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Urban socioeconomic inequality and biodiversity often converge, but not always: A global meta-analysis

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A B S T R A C T

It is through urban biodiversity that the majority of humans experience nature on a daily basis. As cities expand globally, it is increasingly important to understand how biodiversity is shaped by human decisions, institutions, and environments. In some cities, research has documented convergence between high socioeconomic status (SES) and high species diversity. Yet, other studies show that residents with low SES live amid high biodiversity or that SES and biodiversity appear unrelated. This study examines the conditions linked to varying types of relationships between SES and biodiversity. We identified and coded 84 case studies from 34 cities in which researchers assessed SES-biodiversity relationships. We used fuzzy-set Qualitative Comparative Analysis (fsQCA) to evaluate combinations of study design and city-level conditions that explain why SES-biodiversity relationships vary city to city and between plants and animals. While the majority of cases demonstrated increased biodiversity in higher SES neighborhoods, we identified circumstances in which inequality in biodiversity distribution was ameliorated or negated by disturbance, urban form, social policy, or collective human preference. Overall, our meta-analysis highlights the contributions of residential and municipal decisions in differentially promoting biodiversity along socioeconomic lines, situated within each city's environmental and political context. Through identifying conditions under which access to biodiversity is more or less unequal, we call attention to outstanding research questions and raise prospects for better promoting equitable access to biodiversity.

1. Introduction

Recent research has shown that cities are capable of supporting rich and diverse flora and fauna, contrary to the long-held presumption that cities are 'concrete jungles' (Aronson et al., 2014). This biodiversity is important not only for global conservation, as many cities are situated in global biodiversity hotspots, but also because this is the nature that over half the human population experiences on a daily basis. Nature in cities has been linked to positive outcomes for human health and well-being (Sandifer, Sutton-Grier, & Ward, 2015) and understanding the myriad drivers of biodiversity is of paramount importance in order to facilitate urban planning, design, and management for biodiverse, sustainable, and resilient cities.

In particular, researchers and managers are increasingly paying attention to social, economic, and cultural drivers of biodiversity, as evidenced by a number of recent reviews and meta-analyses (e.g., Gerrish & Watkins, 2018; Leong, Dunn, & Trautwein, 2018; Watkins & Gerrish, 2018). Concerns about environmental justice motivate much of this literature linking wealth and social standing with environmental quality and predicting the unequal distribution of resources and biodiversity across the city (Frickel & Elliott, 2018; Logan & Molotch, 1987; Massey, 1996; Pickett & Pearl, 2001). Socioeconomic status (SES) is commonly used to understand how this environmental injustice unfolds. Here, we define SES as a complex measure of social standing and relative power, often related to income, education, occupation, membership in a racial or ethnic group, and access to resources (Pickett & Pearl, 2001). While observers have noticed differences in biotic communities across the city for centuries, direct assessments of SES-biodiversity relationships have been conducted in a limited subset of cities and taxonomic groups (Leong et al., 2018). As such, the exact

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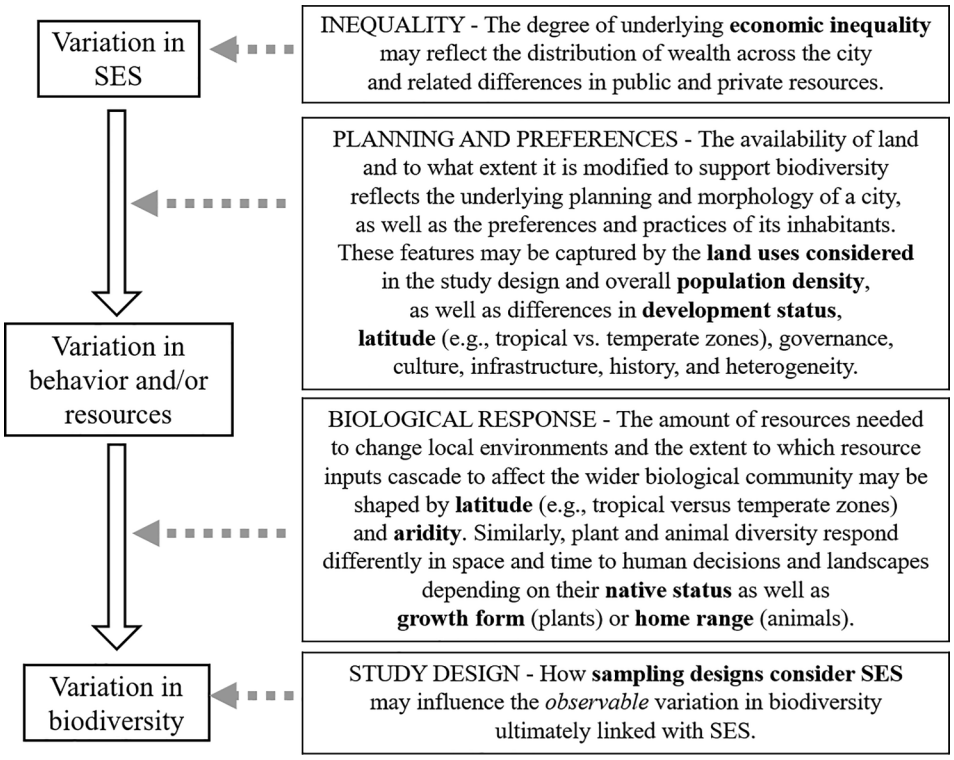

Fig. 1. Conceptual Diagram linking variation in SES with variation in behaviors and resources and subsequent variation in biodiversity (left), as derived from the literature. Causal links (white arrows) are contingent on the presence and character of various contextual factors (right, in caps), which are operationalized as measurable causal conditions (in bold). Note: while we visualize this pathway as linear and unidirectional for logical simplicity, we recognize that there are many feedback loops and circularities possible.

mechanisms through which human activities, as informed by SES, institutional influences, and cultural preferences, contribute to differences in biodiversity across the city are diverse and debated (Aronson et al., 2016). This paper aims to assess the potential mechanisms through which SES shapes spatial distributions of urban biodiversity using a systematic literature review and meta-analysis.

1.1. Theoretical background

Biodiversity varies in response to systematic differences in human behaviors or resources across the city that may be linked either directly or indirectly to SES (Fig. 1; Leong et al., 2018; Warren et al., 2010). Spatial patterns of SES in cities emerge from hierarchical status divisions and power dynamics, which play out across multiple spatial scales (Marcuse & Kempen, 2002; Warren et al., 2010). In some cases, as with horticultural plantings, spatial variation in distribution of biotic communities are a direct result of human actions, shaped by individual preferences but also by parcel sizes, zoning policies and social norms (D'Antona, VanWey, & Hayashi, 2006; Lerman, Turner, & Bang, 2012; Mincey, Schmitt-Harsh, & Thurau, 2013) and therefore may be strongly tied to patterns of SES (Kinzig, Warren, Martin, Hope, & Katti, 2005; Lubbe, Siebert, & Cilliers, 2010). In other cases, as with widely-ranging animals, alignments between SES and biodiversity are indirectly mediated by the distributions of key resources (e.g. vegetation cover; Kinzig et al., 2005; Lerman & Warren, 2011), which are in turn shaped by human actions and policies at multiple scales (Pickett et al., 2017). Depending on the form and context of the alignments between SES and these key resources and behaviors, the outcomes for social inequality in access to biodiversity also vary (Leong et al., 2018). We outline here some of these potential outcomes and the mechanisms that have been invoked to account for them.

The outcome most often observed by researchers is an alignment between high SES and high biodiversity (*i.e.,* "positive SES-biodiversity relationships"). One commonly invoked explanatory mechanism is the "Luxury Effect," through which economic wherewithal allows individuals to live in landscapes with higher biodiversity due to greater opportunities in choosing where to live, active modification of private gardens, or both (Hope et al., 2003). Often, these efforts are motivated by a desire to uphold a certain neighborhood aesthetic or identity (the "Ecology of Prestige"; Grove et al., 2006). Similarly, municipal investments in certain neighborhoods may increase property values and attract wealthier residents while disinvestment in other neighborhoods may pose challenges for biodiversity to persist (Wolch, Byrne, & Newell, 2014). Another commonly invoked mechanism describes a "Hierarchy of Need," in which economic need motivates lower SES residents to cultivate a limited diversity of edible and medicinal plants, while higher SES residents, freed from need, cultivate ornamental plants of greater diversity (Clarke & Jenerette, 2015; Kendal, Williams, & Williams, 2012).

Situations in which high biodiversity is linked with low SES (*i.e.,* "negative SES-biodiversity relationships") appear contrary to the patterns of environmental inequality and biological poverty found in many cities. However, any of the following mechanisms may facilitate such relationships: 1) residents with lower SES may increase biodiversity (e.g., via community gardens) either using minimal resources or through the collective mobilization of political capital (Hamilton & Curran, 2013); 2) residents with lower SES may live in urban areas that happen to be more biodiverse due to a greater presence of native remnant vegetation or spontaneous species, greater heterogeneity in residential yards and gardens, or greater proximity to biodiverse natural areas (S. S. Cilliers, Siebert, Davoren, & Lubbe, 2011; Endsley, Brown, & Bruch, 2018); and 3) residents with higher SES may prefer low biodiversity (e.g., the monoculture lawn; Robbins, 2007; Wheeler et al., 2017) or may be unable to achieve high levels of biodiversity due to some feature of urban form (e.g., dense high rise apartments in the city center; Cohen, Baudoin, Palibrk, Persyn, & Rhein, 2012).

Alternatively, the dominant drivers of biodiversity may not align with SES (*i.e.,* "ambiguous or neutral SES-biodiversity relationships"); rather, drivers related to microclimatic conditions, urban form, or species interactions, for example, may be more relevant (Aronson et al., 2016; Shochat et al., 2010).

Finally, "Legacy Effects", in which past spatial patterns of social inequality continue to shape urban landscapes over time, have also been linked to SES-biodiversity relationships. Legacy effects may result

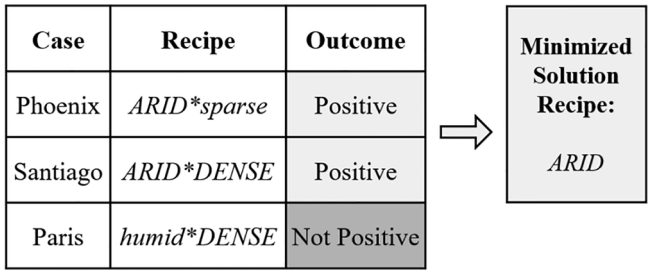

Fig. 2. Example of Boolean analysis. This truth table shows three cases, each represented by recipes of conditions and associated outcomes (*i.e.*, SES-biodiversity relationships). The logically parsimonious solution recipe linked with positive SES-biodiversity relationships is *ARID*, suggesting a relevant mechanism in arid cities that explains positive relationships.

in relationships between SES and biodiversity that are positive, neutral, or negative. For example, histories of colonialism or residential segregation may amplify inequality over time as layers of investment in green spaces and vegetation widen differences in biodiversity across SES groups (Cilliers, Cilliers, Lubbe, & Siebert, 2013). Alternatively, as a city's demographics change, lower SES residents may end up living in areas of previously higher SES, in which past residents had invested material resources in canopy cover or biodiversity then moved away (Grove et al., 2006).

1.2. Study objectives

We systematically assessed relationships between SES and urban biodiversity, seeking common elements underlying different patterns of these relationships (Fig. 1). We hypothesized that certain biophysical and social contextual factors (*sensu* Meyfroidt, 2016) mediate the observable relationship between SES and biodiversity. We asked the following: 1) How often do SES and biodiversity converge in cities across the globe? and 2) How and why do such patterns differ city to city? We tested whether cases in which researchers found positive, neutral, or negative relationships between SES and biodiversity shared similar characteristics. Specifically, we operationalized the hypothesized contextual factors in Fig. 1 into measurable causal conditions (*sensu* Ragin, 2014) that could be compared among cases. We conducted a meta-analysis using Qualitative Comparative Analysis, allowing us to identify configurations of causal conditions linked with different SES-biodiversity relationships. This approach can narrow the field of potential mechanisms for a given set of outcomes to identify those most consistent with the available evidence (Ragin, 2014). Using Qualitative Comparative Analysis thus allowed us to synthesize broad patterns, even from studies with differing methodological approaches, and suggest future directions for research and practice.

2. Methods

This project began within the Urban Biodiversity Research Coordination Network ("UrBioNet"), a global collaborative network for urban biodiversity research and practice. UrBioNet seeks to identify potential causal mechanisms and patterns of variation in biodiversity in cities throughout the world (Aronson et al., 2016). Through a series of workshops and iterative discussions, a working group of ecologists and social scientists developed a protocol for implementing the meta-analysis, articulated inclusion criteria for cases, and selected causal conditions to investigate.

We used Qualitative Comparative Analysis (QCA) to identify patterns among cases with shared features. This method employs Boolean algebra to identify combinations of causal conditions linked with outcomes of interest. QCA is well-suited for testing hypotheses among cases as well as creating empirical typologies (Schneider & Wagemann, 2010), including for analyses of environmental change (e.g., Qin & Liao, 2016; Rudel & Roper, 1996; Zinda & Zhang, 2019).

QCA treats cases as configurations of causal conditions, defined in terms of set membership (Ragin, 2014). A case in Phoenix, United States, for example, is a member in the set of arid cities (by convention, "*ARID*" in caps), alongside Santiago, Chile. Unlike Santiago, however, Phoenix is not a member in the set of dense cities (by convention, "*dense*" in lower case, or for easier interpretation, "*sparse*"). Recipes of conditions, such as *ARID*sparse* and *ARID*DENSE,* imply cases in cities like Phoenix and Santiago. Additionally, each case has an associated outcome condition: a relationship between SES and the diversity of a specific taxon that is either positive, neutral, or negative. Boolean analysis starts by arranging cases into a "truth table," in which rows correspond to cases and columns include the causal conditions and the outcome. Boolean algebraic functions reduce unique combinations of conditions to a set of simplified expressions that are logically sufficient to produce the outcome (Ragin, 2008b). Continuing with our example, if cases in Phoenix and Santiago show positive SES-biodiversity relationships, and a *humid*DENSE* case in Paris does not, we might conclude that *ARID* is the decisive causal condition. Essentially, we used Boolean algebra to produce a minimized solution recipe representing the most parsimonious combination of conditions shared by cases with a common outcome, facilitating further investigation of underlying patterns (Fig. 2). QCA does not assert that any given causal condition, such as *ARID*, is the true cause of the outcome in question (*sensu* Meyfroidt, 2016); rather, causal conditions point us to potential mechanisms discussed by case authors.

Fuzzy-set Qualitative Comparative Analysis (fsQCA), used here, appreciates that cases may differ in their membership in a given condition. For example, Phoenix and Santiago are not equally arid. fsQCA combines Boolean logic with varying set membership, making analyses more sensitive to variation and accounting for uncertainty in measurement. We followed recommendations for coding cases, implementing the analysis, and interpreting the output from Legewie (2013), Ragin (2008a), Rudel (2008), and Schneider and Wagemann (2010).

2.1. Case selection

We developed an inventory of cases from the peer-reviewed academic literature. First, we conducted a Web of Science database search for publications including terms such as "biodiversity" and "socio-economic status" (see Appendix A) and/or cited four key papers (*i.e.,* Hope et al., 2003; Kinzig et al., 2005; Loss, Ruiz, & Brawn, 2009; Lubbe et al., 2010). Reading the publications, we identified citations for other studies we had not yet encountered. Ultimately, this process identified 49 articles. From these, we extracted 84 cases, each of which related SES with the diversity of a single taxonomic group in a single metropolitan or urbanized region (hereafter: "city"), of which there were 34 (Fig. 3). We separately analyzed cases focusing on plants versus animals with the reasoning that humans do not directly modify animal communities to the same extent that they modify plant communities (Leong et al., 2018) (Fig. 4, "Define and Code Cases").

Because fsQCA treats cases as configurations of causal conditions with an associated outcome, there were two basic types of spatial scale information relevant for each case: the spatial scale at which SES and biodiversity information was collected (which, in relation to each other, form the outcome), and the spatial scale at which the causal conditions were collected (discussed below, Section 2.2). Regarding the scale of SES, some cases focused on individual- or household-level indicators, such as income or education (12 cases), while other cases focused on neighborhood-level indicators such as proportion of renters or median household income (72 cases). Regarding the scale of biodiversity, we included any case that reported a measure of species richness, diversity, or evenness, collected at either the scale of a single parcel (23 cases) or multiple parcels (61 cases). As a result, cases were varied in terms of the spatial scale at which both SES and biodiversity information were

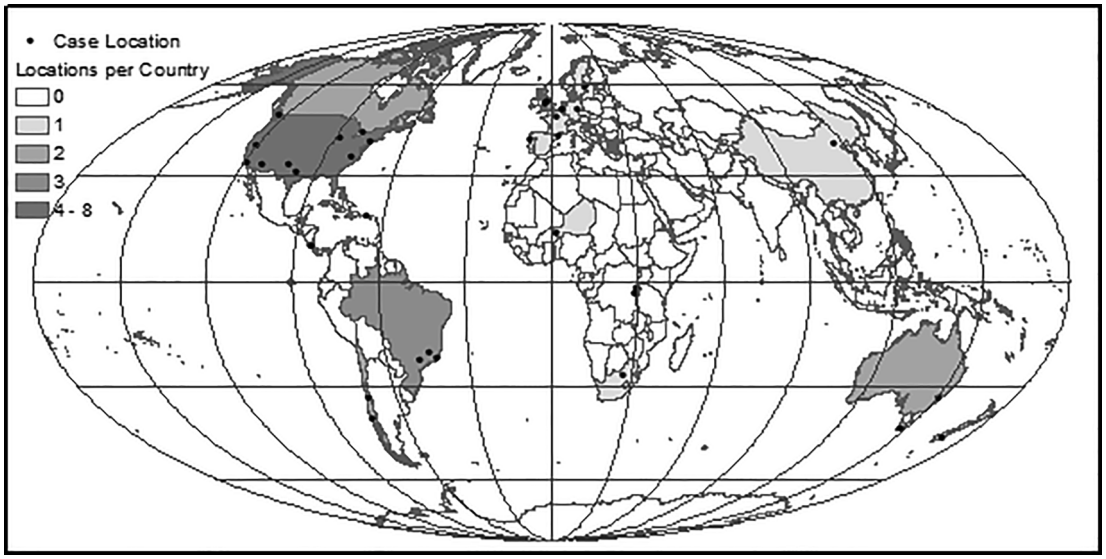

Fig. 3. Locations of the 34 case cities included in the meta-analysis.

collected. We accounted for scale differences in our initial coding scheme but removed them from our final analysis after finding that such information was logically redundant both internally and with other conditions. For example, all household-scale SES cases were also single-parcel biodiversity cases, and all single-parcel biodiversity cases also occurred on residential land. Additionally, all but two animal cases were characterized by either neighborhood-level SES information or multi-parcel biodiversity information.

2.2. Coding outcomes and causal conditions

For each case, we coded three outcome conditions and nine causal conditions. Conditions were calibrated with fuzzy-set membership scores between 1 ("fully in") and 0 ("fully out") based on external criteria. For a case to have a membership score > 0.5 indicates it is "more in than out" of the target set while membership < 0.5 indicates it is "more out than in." At the 0.5 crossover point, membership is maximally ambiguous.

The three outcome conditions (*i.e.*, relationships between SES and biodiversity) were positive, neutral, and negative, facilitating three separate analyses to uncover sets of mechanisms linked with each type of relationship. To code each case with these three outcome conditions, we first categorized cases as having either a positive, neutral, or negative SES-biodiversity relationship, as reported by case authors. We considered neutral cases as those with ambiguous, non-significant, or contradictory relationships between SES and biodiversity. For positive and negative cases, we also coded the reported strength and certainty of the relationship as strong, intermediate, or weak. Each case therefore received one of seven possible codes (Table 1, top row). Next, we assigned three numeric scores to each case reflecting membership in each of the three outcome conditions (Table 1, left column). Cases with neutral relationships were coded at 0.45 for both positive and negative analyses, just below the crossover point of 0.5 to indicate that these cases did not belong in either set but are not full non-members either. For the neutral analysis, we coded neutral and weak relationship cases as members and intermediate and strong relationship cases as non-

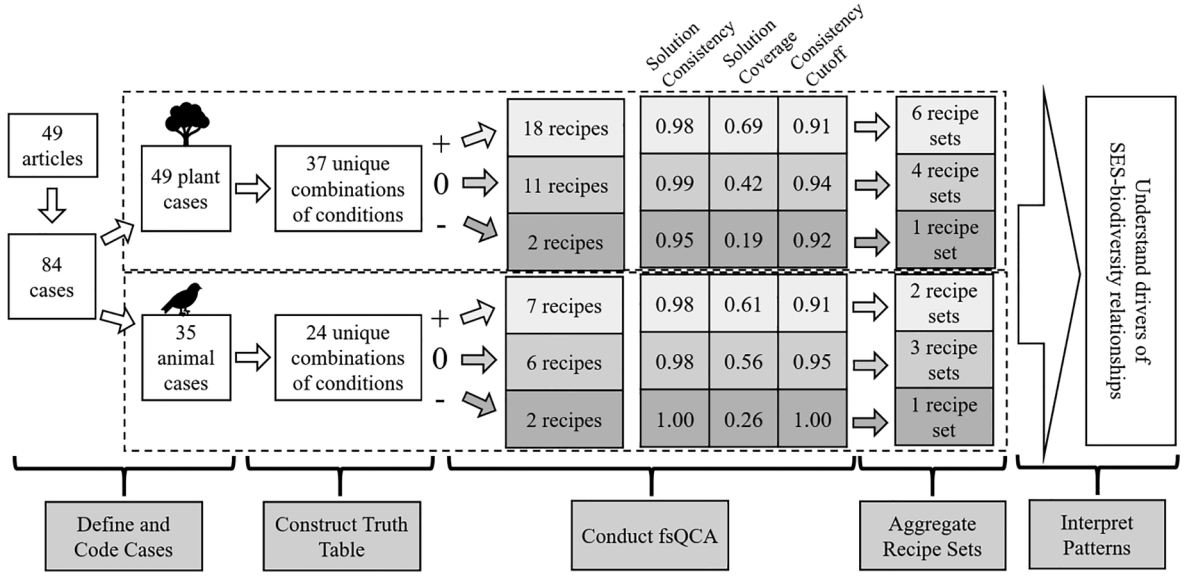

Fig. 4. fsQCA workflow. Articles and the cases within were identified from the literature, categorized as plant- or animal-focused, assembled into truth tables, and analyzed using fsQCA software to produce positive, neutral, and negative solutions consisting of solution recipes. Output values for each analysis are presented along with the final number of recipe sets aggregated. Recipe sets were interpreted in order to refine our understanding of SES-biodiversity relationships.

Table 1
Case membership scores in each of the three outcome conditions (left column), reflecting the strength and direction of each case's SES-biodiversity relationship (top row). Shaded cells include scores > 0.5 and indicate membership in the outcome set with which the analysis is concerned.

	Strong positive	Intermediate positive	Weak positive	Neutral	Weak negative	Intermediate negative	Strong negative
Positive Outcome	1	0.85	0.7	0.45	0.3	0.15	0
Neutral Outcome	0	0.33	0.67	1	0.67	0.33	0
Negative Outcome	0	0.15	0.3	0.45	0.7	0.85	1

members. Two researchers from the UrBioNet working group independently coded each case. The group convened to finalize coding where there was disagreement (see Appendix B, The Outcome).

Causal conditions were coded and calibrated using external information about each case, collected from a variety of sources including the publications themselves, United Nations databases, national censuses, and Wikipedia (Table 2, "Data Source" column, also Appendix B, Causal Conditions). All conditions were conceptualized as causally relevant to our unit of analysis (the SES-biodiversity relationship within the case city), and ranged in spatial scale from city-level to country-level (see Table 2 and Appendix B for details). Indeed, the ability to integrate conditions representing diverse scales and methodologies is an attractive strength of QCA (Ragin, 2014). Information obtained for each city (e.g., aridity) was applied to all cases occurring in that city, with the exception of population density; this information was obtained to match the spatial extent of each case since some studies occurred exclusively within the dense city limits while other studies considered the broader, sparser, metropolitan region (see Table S1 for information about the geographic boundary and study area of each case). As one would expect, cases that were sampled at the municipal level (boundary of the study is a municipal boundary) were typically denser and covered a smaller sampling area than those sampled at the level of a metropolitan region (study area includes multiple municipalities in some way). In this way, the population density condition accounted for variation among cases within the same city in the spatial extents of sampling for the outcome condition (SES-biodiversity relationships).

We calibrated six causal conditions using interval-scale values based on qualitative groupings (Table 2). Membership scores were developed along either a 4-point scale (1, 0.67, 0.33, 0) or a six-point scale (1, 0.8, 0.6, 0.4, 0.2, 0). We calibrated three causal conditions by converting continuous quantitative measures into set membership scores. To do so, we followed the common practice of rescaling variables using theoretically-informed anchor values and the logistic function. The result is simple odds ranging from 1 to 0, with > 0.95 and < 0.05 effectively representing full membership and non-membership, respectively (Ragin, 2008a).

2.3. Analysis

We conducted six analyses using fsQCA software (version 3.0, Ragin & Davey, 2016): a positive, neutral, and negative analysis each for plants and animals. For the plant analyses we used all nine conditions. For the animal analyses, we did not include National Development as a condition because all but one case occurred in a city in a very highly developed country.

For each analysis, fsQCA software generated a truth table in which each row represented a unique combination of conditions (Fig. 4, "Construct Truth Table"). Cases were assigned to rows in which they were members. Each row presents a consistency metric indicating the extent to which member cases demonstrate the outcome and a coverage metric indicating the proportion of cases the row accounts for, adjusting for varying set membership. We used a consistency value of 0.9 as the cut-off for coding rows as demonstrating the outcome. This conservatively high cut-off value ensured that cases not demonstrating the outcome were not treated as demonstrating it (Legewie, 2013). We used the complex solution output, in which fsQCA does not consider simplifying assumptions to reduce recipes (Fig. 4, "Conduct fsQCA").

Within each analysis, we iteratively grouped solution recipes into "recipe sets" based on shared conditions that aligned with relevant mechanisms suggested by case authors (Fig. 4, "Aggregate Recipe Sets"). Specifically, we identified pairs of recipes that differed on single conditions and decided, based on the mechanisms proposed by the authors of the implied cases, whether we could simplify the two recipes without losing any explanatory power (e.g., we can reduce *ARID*sparse* and *ARID*DENSE* to *ARID* if case authors do not suggest any themes relating to land use, population density, or urban form). We repeated this process until we obtained recipe sets that could no longer be reduced without losing important explanatory elements. Recipe sets are therefore parsimonious simplifications of related recipes informed by a dialogue between theory and case knowledge, presented as distilled combinations of conditions that appeared critical to producing the outcome. In addition, for each recipe set, we manually calculated scores of consistency and raw coverage following Ragin (2008b). In defining recipe sets, we sometimes included conditions that were not uniform across all recipes (gray-shaded cells in Tables S5 and S6). In these situations, we felt that the one or two non-conforming cases demonstrated similar enough mechanisms to merit inclusion in a given recipe set. We also aimed to capture the diversity of our solution recipes by defining recipe sets that were mutually exclusive whenever appropriate. We simultaneously aimed to capture some of the inherent ambiguity in our dataset, namely by treating cases with "weak" SES-biodiversity relationships as members in the outcome of both the neutral and either the positive or negative analysis (see Table 1). As such, some weak and some neutral cases were implied by recipe sets from more than one analysis (bolded cases in Tables S5 and S6), allowing for a more honest and nuanced interrogation of how cases relate to each other in different contexts (Fig. 4 "Interpret Patterns" section).

In addition to fsQCA, we conducted Cochran–Mantel–Haenszel tests and Pearson's chi-square association tests to evaluate significant differences in the proportion of outcomes for animal and plant cases for each causal condition.

3. Results

We identified 84 cases from 34 cities encompassing a variety of taxonomic groups, study designs, city conditions, and outcomes (Appendix C). Collectively, most cases showed positive relationships between SES and biodiversity (63%). 12% of cases showed negative

Table 2
Coding and calibration scheme for the measurable conditions detailed in Fig. 1. See Appendix B, Causal Conditions, for more details.

Condition (*MEMBERSHIP* and *non-membership*)	Data Source	Calibration Membership score = Descriptor (Explanation)
Qualitative Groupings		
Taxonomic Group Plant growth form (*WOODY* or *mixed*) — or — Animal home range (*MOBILE* or *low mobility*)	Case publications	1.0 = Trees, shrubs, or woody plants only 0.33 = Mix of woody plants and non-woody plants or not specified 0 = Herbaceous plants only — or — 1.0 = Animals with broad ranges (birds, bats, meso-predators, pollinators) 0 = Animals with small ranges (herpetofauna, small mammals, aquatic invertebrates, indoor arthropods)
Native Status (*NATIVE* or *exotic*)	Case publications	1.0 = Native species only 0.67 = All species: sample includes more native than non-native species, or not specified 0.33 = All species: sample includes more non-native than native species 0 = Non-native species only
Land Uses considered (*PUBLIC* or *residential*)	Case publications	1.0 = Non-residential land uses only 0.67 = Mix of non-residential and residential land uses 0 = Residential land uses only
Economic inequality via the GINI index (*UNEQUAL* or *equal*)	US Census Bureau via American Community Survey (ACS), OECD.Stat (http://stats.oecd.org/), Canback Global Income Distribution Database (C-GIDD); reference year as close to 2010 as possible	1.0 = Very High (GINI > 0.45 using C-GIDD or > 0.5 using ACS; GINI estimates of 1 would indicate complete concentration of wealth in a single household) 0.67 = High (GINI > 0.38) 0.33 = Medium (GINI > 0.30) 0 = Low (GINI < 0.30; GINI estimates of 0 would indicate complete equality or that all households have the same income)
National development via the Human Development Index (*DEVELOPED* or *developing*)	2010 United Nations estimates	1.0 = Very High (HDI > 0.8; surveys suggest different aggregate priorities of individuals in countries with very high HDI (Jahan, 2016)) 0.4 = High (HDI > 0.7) 0.2 = Medium (HDI > 0.55) 0 = Low (HDI < 0.55)
Sampling scheme informed by SES (*INFORMED* or *uninformed*)	Case publications	1.0 = Sampling design informed by variation in SES (stratified by SES or structured to represent SES diversity in city) 0 = Sampling not informed by SES (uniform sampling or stratified by non-SES feature)
Quantitative Anchors		
Density matching spatial extent of case measured in persons/km^2 (*DENSE* or *sparse*)	Case publications, national censuses, and wikipedia, using reference years as close to publication year as possible	0.95 = 8000 persons/km^2 (above this density, individual choices are not likely to affect landscapes due to lack of residential/private green space) 0.5 = 4000 persons/km^2 (distinguishes between Chicago* cases that focus on the dense urban core and the broader lower-density metropolitan area) 0.05 = 1000 persons/km^2 (below this density, individuals are highly likely to have access to residential/private greenspace) *We used Chicago as a reference city for given its classically dense urban core within a sparser, broader, metropolitan matrix.
Latitude in degrees (*TROPICAL* or *temperate*)	Google maps	0.95 = 23.5° (sites below this latitude are considered tropical (American Meteorological Society, 2012)) 0.5 = 35° (sites below this latitude are considered subtropical) 0.05 = 66.5° (sites below this latitude are considered temperate and above are considered polar)
Aridity via the Global Aridity Index, 1950–2000 (*ARID* or *humid*)	Consultative Group for International Agriculture Research (CGIAR) Consortium for Spatial Information (Trabucco & Zomer, 2009)	0.95 = 0.2 (values below which are classified as arid and hyper arid) 0.5 = 0.65 (values above which are classified as humid and below which are dry sub-humid and semi-arid) 0.05 = 1.0 (values above which Mean Annual Precipitation exceeds Mean Annual Evapotranspiration)

relationships, and 25% of cases showed neutral relationships. We conducted six analyses, yielding complex solutions with varying numbers of recipes (Fig. 4). All solutions had high consistency scores, indicating that causal recipes had high agreement in demonstrating each outcome. For both plants and animals, positive analyses yielded the highest solution coverage, followed by the neutral analyses. This indicates that the highest proportion of cases not explained by the solution were negative. Recipes from each solution were aggregated into recipe sets characterized by common mechanisms as discussed by case authors (Tables 3 and 4). For truth tables, full solutions, and cases not represented by solution recipes, see Appendix D.

The plant analyses yielded 11 recipe sets covering a range of mechanisms including municipal investments in public trees, the "hierarchy of need" on residential land, uniform management of public green spaces, and higher biodiversity in higher green space, lower SES districts (Table 3).

The animal analyses yielded 6 recipe sets covering a range of mechanisms such as the conjoint function of residential and non-residential land in increasing biodiversity in higher SES districts, the dominance of urban form in shaping animal communities, and the role of disturbance in fostering negative SES-biodiversity relationships (Table 4).

The recipe sets we identified reveal that there is no one causal condition that consistently mediates relationships between SES and biodiversity. Rather, similar outcomes can be realized through diverse mechanisms and similar mechanisms can give rise to divergent

Table 3
Recipe sets derived from the three plant analyses, described by the relevant conditions in set notation and in narrative format. Shared mechanisms among cases in the recipe set are briefly summarized, along with an illustrative example case. Parameters of fit include Consistency and Raw Coverage. For full recipes, see Appendix D, Table S5.

Set	*Recipe Sets* Cases that focus on:	Shared Mechanisms Among Cases, as Proposed by Case Authors	Case City [case]: Example (Other cities in recipe set)	Parameters of Fit
	Positive Analysis			
A	*WOODY*exotic** *PUBLIC*UNEQUAL** *sparse*TROPICAL* Woody exotic plant diversity across public land uses in unequal sparse tropical cities	Municipalities and residents in higher SES areas increase exotic plant diversity to provide shade, aesthetic, and other ecosystem services. Climatic conditions may demand greater resources to maintain biodiversity, especially in tropical arid cities.	Los Angeles [02A]: Higher income areas have greater (mostly non-native) tree species richness across land uses; proposed explanation is cost of irrigation (Phoenix, Kigali)	Consistency: 0.9937 Coverage: 0.1370
B	*WOODY*NATIVE** *PUBLIC* Woody native plant diversity across public land uses	Municipalities and residents in higher SES areas increase native plant diversity, reflecting greater access to plant materials and planting sites and explicit municipal priorities favoring native species. May be related to unequal lobbying power and municipal priorities across neighborhoods.	Campos dos Goytacazes [39A]: Neighborhoods with higher land values have greater public tree species richness; observation that residents in wealthier neighborhoods plant native trees in public squares (Santiago, Porto)	Consistency: 0.9950 Coverage: 0.1722
C	*mixed*NATIVE** *PUBLIC* Mixed native plant diversity across public land uses	Greater extent of green space surrounding ponds in higher SES neighborhoods. May reflect an overall tendency for native mixed plant diversity to be beyond direct influence of human management.	Halton [18A]: Aquatic plant species richness is greater in public ponds in higher SES areas; indirectly associated with greater amount of surrounding green space (N/A)	Consistency: 0.8716 Coverage: 0.0925
D	*mixed*residential** *sparse*ARID** *(developing + UNEQUAL*INFORMED)* Mixed plant diversity on residential land in sparse arid cities that are **either** developing **or** unequal with sampling informed by SES	Consistent with the "Hierarchy of Need" hypothesis wherein lower SES residents cultivate a limited diversity of utilitarian plants, while higher SES residents cultivate a greater diversity of ornamental plants. Mechanism may be commonly invoked in developing countries, where rates of home food production are higher (Kendal et al., 2012), or the magnitude of difference in home garden diversity may be most noticeable in cases where socioeconomic stratification is profound and incorporated into the sampling design.	Bujumbura [06A]: Home garden species richness is greater in higher SES neighborhoods; authors point to differences in function and size of gardens in wealthier neighborhoods (Beijing Metro, Niamey, Tlokwe, Phoenix)	Consistency: 1.0000 Coverage: 0.1858
E	*residential*sparse** *DEVELOPED*(exotic + equal*INFORMED)* Residential land in sparse developed cities and **either** focus on exotic species **or** occur in an equal city with sampling informed by SES	Individual and community preferences for high biodiversity are associated with high SES. Preference-related factors implicated by authors include ethnicity, education, place attachment, and home ownership (individual-level) and cultural norms, expectations, and policies (community-level). Focus on exotic species may be common as they are often intentionally planted in residential gardens.	Toronto [12A]: Tree species richness was explained by racial variables (correlated positively with percent not visible minorities and negatively with percent South Asian); observation that cultural preferences or neighborhood norms may favor certain species (Maastricht, Dunedin, Hobart, Costa Brava, San Juan, Los Angeles)	Consistency: 0.9388 Coverage: 0.3440
F	*residential*DENSE** *INFORMED* Residential land in dense cities with sampling informed by SES	Neighborhood effects can facilitate differences in biodiversity, as residents with similar SES filter into neighborhoods with distinct forms and opportunities. High plant diversity may reflect either cultural diversity in a neighborhood as residents use yards for self-expression, greater available space for planting, or older neighborhoods that have accrued cultivated species over time. SES-informed sampling highlights these differences among SES areas.	Chicago City [31C]: Floral species richness was explained by number of residential lots, percent white and percent Hispanic; authors suggest diverse neighborhoods may support greater yard diversity (Beijing City, Heredia)	Consistency: 0.9316 Coverage: 0.2467
	Neutral Analysis			
G	*mixed*PUBLIC** *(NATIVE + TROPICAL)* Mixed plant diversity across public land uses and **either** concern native species **or** occur in tropical cities	On public land, greenspace managers may make uniform planting decisions independent of surrounding SES. May be especially relevant for native plants, which have lower maintenance costs compared to non-natives, and tropical cities, where perennial plantings are an important component of managed green spaces.	Phoenix [24B]: Perennial diversity in city parks is not associated with median household income surrounding parks; proposed explanation that greenspace managers consider efficiency and aesthetics rather than SES (Sydney, Paris, Halton)	Consistency: 0.8291 Coverage: 0.1592
H	*PUBLIC*temperate** *uninformed* Public land uses in temperate cities with sampling uninformed by SES	SES-biodiversity relationships may be neutralized via the "Haussmann Paradox," in which higher SES residents live in high-density low-greenspace districts closer to the urban core and lower SES residents live in lower-density higher-greenspace districts further out (Cohen et al., 2012). Higher SES residents	Paris [11A]: Floral richness in public spaces had no relationship to mean incomes; proposed explanation is that higher-status groups live in high-density districts with low vegetation coverage and vice versa (Beijing City, NYC, Chicago Metro, Halton)	Consistency: 0.8095 Coverage: 0.2011

(*continued on next page*)

Table 3 (*continued*)

Set	*Recipe Sets* Cases that focus on:	Shared Mechanisms Among Cases, as Proposed by Case Authors	Case City [case]: Example (Other cities in recipe set)	Parameters of Fit
	Positive Analysis			
I	*WOODY*PUBLIC* (NATIVE + sparse*TROPICAL)* Woody plant diversity across public land uses and **either** concern native species **or** occur in sparse tropical cities	have fewer opportunities to increase plant diversity and there may be a greater abundance of green spaces and community gardens in lower SES areas. Neighborhood characteristics such as building density, age, and degree of urbanization, may be more relevant for woody plant diversity and only somewhat related to SES.	Kigali [41A]: Tree diversity across land uses was related to socioeconomic factors, homestead clustering, and degree of urbanization (Porto)	Consistency: 0.6940 Coverage: 0.2124
J	*mixed*residential* sparse*(developing + humid)* Mixed plant diversity on residential land in sparse cities that are **either** developing **or** humid	Of particular importance are features related to urbanization and land tenure as well as preferences for certain yard or neighborhood types. In humid or developing cities, the cost of increasing and maintaining plant diversity may be lower and the influence of home food production may be higher, respectively.	Rio Claro [15A]: Home garden species richness was not related to monthly family income; rather, age of home garden and concern for aesthetics more important (Maastricht, Hobart, Niamey, Beijing Metro)	Consistency: 0.7773 Coverage: 0.2995
	Negative Analysis			
K	*PUBLIC*UNEQUAL* temperate*uninformed* Public land uses in unequal temperate cities with sampling uninformed by SES	"Haussmann Paradox" as a mechanism for negative, in addition to neutral, SES-biodiversity relationships. Namely, low-SES, low-density areas support greater plant diversity than high-SES, high-density areas.	Chicago Metro [22A]: Invasive species richness was greatest in low-density-low-SES areas further from the downtown core with more vacant land (Beijing City)	Consistency: 0.6953 Coverage: 0.2668

**condition_a* - signifies logical AND: *condition_a* must be present in the solution.

*(*CONDITION_B* + *condition_c*) - signifies logical OR: either *CONDITION_B* or *condition_c* must be present.

outcomes. For example, we observed that similar combinations of conditions can be linked to both positive and neutral SES-biodiversity relationships for woody plants on public land uses, residential plants in sparse cities, and animal diversity in both temperate humid cities and arid cities. We also observed that both neutral and negative SES-plant diversity relationships often take shape in cities where higher SES populations live in denser areas with limited space for biodiversity, a pattern we refer to as the "Haussmann Paradox" (Cohen et al., 2012). In each of these instances and throughout our analysis more generally, it was the combinatorial presence of multiple conditions that provides the context for how SES-biodiversity relationships unfold.

Univariate explorations of conditions and outcomes yield findings consistent with the fsQCA results. Namely, case membership or non-membership in any isolated causal condition was not associated significantly with certain outcomes (CMH X^2 tests, *p-values* > 0.05), with one exception. Animal cases on residential land showed a significantly different composition of outcomes (mostly positive) compared with animal cases on mixed or non-residential land uses (Fig. 5, xyy symbology). A significant CMH X^2 value overall for this condition (*p-value* $= 0.0118$, d.f. $= 4$) suggests that land use plays an important role shaping plant and animal SES-biodiversity relationships. Even in the absence of statistical difference, it was striking to observe differences in outcomes across conditions. For example, only four animal cases occurred in dense cities, none of which showed positive SES-biodiversity relationships (Fig. 5).

Among the remaining conditions, Pearson's chi-square tests identified only three significant differences either between plant and animal cases for a given membership category or between member and non-member cases within a given taxonomic group. Specifically, both for cases that were *TROPICAL* and for cases that were *INFORMED*, plant cases showed fewer negative relationships than animal cases. In addition, within animal cases, *INFORMED* cases featured fewer neutral relationships than *uninformed* cases (see Appendix E).

4. Discussion

In cities around the world, higher SES often converges with higher levels of biodiversity, but not always. Using a systematic meta-analysis, we identified multiple trends explaining divergent types of SES-biodiversity relationships among 49 peer-reviewed articles. Trends toward positive SES-biodiversity relationships corroborate theories previously advanced in the literature related to luxury and legacy effects as well as the importance of political capital and the "Hierarchy of Need." For one, high biodiversity may align with high SES due to differences in non-residential green space quantity, quality, and management. On residential land, positive SES-biodiversity relationships are shaped by differences in preferences and needs and the material resources to act on them, as well as urban forms and residential filtering that shapes what is appropriate or possible in a given neighborhood. Animal diversity is often influenced by interactions between these residential and non-residential components. Trends toward neutral and negative SES-biodiversity relationships are most influenced by parks and urban form. Non-residential green space managers often make planting decisions independent of the SES of the surrounding area, neutralizing relationships. Both neutral and negative SES-biodiversity relationships can be found in cities characterized by a "Haussmann Paradox," in which high-density high-SES areas present fewer opportunities for residents to increase plant diversity relative to lower-density lower-SES areas. Density-related drivers are salient for animals as well, especially in cities where density and SES effects operate independently. Numerous other drivers of biodiversity operate independently of SES, reducing the observable influence of socioeconomics.

The majority of cases demonstrated positive relationships, especially concerning plant diversity. This finding aligns with studies relating SES and biodiversity at the multi-city or regional scale, in which plant diversity tends to show stronger positive relationships with SES

Table 4
Recipe sets derived from the three animal analyses, described by the relevant conditions in set notation and in narrative format. Shared mechanisms among cases in the recipe set are briefly summarized, along with an illustrative example case. Parameters of fit include Consistency and Raw Coverage. For full recipes, see Appendix D, Table S6.

Set	*Recipe Sets* Cases that focus on:	Shared Mechanisms Among Cases, as Proposed by Case Authors	Case City [case]: Example (Other cities in recipe set)	Parameters of Fit
	Positive Analysis			
U	*sparse*temperate** *humid*(exotic + residential)* Sparse temperate humid cities and concern **either** exotic species **or** residential land	High SES yards (via wildlife resources) and surrounding landscapes (via parks and green spaces) function together to increase animal diversity. Possibly related to histories of ethnic and economic segregation wherein greener areas are populated with higher SES residents. May be relevant for exotic animals, which may prefer common plantings such as woody ornamentals; and residential land, where higher SES residents can actively landscape.	Sheffield [17X]: Lower bird species richness in residential neighborhoods with higher deprivation closer to the city center; proposed explanation is reduced bird feeding and fewer habitat features for birds (Leeds, Dunedin, Vancouver, Leipzig, Raleigh, Chicago Metro)	Consistency: 0.8513 Coverage: 0.3842
V	*NATIVE*UNEQUAL* **sparse*ARID* Native animal diversity in unequal sparse arid cities	High SES yards and areas feature native xeric vegetation that supports uncommon native habitat specialists.	Phoenix [27X]: Greater native desert bird diversity in higher income neighborhoods; proposed explanation is cost of higher quality habitat resources and lower proportion of renters (Waco, Lubbock)	Consistency: 0.9128 Coverage: 0.2998
	Neutral Analysis			
W	*MOBILE*temperate** *humid*(equal + uninformed)* Mobile animal diversity in temperate humid cities and are **either** equal **or** have sampling uninformed by SES	Across the city, costs of increasing plant diversity are low and mobile animals may be less dependent on specific plant assemblages. May be especially relevant in cases with low variation in SES, in which features related to urban form, greenspace availability, and diverse human preferences exert a stronger influence over animal diversity.	Chicago City [30X]: Bee species richness had no relation to median household income; authors propose that population density is more important as residents maximize available space with flowering plants (Chicago Metro, Valdivia, Leeds)	Consistency: 0.8018 Coverage: 0.3863
X	*PUBLIC*ARID** *uninformed* Public land uses in arid cities with sampling uninformed by SES	Animal diversity is associated with land use and land planning rather than SES. May be common under study designs focusing on public land uses and not using SES-informed sampling, in which influence of non-residential drivers related to urban form may be more relevant.	Reno [44Z]: Bird species richness in riparian areas related to land use intensity rather than land value; authors suggest some land uses serve as habitat reserves or provide important food resources (Waco)	Consistency: 0.7151 Coverage: 0.1577
Y	*low-mobility*equal* Low-mobility animal diversity in equal cities	Urban form may exert a stronger influence than SES on biodiversity, especially for pond invertebrates and amphibians. More equitable distributions of green and blue spaces may be common in cities with lower economic inequality.	Stockholm [07X]: Aquatic invertebrate species richness associated with building density rather than SES; possible that different urban forms between high and low SES areas offset would-be differences in diversity (Halton)	Consistency: 0.7800 Coverage: 0.1253
	Negative Analysis			
Z	*UNEQUAL*humid** *(exotic*low-mobility + TROPICAL)* Unequal humid cities and **either** concern exotic low-mobility animal diversity **or** are tropical	Studies invoked human disturbance as a driver of animal diversity in unequal humid cities. High disturbance was associated with low-mobility exotic animal diversity in lower SES areas, while in some tropical cities, high disturbance was associated with decreased bird diversity in higher SES areas.	Belo Horizonte [40X]: Wealthier areas are noisier, denser, less covered by canopy, and support lower bird diversity. (Chicago Metro)	Consistency: 0.8629 Coverage: 0.5629

**condition_a* - signifies logical AND: *condition_a* must be present in the solution.
*(*CONDITION_B* + *condition_c*) - signifies logical OR: either *CONDITION_B* or *condition_c* must be present.

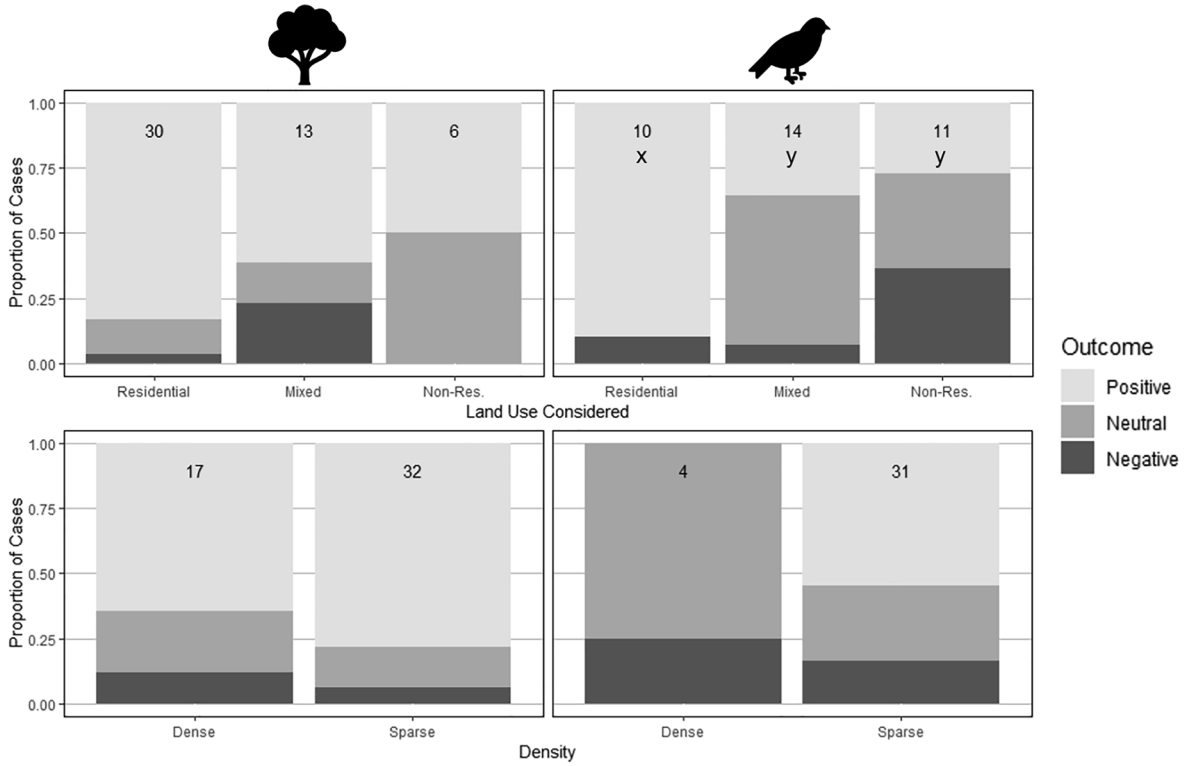

Fig. 5. Proportion of plant and animal cases with positive, neutral, and negative SES-biodiversity relationships for the conditions of Land Use and Density, displayed with the sample size for each taxa*membership subset. For each condition, differences within taxa and differences within membership categories were assessed via Chi square tests; significant differences at $\alpha = 0.05$ are displayed on the figure with xy symbology.

compared with animal diversity (Baldock et al., 2019; Chamberlain, Henry, Reynolds, Caprio, & Amar, 2019; Hand, Freeman, Seddon, Stein, & van Heezik, 2016; Junker et al., 2015; Kuruneri-Chitepo & Shackleton, 2011; Luck, Smallbone, & Sheffield, 2013; MacGregor-Fors & Schondube, 2011; Mills, Cunningham, & Donovan, 2016; Smallbone, Luck, & Wassens, 2011). Our findings also align with seven studies we identified after concluding the analysis that did not meet our original search terms (Escobedo, Clerici, Staudhammer, & Corzo, 2015; Sudha & Ravindranath, 2000; Walker, Colton Flynn, Ovando-Montejo, Ellis, & Frazier, 2017) or were recently published (Avolio, Pataki, Trammell, & Endter-Wada, 2018; Fan, Johnston, Darling, Scott, & Liao, 2019; Nero, Kwapong, Jatta, & Fatunbi, 2018; Steenberg, 2018).

We found our conceptual model (Fig. 1) to be a useful framework for understanding how associations between SES and biodiversity arise. Here, we present four key lessons learned, as informed by our conceptual model. Finally, we identify knowledge gaps to date concerning mechanisms and coverage and offer some new ideas and best practices moving forward.

4.1. Lessons learned

4.1.1. Economic inequality does not necessarily beget inequality in biodiversity distribution

In *UNEQUAL* cities, we may expect environmental injustice to be present, explained by colonial legacies, institutional racism, residential segregation, and exclusionary zoning practices. Alternatively, we may witness a combination of social stratification and housing filtering, wherein lower SES residents are relegated to neighborhoods of lower environmental quality as more mobile residents with higher SES selectively move to more expensive, higher quality neighborhoods (Chowdhury, Larson, Grove, & Polsky, 2011). However, we found that in cities with high economic inequality, high levels of biodiversity may be found in either higher SES areas or lower SES areas. Economic inequality may beget inequality in biodiversity distribution in *TROPICAL* and/or *ARID* cities, for example, where there may be greater tree planting investment in higher SES areas or lower SES residents cannot afford higher quality plantings that support native animal diversity (Recipe Sets A and V). The opposite may be true in *temperate* and/or *humid* cities, where urban form or public policies may more often facilitate higher biodiversity in lower SES areas (Recipe Sets K and Z). That neutral relationships did not rely on conditions of low economic inequality suggests mechanisms neutralizing SES-biodiversity can occur anywhere. As such, economic inequality within cities may be less relevant than the character of cities' public policies and poverty-related interventions (Leong et al., 2018).

4.1.2. Drivers of positive SES-biodiversity relationships are primarily residential

Opportunities for residents to transform material resources into those promoting biodiversity vary greatly within and among cities. Positive relationships were common on *residential* lands and in *sparse* cities (e.g., Recipe Sets D-F and U-V; also Fig. 5), where residents have larger gardens and yards in which to convert resources into biodiversity. In many cases, higher SES residents appeared to prefer greater biodiversity and achieved higher levels through intentional plantings or by providing food or habitat resources for animals (*e.g.*, bird feeders, fruiting or mature trees, vegetative complexity, nesting sites). Such preferences may be related directly to SES (e.g., Hope et al., 2003), or indirectly via cultural norms (*e.g.*, Grove et al., 2006) or feedback loops from living in high biodiversity settings (*e.g.*, Lerman & Warren, 2011). However, biodiversity isn't favored in all settings. Biodiverse yards may convey disorder (Lubbe et al., 2010), include undesirable elements like trees (Kirkpatrick, Daniels, & Zagorski, 2007), or signal lack of care (Robbins, 2007). The recipe sets we identified capture some of these differences in preferences and practices and also allow for a greater interrogation of patterns. For example, while positive SES-biodiversity

relationships were linked to *residential* land in cities in both *developing* and *DEVELOPED* countries, case authors pointed to different underlying mechanisms, namely the "Hierarchy of Need" and differences in cultural preferences, respectively (Recipe Sets D and E).

It was surprising that the "Hierarchy of Need" was a prevalent explanation in cases in developing nations given that food insecurity motivates plant community composition in highly developed nations as well (*e.g.*, Clarke & Jenerette, 2015; Douglas & Lawrence, 2011; McClintock, Mahmoudi, Simpson, & Santos, 2016). Indeed, poverty and disadvantage can be high regardless of development status, especially for racial and ethnic minorities (Jahan, 2016). One explanation for this contradiction may be that the "Hierarchy of Need" hypothesis is particularly salient in *developing*ARID* cities given the higher relative cost of purchasing and irrigating ornamental species compared to *DEVELOPED*ARID* cities or *developing*humid* cities (e.g., Rayol, Do Vale, & Miranda, 2017). Indeed, home food production is less common in gardens in western temperate and colder climate countries (Kendal et al., 2012), which also tend to be of higher development status. Alternatively, the "Hierarchy of Need" hypothesis may be commonly invoked in developing nations given coinciding histories of segregation, colonialism, disenfranchisement, and participation in markets among higher SES households (Lubbe et al., 2010).

Just as residential drivers commonly facilitate positive SES-biodiversity relationships, non-residential drivers related to green space planning and urban form facilitate neutral and negative relationships (Recipe Sets H and K). We were intrigued by the explanatory potential of the "Haussmann Paradox," in which low-SES, low-density areas support equal or greater biodiversity than high-SES, high-density areas (Cohen et al., 2012). The paradox is named for Baron Haussmann, the urban planner responsible for imposing this form upon the Paris landscape in the mid-1800s. During that era, industrial development influenced the spatial arrangement of various social classes, such that working-class residents lived further from the dense urban core and closer to factories as well as non-residential green spaces like woodlands and cemeteries. While industrial areas were later converted to housing and more green space, the urban core maintained its high density and low green space character. It is not surprising, therefore, that "Haussmann Paradox" cases concern *PUBLIC* land uses, which include these non-residential green spaces. Further, many, but not all, "Haussmann Paradox" cities have dense urban cores, further highlighting the importance of building density and greenspace availability as a mechanism. The importance of density, rather than SES, as a component of "Haussmann Paradox" cases may explain the relevance of the *uninformed* condition, wherein researchers may be more likely to observe non-SES effects. Finally, it is interesting that only *temperate* cities demonstrate the "Haussmann Paradox," suggesting similar trajectories of development over time in higher latitudes, potentially related to histories of industrialization. However, this interactive relationship between SES and density may be more global than our *temperate* condition suggests. In South Africa, for example, Chamberlain et al. (2019) found that native bird species richness was mediated by a similar interaction between SES and urbanization levels. The mechanisms behind this outcome relate to the "Haussmann Paradox" in that green space availability declines with both urbanization and density, but other factors may also influence bird species richness, such as disturbance associated with higher levels of urbanization (see Recipe Set Z).

4.1.3. Biodiversity responds to SES-related decisions differently throughout the world

Different environmental limitations across the world's cities shape the way resource inputs and management decisions influence biodiversity. Often, the challenges of heat and water scarcity in *TROPICAL ARID* cities necessitate greater material resource inputs in order to influence biodiversity compared with *humid* or *temperate* cities. This feature was linked to positive relationships for woody plant diversity on public land (e.g., municipal investments in tree-related ecosystem services in higher SES areas; Recipe Sets A and B) and for mixed plant diversity on residential land (e.g., the "Hierarchy of Need"; Recipe Set D). In contrast, favorable climates in humid and temperate regions appeared to support neutral and negative relationships. The lower demand for material resources makes it easier for actors to increase biodiversity evenly across the city or specifically in lower SES areas. There are also important combinatorial patterns concerning taxonomic group, native status, and aridity. For example, higher SES areas in arid cities tend to feature higher native animal diversity and lower exotic animal diversity. Humid cities often show the opposite pattern, in which higher SES areas feature greater exotic animal species diversity. These contrasting trends may be related to different yard typologies in arid versus humid cities. In the former city type, higher SES residents tend to plant native plant species, while in the latter, tend to plant exotic plant species.

4.1.4. Some study designs more often detect inequality in biodiversity distribution than others

When researchers inform their sampling with SES, they may be more likely to observe systematic differences in biodiversity across SES groups. Indeed, the majority of neutral relationship cases were observed when sampling was not informed by SES. This finding may reflect a publication bias (*i.e.*, if SES-informed sampling indicates a SES-driven hypothesis and researchers find no SES influence, those results are less likely to be reported) or conversely that stratifying by SES may elevate type II errors. Regardless, while unequal biodiversity distributions may exist in any city, our ability to detect and understand such patterns may be limited by the study designs employed (see Box 1).

Box 1
Strategies for addressing research needs identified by the meta-analysis.

Research Needs	Strategy
Clarify mechanism.	Collect information about presence, absence, or quality of intermediate features that link SES and biodiversity (e.g., expensive bird food, paying for irrigation, yard size…)
Facilitate theory-building.	Link mechanisms to precise characterizations of cities (*e.g.*, colonial history, rapid growth, city age, informal settlements, zoning frameworks, residential turnover, available lawn care services, winter temperatures, housing/population density gradients…)
Facilitate comparisons.	Collect/report SES and biodiversity data in a similar way to others focusing on the region or taxonomic group (*e.g.*, median household income, measure of deprivation, species richness, alpha diversity…)
Expand coverage.	Consider a wider diversity of cities (*e.g.*, developing, super young, high latitudes, the Pacific Islands, North Africa, the Middle East, Asia) Consider taxa beyond birds and woody plants (*e.g.*, herbaceous plants, herpetofauna, invertebrates, mammals, also fish, fungi, and microbes…)
Increase detectability.	Ensure that sampling occurs along a wide enough SES gradient for effectively capturing the range of situations across the city.
Consider human or conservation outcomes.	Measure health, well-being, or conservation outcomes associated with SES-biodiversity relationships (*e.g.*, prevalence of nuisance or hazard species, charismatic species, rare or specialist species…)

4.2. The complexity of spatial scale

One particularly challenging element of the meta-analysis was that the spatial scale of sampling varied in complex ways across the studies (see Sections 2.1 and 2.2). Critically, since data for most causal conditions were coded at the level of an entire city, heterogeneities within cities may be obscured in the analysis. For example, characterizing an entire municipality as either 'dense' or 'sparse' ignores density gradients that occur within cities and that might or might not align with SES gradients, thereby shaping outcomes for SES-biodiversity relationships. While we accounted for some of this complexity through the careful alignment of the density condition with the sampling area for each case (Table S1), the existence of density gradients could not be rigorously assessed and compared across cases for this analysis. The recurring importance of density in our recipes suggests this is an important next step for research. That is, there is a need for spatially explicit, quantitative analyses that address the relationships among housing or population density, SES, and biodiversity.

4.3. Opportunities for further study

A key future goal for researchers should be to clarify the mechanisms that shape biodiversity and are related directly to SES. Biological communities do not respond directly to human SES but rather to the absence, presence, or quality of some intermediate resource, feature, or condition connected to SES (Fig. 1). Most case authors, when justifying their inclusion of SES variables in their analyses, acknowledged that SES proxied for other, challenging-to-measure, features. If authors did find a relationship between SES and biodiversity, they often speculated about those unmeasured mechanisms. Moving forward, researchers should focus on these mechanisms explicitly. Relatedly, researchers would benefit from more precise characterizations of cities regarding conditions that may link socioeconomic inequality with biodiversity. For example, Silva, García, Estay, Barbosa, and Chapman (2015) suggested that non-municipal green space plays an important role in supporting bird diversity widely across Latin American cities. While this regional characterization may indeed be useful, the relevant underlying mechanisms might instead be both shared among Latin American cities and found elsewhere. There are numerous other conditions that may provide useful insights about underlying mechanisms, such as the role of high and low temperatures (Jenerette et al., 2016; Kendal et al., 2012), where individuals with high or low SES end up living (e.g., on the urban periphery or in the downtown core), and the means through which individuals obtain plants or wildlife resources (Torres-Camacho et al., 2017).

In addition, researchers should consider a wider diversity of taxonomic groups and geographic locations in future studies. The majority (82%) of cases we found concerned either woody plants or birds and only one case concerned indoor biodiversity (*i.e.*, arthropods; Leong, Bertone, Bayless, Dunn, & Trautwein, 2016) despite the fact that individual residents often have considerably more control over this aspect of their landscape. Biodiversity on non-residential land uses also requires further investigation as residents have the least control over these spaces. The biodiversity of ponds, public parks, cemeteries, community gardens, forest fragments, and other types of urban commons is likely influenced by a more heterogeneous set of actors and features a more blurred distinction between the private and public and the formal and informal (Seto, Sánchez-Rodríguez, & Fragkias, 2010; Sletto & Palmer, 2017). Regarding city conditions, there is an urgent need to understand how SES-biodiversity relationships unfold in *developing* countries (only 23% of cases occurred in developing cases). The research and publication bias favoring very highly developed countries exacerbates the already wide knowledge gap concerning the drivers of biodiversity in developing countries (Aronson et al., 2016; Botzat, Fischer, & Kowarik, 2016; Chamberlain et al., 2019). Future research should also consider cities undergoing development in recent decades. Most cities included in our meta-analysis were rather old, with only two cities undergoing urbanization post-1950. Yet global urban development has increased in pace since 1950, accompanied by changes in urban form and location. It is possible that newer urban centers, primarily in Asia and Africa, show different SES-biodiversity relationships compared with those we considered in our meta-analysis (Seto et al., 2010). In addition, there were large swatches of the globe without case representation (Fig. 3).

For both the plant and animal analyses, there were key combinations of conditions captured by few, if any, available cases. Critically, there was only one animal case in a *developing* country city (Belo Horizonte, Brazil), and all *ARID* animal cases occurred in the southwestern US and were further characterized as *sparse*, *DEVELOPED* and *UNEQUAL*. These coverage issues could be resolved by either expanding investigations to new cities or conducting analyses in cities where research has already taken place (for recommendations, see Appendix F). Among our 34 cities, 20 were each only represented by one case (24% of total cases) while two cities, Phoenix and Chicago, were together represented by 25 cases (30% of total cases). The diversity of cases in these two cities allowed us to explore how different taxonomic groups, land uses, and study designs led to different patterns.

Overall, a greater quantity and diversity of studies that consider SES-related mechanisms in shaping urban biodiversity is needed. Just as we found that positive SES-biodiversity relationships were most common, it is possible that the body of research and theory highlighting such relationships has exerted a publication bias limiting our theoretical understanding of how non-positive relationships come to be. Indeed, we had the lowest solution coverage for the negative, and to a lesser extent neutral, analysis, suggesting there may be causal conditions we did not consider. As more studies include considerations of SES in their designs, we may gain important insights into the drivers of neutral and negative relationships. See Box 1 for an overview of strategies to address research needs identified by the meta-analysis.

4.4. Implications

When socioeconomic inequality converges with disparities in biodiversity, there are material consequences for a city's people, plants, and animals. First, residents with lower SES living in lower biodiversity settings could receive fewer ecosystem services, including health and well-being outcomes (Cilliers et al., 2013; Sandifer et al., 2015; Schwarz et al., 2017; Turner, Nakamura, & Dinetti, 2004). Second, unequal biodiversity distribution across the city implies pockets of low biodiversity, which may challenge the persistence of certain uncommon species or biological communities (Bonnington, Gaston, & Evans, 2015; Lepczyk et al., 2017). That these pockets may be socioeconomic in nature makes them more dynamic and challenging to manage. While promoting biodiversity may appear straightforward with the right interventions (Aronson et al., 2017; Savard, Clergeau, & Mennechez, 2000), we propose that unequal biodiversity distribution is not simply an ecological problem to solve but rather an ecological manifestation of social inequality. Different histories of urban development will shape these inequalities in different ways, be it through unequal access to material resources, public services, or municipal investments, thus demanding different solutions.

We nonetheless suggest three strategies to address convergence between biodiversity and SES. First and foremost, cities and countries could aggressively work to reduce socioeconomic inequality, which, beyond its frequent association with biodiversity differences across the city, often results in other negative effects (United Nations, 2015). Second, cities could engage in more participatory and inclusive approaches to conserving or promoting biodiversity that incorporate the needs, goals, and objectives of local residents (Krasny, Lundholm, Shava, Lee, & Kobori, 2013; Silva & Krasny, 2016). Meanwhile, cities could reduce barriers for residents to increase biodiversity where they live by subsidizing the cost of native plants or those that benefit animal

specialists and by re-evaluating policies that may restrict biodiversity-friendly activities (Lerman et al., 2012). These approaches can help empower residents to make neighborhoods as a whole more biodiverse and to align these changes with residents' preferences (Belaire, Whelan, & Minor, 2014). Finally, cities could expand and protect high quality public green spaces for native plant and animal diversity in lower SES areas (Chamberlain et al., 2019; McKinney, 2002). Such progressive urban planning can help mitigate inequality and its biodiversity effects, and in some cases provide additional ecosystem services to lower SES residents, for example through community gardens (Cilliers et al., 2018). Studies in sub-Saharan Africa have shown, however, that stakeholders are often not aware of the benefits of urban green spaces (Girma, Terefe, Pauleit, & Kindu, 2019) and that targeted greening and conservation rarely happen, especially in informal settlements (Roy, Shemdoe, Hulme, Mwageni, & Gough, 2018). When targeted greening does occur, it can sometimes have negative effects, such as an increase in ecosystem disservices or a rise in property values that displace original residents (Cilliers & Cilliers, 2015; Wolch et al., 2014). The alternative (*i.e.*, status quo) may not be much better. We found that municipal decisions often increased inequality in biodiversity distribution in the form of street tree plantings in wealthier neighborhoods (Recipe Sets A and B) and greenspaces near wealthier areas that supported animal diversity (Recipe Set U). Instead, progressive urban planning can reduce inequality but demands the intentional marshalling of resources and political will, as well as the use of participatory processes (Girma et al., 2019).

As the global urban population grows, we must look toward the future and consider how urban growth scenarios will impact both biodiversity and socioeconomic inequality (Seto, Guneralp, & Hutyra, 2012). Many cities are located in biodiversity hotspots and cities in general are responsible for habitat fragmentation, species extirpations, and ultimately biodiversity loss. As cities expand, different conservation strategies are needed depending on the nature of potential biodiversity impact and the governance capacity (Huang, McDonald, & Seto, 2018). Especially for peri-urban communities, informal settlements on the formal boundaries of cities, or areas with intact remnant vegetation, careful urban growth should attempt to maintain biotic communities while accommodating human needs. Sometimes there will not be an ideal growth scenario (Sushinsky, Rhodes, Shanahan, Possingham, & Fuller, 2017), but with a more nuanced and global understanding of how biodiversity and socioeconomic inequality converge in cities, we can better address inequality of nature experiences now and in the future while at the same time promoting biodiversity conservation and urban sustainability.

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Appendix A. Supplementary data

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