research and theoretical gaps in the literature with respect to how (or whether) conservation can succeed on an urbanizing planet. Prior work in urban ecology and conservation science had primarily focused on reserve design (e.g., [46]), ignoring potential variation in urban extent, intensity, and form and how it could affect conservation goals. As a result, most urban

areas were implicitly treated as monolithic “threats” without considering the ability of urban planners and communities to further shape ecological responses (e.g., [47]). Although three prior empirical urban studies had independently used many elements of the sparing-sharing framework [48–50], Lin and Fuller explicitly drew the parallel between cities and agriculture. They stopped short, however, of indicating exactly which urban indicator should be substituted for agricultural yield in the sparing-sharing model (Fig. 1). With respect to scale, they argued for the need to conduct regional or whole-city analyses to capture effects of alternative forms of urbanization on biodiversity. It has now been nearly a decade since the sparing-sharing framework was formally introduced into the urban context, but the resulting research has yet to be reviewed as a coherent body of work. To assess whether actionable conclusions can be derived from the urban sparing-sharing framework, we take stock of this literature, asking:

1. What is the geographic scope of urban sparing-sharing research?
2. What study designs and urban indicators have been used?
3. Which taxonomic groups, processes, or ecosystem services have been assessed, and what have been their responses?
4. How have urban studies dealt with issues of spatial scale and connectivity?

To address these questions, we review the urban sparing-sharing literature from 2010 to 2021. In each section, we point to knowledge gaps and future directions needed to inform basic ecology and urban planning.

Methods

To conduct the systematic review, we searched the Clarivate Web of Science Core Collection in “all fields” for the phrase “(urban OR urbaniz* OR suburban OR city OR cities) AND ((sparing AND sharing) OR (land-sharing))” with a date range set from 1 January 2011 to 31 December 2021. We used this time frame in the spirit of this journal’s current, 10-year scope, and in recognition that most target literature would follow Lin and Fuller’s 2013 statement of urban sparing-sharing. We performed the search on 20 January 2022 and retrieved 134 results. This search was fairly restrictive because our goal was to retrieve papers that specifically addressed the sparing-sharing framework by comparing alternative development scenarios matched for total area and/or population, and not papers that addressed densification or sprawl alone.

Three of the authors independently reviewed titles and abstracts of all 134 studies for relevance. Relevant studies

had to be urban in context, ecological in scope, and had to address effects of landscape configuration. The 25 studies marked as relevant by at least one person were reviewed completely (Figs. S1, S2, Data S1). We also reviewed cited references of all relevant papers, and retrieved four additional studies, two of which were slightly older than the original date range (2010). Thus, we reviewed 29 studies in total. From this set, we excluded articles that did not provide explicit tests of landscape configuration while controlling for amount of green space or human population within a fixed area. For studies that used the shape of species' density-urbanization curves to determine the preferred landscape configuration (Fig. 1), the urbanization axis had to be a quantitative measure of human density, building density, or built cover; we did not accept proxies such as distance to city center, or qualitative indices, which could distort the shape of the curve and may not accurately represent the degree of urbanization [51]. This process resulted in a final set of 15 studies conducted in 22 cities (Figs. S1, S2, Data S1).

For each study, we recorded attributes of the study area and the focal taxa or responses (Data S2). We recorded the location and population of the focal city or the metropolitan area or agglomeration of which it was a part, in the year the data were collected (Data S3). Population data were obtained from OECD.stat "Metropolitan areas" or [1] (File 22 at <https://population.un.org/wup/Download/>). Information for smaller cities (population < 300,000) was obtained directly from municipal websites or open data portals such as datacommons.org (Data S3). We recorded the biome in which each city was located [49], and whether spared land had been converted to agriculture, if reported. We recorded the reported urban land use and the metric used to define urban areas (e.g., housing density, percent impervious), and we noted the sample size, sample unit (e.g., area, individual residence), and the scales used for both sampling and predicting ecological outcomes.

For each study, we recorded the type of response assessed and categorized it as an individual species response, a community metric (e.g., species richness), or an ecosystem service/process (e.g., carbon sequestration). We noted the taxon and the number of species examined. We recorded the number of responses that "preferred" sparing, sharing, or an intermediate or ambiguous configuration (Data S4). In some studies, the ideal configuration depended on urbanization level; for example, at low levels of development, sharing might be preferred, while at a high levels, sparing might be preferred. In such cases, we recorded the ideal configuration at the average urbanization level of the study area. Where possible, we also categorized responses as urban winners, losers, or neither. This was possible for studies that reported density-urbanization

curves (Fig. 1) or comparable functional relationships, either graphically or as modeled coefficients. Winners were those whose density increased monotonically across the urban gradient; losers decreased; and responses categorized as "neither" had flat or hump-shaped relationships. Thus, there were nine possible combinations of sparing-sharing and winner-loser (Fig. S3).

We did not attempt a formal meta-analysis because of the small number of studies and the variety of study designs. However, we did address the following questions statistically using data extracted from the reviewed papers. Analyses were performed in R version 3.5.1 [52]. First, as part of overall Q3, we addressed three questions by constructing contingency tables and subjecting them to Fisher's exact tests:

- Q3a. Do different response groups respond differently to sparing versus sharing? We tested a 3×3 contingency table of response group (individual species, community metrics, or ecosystem services/processes) vs. preferred configuration (sparing, sharing, neither).
- Q3b. Among individual species responses, do different taxa respond differently to sparing vs. sharing? We tested a 4×3 contingency table of taxa (birds, insects, mammals, plants) vs. preferred configuration (sparing, sharing, neither).
- Q3c. Are urban winners and losers equally likely to benefit from sparing or sharing? We constructed a 3×3 contingency table of response direction (winner, loser, neither) vs. preferred configuration (sparing, sharing, neither) (Fig. S3). We also subdivided this global table into six 3×3 tables—one per response group (individual species of birds, mammals, insects, or plants; community metrics; and ecosystem services/processes) and subjected the six resulting p values to a sequential Bonferroni correction [53].

We populated these contingency tables with counts of individual measurements and individual species, often including multiple measurements from each study. We acknowledge that this approach does not control for any systematic bias of individual studies (i.e., cannot include a random effect of study), but we believe it provides a useful summary of the literature to date.

Finally, as part of overall Q4, we asked whether studies vary the grain size of their sampling according to the type of response under study. Here, we constructed a linear mixed model in which (log-transformed) size of sampling site was the dependent variable and response group (species, community metric, or process/service) was the predictor. This model included a random effect of study, was fit using "lme4" [54] and tested for significance using a type II Wald X^2 test in "car" [55] followed by a Tukey test in "multcomp" [56].

Results and Discussion

What Is the Geographic Scope of Urban Sparing-Sharing Research?

Studies were located in Europe, Australia, North America, and Asia (Fig. 2, Data S3). Most studies included a single city or metropolitan area. Exceptions were two studies that sampled the same set of nine European cities in six countries [57, 58] and a review paper that reanalyzed data from several primary studies [59]. From the latter, we extracted results for three cities (2 North American, 1 European). The 22 focal cities had a median absolute latitude of 47.8° (range 22.5–66.5). Of these, 20 were in temperate latitudes, one was in the tropics (Shenzhen, China [60]), and one was within the arctic circle (Rovaniemi, Finland—which was pooled for analysis with 8 other European cities in the primary studies [57, 58]). Study sites were located in urban areas with a median population size of 1.05 million at the time of sampling, with a range from 62,000 (Rovaniemi, Finland) to 35.44 million (Tokyo, Japan) (Fig. S5). Two of the 22 cities (Tokyo, Japan, and Shenzhen, China) satisfied the definition of “megacities” with populations of 10 million or more. All cities were located in forested or wooded biomes (Fig. S4). In most studies, the land spared from urbanization was forested, or included mixed urban green spaces such

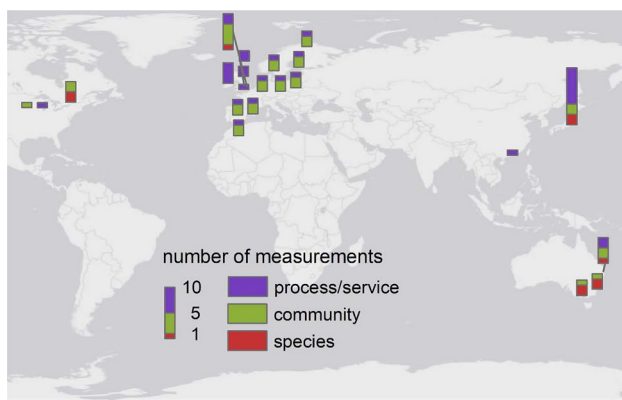


Fig. 2 Global map of urban sparing-sharing studies reviewed, by type of response measured: individual species outcomes (e.g., abundance, occupancy), community-level metrics (e.g., richness, aggregate abundance), or ecosystem processes or services (e.g., soil retention, green space access). In the species category, a single measurement refers to a single community in which individual species responses were measured (e.g., carabid beetles), regardless of the number of species in the community. Individual studies often included more than one response or more than one measurement. Most primary studies included a single city or metropolitan area; exceptions are two studies with sites in nine European cities. Although these studies analyzed data from the nine cities jointly, each city is mapped separately. Esri base map represents data from Esri, HERE, Garmin, FAO, NOAA, USGS, © OpenStreetMap contributors, and the GIS User Community

as recreational parks and remnant vegetation; in four cities, spared land was dominated by agriculture. Thus, the definition of spared land in an urban context differs from that in an agricultural context; the land spared from urban development was often still subject to some form of human use that may blur the distinction between sparing and sharing.

As is common in urban ecological research, cities in the tropics and the Global South were underrepresented [61, 62]. This is all the more striking because much of the projected urban growth is expected to happen in these areas and much of it in megacities [2]. North America also appears to be under-explored in terms of the urban sparing-sharing framework. Although North America was represented by measurements in three metropolitan areas [48, 49, 59], all were precursors to Lin and Fuller’s 2013 call to action [45], after which no further North American work appeared. Because the ecological effects of urbanization likely depend on differences in urban environments, human culture, and the background ecosystem and climate in which the urbanization occurs [63, 64], results from one region may not apply to another. For example, sparing agricultural land on an urban periphery likely has different ecological effects than sparing habitats that are not intensively managed or altered by humans. Thus, to the extent that people and governments in these underrepresented regions seek to use biological conservation as a criterion to manage urban form, additional research is needed to fill these geographical gaps. Arid, semi-arid, and mountainous regions may represent especially urgent research needs, as these areas face accelerated and compounding climate stressors [65].

What Study Designs and Urban Indicators Have Been Used?

Studies employed four overall approaches to compare the outcomes of sharing-sparing landscape configurations.

Curve Shape

As outlined in the introduction and Fig. 1, the classical assessment of sparing-sharing fits density-urbanization curves for each species (or other response). Curve shape then indicates whether sparing or sharing will produce the larger population, greater diversity, or higher level of ecosystem service (Fig. 1, Fig. S3). Five studies used this approach [59, 66–68, 69•]. With one exception ([70] as analyzed by [59]), these followed the recommendation [35] to root the sampling gradient in spared land with 0% urban development. Some studies expanded upon the basic curve shapes by fitting generalized additive models or other exponential functions with multiple inflection points so that sparing might be favored at some levels of urbanization, while sharing might be favored at others [67, 68, 69•].

Simulation

In this approach, focal taxa or services are sampled or modeled in sites that represent different urban intensities. Then, one of two approaches was used. In the first, simulated landscapes draw from these sampled communities to simulate effects of different development patterns. For example, a simulated shared landscape draws its community entirely from samples taken in low-intensity development, while a spared landscape populates part of the simulated area with high-urban communities and the remainder with non-urban communities [48–50, 67, 68, 69•, 71]. In the second approach, the effects of implementing a sharing landscape are modeled over time, allowing for an assessment of the accumulated value in ecosystem services [60].

Paired Landscapes

Members of each landscape pair have overall equal amounts of housing, human population, sealed surface, or green space, but differ in the configuration of that green space. Although urbanization level is matched within pairs, it may differ among pairs. Studies using this design [57, 58, 72] did not attempt to ask whether the best configuration differed across urbanization levels. In principle, they could do so, if pairs were replicated adequately across urbanization levels.

Observational

One study [73] overlaid an entire city with contiguous hexagonal landscapes and analyzed proxies for ecosystem services as a function of landscape characteristics. Although greenspace amount and configuration were correlated across landscapes, the authors attempted to isolate effects of configuration by including greenspace amount as a covariate. Although such an approach is reasonable in exploratory studies, it provides weak conclusions because estimated outcomes for some landscape combinations (e.g., low-urban/sharing) may be based on very few data points, and collinear predictors may distort parameter estimates [74].

In all study designs, alternative landscapes must be matched for their ability to meet the same level of human need in the same total area. In classical agricultural applications, yield is the benchmark for assessing these intensity-area tradeoffs. In the reviewed studies, housing was a common target, because urban sprawl is usually driven by residential development [24], and because many cities must plan to accommodate projected population growth. Thus, studies attempted to match alternative landscapes for number of humans housed (analogous to number of humans fed by agriculture) and common urban metrics were housing density [48–50, 66, 71], building density [68], and human population density [67, 69•]. Other studies matched landscapes

on the basis of proxies that may not have a consistent relationship with housing or any other specific per-capita benefit to urban humans. For example, some paired designs matched landscapes for total greenspace amount, rather than human population [57, 58, 72], and several studies used percent impervious surface or built land cover in place of yield [59, 73, 75]. We recommend number of humans housed as a suitable metric for comparison to yield, over less direct proxies such as impervious surface. Overall, “yield” (level of production of some benefit or commodity per unit area) in an urban setting is complex and multifaceted, and the urban literature has not yet produced an explicit discussion of which variable (or variables) should be selected for analysis. Cities also produce knowledge, culture, goods, and economic activity [76], all of which represent valuable social welfare outcomes. Although the area requirements of these city-produced benefits are less obvious than those of housing, their relationships to conservation and urban form merit attention in future work. A metric that may warrant examination is the sustainable cities indicator put forth by the United Nations 2030 Agenda for Sustainable Development [77]. This land use efficiency metric is the ratio of the expansion of developed land to the population growth rate over a given time period and for a given area. As it measures the form of urbanization patterns, this versatile metric is broadly linked to not only environmental, but also economic and social dimensions of land change and has the potential to control for legacy effects that might otherwise make comparisons difficult [77, 78].

Which Taxonomic Groups, Processes, or Ecosystem Services Have Been Assessed, and What Were Their Responses?

Studies assessed the responses of individual species or community metrics for birds [49, 50, 57, 58, 69•], mammals [66, 71], insects [48, 59, 68], and plants [67]. They assessed indicators of ecosystem services and processes including carbon sequestration [59, 67], greenspace access [72, 73], air quality [73], climate [59, 73, 75], soil retention [60], water infiltration [59], and predation [58]. Examining pooled results across studies, the preferred configurations differed among response groups (Fisher’s exact test, $p < 0.01$, Fig. 3). Individual species were most likely to benefit from sparing (51% of 296 species), whereas processes and services were more likely to benefit from sharing (50% of 26 measurements). Community metrics such as diversity, richness, and pooled abundance were least conclusive, with only a plurality of measurements in favor of sparing (43% of 21 measurements). The latter may be symptomatic of the various ways community metrics were assessed. Some studies measured community metrics per landscape, without accounting for potential biotic homogenization among landscapes, a known problem and the source

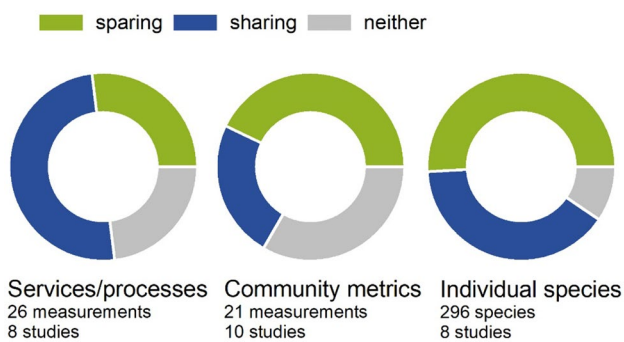


Fig. 3 Proportion of services, community metrics, and individual species that benefit from urban sparing, sharing, or neither, extracted from 15 publications

of the recommendation to conduct sparing-sharing analyses at the species level [36•]. Even studies that did simulations based on individual-species data could have missed homogenization (loss of species turnover among sites) if their simulated landscapes were smaller than an entire city.

We further examined individual species responses for each taxon separately. Responses differed among taxa (Fisher’s exact test, $p < 0.001$, Fig. 4), with 72% of mammals preferring sparing, about half of birds and insects, and only 20% of plants. The latter value was based on a single study of trees in Cambridge, England, where spared land was not forested [67]. There, the authors simulated a scenario in which forest was restored on spared land, which reversed the overall outcome in favor of sparing (we did not include the result of that simulation in our analysis because we assigned individual species to sparing/sharing outcomes on the basis of density-urbanization curves, which only represented actual—not hypothetically restored—conditions).

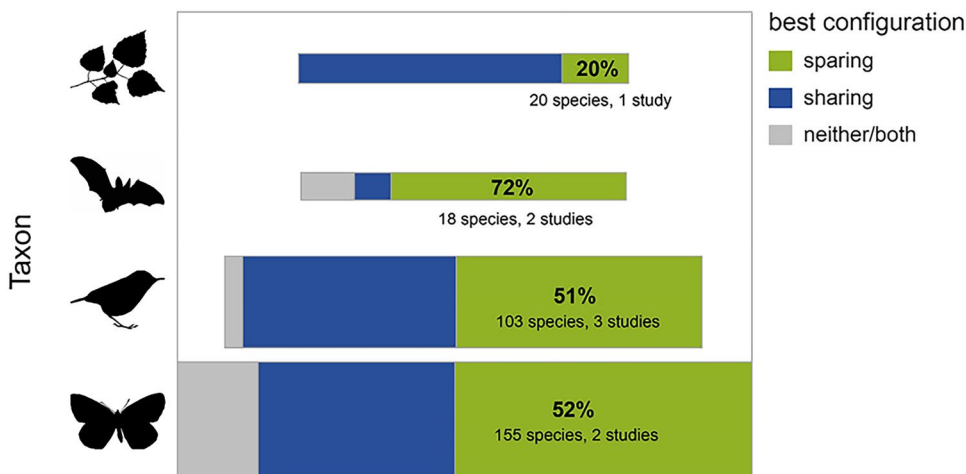
Finally, we were able to identify urban winners and losers (Fig. S3) from six studies of individual species responses (two bird studies including 64 responses; two

mammal studies with 18 responses; one insect study with 61 responses; and one plant study with 20 responses) and from six studies of community metrics (8 measurements) and two of services/processes (8 measurements). In this subset of studies, preferred configuration (sparing/sharing) depended on response direction (winner/loser) for birds and mammals, but not insects, plants, community metrics, or processes/services (Fig. S6, Fisher’s exact test with sequential Bonferroni correction at $\alpha = 0.05$). Across all groups, most losers preferred sparing (77%), while most winners preferred sharing (89% of the very few winners). However, a large number of responses were classified as neither winners nor losers, and in this category, 46% of species/responses preferred sparing and 46% preferred sparing.

Overall, although most individual species did prefer sparing, that majority was not as large as in agricultural studies, where at least 64% of 1591 species assessed were losers that preferred sparing [36•]. Here, that total was 37% of 163 species, suggesting that decisions between sharing and sparing are more nuanced in urban than agricultural settings. One of these nuances may arise from the background landscape in which urbanization occurs, whereas agricultural intensification may spare adjacent undisturbed environments, urban growth occurs in a variety of background landscapes, from relatively undisturbed areas to long-inhabited agricultural areas. In other words, compact urban development and compact agriculture may “spare” very different baseline landscapes. Similarly, in cities, shared land may include small parks and private yards or gardens where management practices differ widely within and among cities. Quantifying these potential nuances will be important to developing predictive models of urban sparing-sharing.

Integrating results across multiple species—or across species and processes—also remains a challenge. Choosing a single ecological response metric, multiple metrics, or an aggregated index will invariably result in an incomplete picture of the ecological consequences of landscape

Fig. 4 Sparing was the preferred development pattern for most animals (including mammals, birds, and insects), but the single study of plants (trees) found that most taxa benefited from sharing; the same study suggested that restoring urban green spaces to woodlands would reverse this pattern. The overall size of each mosaic plot represents the number of species or measurements included; colored blocks represent the proportion of species that favor sparing, sharing, or neither. Text percentages indicate the percent of species that favor sharing



configuration. The original formulation of the sparing-sharing framework [32] simply favored the development pattern that minimized the total number of extinctions in the landscape. Very few urban studies—with the exception of [50]—examined the number of species committed to area-wide extinction under alternative development patterns. One noteworthy approach was that of Geschke et al. [69], which sought the landscape configuration that would maximize the citywide geometric mean of bird relative abundance across all species, while meeting housing targets. This approach upweighted changes in rare species, captured effects of biotic homogenization among sites, and determined that an intermediate configuration was slightly better than extreme sparing to optimize regional bird diversity.

To incorporate not only species, but also ecosystem processes or services, into the urban optimization process, new approaches are needed. In non-urban settings, decision-support software such as Marxan with Zones [79] has helped identify optimal distribution of land uses relative to specific, conflicting management objectives. For example, Law et al. [80] showed that multiple landscape configurations—allocated among conservation, oil-palm plantation, and small-holder farming—could meet competing stakeholder goals for timber production, biodiversity conservation, and carbon emissions, with optimal solutions including a mix of sparing and sharing. Similar approaches in urban areas could optimize allocation of spared and shared land to meet multiple goals, such as maintaining regional biodiversity, protecting priority species, providing ecosystem services, and meeting housing targets. We did not recover any urban examples of this approach to sparing-sharing (but see [81]). New decision-support metrics that leverage participatory mapping and modeling approaches for community engagement could generate buy-in and include previously marginalized or excluded voices in necessary (but often difficult and contentious) discussions about future planning [82].

How Have Urban Studies Dealt with Issues of Spatial Scale and Connectivity?

Studies of sparing-sharing require researchers to make decisions on at least three spatial scales: the size of study sites within which data are collected (grain size); the size of the overall landscape in which study sites are located; and finally, the scale at which sparing-sharing is assessed.

Grain size—the area represented by individual measurements of response variables—ranged from 0.0009 (corresponding to a single 30 m × 30 m pixel in a landscape raster) to 7.1 km² (the area of a circle with a 1.5 km radius). Most studies defined grain size a priori with some mechanistic justification; one [73] performed all analyses at three grain sizes; and one performed model selection to determine the area that should be associated with each sampling point [66].

Studies used larger grain sizes when investigating ecosystem processes and services (mean ± SE = 1.4 ± 0.5 km²) than when investigating individual species (0.16 ± 0.17 km²) or community metrics (0.20 ± 0.17 km²).

The landscape scale was generally one city or metropolitan area, ranging from 41 to 8944 km², with one multi-city study spread over 1.2 million km². Even so, studies did not necessarily assess ecological outcomes at the whole-city scale. For example, one study sampled 35 1 km² study sites across > 2000 km² of Tokyo, Japan, to develop species-specific density-urbanization curves for butterflies and carabid beetles [68]. However, the study restricted predictions about diversity and extinctions to the scale of the 1 km² squares, not the whole city. Studies that did assess whole-city outcomes did so by selecting a future population projection and simulating the addition of those dwellings to the existing “baseline” landscape in ways that either developed existing greenspace at a low-density (sharing) or subdivided parcels to densify residential areas while leaving public greenspace intact (sparing). Then, they used species’ density-urbanization curves from the same cities to populate these new, simulated landscapes [50].

Crucially, however, most studies were ambiguous about the scale at which sparing and sharing were actually defined. That is, how large did a habitat patch have to be to count as “spared”? Exceptions were studies that simulated small landscapes of pre-defined size, such as [48, 49, 68] or those that selected small, paired landscapes as study areas. For example, [57] considered a 0.25 km² landscape to be “spared” if more than 50% of its greenspace was aggregated in a single patch. However, whole-city simulations—arguably the most useful from a city-planning perspective—were notably ambiguous. They simulated the addition of new residences in ways that preserved or divided existing greenspaces, but they did not report the size of those greenspaces, the percent of the total metropolitan area that was greenspace, or any metric of greenspace aggregation. The absence of this information makes results difficult to interpret or generalize among cities. Depending on each city’s baseline configuration, sharing development in one city could yield a configuration very similar to sparing development in another city. This contingency hinders comparison and generalization, and future work would benefit from multi-city studies that explicitly make such comparisons—as well as careful reporting of baseline, city-wide habitat amount, and configuration in single-city studies.

Finally, no study attempted to account for the connectivity of urban greenspace in predicting biodiversity outcomes. Indeed, the classical sparing-sharing framework assumes that any spared patch would host a similar species population density, or provide a similar level of ecosystem service per unit area, regardless of patch size, matrix quality (until the ambiguous transition from sparing to sharing is crossed), or

connectedness to other patches. If future patches are smaller, more isolated, or qualitatively distinct from those sampled to develop density-yield curves (Fig. 1, Fig. S3), then the classical assessment will overestimate diversity or service provision of spared patches. Likewise, the existence of large or higher quality patches that act as sources for smaller or lower quality patches nearby could lead to more species or higher populations supported. Metacommunity theory provides an avenue to predict biodiversity not only on the basis of habitat quality but also connectivity, by integrating the roles of dispersal, environmental filtering, biotic interactions, and neutral processes [83]. Urban ecology and conservation biology have increasingly acknowledged the importance of metacommunity processes for understanding and managing complex landscapes [84–87]. Empirical research continues to document the ability of different species to disperse through urban matrices [88–90], and the increasing availability of metacommunity simulation models [91–93] suggests a way to incorporate dispersal into assessments of spared and shared landscapes. Simulated landscapes could be initially populated using density-urbanization curves (as they are now), but their trajectories over time could then be simulated on the basis of patch sizes and arrangement, and species' dispersal abilities within the simulated landscapes.

Summary and Conclusions

The sparing-sharing framework is an important example of a means to reconcile and harmonize ecological integrity and human wellbeing in the Anthropocene. Whereas agricultural and ecological research communities have a long history of considering tradeoffs and synergies between these systems (e.g., [94, 95]), urban ecology is still a relatively nascent subdiscipline that lacks this history. While conservation science has taken steps to view urban landscapes as an integral part of conservation planning (e.g., [96, 97]), it is still rare to see explicit consideration of human-centered objectives, such as improving societal welfare or housing availability (but see [47]). In this sense, the application of the sparing-sharing framework to urban landscapes is an advance.

This review finds, however, that urban research using this framework has not yet produced strong conclusions that are generalizable to additional taxa or cities. As a result, it does not provide actionable recommendations for city planners, urban developers, and conservationists. Neither individual taxa, community metrics, nor ecosystem services show an overwhelming majority in favor of one development pattern over the other, as they do in agricultural studies to date. Instead, each configuration produces winners and losers. To evaluate potential human and conservation outcomes of actual urban planning and zoning decisions—such as the distribution and density of new housing, and preservation

or creation of greenspace—additional insights are needed. Here, we summarize specific areas for progress identified throughout the review.

1. Assessments of urban landscape configurations will be more informative if they explicitly optimize across multiple, sometimes competing, objectives, rather than seeking a majority rules conclusion. Future analyses could parameterize optimization algorithms that not only maximize biodiversity while meeting housing targets—as in the classical framework—but also give weight to other stakeholder priorities such as ecosystem service provision, protection of target species, or economic activity. The range of possible configurations will include not only extreme sparing and sharing (the classical one- and two-compartment landscapes) but also mixed or multi-compartment configurations. A related consideration is that changing how shared land is managed could have greater ecological consequences than changing configuration per se [98•], and this possibility should not be overlooked in urban scenarios. In fact, differences in management among the small green spaces characteristic of sharing could be one reason why our results are more mixed than expected in terms of fragmentation alone [44]. Few urban sparing-sharing studies have adopted any of these approaches (but see [67, 69•]), and these advances are needed to increase relevance and realism when assessing alternative urban configurations.
2. To facilitate comparability of results among cities, the roles of spatial scale, connectivity, and land management need to be more explicitly examined. In agricultural landscapes, optimal ecological outcomes and ecosystem services likely result from multi-scale land sparing and land sharing elements situated within a heterogeneous connected landscape [43•], and we suspect that is the case in the urban context as well. Studies that simulate changes to real-world landscapes, particularly whole cities, would benefit from defining the size and total area of green spaces involved, and examining the consequences of altered connectivity for the species and services in the alternative landscape configurations. Both the movement of non-human species and the provision of ecosystem services that depend on green-space access will depend on sparing scale and connectivity.
3. Additional geographic and taxonomic representation is needed to understand how optimal urban configurations differ systematically across biomes, land uses, or governance structures. Geographic representation among studies is currently weak, with few studies outside of Europe, Australia, and Japan, and few comparative or multi-city studies. Taxonomic representation is similarly weak, with only eight studies providing species-level data, and none addressing reptiles, amphibians, fish, or

aquatic invertebrates. The ecological consequences of land sparing likely differ when a city develops within a background biome or landscape of high versus low biodiversity. Scale will again intersect with this issue, as there are likely many cases where island biogeography theory (or its more nuanced derivatives [99]) applies in the sparing-sharing context. But whether the urban area of interest represents the “island” or the “ocean” will depend on the scale of analysis, the background ecological context, and the taxa considered. Future work could take on these comparisons to suggest how broadly results from any given city, region, or taxon may apply.

The key insight of the sparing-sharing framework is that choices between alternative landscape configurations are only meaningful when those landscapes are matched for total area and the level of human needs met. In other words, it is not enough to document detriments of sprawl; these must be weighed against alternative configurations that accommodate the same number of people and their livelihoods. This key insight can be retained while continuing to adopt and develop new and geographically representative approaches to evaluating land use tradeoffs in the world’s growing cities to support ecological outcomes, human populations, and human wellbeing.

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Conflict of Interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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References

Papers of particular interest, published recently, have been highlighted as:

- Of importance

1. United Nations. World urbanization prospects: The 2018 Revision. New York: United Nations, Population Division; 2018.
2. Gao J, O’Neill BC. Mapping global urban land for the 21st century with data-driven simulations and Shared Socioeconomic Pathways. *Nat Commun.* 2020;11:1–12.
3. Li X, Zhou Y, Eom J, Yu S, Asrar GR. Projecting global urban area growth through 2100 based on historical time series data and future shared socioeconomic pathways. *Earth’s Future.* 2019;7:351–62.
4. Seto KC, Fragkias M, Güneralp B, Reilly MK. A meta-analysis of global urban land expansion. *PLoS ONE.* 2011;6: e23777.
5. Liu Z, He C, Zhou Y, Wu J. How much of the world’s land has been urbanized, really? A hierarchical framework for avoiding confusion. *Landscape Ecol.* 2014;29:763–71.
6. FAO. Food and Agriculture Organization of the United Nations, Statistical Database, Land Use Domain. 2021. <https://www.fao.org/faostat/en/#data/RL>. Accessed 4 May 2022.
7. Gaston KJ. Biodiversity and extinction: species and people. *Prog Physical Geogr.* 2005;29:239–47.
8. Güneralp B, Seto K. Futures of global urban expansion: uncertainties and implications for biodiversity conservation. *Environ Res Lett.* 2013;8: 014025.
9. Kühn I, Brandl R, Klotz S. The flora of German cities is naturally species rich. *Evol Ecol Res.* 2004;6:749–64.
10. Cincotta RP, Wisniewski J, Engelman R. Human population in the biodiversity hotspots. *Nature.* 2000;404:990–2.
11. Luck GW. A review of the relationships between human population density and biodiversity. *Biol Rev.* 2007;82:607–45.
12. Soga M, Gaston KJ. Extinction of experience: the loss of human–nature interactions. *Front Ecol Environ.* 2016;14:94–101.
13. Gaston KJ, Soga M. Extinction of experience: the need to be more specific. *People Nat.* 2020;2:575–81.
14. Rook GA. Regulation of the immune system by biodiversity from the natural environment: an ecosystem service essential to health. *Proc Natl Acad Sci USA.* 2013;110:18360–7.
15. Gaston KJ. Urban ecology. In: Gaston KJ, editor. *Urban ecology.* Oxford University Press; 2010. p. 1–9.
16. Dearborn DC, Kark S. Motivations for conserving urban biodiversity. *Conserv Biol.* 2010;24:432–40.
17. Dunn RR, Gavin MC, Sanchez MC, Solomon JN. The pigeon paradox: dependence of global conservation on urban nature. *Conserv Biol.* 2006;20:1814–6.
18. Seto KC, Sánchez-Rodríguez R, Fragkias M. The new geography of contemporary urbanization and the environment. *Annu Rev Environ Res.* 2010;35:167–94.
19. Marzluff JM, Bowman R, Donnelly R. A historical perspective on urban bird research: trends, terms, and approaches. In: *Avian ecology and conservation in an urbanizing world.* Springer; 2001. p. 1–17.
20. Adams MA, Frank LD, Schipperijn J, Smith G, Chapman J, Christiansen LB, et al. International variation in neighborhood walkability, transit, and recreation environments using geographic information systems: the IPEN adult study. *Int J Health Geogr.* 2014;13:17. <https://doi.org/10.1186/1476-072x-13-43>.
21. Schneider A, Woodcock CE. Compact, dispersed, fragmented, extensive? A comparison of urban growth in twenty-five global cities using remotely sensed data, pattern metrics and census information. *Urban Stud.* 2008;45:659–92.
22. Güneralp B, Reba M, Hales BU, Wentz EA, Seto KC. Trends in urban land expansion, density, and land transitions from 1970 to 2010: a global synthesis. *Environ Res Lett.* 2020;15: 044015.
23. Liu X, Huang Y, Xu X, Li X, Li X, Ciais P, et al. High-spatiotemporal-resolution mapping of global urban change from 1985 to 2015. *Nat Sustain.* 2020;3:564–70.

24. Terando AJ, Costanza J, Belyea C, Dunn RR, McKerron A, Collazo JA. The southern megalopolis: using the past to predict the future of urban sprawl in the southeast US. *PLoS ONE*. 2014;9: e102261.
25. Zhao L. Urban growth and climate adaptation. *Nat Clim Change*. 2018;8:1034.
26. McGrane SJ. Impacts of urbanisation on hydrological and water quality dynamics, and urban water management: a review. *Hydrolog Sci J*. 2016;61:2295–311.
27. Moore M, Gould P, Keary BS. Global urbanization and impact on health. *Int J Hyg Environ Health*. 2003;206:269–78.
28. Sutton PC, Anderson SJ, Elvidge CD, Tuttle BT, Ghosh T. Paving the planet: impervious surface as proxy measure of the human ecological footprint. *Prog Physical Geogr*. 2009;33:510–27.
29. Artmann M, Inostroza L, Fan P. Urban sprawl, compact urban development and green cities. How much do we know, how much do we agree? *Ecol Indicators*. 2019;96:3–99.
30. Ewing R, Meakins G, Hamidi S, Nelson AC. Relationship between urban sprawl and physical activity, obesity, and morbidity - update and refinement. *Health Place*. 2014;26:118–26. <https://doi.org/10.1016/j.healthplace.2013.12.008>.
31. Burchell RW, Mukherji S. Conventional development versus managed growth: the costs of sprawl. *Am J Public Health*. 2003;93:1534–40.
32. Green RE, Cornell SJ, Scharlemann JP, Balmford A. Farming and the fate of wild nature. *Science*. 2005;307:550–5.
33. Van Noordwijk M, Tomich T, De Foresta H, Michon G. To segregate-or to integrate? The question of balance between production and biodiversity conservation in complex agroforestry systems. *Agroforestry Today (ICRAF)*. 1997;9:6–9.
34. Gabriel D, Carver SJ, Durham H, Kunin WE, Palmer RC, Sait SM, et al. The spatial aggregation of organic farming in England and its underlying environmental correlates. *J Appl Ecol*. 2009;46:323–33.
35. Phalan B, Balmford A, Green RE, Scharlemann JP. Minimising the harm to biodiversity of producing more food globally. *Food Policy*. 2011;36:S62–71.
36. Balmford A. Concentrating vs. spreading our footprint: how to meet humanity's needs at least cost to nature. *J Zool*. 2021;315:79–109. **Reviews evidence to date in agricultural sparing-sharing research, and highlights selected non-agricultural applications.**
37. Phalan BT. What have we learned from the land sparing-sharing model? *Sustainability*. 2018;10:1760.
38. Kremen C. Reframing the land-sparing/land-sharing debate for biodiversity conservation. *Ann N Y Acad Sci*. 2015;1355:52–76.
39. Ekroos J, Ödman AM, Andersson GK, Birkhofer K, Herbertsson L, Klatt BK, et al. Sparing land for biodiversity at multiple spatial scales. *Front Ecol Evol*. 2016;3:145.
40. Fischer J, Abson DJ, Butsic V, Chappell MJ, Ekroos J, Hanspach J, et al. Land sparing versus land sharing: moving forward. *Conserv Lett*. 2014;7:149–57.
41. Balmford A, Green R, Phalan B. Land for food and land for nature? *Daedalus*. 2015;144:57–75.
42. Kremen C, Merenlender AM. Landscapes that work for biodiversity and people. *Science*. 2018;362:eaau6020.
43. Grass I, Loos J, Baensch S, Batáry P, Librán-Embid F, Ficiyan A, et al. Land-sharing/-sparing connectivity landscapes for ecosystem services and biodiversity conservation. *People and Nature*. 2019;1:262–72. **A non-urban perspective piece highlighting the need to incorporate landscape connectivity into the sharing-sparing approach.**
44. Fahrig L. Ecological responses to habitat fragmentation per se. *Annu Rev Ecol Syst*. 2017;48:1–23.
45. Lin BB, Fuller RA. Sharing or sparing? How should we grow the world's cities? *J Appl Ecol*. 2013;50:1161–8.
46. Soulé ME. Land use planning and wildlife maintenance. In: *Urban Ecology*. Springer; 2008. p. 699–713.
47. Wittig R, Breuste J, Finke L, Kleyer M, Rebele F, Reidl K, et al. What should an ideal city look like from an ecological view? Ecological demands on the future city. In: *Urban Ecology*. Springer; 2008. p. 691–8.
48. Gagné SA, Fahrig L. The trade-off between housing density and sprawl area: minimizing impacts to carabid beetles (Coleoptera: Carabidae). *Ecol Soc*. 2010;15:12.
49. Gagné SA, Fahrig L. The trade-off between housing density and sprawl area: minimising impacts to forest breeding birds. *Basic Appl Ecol*. 2010;11:723–33.
50. Sushinsky JR, Rhodes JR, Possingham HP, Gill TK, Fuller RA. How should we grow cities to minimize their biodiversity impacts? *Global Change Biol*. 2013;19:401–10.
51. Szulkin M, Garroway CJ, Corsini M, Kotarba AZ, Dominoni D. How to quantify urbanization when testing for urban evolution? In: *Urban Evolutionary Biology*. Oxford; 2020. p. 13.
52. R Core Team. R: A Language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2013.
53. Holm S. A simple sequentially rejective multiple test procedure. *Scand J Stat*. 1979;6:65–70.
54. Bates D, Maechler M, Bolker B, Walker S. Fitting linear mixed-effects models using lme4. *J Stat Softw*. 2015;67:1–48.
55. Fox J, Weisberg S. An R companion to applied regression. 3rd ed. Thousand Oaks, CA: Sage; 2019.
56. Hothorn T, Bretz F, Westfall P. Simultaneous inference in general parametric models. *Biom J J Math Methods Biosci*. 2008;50:346–63.
57. Ibáñez-Álamo JD, Morelli F, Benedetti Y, Rubio E, Jokimäki J, Pérez-Contreras T, et al. Biodiversity within the city: effects of land sharing and land sparing urban development on avian diversity. *Sci Total Environ*. 2020;707: 135477.
58. Jokimäki J, Suhonen J, Benedetti Y, Diaz M, Kaisanlahti-Jokimäki ML, Morelli F, et al. Land-sharing vs. land-sparing urban development modulate predator-prey interactions in Europe. *Ecol Appl*. 2020;30:e02049.
59. Stott I, Soga M, Inger R, Gaston KJ. Land sparing is crucial for urban ecosystem services. *Front Ecol Environ*. 2015;13:387–93.
60. Hu T, Peng J, Liu Y, Wu J, Li W, Zhou B. Evidence of green space sparing to ecosystem service improvement in urban regions: a case study of China's ecological red line policy. *J Clean Prod*. 2020;251: 119678.
61. Lahr EC, Dunn RR, Frank SD. Getting ahead of the curve: cities as surrogates for global change. *Proc Roy Soc B*. 2018;285:20180643.
62. Aronson MF, La Sorte FA, Nilon CH, Katti M, Goddard MA, Lepczyk CA, et al. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proc Roy Soc B*. 2014;281:20133330.
63. Diamond SE, Dunn RR, Frank SD, Haddad NM, Martin RA. Shared and unique responses of insects to the interaction of urbanization and background climate. *Curr Opin Insect Sci*. 2015;11:71–7.
64. Youngsteadt E, Terando AJ. Ecology of urban climates: the need for a landscape biophysics in cities. In: Barbosa P, editor. *Urban Ecology: Its Nature and Challenges*. Wallingford, UK: CABI; 2020.
65. IPCC. Climate Change 2022: Impacts, adaptation and vulnerability: contribution of working group II to the sixth assessment report of the intergovernmental panel on climate change. Cambridge: Cambridge University Press; 2022. in press.
66. Caryl FM, Lumsden LF, van der Ree R, Wintle BA. Functional responses of insectivorous bats to increasing housing density support 'land-sparing' rather than 'land-sharing' urban growth strategies. *J Appl Ecol*. 2016;53:191–201.
67. Collas L, Green RE, Ross A, Wastell JH, Balmford A. Urban development, land sharing and land sparing: the importance of considering restoration. *J Appl Ecol*. 2017;54:1865–73.

68. Soga M, Yamaura Y, Koike S, Gaston KJ. Land sharing vs. land sparing: does the compact city reconcile urban development and biodiversity conservation? *J Appl Ecol*. 2014;51:1378–86.
69. ● Geschke A, James S, Bennett AF, Nimmo DG. Compact cities or sprawling suburbs? Optimising the distribution of people in cities to maximise species diversity. *J Appl Ecol*. 2018;55:2320–31. **Takes an optimization approach, considering multiple landscape compartments with urban densities between the sparing-sharing extremes; the solution that optimizes geometric mean of bird abundance across species includes some lower-density housing than extreme sparing.**
70. Wang L, Lyons J, Kanehl P, Bannerman R. Impacts of urbanization on stream habitat and fish across multiple spatial scales. *Environ Manag*. 2001;28:255–66.
71. Villaseñor NR, Tulloch AI, Driscoll DA, Gibbons P, Lindenmayer DB. Compact development minimizes the impacts of urban growth on native mammals. *J Appl Ecol*. 2017;54:794–804.
72. Soga M, Yamaura Y, Aikoh T, Shoji Y, Kubo T, Gaston KJ. Reducing the extinction of experience: association between urban form and recreational use of public greenspace. *Landscape Urban Plann*. 2015;143:69–75.
73. Dennis M, Scaletta KL, James P. Evaluating urban environmental and ecological landscape characteristics as a function of land-sharing-sparing, urbanity and scale. *PLoS ONE*. 2019;14: e0215796.
74. Graham MH. Confronting multicollinearity in ecological multiple regression. *Ecology*. 2003;84:2809–15.
75. Osborne PE, Alvares-Sanches T. Quantifying how landscape composition and configuration affect urban land surface temperatures using machine learning and neutral landscapes. *Comput Environ Urban*. 2019;76:80–90.
76. Bettencourt LM. The origins of scaling in cities. *Science*. 2013;340:1438–41.
77. United Nations. Sustainable development goals metadata repository-SDG indicator metadata (Format Version 1.0). New York: United Nations, Department of Economic and Social Affairs, Statistics Division; 2021. <https://unstats.un.org/sdgs/metadata/files/Metadata-11-03-01.pdf>. Accessed 22 May 2022.
78. Vogler JB, Vukomanovic J. Trends in United States human footprint revealed by new spatial metrics of urbanization and per capita land change. *Sustainability*. 2021;13:12852.
79. Watts ME, Ball IR, Stewart RS, Klein CJ, Wilson K, Steinback C, et al. Marxan with zones: software for optimal conservation based land-and sea-use zoning. *Environ Model Softw*. 2009;24:1513–21.
80. Law EA, Bryan BA, Meijaard E, Mallawaarachchi T, Struebig MJ, Watts ME, et al. Mixed policies give more options in multi-functional tropical forest landscapes. *J Appl Ecol*. 2017;54:51–60.
81. Lin J, Li X. Large-scale ecological red line planning in urban agglomerations using a semi-automatic intelligent zoning method. *Sustain Cities Soc*. 2019;46: 101410.
82. Vukomanovic J, Smart L. GIS participatory modeling. In: Wilson JP, editor. *The geographic information science & technology body of knowledge* (1st Quarter 2021 Edition). University Consortium for Geographic Information Science; 2021.
83. Leibold MA, Holyoak M, Mouquet N, Amarasekare P, Chase JM, Hoopes MF, et al. The metacommunity concept: a framework for multi-scale community ecology. *Ecol Lett*. 2004;7:601–13.
84. Andrade R, Franklin J, Larson KL, Swan CM, Lerman SB, Bateman HL, et al. Predicting the assembly of novel communities in urban ecosystems. *Landscape Ecol*. 2021;36:1–15.
85. Chase JM, Jeliakov A, Ladouceur E, Viana DS. Biodiversity conservation through the lens of metacommunity ecology. *Ann N Y Acad Sci*. 2020;1469:86–104.
86. Fahrig L, Watling JI, Arnillas CA, Arroyo-Rodríguez V, Jörgen-Hickfang T, Müller J, et al. Resolving the SLOSS dilemma for biodiversity conservation: a research agenda. *Biol Rev*. 2022;97:99–114.
87. Daigle RM, Metaxas A, Balbar AC, McGowan J, Trembl EA, Kuempel CD, et al. Operationalizing ecological connectivity in spatial conservation planning with Marxan Connect. *Methods Ecol Evol*. 2020;11:570–9.
88. Richardson JL, Michaelides S, Combs M, Djan M, Bisch L, Barrett K, et al. Dispersal ability predicts spatial genetic structure in native mammals persisting across an urbanization gradient. *Evol Appl*. 2021;14:163–77.
89. Johansson V, Koffman A, Hedblom M, Deboni G, Andersson P. Estimates of accessible food resources for pollinators in urban landscapes should take landscape friction into account. *Ecosphere*. 2018;9: e02486.
90. Shimazaki A, Yamaura Y, Senzaki M, Yabuhara Y, Akasaka T, Nakamura F. Urban permeability for birds: an approach combining mobbing-call experiments and circuit theory. *Urban For Urban Green*. 2016;19:167–75.
91. Sokol ER, Brown BL, Carey CC, Tornwall BM, Swan CM, Barrett J. Linking management to biodiversity in built ponds using meta-community simulations. *Ecol Model*. 2015;296:36–45.
92. Keyel AC, Gerstenlauer JL, Wiegand K. SpatialDemography: a spatially explicit, stage-structured, metacommunity model. *Ecography*. 2016;39:1129–37.
93. Thompson PL, Guzman LM, De Meester L, Horváth Z, Ptasnik R, Vanschoenwinkel B, et al. A process-based metacommunity framework linking local and regional scale community ecology. *Ecol Lett*. 2020;23:1314–29.
94. Paoletti M, Pimentel D, Stinner B, Stinner D. Agroecosystem biodiversity: matching production and conservation biology. *Agric Ecosyst Environ*. 1992;40:3–23.
95. Thomas VG, Kevan PG. Basic principles of agroecology and sustainable agriculture. *J Agric Environ Ethics*. 1993;6:1–19.
96. Parish J. Re-wilding Parkdale? Environmental gentrification, settler colonialism, and the reconfiguration of nature in 21st century Toronto. *Environ Plann E Nat Space*. 2020;3:263–86.
97. Garrard GE, Williams NS, Mata L, Thomas J, Bekessy SA. Biodiversity sensitive urban design. *Conserv Lett*. 2018;11: e12411.
98. ● Runting RK, Griscom BW, Struebig MJ, Satar M, Meijaard E, Burivalova Z, et al. Larger gains from improved management over sparing–sharing for tropical forests. *Nat Sustainability*. 2019;2:53–61. **A non-urban example highlighting the possibility that altering land-management practices in shared land may affect ecological outcomes as much or more than configuration; an area that urban research should pursue.**
99. Dickson BG, Albano CM, Anantharaman R, Beier P, Fargione J, Graves TA, et al. Circuit-theory applications to connectivity science and conservation. *Conserv Biol*. 2019;33:239–49.

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