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Urbanization is not associated with increased abundance or decreased richness of terrestrial animals - dissecting the literature through meta-analysis

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Abstract The widely accepted consensus is that urbanization increases abundance but reduces species richness of animals. This assumption is the premise for empirical tests and theoretical explanations. We studied the association of urbanization with abundance and species richness of different animal taxa in 20 and 26 published articles reporting abundances and richness, respectively via meta-analysis. Because some articles had multiple estimates, we analyzed 40 and 58 estimates of abundance and richness, respectively. Contrary to conventional wisdom, the overall abundance of terrestrial animals was not higher in urban areas, but instead actually lower, while we failed to confirm the conventional thinking of lower species richness with

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urbanization. These findings cannot, however, be generalized across all cities and animal species, as conflicting differences were reported among geographical regions, animal taxa. Our results question the conventional wisdom that urbanization generally increases abundances while reducing species richness, and highlights the variability of urbanization effects on diversity among taxa and geographic regions.

Keywords Species richness · Abundance · Cities · Urbanization · Meta-analysis

Introduction

Urbanized areas are a rapidly expanding habitat type worldwide, as the world's population shifts disproportionately to cities (Grimm et al. 2008). Urbanization brings about dramatic changes to land use as croplands, old fields, forests, and natural areas give way to cities and suburbs and their buildings, roads, airports, gardens, and parks (Faeth et al. 2005). About 3 % of the world's land area is now urbanized, but the effects of urbanization on climate, resources, pollution, and biodiversity extend far beyond the areal boundaries of cities (Grimm et al. 2008).

Within urban habitats, biological communities are dramatically altered in terms of species composition, abundances, richness and evenness (e.g., Shochat et al. 2010). The widely accepted consensus is that human activities in urbanized areas result in a reduction in species richness, evenness and diversity of animals whilst abundances of these same animals is thought to increase (e.g. Marzluff 2001; Marzluff and Ewing 2001; Chace and Walsh 2006; Grimm et al. 2008; Shochat et al. 2010). The pattern of decreased species richness but increased abundances is thought to be particularly evident for birds (Chace and Walsh 2006; McKinney 2008; Shochat et al. 2010) and, to a lesser extent, for arthropods (Raupp et al. 2010; Faeth et al. 2011), two of the most frequently studied groups in urban studies.

Explanations for reduced richness in cities compared to wildlands include habitat loss and fragmentation (McKinney 2008), applications of island biogeography theory (Faeth and Kane 1978; Niemelä 1999; Marzluff 2005), the intermediate disturbance hypothesis (Connell 1978), the disturbance-stress hypothesis (Menge and Sutherland 1987), metapopulation and metacommunity theory (Leibold et al. 2004), and socio-ecological theory (Swan et al. 2011) – all with varying levels of support (e.g., Swan et al. 2011; Faeth et al. 2011).

The pattern of species richness decline while abundances increase as a result of urbanization, termed *the density-diversity paradox* (Shochat et al. 2010), is perplexing, because richness is generally expected to increase as the number of individuals increase in biological communities (e.g., Srivastava and Lawton 1998; Chiari et al. 2010). One explanation for the increased abundance and decreased richness of animal species in cities is that synanthropic urban species outcompete and exclude native species (Shochat et al. 2010). These urban generalists increase in numbers due to their competitive superior abilities, human subsidized food resources, and lowered predation pressure in cities relative to wildlands, and thus decrease community evenness (Shochat et al. 2010).

However, theoretical explanations for patterns of diversity and abundance in cities, and ensuing empirical tests of the explanations, may be premature if these patterns are either not real or not consistent across cities that are typically characterized by enormous heterogeneity. For no obvious reason, traditional literature surveys have been preferred over systematic reviews in attempts to reveal the overall trends of the effects of urbanization on diversity of

animals. Out of 16 published articles we found that review diversity effects of urbanization on animals, only three (McKinney 2006, 2008; Niemelä and Kotze 2009) are based on some statistical analyses. To our knowledge, meta-analysis has not been used to examine the overall trends in the literature.

We studied the association of urbanization with abundance and species richness of different animal taxa in published articles via meta-analysis. We asked if there is a general pattern of associations of urbanization with abundance and species richness and if these associations vary among animal taxa (mammals, birds and arthropods) and land use type (urban compared to wildland, agriculturally-managed and suburban/exurban areas). We also compared the association between urbanization with abundance and species richness of animals in different climate zones and compared the findings between European cities and cities in the USA. Based on previous review articles (e.g., McKinney 2008; Raupp et al. 2010; Shochat et al. 2010; Faeth et al. 2011), we expected that species richness would be lower and the abundances of terrestrial animals would be higher in urbanized areas compared to other areas. In addition, we expected that the effects on species richness and abundance to vary in different climatic regimes (Faeth et al. 2011). Furthermore, we hypothesized that the associations of urbanization with abundances and species richness of animals are more negative in the USA than in Europe, because cities in the USA tend to be younger and expanding into forest/native habitats while European cities tend to be older and expand into agricultural land (Sattler 2011).

Literature survey and meta-analysis

Web of Science database was used to identify articles with abstracts containing words "urban", "ecology" and "biodiversity" in June 2013. Each paper was examined to see if it contained information about changes in abundance (representation of a species in a particular landscape usually measured as the number of individuals found per sample) or species richness (a count of species within a particular landscape usually measured as the number of species found per sample) related to urbanization. Articles that reported species richness or abundance (number of individuals) data of terrestrial animals along some gradient of urbanization were selected. Only studies including paired comparisons of non-urban and urban parameters were considered. These studies used the same methodology over a similar time period at the same scales in both non-urban and urban landscapes. The final data set included in the statistical synthesis consisted of 31 published articles (Table 1). The climate zone of each study location was either self-identified in the papers or was obvious from the city locations.

Table 1 The articles included in the statistical synthesis presenting the association among urbanization and a) abundance, b) species richness and c) both abundance and species richness of terrestrial animals

a) Bergh et al. 2009; Dickman and Doncaster 1989; Møller 2011; Sumoski et al. 2009; Walker and Schochat 2010

b) Clergeau et al. 2001; Coleman and Barclay 2012; Gagné and Fahrig 2010b; Kozlov and Zvereva 1997; Kudavidanage et al. 2012; Magura et al. 2010; MacGregor-Fors et al. 2010; Menke et al. 2011; Reis et al. 2012; Sattler et al. 2011; Öckinger et al. 2009

c) Banville and Bateman 2012; Buczkowski and Richmond 2012; Gagné and Fahrig 2010a; Hornung et al. 2007; Lessard and Buddle 2005; McIntyre et al. 2001; McKinney et al. 2011; McKinney and Paton 2009; Niemelä et al. 2002; Rango 2005; van Rensburg et al. 2009; Sandström et al. 2006; Smith and Chow-Fraser 2010; Su et al. 2011; Tóthmérész et al., 2011

Fig. 1 Estimated standardized mean differences (Hedge' g) and 95 % confidence intervals for abundances of ▶
animals for each study and the overall mean difference. A negative estimate means the study reported lower
abundance and a positive estimate means that the study reported higher abundance in urban areas compared to
non-urban areas. The size of the box indicates the weight assigned to that study in determining the overall mean
difference

Land use types in each paper were divided into the following categories: "urban",
"suburban/exurban", "agricultural" and "wildland". The papers included in the meta-analysis
presented at least one dual comparison. The included articles provided variable details
of definition on the urban habitat investigated; 10 out of the total number of 31
articles did not provide any definition on how the urban habitat had been defined. In
the rest of the selected articles the categories were based on a) the proportion of
impervious surface (PIS): urban (PIS > 50 %), suburban (20 % < PIS < 50 %) and
rural (PIS <20 %) defined by McKinney 2002 and/or b) building density. In the latter
category of articles, the urban classification included all landscapes in which buildings
dominated, including commercial, industrial and residential built-up areas with apart-
ment houses, offices and small amount of green space (e.g., small gardens, parks and
small urban woods). The suburban/exurban class included all landscapes that included
single family residential areas, apartment complexes with pathways, parks and roads. The rural
class was further divided into agricultural and wildland classes. Agricultural class included
farmlands with nearby natural areas, grasslands, semi-natural meadows and arable lands.
Wildland class included areas with natural vegetation with low human disturbance. We want
to emphasize that the definitions provided varied between research papers, presumably
reflecting regional, national or cultural differences and therefore the description provided by
McKinney (2002) only provides a wide framework for the definition of different classes.

Based on the original data provided in the included papers, for each paper we estimated an
effect size between urbanized and other areas using standardized mean differences, which can
be considered comparable across studies (Hedges and Olkin 1985). However, since the
standardized mean difference estimates can be biased in small samples, they were corrected
to remove bias (Hedges 1981. A random effects model was used, because all studies are not
expected to estimate a common effect size (Boronstein et al. 2009) due to markedly variable
city locations, conditions and research methods applied in individual studies. Several papers
reported multiple comparisons of urbanization and surrounding areas, compared several
taxonomic animal groups or had included several cities in different countries. Thus, we
investigated the need to incorporate a multilevel structure to the model. The multilevel model
essentially treats each paper with multiple estimates as a "cluster" of repeated observations,
and allows the model to account for dependencies between such estimates. For the purposes of
estimating overall mean differences, in the multilevel model each cluster supplies one input,
the same as papers with only one estimate. We found that variation between papers was large
compared to that for different estimates within the same paper, with intraclass correlations
close to 0.90 for both species abundance and richness, and thus employed a multilevel model.
This model was first used to estimate an overall mean difference between urban areas and non-
urban areas and compute estimates of heterogeneity using all papers. *P*-values for the test that
the average difference for the population of studies was nonzero were calculated, as were 95 %
confidence intervals for the average difference. Chi-square tests based on Cochran's *Q* statistic
(Viechtbauer 2007) were used to assess evidence of heterogeneity. Next, covariates
representing taxon, geographic location, climate and type of non-urban area were added to
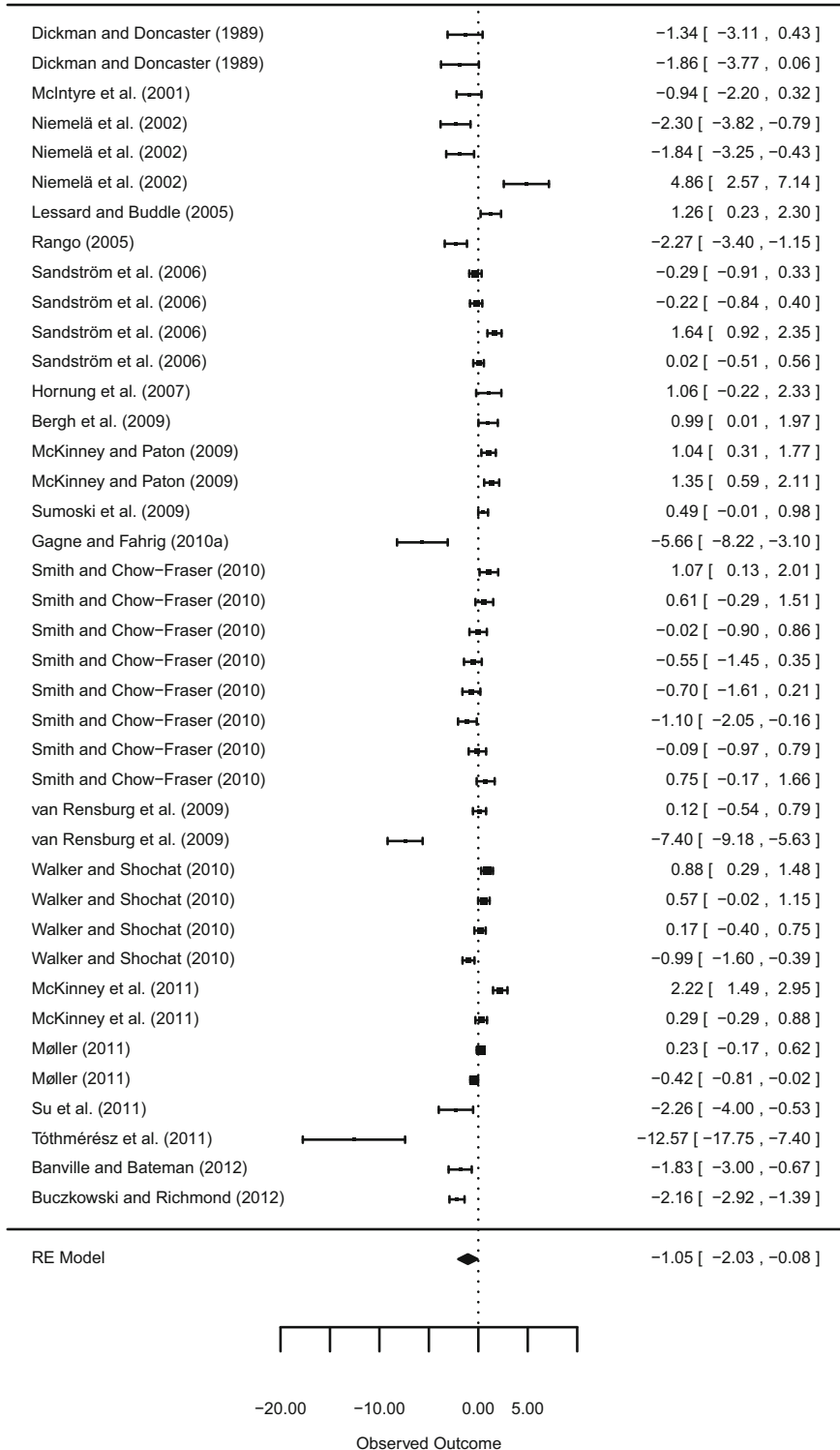
Dickman and Doncaster (1989)	−1.34 [−3.11 , 0.43]
Dickman and Doncaster (1989)	−1.86 [−3.77 , 0.06]
McIntyre et al. (2001)	−0.94 [−2.20 , 0.32]
Niemelä et al. (2002)	−2.30 [−3.82 , −0.79]
Niemelä et al. (2002)	−1.84 [−3.25 , −0.43]
Niemelä et al. (2002)	4.86 [2.57 , 7.14]
Lessard and Buddle (2005)	1.26 [0.23 , 2.30]
Rango (2005)	−2.27 [−3.40 , −1.15]
Sandström et al. (2006)	−0.29 [−0.91 , 0.33]
Sandström et al. (2006)	−0.22 [−0.84 , 0.40]
Sandström et al. (2006)	1.64 [0.92 , 2.35]
Sandström et al. (2006)	0.02 [−0.51 , 0.56]
Hornung et al. (2007)	1.06 [−0.22 , 2.33]
Bergh et al. (2009)	0.99 [0.01 , 1.97]
McKinney and Paton (2009)	1.04 [0.31 , 1.77]
McKinney and Paton (2009)	1.35 [0.59 , 2.11]
Sumoski et al. (2009)	0.49 [−0.01 , 0.98]
Gagne and Fahrig (2010a)	−5.66 [−8.22 , −3.10]
Smith and Chow−Fraser (2010)	1.07 [0.13 , 2.01]
Smith and Chow−Fraser (2010)	0.61 [−0.29 , 1.51]
Smith and Chow−Fraser (2010)	−0.02 [−0.90 , 0.86]
Smith and Chow−Fraser (2010)	−0.55 [−1.45 , 0.35]
Smith and Chow−Fraser (2010)	−0.70 [−1.61 , 0.21]
Smith and Chow−Fraser (2010)	−1.10 [−2.05 , −0.16]
Smith and Chow−Fraser (2010)	−0.09 [−0.97 , 0.79]
Smith and Chow−Fraser (2010)	0.75 [−0.17 , 1.66]
van Rensburg et al. (2009)	0.12 [−0.54 , 0.79]
van Rensburg et al. (2009)	−7.40 [−9.18 , −5.63]
Walker and Shochat (2010)	0.88 [0.29 , 1.48]
Walker and Shochat (2010)	0.57 [−0.02 , 1.15]
Walker and Shochat (2010)	0.17 [−0.40 , 0.75]
Walker and Shochat (2010)	−0.99 [−1.60 , −0.39]
McKinney et al. (2011)	2.22 [1.49 , 2.95]
McKinney et al. (2011)	0.29 [−0.29 , 0.88]
Møller (2011)	0.23 [−0.17 , 0.62]
Møller (2011)	−0.42 [−0.81 , −0.02]
Su et al. (2011)	−2.26 [−4.00 , −0.53]
Tóthmérész et al. (2011)	−12.57 [−17.75 , −7.40]
Banville and Bateman (2012)	−1.83 [−3.00 , −0.67]
Buczkowski and Richmond (2012)	−2.16 [−2.92 , −1.39]
RE Model	−1.05 [−2.03 , −0.08]

−20.00   −10.00   0.00 5.00

Observed Outcome

Fig. 2 Estimated standardized mean differences (Hedge' g) and 95 % confidence intervals for species richness of ▶ animals for each study and the overall mean difference. A negative estimate means the study reported lower richness and a positive estimate means that the study reported higher richness in urban areas compared to non-urban areas. The size of the box indicates the weight assigned to that study in determining the overall mean difference

the model and assessed to determine if these helped to reduce unexplained variability, and Q chi-square tests were used to assess evidence that the covariates significantly reduced amount of heterogeneity. Where sufficient sample sizes allowed, separate mean difference estimates were obtained for subpopulations defined by the covariates, and again p-values and 95 % confidence intervals for the average difference calculated. Restricted maximum likelihood was used to estimate model parameters in each case.

Publication bias was assessed by examining funnel plots, computing rank correlation (using Kendall's tau statistic) tests, and calculating fail-safe estimates. Sensitivity of the results to extreme estimates was also examined. Finally, we checked to see if restricting the analysis to studies with a detailed definition of urban classes affected the results. The metaphor package (Viechtbauer 2010) in the R software environment (R Core Team 2014) was used for all analyses.
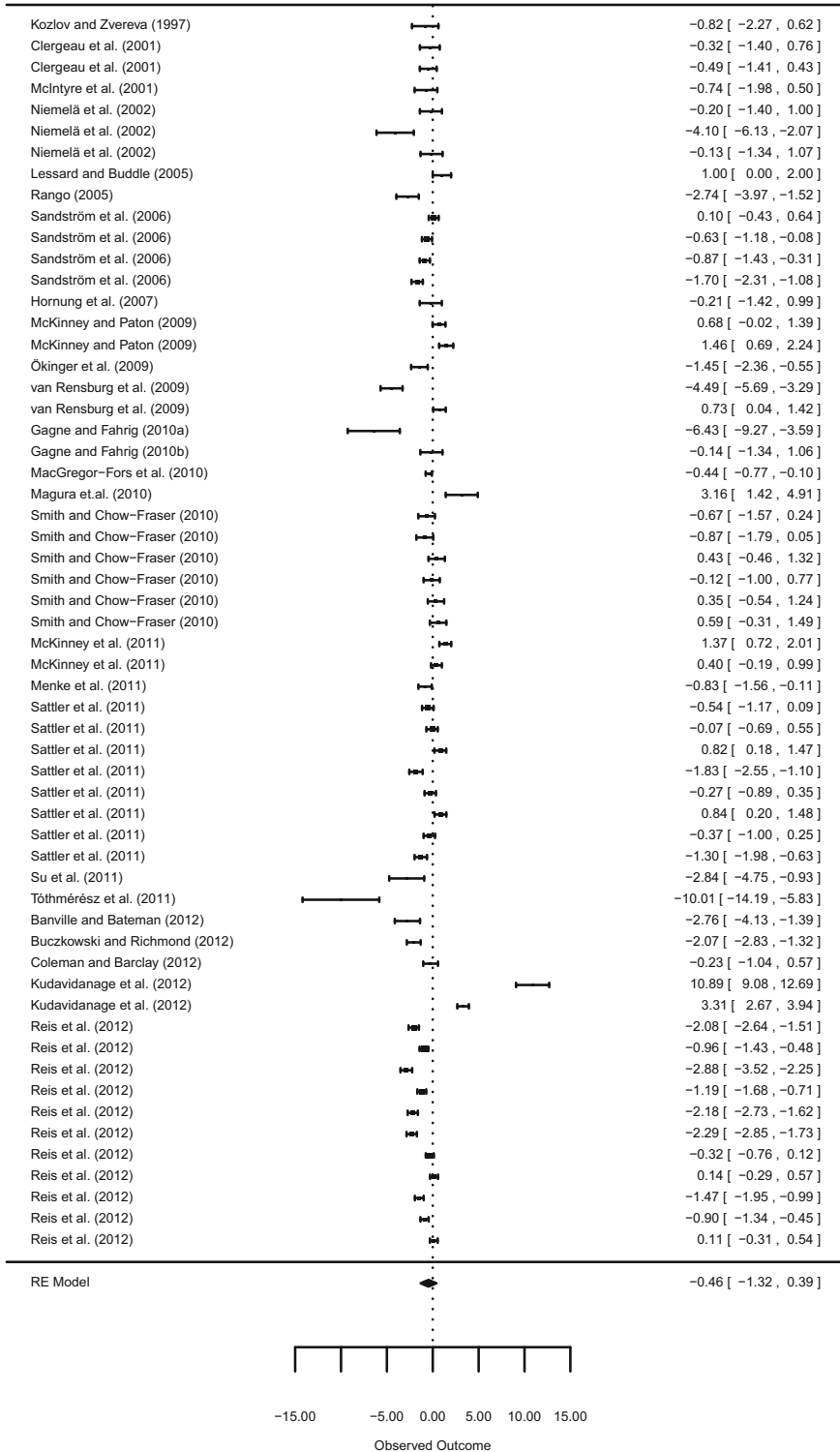
Results

Abundance

Urbanization was associated with lower overall abundance of terrestrial animals ($n = 40$, $g = -1.05$, $p = 0.034$, 95 % CI: -2.03, -0.08) (Fig. 1). There was strong evidence of unexplained between-study heterogeneity ($Q(39\ df) = 351.7$, $p < 0.001$). Covariates representing taxon, geographic location, climate and type of non-urban area, as well as all first-order interactions, were introduced into the model, indicating the need account for dependencies between estimates from the same paper. Thus, the results we report below are based on the multilevel model.

We first investigated the need to account for interaction between covariates. Since only the interaction between taxon and geographic area was statistically significant, other interaction terms were dropped from the model. The covariates accounted for a significant amount of heterogeneity ($Q(12\ df) = 39.2$, $p < 0.001$), although there was still significant unexplained heterogeneity ($Q(27\ df) = 195.1$, $p < 0.001$). Studies conducted in Europe ($g = -6.39$, $p < 0.001$, 95 % CI:-8.74, 4.05) and in particular European studies on arthropods ($g = -4.13$, $p = 0.006$, 95 % CI:-7.10, 1.16) tended to report lower abundance in urban areas (Fig. 2).

Species richness

The studies suggested that urbanization was associated with lower overall species richness of terrestrial animals, although the association was not statistically significant ($n = 58$, $g = -0.46$, $p = 0.289$, 95 % CI:-1.32, 0.39) (Fig. 3). As in the case of species abundance, there was a substantial amount of unexplained between study heterogeneity ($Q(57\ df) = 847.2$, $p < 0.001$). As before, since only the interaction between taxon and geographic was statistically significant, the other interaction terms were dropped from the model and the model refit. The covariates accounted for a
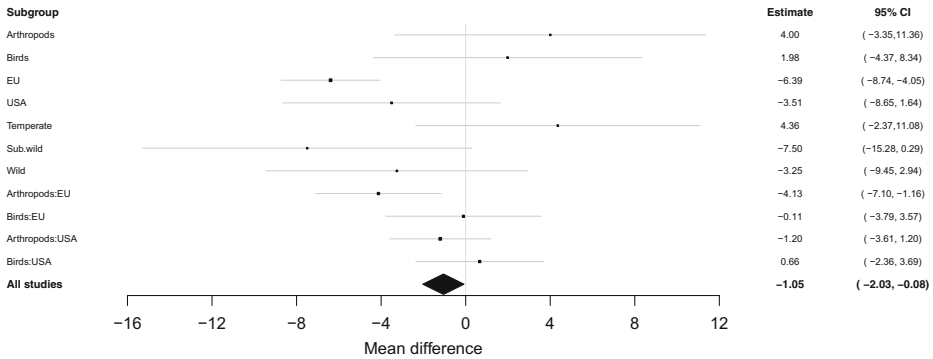
Study		Observed Outcome
Kozlov and Zvereva (1997)		−0.82 [−2.27 , 0.62]
Clergeau et al. (2001)		−0.32 [−1.40 , 0.76]
Clergeau et al. (2001)		−0.49 [−1.41 , 0.43]
McIntyre et al. (2001)		−0.74 [−1.98 , 0.50]
Niemelä et al. (2002)		−0.20 [−1.40 , 1.00]
Niemelä et al. (2002)		−4.10 [−6.13 , −2.07]
Niemelä et al. (2002)		−0.13 [−1.34 , 1.07]
Lessard and Buddle (2005)		1.00 [0.00 , 2.00]
Rango (2005)		−2.74 [−3.97 , −1.52]
Sandström et al. (2006)		0.10 [−0.43 , 0.64]
Sandström et al. (2006)		−0.63 [−1.18 , −0.08]
Sandström et al. (2006)		−0.87 [−1.43 , −0.31]
Sandström et al. (2006)		−1.70 [−2.31 , −1.08]
Hornung et al. (2007)		−0.21 [−1.42 , 0.99]
McKinney and Paton (2009)		0.68 [−0.02 , 1.39]
McKinney and Paton (2009)		1.46 [0.69 , 2.24]
Ökinger et al. (2009)		−1.45 [−2.36 , −0.55]
van Rensburg et al. (2009)		−4.49 [−5.69 , −3.29]
van Rensburg et al. (2009)		0.73 [0.04 , 1.42]
Gagne and Fahrig (2010a)		−6.43 [−9.27 , −3.59]
Gagne and Fahrig (2010b)		−0.14 [−1.34 , 1.06]
MacGregor−Fors et al. (2010)		−0.44 [−0.77 , −0.10]
Magura et al. (2010)		3.16 [1.42 , 4.91]
Smith and Chow−Fraser (2010)		−0.67 [−1.57 , 0.24]
Smith and Chow−Fraser (2010)		−0.87 [−1.79 , 0.05]
Smith and Chow−Fraser (2010)		0.43 [−0.46 , 1.32]
Smith and Chow−Fraser (2010)		−0.12 [−1.00 , 0.77]
Smith and Chow−Fraser (2010)		0.35 [−0.54 , 1.24]
Smith and Chow−Fraser (2010)		0.59 [−0.31 , 1.49]
McKinney et al. (2011)		1.37 [0.72 , 2.01]
McKinney et al. (2011)		0.40 [−0.19 , 0.99]
Menke et al. (2011)		−0.83 [−1.56 , −0.11]
Sattler et al. (2011)		−0.54 [−1.17 , 0.09]
Sattler et al. (2011)		−0.07 [−0.69 , 0.55]
Sattler et al. (2011)		0.82 [0.18 , 1.47]
Sattler et al. (2011)		−1.83 [−2.55 , −1.10]
Sattler et al. (2011)		−0.27 [−0.89 , 0.35]
Sattler et al. (2011)		0.84 [0.20 , 1.48]
Sattler et al. (2011)		−0.37 [−1.00 , 0.25]
Sattler et al. (2011)		−1.30 [−1.98 , −0.63]
Su et al. (2011)		−2.84 [−4.75 , −0.93]
Tóthmérész et al. (2011)		−10.01 [−14.19 , −5.83]
Banville and Bateman (2012)		−2.76 [−4.13 , −1.39]
Buczkowski and Richmond (2012)		−2.07 [−2.83 , −1.32]
Coleman and Barclay (2012)		−0.23 [−1.04 , 0.57]
Kudavidanage et al. (2012)		10.89 [9.08 , 12.69]
Kudavidanage et al. (2012)		3.31 [2.67 , 3.94]
Reis et al. (2012)		−2.08 [−2.64 , −1.51]
Reis et al. (2012)		−0.96 [−1.43 , −0.48]
Reis et al. (2012)		−2.88 [−3.52 , −2.25]
Reis et al. (2012)		−1.19 [−1.68 , −0.71]
Reis et al. (2012)		−2.18 [−2.73 , −1.62]
Reis et al. (2012)		−2.29 [−2.85 , −1.73]
Reis et al. (2012)		−0.32 [−0.76 , 0.12]
Reis et al. (2012)		0.14 [−0.29 , 0.57]
Reis et al. (2012)		−1.47 [−1.95 , −0.99]
Reis et al. (2012)		−0.90 [−1.34 , −0.45]
Reis et al. (2012)		0.11 [−0.31 , 0.54]
RE Model		−0.46 [−1.32 , 0.39]

−15.00   −5.00   0.00   5.00   10.00   15.00

Observed Outcome

Fig. 3 Estimated standardized mean differences (Hedge' g) and 95 % confidence intervals for abundance of animals for each subpopulation and the overall mean difference. A negative estimate means the study reported lower abundance and a positive estimate means that the study reported higher abundance in urban areas compared to non-urban areas

statistically significant reduction in heterogeneity ($Q(20\ df) = 84.7$, $p < 0.001$), although there was still significant unexplained heterogeneity ($Q(37\ df) = 360.5$, $p < 0.001$). European studies tended to report lower species richness ($g = -2.87$, $p = 0.009$, 95 % CI:-5.03, −0.72) (Fig. 4).

Publication bias

First we consider the model without covariates. There was some tendency for studies finding evidence of higher abundance in urban areas to have greater precision ($tau = -0.26$, $p = 0.016$) (Fig. 5). For species richness, the funnel plot (Fig. 6) did not exhibit obvious asymmetry ($tau = -0.05$, $p = 0.566$), although there was a great deal of variability in study estimates apparent.

Overall there appears to be more balance in the precision of studies reporting higher abundance and those reporting lower abundance, although there is still evidence that more studies found higher abundance ($tau = -0.26$, $p = 0.016$) (Fig. 7). For species richness, the funnel plot (Fig. 8) was much improved over the case without covariates, with most studies within the expected range, and again no obvious evidence of asymmetry or bias ($tau = -0.05$, $p = 0.566$).
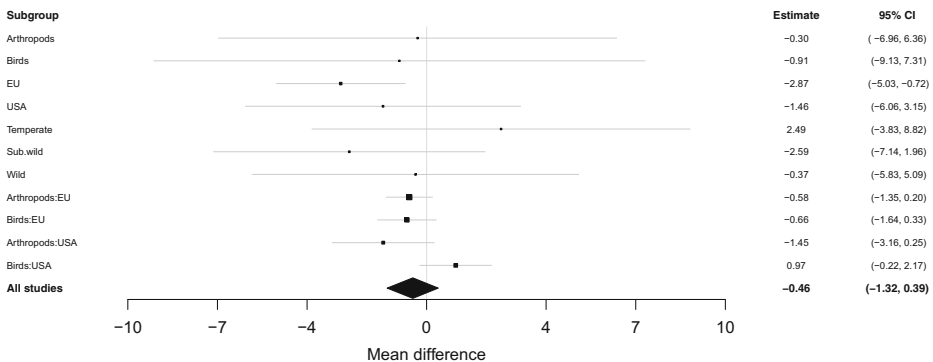
Fig. 4 Estimated standardized mean differences (Hedge' g) and 95 % confidence intervals for species richness for each study and the overall mean difference. A negative estimate means the study reported lower richness and a positive estimate means that the study reported higher richness in urban areas compared to non-urban areas

Fig. 5 Plot of standard error of standardized mean difference versus estimated standardized mean difference, all studies reporting abundance
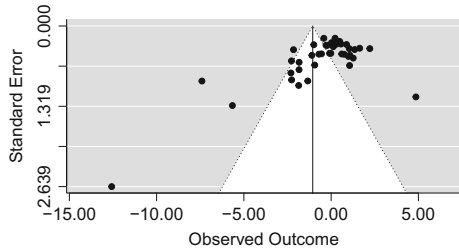

It is sometimes assumed that the lack of inclusion of unpublished studies that did not find differences could be biasing the results. Thus, we calculated Orwin's fail-safe N, which suggested that 40 studies for species abundance and 58 studies for species richness, each with and observed mean difference of 0, would need to be added to the analysis before the respective confidence interval for the overall mean difference would no longer exclude 0. It seems unlikely that that many studies with no observed differences were excluded, although the fail-safe values calculated do not exceed the critical value of $5*n + 10$ (Rosenthal 1995), and according to this rule of thumb publication bias cannot be ruled out.

Sensitivity analysis

Urban definition

Not all studies included a detailed definition of the urban habitat studied. When restricted to studies with detailed definitions for urban classes, while there was still evidence of decreased abundance, the difference was no longer statistically significant ($n = 20$, $g = -0.72$, $p = 0.398$, 95 % CI:-2.38, 0.95). The results for species richness did not depend on whether or not the papers without definitions of urbanization categories were excluded from the analyses.

When restricted to studies with detailed definitions for urban classes, no significant contribution of covariates to reducing heterogeneity was observed.

Effect of outliers

Several studies reported estimated differences that were unusually extreme, relative to most other studies. In particular, Tóthmérész et al. (2011) reported a much larger decrease in both species abundance and richness for urban areas, while van Rensburg et al. (2009) reported a smaller but still relatively large decrease in species richness. On the other hand, Niemelä et al. (2002) and Kudavidanage et al. (2012) reported unusually large increases for urban areas in

Fig. 6 Plot of standard error of standardized mean difference versus estimated standardized mean difference, all studies reporting species richness
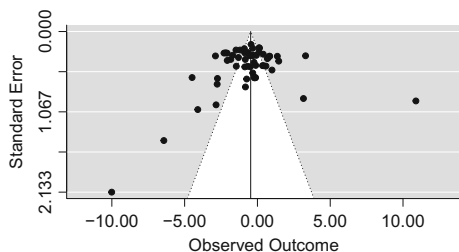
Fig. 7 Plot of standard error of
standardized mean difference
versus residual (difference between
estimated standardized mean
difference and that predicted by
regression model including all
covariates), all studies reporting
abundance
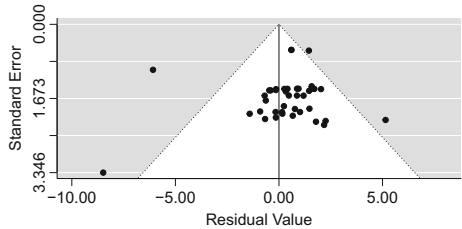
species abundance and species richness, respectively. Thus, estimates were recomputed, omitting one or more of these estimates (Table 2). In all cases, omission of one or more extreme estimates resulted in an estimated difference smaller in magnitude and no longer statistically significant at the 0.05 level.

Discussion

Contrary to conventional wisdom that animal abundances are higher in cities despite lower species richness (Marzluff 2001; Marzluff and Ewing 2001; Chace and Walsh 2006; Grimm et al. 2008; Shochat et al. 2010), our meta-analysis shows that urbanization is associated with decreased overall abundance and may not be associated with overall species richness of terrestrial animals. However, our results also show that these conclusions cannot be generalized across all cities – negative associations for both abundance and species richness of animals were only found in Europe and not in the USA. Furthermore, the sensitivity analyses suggest that the finding of decreased abundance is sensitive to outliers, i.e., while there was still evidence of decreased abundance, the difference was no longer statistically significant when one or two studies that showed unusually large decreases of abundance by urbanization were omitted from the analyses. The statistical evidence of decreased abundance also disappeared when restricting to studies with detailed urban definitions. Our analyses do not consider potential species turnover in urban compared to non-urban areas which might also affect diversity. Despite these limitations, we believe that our results suggest that the widely accepted notion that urbanization results in reduced species richness but increased abundance (the density-diversity paradox, Shochat et al. 2004, 2006) may not generally hold. If so, then the development of conceptual models to explain, and mechanistic experiments to test, the density-diversity paradox may be unnecessary.

Structural, age and development differences between European cities and cities in the USA may explain some of the found variation in results of this meta-analysis. For instance, road systems, transportation and the cityscapes often differ among European and US cities.

Fig. 8 Plot of standard error of
standardized mean difference
versus residual (difference between
estimated standardized mean
difference and that predicted by
regression model including all
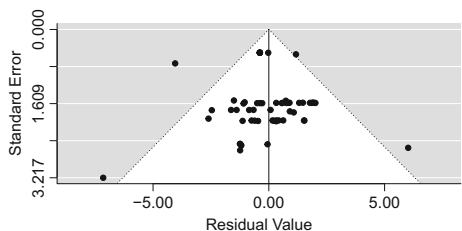covariates), all studies reporting
species richness

Table 2 Estimates of population mean of differences between urban and other types of habitats when certain studies were omitted from the analysis

Studies omitted	Abundance	Richness
None	$g = -1.05$ ($p = 0.034$)	$g = -0.46$ ($p = 0.289$)
Tóthmérész et al. (2011)	$g = -0.79$ ($p = 0.069$)	$g = -0.27$ ($p = 0.500$)
Kudavidanage et al. (2012)	(did not reported abundance)	$g = -0.41$ ($p = 0.320$)
Tóthmérész et al. (2011) and van Rensburg et al. (2009)	$g = -0.69$ ($p = 0.103$)	$g = -0.22$ ($p = 0.539$)
Tóthmérész et al. (2011), van Rensburg et al. (2009) and Niemelä et al. (2002)	$g = -0.83$ ($p = 0.058$)	$g = -0.23$ ($p = 0.539$)

Furthermore, European cities tend to be much older, more densely built, and have less green space than cities in the USA. In general, low to moderate levels of housing density may have neutral or even positive effects on abundances and/or species richness of animals (McKinney 2002). This positive effect of moderate levels of urbanization on abundances and richness has been explained via the intermediate disturbance hypothesis (e.g., Blair and Launer 1997; McKinney 2002), where local species diversity is maximized when ecological disturbance is neither too rare nor too frequent. Furthermore, cities in Europe tend to be surrounded by agriculturally managed areas while cities in the USA are often located close to wildlands. This may contribute to higher arthropod diversity in urban and suburban areas in the USA.

Conventional ecological theories and hypotheses such as productivity-richness theory (e.g. Ricklefs 1973; Abrams 1995), the more individuals -hypothesis (e.g. Srivastava and Lawton 1998; Chiari et al. 2010), habitat loss and fragmentation (McKinney 2008), island biogeography theory (Faeth and Kane 1978; Niemelä 1999; Marzluff 2005), the intermediate disturbance -hypothesis (Connell 1978), the disturbance-stress -hypothesis (Menge and Sutherland 1987), and metapopulation and metacommunity theory (Leibold et al. 2004) may be sufficient to explain how urbanization decreases species richness and abundance of terrestrial animals in Europe. Most of these theories explain how highly fragmented and smaller habitats support lower numbers of species and/or individuals than less fragmented and larger habitats, with varying levels of empirical support collected from urban habitats (e.g., Faeth et al. 2011).

The lack of systematical analysis of the effects of urbanization on species richness and abundance of terrestrial animals may have led to erroneous conclusions and generalizations that are widely accepted and form an unsound foundation for future research. We are not arguing that urbanization does not affect species richness and abundances for specific taxa or taxonomic groups or for specific urban areas. Instead, we argue that previous generalizations about the effects of urbanization on richness and abundances may not hold across cities. Contrary to conventional wisdom, our meta-analysis revealed only negative or neutral associations between urbanization, species richness and abundance of animals. It may be that the effects of urbanization vary so greatly by taxonomic group, geographic region, climatic zone and idiosyncrasies of each city that generalizations about the urbanization and its effects on species richness and abundances are not possible.

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