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How and where sprawl and compact residential development are compared determines what's better for biodiversity

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Residential development profoundly changes biodiversity. A central issue in the management of these impacts is the role of urban form. We report the results of the first meta-analyses of the biodiversity value of compact versus dispersed residential developments. We identified six studies that compared biodiversity responses between existing developments and 14 studies that modeled the projected impacts of urban form. We show that the relative effects of compact versus dispersed developments are varied within and across studies, precluding any general statement about the benefits of one type of urban form over another. Variability in effect sizes resulted from the expected variability among biodiversity responses and the influence of spatial scale and local conditions, e.g., private and public landscape management practices. We suggest that future research on the effects of compact and dispersed developments on biodiversity should be designed with local planning and other conditions in mind and in collaboration with planning practitioners and local decision-makers and community members. Future research should also ideally thoroughly characterize the urban forms being compared in terms of their variation in landscape structure and socio-ecological context that is likely to impact biodiversity.

Of the five most important determinants of biodiversity loss, land use and land cover change are expected to have the most substantial influence on the diversity and community structure of terrestrial and freshwater organisms by the end of this century¹. Among the fastest growing and least reversible drivers of global land use and land cover change are continued population growth within cities and the expansion of urban residential development².

Residential development profoundly changes biodiversity. The addition of buildings, roads, and other human-made structures to an undeveloped landscape changes the amount and spatial arrangement of habitat for plant and animal species. For example, urbanization in the US Southeast is projected to reduce the total amount of forest in the region by approximately 9% and mean patch area by 15%, whereas the number of forest patches are projected to increase by 7%³. These and associated changes in human activities that impact habitat quality alter plant and animal community structure and function in urbanized landscapes. For birds, urban and suburban landscapes host approximately 30–70% of the species in natural landscapes, and these species may be filtered by dietary habit, nesting location, and reproductive output^{4,5}. Across plants, beetles, hoverflies, mammals, reptiles, and amphibians, in addition to birds, sites subjected to moderate or intensive urban land use host an average of 34–50% of the species that occur in undeveloped sites⁶. In addition, urban amphibian, bat, bee, carabid beetle, and reptile communities are characterized by novel

suites of traits that result from the interaction between species life history and landscape structure⁷.

A central issue in the management of these impacts is the role of urban form, or the degree of centralization (or decentralization) of the urban structure, a metric for appraising the impact of development patterns on the natural landscape⁸. The optimal spatial arrangement of urban land uses along a continuum of development types (where compact development represents one endpoint and sprawl, the other) has been the subject of debate in the planning literature for decades, largely driven by an effort to mitigate or avoid the presumed, and often undesirable, impacts of urban sprawl⁹. A 1974 report prepared by the Real Estate Research Corporation was among the first to identify the need for an improved understanding of the relative effects of alternative patterns of (largely residential) development¹⁰. An early attempt to quantify the economic and environmental costs of planned, high-density development and low-density sprawl, this report proposed development decision-making guidance for planners and managers and laid the foundation for such influential works as Gordon and Richardson's "Are compact cities desirable?"¹¹ and Ewing's counterpoint "Is Los Angeles-style sprawl desirable?"¹². Now considered classics in the planning literature, the decades since their publication have seen many subsequent attempts to measure sprawl and more broadly assess the environmental impacts of urban form^{13–17}.

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The contrast between compact and sprawling urban forms is analogous to the land sparing/land sharing dichotomy. First proposed by Green et al.¹⁸, the sharing or sparing debate emerged as an agroecological framework for understanding the trade-off between two divergent approaches to farming. For a given landscape size and agricultural production, land sparing is when high yield farming occurs over a relatively small area, leaving space for the preservation of natural habitats. On the other hand, land sharing, otherwise known as wildlife-friendly farming or nature farming¹⁹, is when landscapes are dominated by a mosaic of lower intensity agricultural practices and remnants of biodiversity-supporting vegetation.

The land sparing/land sharing model has been translated from its original agroecological context to an urban one²⁰. In urban landscapes, agricultural production is replaced by total human population and agricultural yield by housing density. Land sparing scenarios are those in which high-density residential development is restricted in extent and interspersed with patches of natural or semi-natural habitat. For example, conservation subdivisions concentrate residential development in a portion of a parcel at higher density than is typical and devote the remainder of the space to recreation or low-intensity agricultural use²¹. At the other end of the spectrum, land sharing scenarios are those in which low-density housing typically dominates landscapes and greenspace is more dispersed, often occurring in backyards. Importantly, greenspace management is likely to vary significantly in urban land sharing and land sparing scenarios depending on the ownership and differing human uses of remaining natural space.

To our knowledge, only two reviews of the ecological effects of urban form have been published. The first, that of Stott et al.²², used case studies of ecosystem service provision along urbanization gradients to show that land sparing better maintains aboveground carbon storage, water infiltration, agricultural production, pollination, and summer temperature regulation, whereas land sharing supports human well-being and air purification. More recently, Youngsteadt et al.²³ reviewed 15 studies published since 2010 that compared urban developments of differing configurations with similar amounts of green space or human populations within a fixed area. Approximately half (51%) of individual species, a plurality (43%) of community metrics, and half (50%) of ecosystem services and processes measured in studies had more positive values in land sparing than land sharing scenarios.

Our objective was to synthesize the results of existing studies on the biodiversity effects of urban form to determine whether biodiversity is higher in compact or dispersed residential developments. We adopted the land sparing/land sharing approach in that we sought to compare development patterns that varied in housing density whilst keeping landscape area and human population size constant. However, we deliberately use the terms “compact development” and “dispersed development” rather than “land sparing” and “land sharing”, respectively, in recognition that (1) variation in development pattern is an element of variation in urban form and (2) the terms coincide with those used by planners and decision-makers. We acknowledge the simplicity of the dichotomous comparison inherent in our objective that does not capture the large variety of urban forms. However, many studies adopting a dichotomous perspective have now been published, necessitating its use in our synthesis.

We addressed our research objective in parts by asking (1) what are the characteristics of empirical or modeling studies that compared one or more biodiversity responses in compact and dispersed developments?, (2) What is the overall effect of compact and dispersed developments on biodiversity in empirical studies and in modeling studies?, and (3) what are the effects of moderator variables, such as urban form extent, latitude, and type of biodiversity response, on biodiversity effect sizes? Our synthesis differs from the review by Youngsteadt et al.²³ in that we performed a meta-analysis focusing on developments of similar extent with similar numbers of dwellings or people that differed in residential density. In this way, the comparisons of the spatial arrangement of development were not confounded by human population size. In contrast, the developments considered by Youngsteadt et al.²³ potentially varied in both development pattern and population size. In addition, we considered studies carried out over a broader timespan than those included in Youngsteadt et al.’s review²³. To our knowledge, ours are the first meta-analyses of the effects of urban form on biodiversity.

Results

Literature search

Our initial search of Web of Science yielded 17,210 records (Fig. 1). Of the first 100 records, we selected 55 for further consideration. Backward and forward citation searching of those studies that met our inclusion criteria

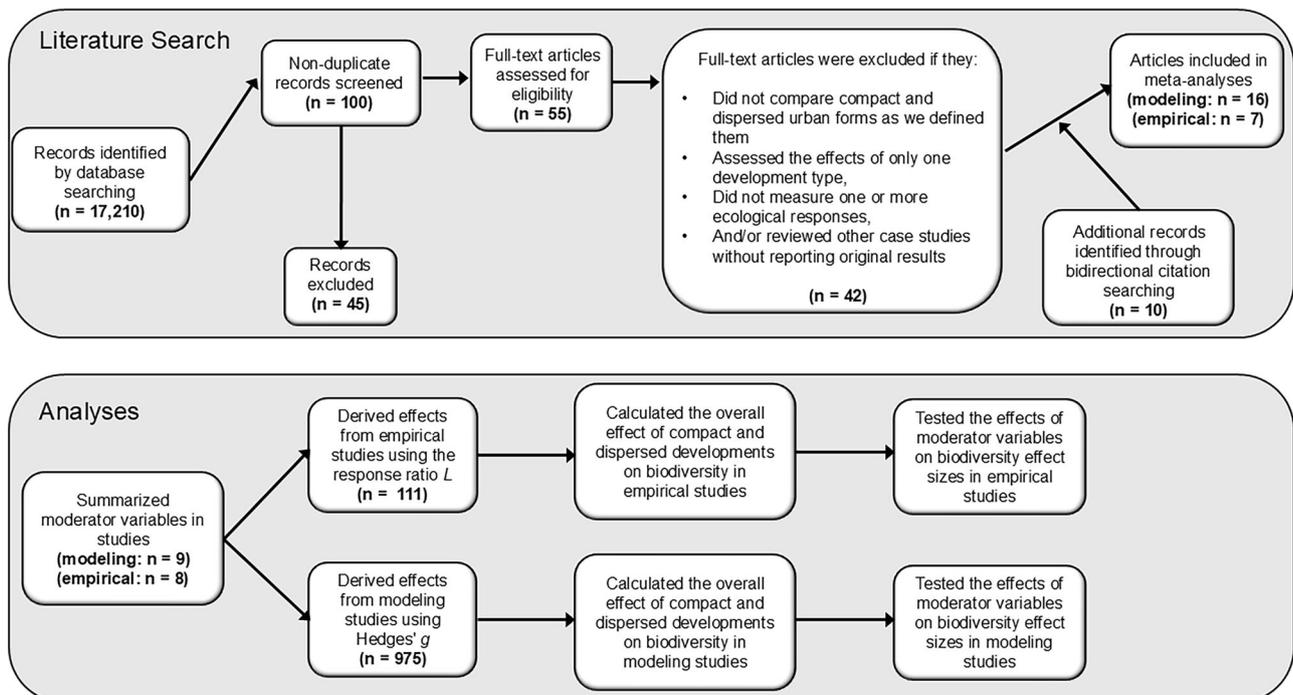


Fig. 1 | Workflow to identify studies that compared biodiversity responses between compact and dispersed developments and to analyze the overall and moderator-mediated effects of urban form on biodiversity.

resulted in 10 additional studies. Using ProQuest, we identified four dissertations that met our inclusion criteria but published articles describing them were already included in our Web of Science search results. No additional studies that had not already been detected by Web of Science or ProQuest were uncovered by our Google Scholar query.

Characteristics of selected studies

Twenty-three journal articles met our criteria for inclusion in meta-analyses. Of these, 30% (7 articles, 6 studies) compared biodiversity responses between existing dispersed and compact developments and 70% (16 articles, 14 studies) modeled the projected biodiversity impacts of urban form (Tables 1, 2; Supplementary Data). Articles were published between 1997 and 2020, with 83% being published in or since 2010. The number of authors of each empirical article ranged from 1 to 12, averaging 5.00 ± 1.70 (SE) authors. Seventy-one percent of empirical articles were authored by multidisciplinary teams. The number of authors of each modeling article varied less among articles, with a mean of 3.75 ± 0.34 (SE) authors. Modeling articles were more likely to have been authored by a multidisciplinary team (63%) than not (37%).

The majority of studies took place in eastern North America (35%) or western Europe (20%). A single study was global in extent²⁴, a single study was carried out in Japan²⁵, and four studies occurred in the Southern Hemisphere, all of which were carried out along the southeastern coast of Australia^{26–29}. As a result, only three of Earth’s fourteen biomes, Temperate Broadleaf and Mixed Forests, Temperate Coniferous Forests, and Temperate Grasslands, Savannas, and Shrublands, were represented by studies. Study locations occurred in the mid-latitudes, between 27 and 52 degrees North or South.

Urban form extent varied considerably across studies, with a mean of 0.78 ± 0.28 (SE) km² for empirical studies and 3455.31 ± 1943.89 (SE) km² for modeling studies (Tables 1, 2). Urbanization intensity, as indicated by the human population size of modeled scenarios of urban form, varied considerably as well ($386,546,766 \pm 385,650,375$ (SE) people; excluding the global study with a very large urbanization intensity: $896,517 \pm 324,300$ (SE) people).

Study responses were predominantly measures of the biodiversity of different taxonomic groups (Fig. 2). Eighty-nine percent of effects in empirical studies were calculated using measures of the diversity of different taxonomic groups, Aves and Arachnida being the most common. The remainder of effects in empirical studies were calculated using measures of habitat amount or aquatic biomass. Similarly, 85% of effects derived from modeling studies represented measures of the diversity of different taxonomic groups, Aves and Mammalia being the most common. The remainder of effects in modeling studies were measures of carbon uptake, habitat amount, habitat quality, connectivity, and fragmentation.

Empirical studies: The overall effect of compact and dispersed developments on biodiversity

Of 111 effects derived from empirical studies, 64 (58%) were positive, indicating that compact development was associated with more positive biodiversity responses than dispersed development, 45 (40%) were negative, indicating that dispersed development was associated with more positive biodiversity responses than compact development, and 2 (2%) were nil, indicating no difference in biodiversity responses between compact and dispersed development (Supplementary Data). When averaged for each study, Hedges’ *g* was significant and positive in one study, positive but not significant in three studies, and negative but not significant in the remaining two studies (Fig. 3). The overall effect of urban form on biodiversity across studies was positive but not significant (Hedges’ $g = 0.01$ (95% CI: $-0.07-0.08$)) (Fig. 3). Significant heterogeneity existed among effect sizes ($Q = 211.74, p < 0.0001$).

Empirical studies: the effects of moderator variables on biodiversity effect sizes

The model that included urban form extent and type of biodiversity response qualified as the best model of the effects of moderator variables on

Table 1 | Moderator variable values of selected empirical studies of the effects of urban form on biodiversity

Study ID	Article citation	Number of authors	Multi-disciplinary	Latitude (°N)	Biome	Urban form extent (mean ± SD km ²)	Biodiversity response group	Specific type of biodiversity response
1	Göçmen ⁴³	1	No	43	Temperate Broadleaf and Mixed Forests	0.32 ± 0.10	Landscape structure	Habitat amount
2	Ibáñez-Álamo et al. ³³	12	Yes	47	Temperate Broadleaf and Mixed Forests	0.25 ± 0.00	Ecosystem structure	Aves
2	Jokimäki et al. ³⁴	11	Yes	47	Temperate Broadleaf and Mixed Forests	0.25 ± 0.00	Ecosystem structure	Aves
3	Kleppel et al. ³²	3	Yes	42	Temperate Broadleaf and Mixed Forests	1.38 ± 0.17	Ecosystem structure	Plantae, Aquatic biomass
4	Lenth et al. ³⁶	3	No	40	Temperate Grasslands, Savannas, and Shrublands	0.79 ± 0.19	Ecosystem structure	Aves, Mammalia, Plantae
5	Suarez-Rubio & Lookingbill ³⁵	2	Yes	39	Temperate Broadleaf and Mixed Forests	1.82 ± 1.35	Ecosystem structure	Aves
6	Varet et al. ³¹	3	Yes	48	Temperate Broadleaf and Mixed Forests	0.12 ± 0.00	Ecosystem structure	Insecta, Arachnida

Urban form extent is the average areal extent of compact and dispersed developments in studies.

Table 2 | Moderator variable values of selected modeling studies of the effects of urban form on biodiversity

Study ID	Article citation	Number of authors	Multi-disciplinary	Latitude	Biome	Urban form extent (mean ± SD km ²)	Urbanization intensity (mean ± SD number of residents)	Biodiversity response group	Specific type of biodiversity response
1	Collas et al. ⁶⁰	5	No	52°N	Temperate Broadleaf and Mixed Forests	41 ± 0	150,900 ± 0	Ecosystem structure, Ecosystem function	Plantae, Carbon uptake
2	Dorning et al. ⁶¹	4	Yes	36°N	Temperate Broadleaf and Mixed Forests	11,484 ± 0	969,127 ± 0	Landscape structure	Habitat amount, Fragmentation
3	Gagné & Fahrig ⁶²	2	No	45°N	Temperate Broadleaf and Mixed Forests	23 ± 0	1780 ± 0	Ecosystem structure	Aves
3	Gagné & Fahrig ⁶³	2	No	45°N	Temperate Broadleaf and Mixed Forests	23 ± 0	1780 ± 0	Ecosystem structure	Insecta
4	Geschke et al. ²⁷	4	Yes	38°S	Temperate Broadleaf and Mixed Forests	964 ± 0	3,567,100 ± 823,150	Ecosystem structure	Aves
5	McDonald et al. ²⁴	3	Yes	N/A	N/A	N/A	5,400,000,000 ± 0	Ecosystem structure	N/A
6	Penteado ⁶⁴	1	No	45°N	Temperate Broadleaf and Mixed Forests	19 ± 0	51,000 ± 0	Landscape structure	Habitat amount
7	Shoemaker et al. ⁵²	3	Yes	35°N	Temperate Broadleaf and Mixed Forests	3460 ± 0	1,480,000 ± 0	Landscape structure	Habitat amount
8	Soga et al. ²⁵	4	Yes	35°N	Temperate Broadleaf and Mixed Forests	1 ± 0	5940 ± 3270	Ecosystem structure	Insecta
9	Sushinsky et al. ²⁸	5	Yes	27°S	Temperate Broadleaf and Mixed Forests	636 ± 0	2,040,069 ± 0	Ecosystem structure	Aves
9	Sushinsky et al. ²⁹	5	Yes	27°S	Temperate Broadleaf and Mixed Forests	636 ± 0	2,040,069 ± 0	Ecosystem structure, Landscape structure	Aves, Habitat amount
10	Tannier et al. ⁶⁵	4	No	47°N	Temperate Broadleaf and Mixed Forests	3600 ± 0	473,200 ± 0	Ecosystem function	Connectivity
11	Theobald et al. ⁶⁶	3	No	40°N	Temperate Coniferous Forests	3 ± 0	40 ± 0	Landscape structure	Habitat quality
12	Thorn et al. ⁶⁷	6	Yes	44°N	Temperate Broadleaf and Mixed Forests	24,214 ± 0	2,800,000 ± 0	Landscape structure	Habitat quality
13	Vaughn et al. ⁴⁴	4	Yes	30°N	Temperate Coniferous Forests	7 ± 0	4367 ± 0	Ecosystem function	Carbon uptake
14	Villaseñor et al. ²⁶	5	Yes	33°S	Temperate Broadleaf and Mixed Forests	467 ± 0	111,200 ± 5964	Ecosystem structure	Mammalia

Urban form extent is the areal extent of development scenarios in studies. Urbanization intensity is the average number of residents in modeled scenarios.

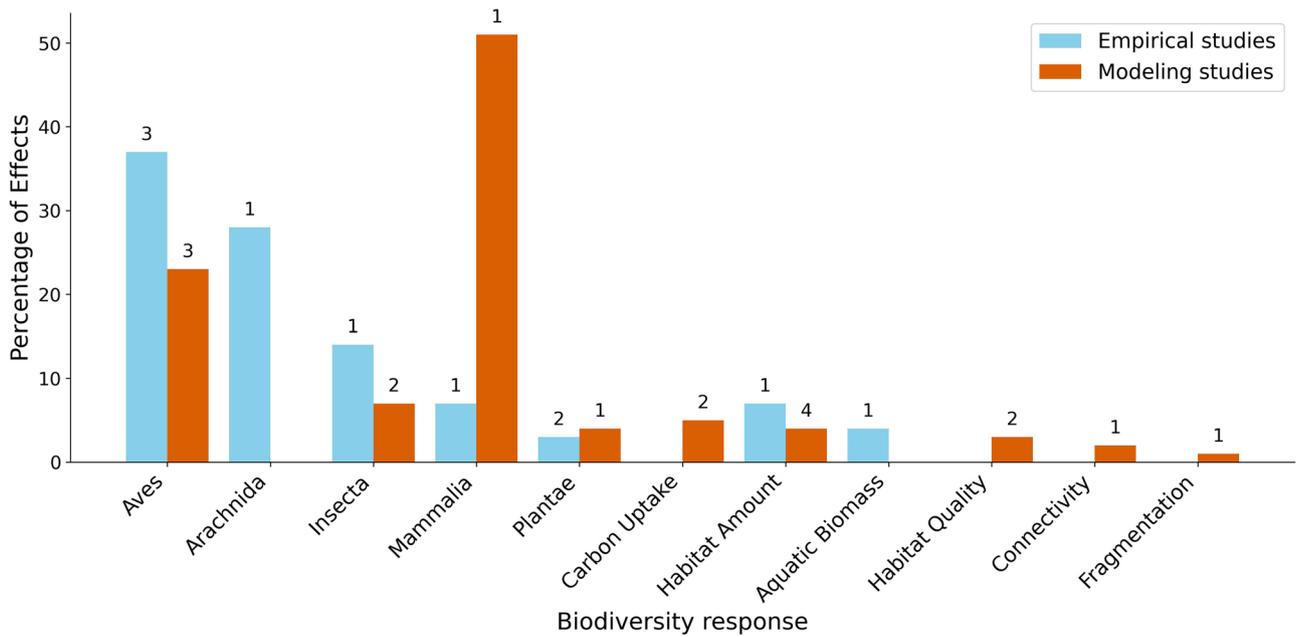


Fig. 2 | The percentage of effects in empirical and modeling studies of compact and dispersed residential developments representing different types of biodiversity response, including the diversity of taxonomic groups.

Fig. 3 | The mean (95% CI) effects of urban form on biodiversity across selected empirical studies.

Positive effect sizes indicate that biodiversity responses were more positive in compact developments than dispersed developments. Negative effect sizes indicate that biodiversity responses were more positive in dispersed developments.

Göçmen²⁶

Ibáñez-Álamo et al.⁵⁰
& Jokimäki et al.⁵¹

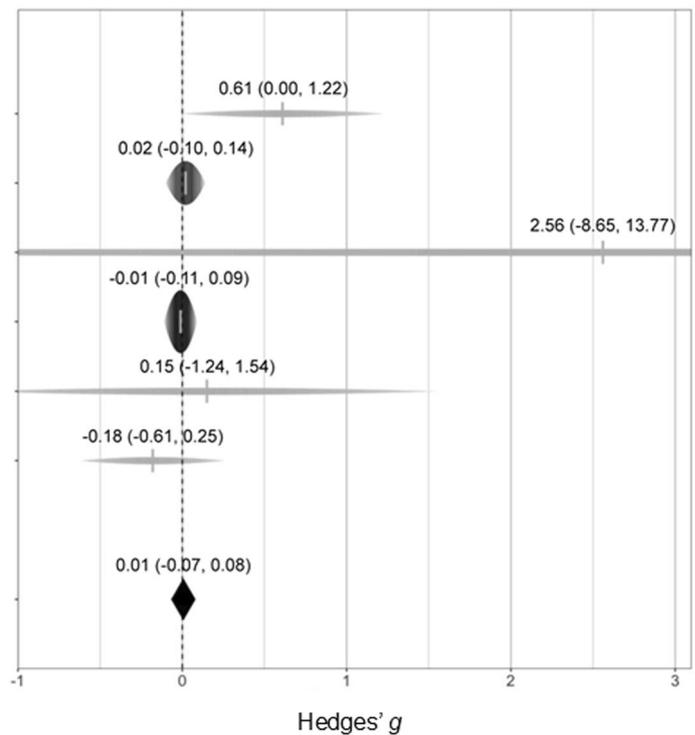
Kleppel et al.⁴⁹

Lenth et al.⁵⁸

Suarez-Rubio
& Lookingbill⁵⁹

Varet et al.⁴⁸

Overall Effect



empirical study effect sizes (Table 3, Supplementary Table 1). The model intercept was significant and negative, suggesting that, all else being equal, biodiversity responses were more positive in dispersed developments than compact developments. However, significant and positive coefficients for urban form extent, aquatic biomass, and habitat amount show that this overall pattern is reversed for developments of large spatial extent or when measures of aquatic biomass or habitat amount are used as responses. In these cases, biodiversity responses are more positive in compact developments (Fig. 4). All other moderator variable coefficients were non-significant.

Modeling studies: the overall effect of compact and dispersed developments on biodiversity

Of 975 effects derived from modeling studies, 488 (50%) were positive, indicating that compact development was associated with more positive biodiversity responses than dispersed development, 480 (49%) were negative, indicating that dispersed development was associated with more positive biodiversity responses than compact development, and 7 (1%) were nil, indicating no difference in biodiversity responses between compact and dispersed development (Supplementary Data). When averaged for each study, the response ratio, *L*, was significant and positive in nine studies,

Table 3 | The best model of the effects of moderator variables on empirical study effect sizes that estimated the effects of urban form on biodiversity

Intercept	Urban form extent	Aves	Insecta	Plantae	Mammalia	Aquatic biomass	Habitat amount	AIC
-0.29* (0.13)	0.10* (0.03)	0.25 (0.14)	0.39 (0.22)	-0.08 (0.40)	0.43 (0.23)	1.01* (0.44)	0.79* (0.17)	224.90

Urban form extent is the average areal extent of compact and dispersed developments in studies and Aves, Insecta, Plantae, Mammalia, aquatic biomass, and habitat amount are specific types of biodiversity responses measured in studies. Coefficients and their standard errors in parentheses are shown. Significant ($p < 0.05$) moderator variable effects are indicated by an asterisk.

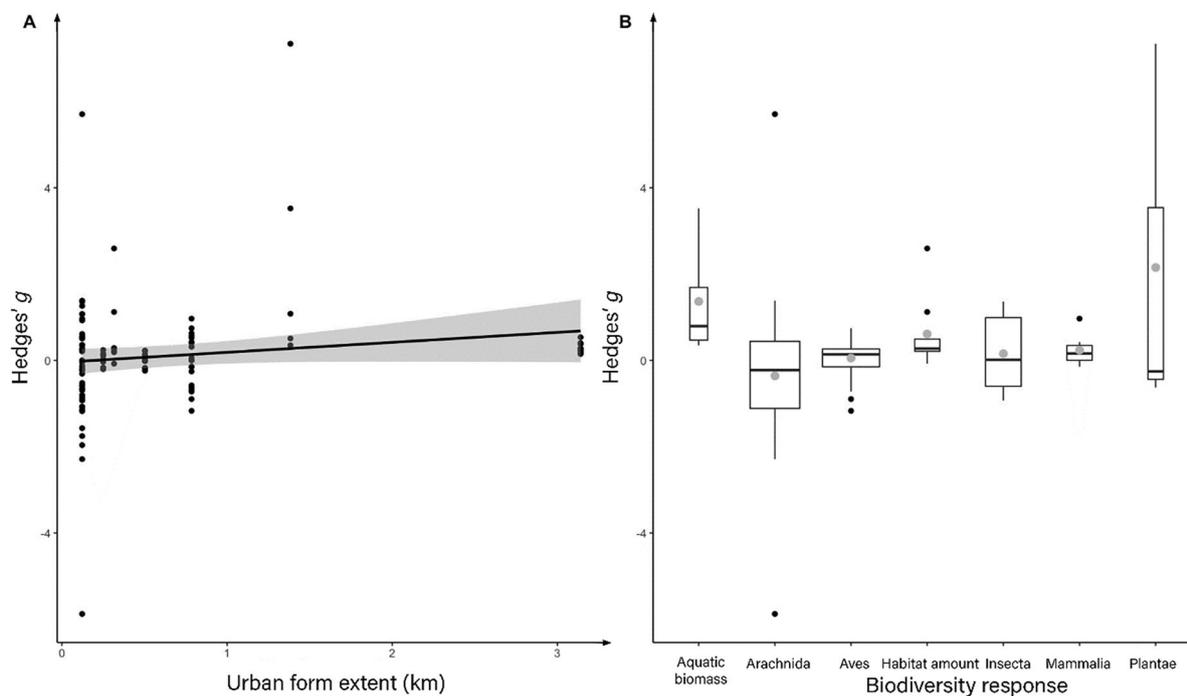


Fig. 4 | Empirical study effect sizes with respect to the spatial extent of compact and dispersed developments. A and the type of biodiversity response measured in studies (**B**). Positive effect sizes indicate that biodiversity responses were more

positive in compact developments than dispersed developments. Negative effect sizes indicate that biodiversity responses were more positive in dispersed developments.

positive but not significant in one study, significant and negative in two studies, and negative but not significant in two studies (Fig. 5). The overall effect of urban form on biodiversity across studies was significant and positive ($L = 0.08$ (95% CI: 0.07–0.08)) (Fig. 5).

Modeling studies: the effects of moderator variables on biodiversity effect sizes

Four models qualified as the best models of the effects of moderator variables on modeling study effect sizes (Table 4, Supplementary Table 2). One model contained latitude, one model contained urban form extent, one model contained the biome Temperate Coniferous Forests, and the final model contained latitude and Temperate Coniferous Forests. The intercept coefficient in each model was positive, as were all moderator variable coefficients except for urban form extent, which was negative. The only significant coefficient was that of latitude in the top-ranked model (Fig. 6), indicating that studies conducted in the northern hemisphere were more likely to find more positive biodiversity responses in compact compared to dispersed developments.

Discussion

In this paper, we sought to determine whether biodiversity is higher in compact or dispersed residential developments. To do so, we asked (1) what is the overall effect of compact and dispersed developments on biodiversity in empirical studies and in modeling studies?, and (2) what are the effects of moderator variables, such as urban form extent, latitude, and type of biodiversity response, on biodiversity effect sizes? In empirical studies,

biodiversity responses were generally higher in dispersed developments compared to compact ones, although considerable variability in effect magnitude and direction occurred within and among studies. The overall effect of urban form on biodiversity in empirical studies was influenced by urban form extent and the type of response. Specifically, biodiversity responses were higher in compact developments when the spatial extent of studied areas was larger and when habitat amount and aquatic biomass were measured. In modeling studies, biodiversity responses were generally higher in compact than dispersed developments. This result was likely driven by studies carried out in the northern hemisphere. In the following, we first compare our results to those of Youngsteadt et al.²³, who synthesized biodiversity responses to urban land sparing and land sharing scenarios. We then discuss each of the moderator variable effects in our analyses in turn and the broader influence of context in determining the magnitude and direction of biodiversity differences between compact and dispersed developments. Next, we address the limitations of our approach and suggest avenues of future research based on our results. We conclude that the answer to our overarching research question—is biodiversity higher in compact or dispersed residential developments?—is: it depends. Variability among types of biodiversity response and the influence of context preclude any general statement about the benefits of one urban form over another.

Our findings are similar to those of the only other synthesis of the effects of urban form on biodiversity in that they do not provide a clear answer to the question of whether compact or dispersed development is better. Youngsteadt et al.²³ reviewed studies published since 2010 that compared urban developments of differing configurations with similar

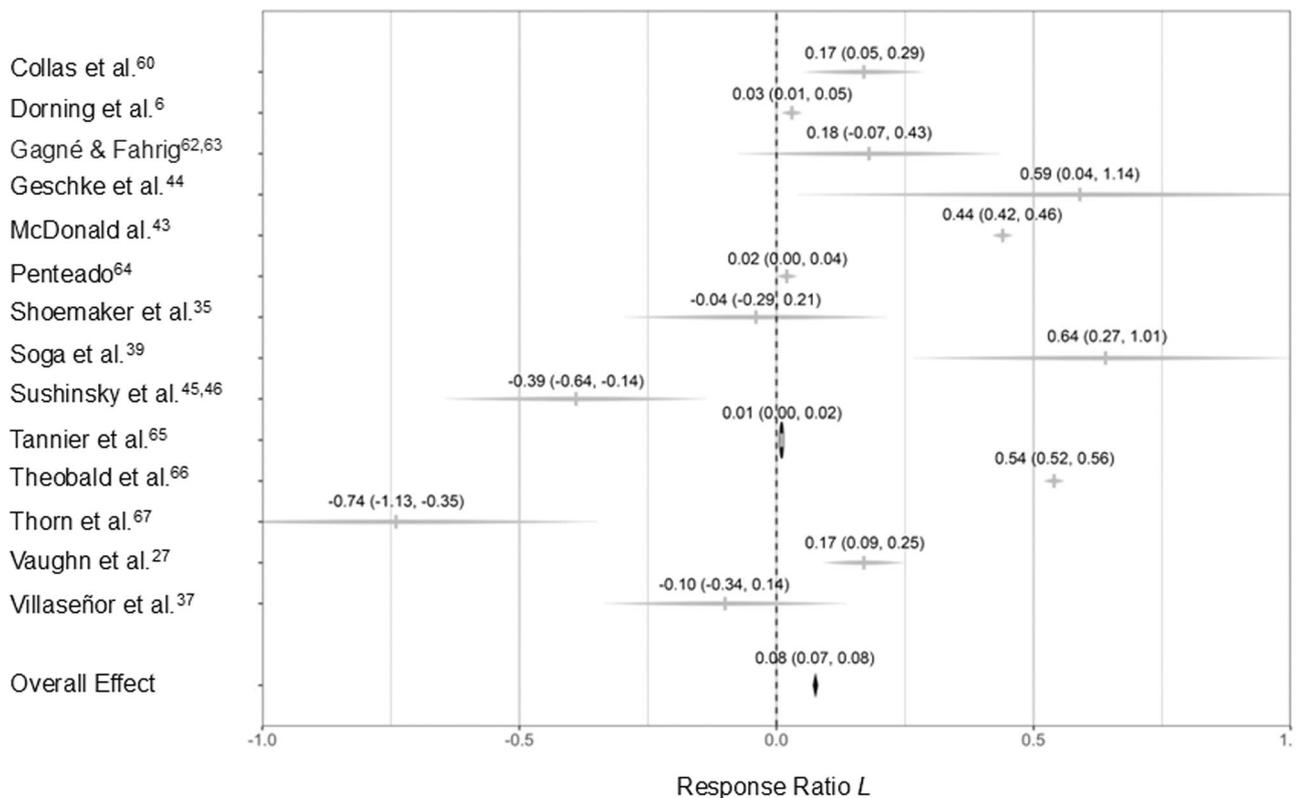


Fig. 5 | The mean (95% CI) effects of urban form on biodiversity across selected modeling studies. Positive effect sizes indicate that biodiversity responses were more positive in compact developments than dispersed developments. Negative effect sizes indicate that biodiversity responses were more positive in dispersed developments.

Table 4 | The best models of the effects of moderator variables on modeling study effect sizes that estimated the effects of urban form on biodiversity

Intercept	Latitude	Urban form extent	Temperate Coniferous Forests	AIC
0.02 (0.07)	0.004* (0.002)			4265.53
0.11 (0.12)		-2.54×10^{-5} (3.12×10^{-5})		4267.17
0.04 (0.11)			0.28 (0.35)	4267.22
0.01 (0.08)	0.004 (0.002)		0.17 (0.32)	4267.24

Urban form extent is the areal extent of development scenarios in studies and urbanization intensity is the average number of residents in modeled scenarios. Coefficients and their standard errors in parentheses are shown. Significant ($p < 0.05$) moderator variable effects are indicated by an asterisk.

amounts of green space or human populations within a fixed area and concluded that “existing ecological research does not favor one pattern or the other”. The outcomes of our and of Youngsteadt et al.’s review²³ are not unexpected. Species are hypothesized to vary in their responses to urban form based on their functional responses to urbanization intensity, or density-yield curves sensu the agricultural land sparing/sharing framework¹⁸. Some species may benefit from compact development and some from dispersed development, whereas others may show no difference between development types²³. This response variety among species is likely to translate into the variability in the magnitude and direction of effect sizes we observed within and among studies, and ultimately into an ambiguous overall response of biodiversity to differing urban forms. In addition, neither Youngsteadt et al.²³ nor this review considered possible variation in the quality, amount, and connectivity of habitat between development types. Such variation is likely given the occurrence of land use types other than residential in some of the developments reviewed here and by Youngsteadt et al.²³ and the variability in land management between public and private lands and among land uses in urban landscapes³⁰. Species respond differently to such factors. As such, comparisons between development types that do not explicitly consider variation in the quality, amount, and connectivity of habitat may not yield a definitive answer.

Urban form extent, or the average spatial extent of the areas in which urban form and biodiversity responses were measured, had a significant positive influence on effect sizes in empirical studies. In other words, biodiversity responses, i.e., species diversity, abundance, and occurrence, and habitat amount, were more positive in compact developments than dispersed developments when study sites were larger. This effect may be explained by the fact that larger compact development sites include larger areas of non-urban land that host more species and individuals and more habitat. The urban form extent effect may also be explained by an increase in the difference in the relative proportion of non-urban land between compact and dispersed developments as study site size increases. For example, in Varet et al.³¹, the study with the smallest sites, the proportion of compact sites in non-urban land was 1.76 times that in dispersed sites, whereas the proportion of compact sites in non-urban land used by Kleppel et al.³², the study with the second largest sites, was 2.25 times that in dispersed sites. However, the compact and dispersed sites in at least two empirical studies were distinguished not by the difference in amount of non-urban land, but by its configuration. For example, the sites studied by Ibáñez-Álamo et al.³³ and Jokimäki et al.³⁴ contained the same proportion of green space, but the green space in compact sites was more contiguous than that in dispersed sites. Thus, the positive effect of urban form extent may also be due to the

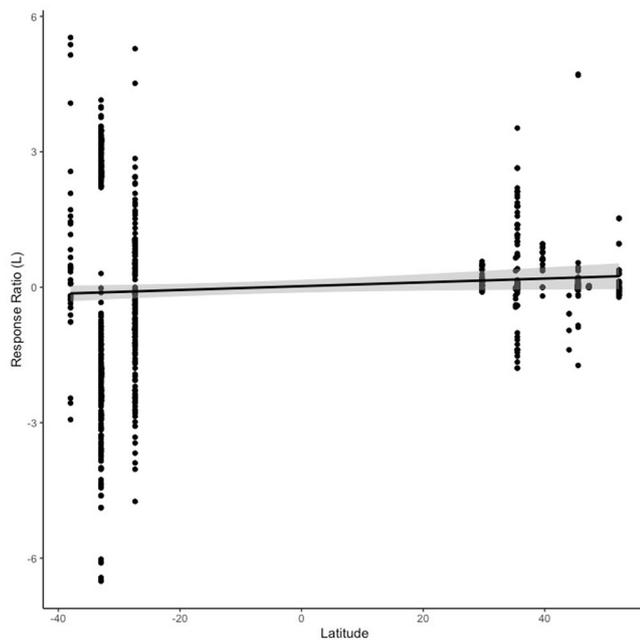


Fig. 6 | Modeling study effect sizes with respect to the latitude of study areas. Positive effect sizes indicate that biodiversity responses were more positive in compact developments than dispersed developments. Negative effect sizes indicate that biodiversity responses were more positive in dispersed developments.

impact of spatial scale interacting in complex ways with the species studied and site characteristics³⁵. We note that the number of empirical studies examined in our meta-analysis was small, thus necessitating additional investigations of the impact of spatial scale on the effect of urban form in general and on site characteristics such as the proportion of sites that are non-urban land in particular.

The responses of habitat amount and aquatic biomass also had significant positive influences on effect sizes in empirical studies. Values of habitat amount and aquatic biomass were significantly higher in compact developments than dispersed developments. Habitat amount and aquatic biomass were each measured in a single study. Thus, these significant effects may represent unmeasured aspects of study design or site characteristics rather than indications that these specific biodiversity responses are particularly influenced by urban form.

The only moderator variable to influence effect sizes in modeling studies was study latitude. Studies conducted in the northern hemisphere were more likely to report more positive biodiversity responses in compact compared to dispersed developments. The only studies conducted in the southern hemisphere were carried out along the southeastern coast of Australia, whereas those carried out in the northern hemisphere occurred primarily in western Europe and eastern North America. The significant effect of latitude may thus represent differences between these locations of the world in site characteristics, e.g., construction design, landscaping styles, the type and diversity of non-urban land uses, and in species' evolutionary histories, habitats, and behaviors, not to mention differences in topography, insolation, and rainfall, among other factors.

A major take-away from our results, given the influence of urban form extent, type of biodiversity response, and latitude, is the strong dependence of effect sizes on local context. The importance of context means that the answer to the question of whether compact or dispersed development is better for biodiversity will vary depending on local conditions. Local conditions may include the absolute values and range of development densities in study sites; construction type, e.g., single- or multi-family, and design, e.g., bird-friendly, green building; the occurrence, size, and spatial arrangement of green spaces within developed areas; private and public landscape management practices in developed areas; the areal extent (both in absolute

terms and in relation to the size and density of the human population accommodated in developed areas) and uses of non-urban land; and the many environmental factors that drive ecological systems, such as temperature, moisture, soil type, and topography.

Our synthesis of the effects of urban form on biodiversity is not without its limitations. First, we set out to compare what we assumed were two distinct urban forms that primarily varied in residential development density. However, given the effect of context on our results, it is highly likely that urban forms compared in studies varied in many other ways that may have impacted biodiversity, e.g., the amount, quality, and connectivity of habitat. As it stands, it is unclear exactly how dispersed and compact developments varied in structure in the studies we reviewed and relatedly, how distinct compact and dispersed developments within and among studies really were. In an agricultural context, a recent review noted the fuzzy conceptualization of land sparing and land sharing scenarios, in some cases resulting in scenarios assumed to represent distinct forms having very similar structure³⁶. This possibility may significantly impede or bias the identification of the relative effects of land sparing and land sharing scenarios or compact and dispersed urban forms.

Second, we performed our literature review in 2019 and 2020, seeking to identify all existing studies that compared biodiversity in compact and dispersed developments. However, studies that may have qualified for our review have been published since 2020. For example, Penteado³⁷ investigated the impacts of varying the amount and configuration of open space in compact and dispersed development scenarios on the population sizes of three species in Portland, Oregon, USA. In addition, Suhonen et al.³⁸ estimated bird occupancy-frequency distributions in paired land sparing and land sharing landscapes in European cities. Thus, our review should not be considered exhaustive. Rather, the effect sizes we collated (Supplementary Data) should be used to reexamine our research objective in the future using new data.

The question of whether compact or dispersed development is better for biodiversity is inherently a practical one. In other words, the purpose of answering the question is to provide guidance to municipal planners and others charged with planning and developing residential areas. Based on this fact, the expected variability in effects sizes across biodiversity response measures, and our findings of the importance of context, we recommend that future research on the effects of urban form be localized – designed with local planning and other conditions in mind and in collaboration with planning practitioners and local decision-makers and community members. Future urban form study sites should ideally conform to real or expected development densities, sites of future development, and construction types and designs based on local population projections, zoning and other regulations, and comprehensive plans. As such, study sites may encompass a continuum or variety of urban forms between the end points of maximally compact or maximally dispersed. In addition, study sites should be thoroughly characterized, not only in terms of differing residential development density, but in the amounts and configurations of land covers and land uses, and to the extent it is feasible, in the many factors that may influence the biodiversity response of interest³⁶. In this way, planners and researchers will have a better understanding of exactly what is being compared. It has been suggested that regional or whole-city spatial scales are most appropriate for determining the impacts of compact and dispersed urban forms because they are generally broad enough to encompass the scales at which biodiversity responds to variation in land use²⁰. Thus, these study design issues are best addressed using a modeling approach. We also recommend that community members and other stakeholders participate in the selection of biodiversity outcomes in future urban form research. Community support is a major determinant of local conservation outcomes³⁹. Research that shows a difference between compact and dispersed development in one or more measures of importance to local communities will have a greater likelihood of convincing decision-makers to change regulations, policies, and practice. Finally, the impact of place on the likelihood of implementation should not be ignored⁴⁰. Practitioners

and decision-makers are more likely to take action when local neighborhoods, green spaces, and species are concerned.

In conclusion, we show that the effects of compact and dispersed residential developments on biodiversity are varied within and across existing studies, precluding any general statement about the benefits of one urban form over another. The variability in effect sizes we observed was a result of expected variability among biodiversity responses and the influence of context. We suggest that future research on the effects of compact and dispersed development on biodiversity should be localized in order to increase the likelihood of implementation, i.e., designed with local planning and other conditions in mind and in collaboration with planning practitioners and local decision-makers and community members. Such localized research should ideally thoroughly characterize the urban forms being compared in terms of their variation in landscape structure and socio-ecological context that is likely to impact the biodiversity responses of interest. If this occurs, future syntheses could investigate the specific aspects of urban form, along a continuum between dispersed and compact, that most strongly affect biodiversity.

Methods

Literature search and selection of studies

In 2019–2020, we conducted a comprehensive search of the literature using standard methods (Fig. 1)⁴¹. We began with a review of extant literature known to the authors, using key publications to establish baseline qualifications for all studies included in our analyses. We then searched for additional studies using Web of Science and combinations of keywords describing urban form (compact development, dispersed development, land-sharing, land-sparing, urban sprawl, housing density-sprawl area tradeoff, development pattern, and urban form) and biodiversity responses (species, ecosystem, species richness, abundance, animal, plant, flora, fauna, lichen, bird, mammal, tree, frog, toad, amphibian, salamander, reptile, snake, turtle, lizard, invertebrate, insect, fish, and habitat) (Supplementary Note 1). We applied the asterisk wildcard feature to all keywords to include all possible derivatives. We included keywords from publications we were already familiar with to ensure that these publications, as well as any additional publications using similar terms that we were unaware of, were captured in our review. Our search encompassed book chapters, conference proceedings, reviews, editorials, letters, notes, corrections, and early access articles written in English since 1900 (the earliest year available in Web of Science) and originating from any geographic area. We refined our search by excluding irrelevant categories, e.g., oceanography, virology. The resulting studies were sorted by relevance and the titles and abstracts of the first 100 studies were read. We chose to rank studies by relevance because of the very large number of results from our initial search (Fig. 1). However, we recognize that this choice may have led to potentially important studies being omitted from our review. We carried out identical searches of Google Scholar and the ProQuest database to potentially find additional studies relevant to our objective, including unpublished dissertations and theses. Once a study met the criteria to be included in our review (see below), we performed a bidirectional citation search of its cited and citing articles. Concurrent to keyword searching, these processes, known as forward and backward citation searching, respectively, were employed in an effort to carry out a truly exhaustive query that returned as many relevant studies as possible⁴².

Studies needed to meet three key criteria to be eligible for inclusion in our review. First, they needed to explicitly compare actual or modeled instances of compact and dispersed patterns of residential development. To do so, studies needed to compare sites or scenarios of similar extent that contained a similar number of dwellings or people, but that differed in residential density. For example, Göçmen⁴³ compared 26 existing conservation or traditional subdivisions with a roughly equal number of dwellings (51.31 ± 44.67 lots) and a roughly equal areal extent (95.96 ± 84.94 acres) in Waukesha County, Wisconsin, USA. Other studies inferred the effects of urban form using scenario modeling. For example, Vaughn et al.⁴⁴ compared eight development scenarios that each

accommodated 1835 dwellings within the proposed area for a subdivision in Gainesville, Florida, USA. Compact patterns were created by planning for higher density in key areas with the remainder of the subdivision area undeveloped. Some studies were repeatedly detected via database and citation searching but were ultimately excluded from our review because they reported the biodiversity effects of either compact or dispersed development, but not both⁴⁵.

Second, for inclusion in our review, studies needed to assess the effects of compact and dispersed urban form on one or more biodiversity responses. Responses could include strict measures of biodiversity (the variety of organisms at all levels, from genetic variants of a single species to genera, families, and higher levels of taxonomic organization), habitat composition and configuration, or ecosystem structure and function. We excluded studies from our review that focused on environmental but non-ecological responses, e.g., air quality⁴⁶. Third, studies needed to report original results. Thus, related review articles were excluded from meta-analyses.

Effect sizes

We calculated the standardized difference in biodiversity response between compact and dispersed urban forms in each study using Hedges' g ⁴⁷ for empirical studies that estimated the effects of urban form in actual developments or the response ratio (L)⁴⁸ for modeling studies that projected the effects of urban form using hypothetical scenarios (Fig. 1).

Hedges' g is given by:

$$g = J(df)d \quad (1)$$

where J is a correction factor for small samples given by:

$$J(df) = 1 - (3/(4df - 1)) \quad (2)$$

and Cohen's d , the standardized mean difference, is given by:

$$d = (Y_1 - Y_2)/S_{pooled} \quad (3)$$

and df is the degrees of freedom used in computing the pooled sample standard deviation, S_{pooled} , across two independent groups with means Y_1 (experimental group) and Y_2 (control group) which is given by:

$$S_{pooled} = \sqrt{(n_1 - 1)S_1^2 + (n_2 - 1)S_2^2} \quad (4)$$

where n_1 and n_2 represent group sample sizes and S_1 and S_2 represent group standard deviations.

Our use of Hedges' g minimized bias due to small sample size (number of empirical studies) and controlled for variation in group size among studies ($2 \leq n \leq 45$)⁴⁹.

We chose to use an alternate measure of standardized effect size for modeling studies because these studies either did not replicate compact and dispersed scenarios ($n = 1$) and thus we could not calculate S_{pooled} or because studies created an arbitrary and large number of scenario replicates using randomization algorithms, thus artificially reducing S_{pooled} and increasing Hedges' g . Instead, we employed the unitless response ratio, L , as the measure of effect size for modeling studies⁴⁸. L , or the ratio of the outcome in the experimental group to that of the control group, is often used as a measure of effect magnitude in ecology⁴⁸, particularly in cases where experiments or interventions are costly and replication is rare, such as stream restoration⁵⁰.

L is given by:

$$L = \ln(X_e/X_c) \quad (5)$$

where X_e is the outcome in the experimental group and X_c is the outcome in the control group. We used the mean of outcomes for modeling studies that created an arbitrary number of replicates in each group.

Table 5 | Moderator variables used in meta-analyses

Category	Variable name	Variable description
Publication characteristics	study	Unique number assigned to each study
	multidisciplinary	0 if all authors are of the same disciplinary affiliation; 1 if more than one disciplinary affiliation is represented
	totalauthors	Number of authors
Geographic context	latitude	Latitude of study as indicated by the authors or approximate latitudinal midpoint if not described in the paper and/or for large study areas
	biome	1 of 14 terrestrial biomes characterized by distinct and naturally occurring communities of flora and fauna (Olson 2001)
Extent and intensity	ufextent	<i>Urban form extent</i> . Average spatial extent (km) of the areas in which urban form and biodiversity responses were empirically measured or modeled.
	humanpoptotal	<i>Human population</i> . Average number of people residing in areas in which urban form and biodiversity responses were modeled.
Biodiversity response	bioendpointgroup	<i>Biodiversity endpoint group</i> . One of the following three categories: ecosystem structure, ecosystem function, landscape structure
	bioendpoint	<i>Biodiversity endpoint</i> . Type of biodiversity response: Aves = Members of the class Aves Insecta = Members of the class Insecta Arachnida = Members of the class Arachnida Plantae = Terrestrial members of the class Plantae Mammalia = Members of the class Mammalia Aquatic biomass = biomass of aquatic plants, phytoplankton, and zooplankton Carbon uptake = Carbon storage and sequestration Habitat quality Habitat amount Fragmentation Connectivity

The variable humanpoptotal was measured for modeling studies only.

In our calculations of effect size, we considered compact urban form as the experiment and dispersed urban form as the control. As a result, positive Hedges' g or L values indicated that a given biodiversity response was greater in magnitude in compact compared to dispersed development and negative values indicated that dispersed rather than compact development elicited a larger response.

We calculated effects in each study using data in tables, in the main text, in supplementary material and appendices, and, most frequently, in figures using the WebPlotDigitizer tool⁵¹. In one instance, we requested raw data from the authors⁵² because figure values could not be accurately digitized. In the event that an empirical study's results were reported in units that could not be directly used to calculate Cohen's d , we first used mean values and summary statistics to calculate the correlation coefficient (r) and converted r to Cohen's d and Hedges' g using formulas in Cooper et al.⁵³.

Effects were calculated for each biodiversity response in each study and for all possible comparisons of dispersed and compact modeling scenarios at each projected time period. For modeling studies, we did not calculate effects using dispersed scenarios having a biodiversity response value of 0 because division by 0 in the L formula is not possible. In a few modeling studies, biodiversity response values were reported as a negative number. For instance, Villaseñor et al.²⁶ measured the percent change in abundance of three species of ground-dwelling mammals and four arboreal marsupials under contrasting development scenarios, and it was not uncommon for abundance to decrease under one instance of urban form (eliciting means expressed as a negative value) and for abundance to increase (positive value) under the contrasting scenario. To calculate effects where one of the paired biodiversity response values was negative, we divided the absolute value of each group mean by the sum of absolute mean values, then used these new values in the L formula. Finally, we reversed the direction of L if a smaller value of the biodiversity response, e.g., number of local extinctions, indicated a more positive outcome.

Moderator variables

We recorded several moderator variables of potential importance in predicting the effects of urban form on biodiversity responses (Table 5). For each article, we recorded the number of authors and denoted whether authorship was multidisciplinary or not based on authors' affiliations. We assigned each study a unique identifier. Studies were instances of research using the same study sites or scenarios and could be described in multiple articles. For each study, we recorded latitude as stated by the authors or as the latitudinal midpoint of the study area measured using Google Earth. We also assigned each study to one of 14 biomes defined by Olson et al.⁵⁴.

We hypothesized that urban form extent and urbanization intensity might influence the difference between compact and dispersed

development patterns. We defined urban form extent as the average spatial extent of the areas in which urban form and biodiversity responses were empirically measured or modeled. For example, Soga et al.²⁵ calculated the responses of ground beetle and butterfly species to land sharing and land sparing scenarios in 1 km² grid cells in Tokyo, Japan, for an urban form extent of 1 km². We approximated urbanization intensity for each modeling study using the average number of people residing in areas in which urban form and biodiversity responses were modeled. We recorded human population sizes using data described by authors. In studies where only the number of dwellings was given, we multiplied the number of dwellings by the average household size for the study area. We did not record urbanization intensity for empirical studies due to a lack of information provided by authors.

We classified the types of biodiversity responses in studies as measures of the diversity of one of seven taxonomic groups (Aves, Insecta, Arachnida, Plantae, and Mammalia), or measures of aquatic biomass, carbon uptake, habitat quality, habitat amount, fragmentation, or connectivity. We further grouped biodiversity response types into three broad categories, namely ecosystem structure, ecosystem function, and landscape structure, using the criteria of Smucker and Detenbeck⁵⁰.

Meta-analyses

We calculated the overall effect of urban form on biodiversity responses as the mean effect size across studies and used the Q statistic to measure heterogeneity among effect sizes for empirical studies. Q could not be used to measure heterogeneity for modeling studies because effect size variance (required for its calculation) could not be estimated given the nature of our data, where n was either arbitrarily inflated or undefined, thus warranting the use of the response ratio L rather than Hedges' g . We then used mixed effects, multi-level models to assess the influence of moderator variables on effect sizes. We analyzed empirical and modeling studies separately due to their different methodological approaches and our use of different measures of standardized effect size for these two groups (Fig. 1). For each set of analyses, we evaluated multiple models that contained different combinations of moderator variables and used AIC to choose the best models ($\Delta AIC < 2$) (Table 6). In each model, we accounted for the interdependence of effect sizes within studies using a random study variable, whereby intercepts were allowed to vary among studies. All moderator variables were considered to have fixed effects.

All model residuals conformed to the assumptions of normality and equality of variance. All analyses were carried out using R Statistical Software, version 4.0.3⁵⁵ and the lme4 and metafor packages for modeling and empirical studies, respectively^{56,57}.

Table 6 | Mixed-effects, multi-level models of the effects of urban form on biodiversity

Model	Moderator variables	Description
0	None	Intercept-only model
1	multidisciplinary	Models 1–8 each contain one of the eight moderator variables extracted from studies
2	totalauthors	
3	latitude	
4	biome	
5	bioendpointgroup	
6	bioendpoint	
7	ufextent	
8 ^a	humanpoptotal	
9 ^a	ufextent, humanpoptotal	Urban form extent + urbanization intensity
10	latitude, biome	Geographic context
11	totalauthors, multidisciplinary	Author characteristics
12	ufextent, bioendpointgroup	Urban form extent + biodiversity response group
13 ^a	ufextent, humanpoptotal, bioendpointgroup	Urban form extent + urbanization intensity + biodiversity response group
14	latitude, biome, bioendpointgroup	Geographic context + biodiversity response group
15	totalauthors, multidisciplinary, bioendpointgroup	Author characteristics + biodiversity response group
16	ufextent, bioendpoint	Urban form extent + specific type of biodiversity response
17 ^a	ufextent, humanpoptotal, bioendpoint	Urban form extent + urbanization intensity + specific type of biodiversity response
18	latitude, biome, bioendpoint	Geographic context + specific type of biodiversity response
19	totalauthors, multidisciplinary, bioendpoint	Author characteristics + specific type of biodiversity response

^aThat were used for modeling studies only. See Table 1 for moderator variable descriptions. Empirical and modeling studies were analyzed separately using the same models, with the exception of models marked with an.

Data availability

The data necessary to interpret, replicate and build upon the methods or findings reported in this article are provided within the Supplementary Data file.

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Author contributions

C.A.B. and S.A.G. contributed extensively to the work presented in this paper. All authors have read and approved the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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