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Effects of urbanization on species richness: A review of plants and animals

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Abstract Many studies have described the effects of urbanization on species richness. These studies indicate that urbanization can increase or decrease species richness, depending on several variables. Some of these variables include: taxonomic group, spatial scale of analysis, and intensity of urbanization. Recent reviews of birds (the most-studied group) indicate that species richness decreases with increasing urbanization in most cases but produces no change or even increases richness in some studies. Here I expand beyond the bird studies by reviewing 105 studies on the effects of urbanization on the species richness of non-avian species: mammals, reptiles, amphibians, invertebrates and plants. For all groups, species richness tends to be reduced in areas with extreme urbanization (i.e., central urban core areas). However, the effects of moderate levels of urbanization (i.e., suburban areas) vary significantly among groups. Most of the plant studies (about 65%) indicate increasing species richness with moderate urbanization whereas only a minority of invertebrate studies (about 30%) and a very small minority of non-avian vertebrate studies (about 12%) show increasing species richness. Possible explanations for these results are discussed, including the importance of nonnative species importation, spatial heterogeneity, intermediate disturbance and scale as major factors influencing species richness.

Keywords Urban · Biodiversity · Urbanization · Species richness · Anthropogenic

Introduction

Biodiversity plays several important roles in urban environments. These roles include ecosystem services such as air and water purification (Bolund and Hunhammar 1999) and amenity values such as aesthetic enjoyment and recreation (Miller 2005, 2006). In addition, urban biodiversity has an important role in educating an increasingly urban population about nature and species conservation (Miller and Hobbs 2002).

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As urbanization is spreading rapidly across the globe, a basic challenge for conservation is to understand how it affects biodiversity (McKinney 2002). Although urbanization is a major cause of native species extinction (Czech et al. 2000), the complex nature of urban land use can have a complicated influence on local biodiversity. On one hand, some aspects of urbanization promote the loss of species diversity. One of these is a species-area effect: a large expanse of impervious surface in urban areas reduces and fragments the area available for plants and animals. For example, over 80% of most central (downtown) urban areas are covered by pavement and buildings (Blair and Launer 1997), leaving less than 20% as vegetated area. Another negative impact on biodiversity is structural simplification of vegetation in many areas. Landscaping and maintenance of residential and commercial areas typically involves removal of shrubs and dead wood and an increase in grasses and herbs (Marzluff and Ewing 2001). This has a negative impact on the diversity of birds and other animals, whose diversity tends to correlate with vegetative complexity and plant species-richness (Savard et al. 2000).

On the other hand, some aspects of urbanization can promote increasing levels of biodiversity, usually by the addition of nonnative species that replace native species faster than they are lost (McKinney 2002, 2006a). Urban areas have extremely high spatial habitat heterogeneity produced by many different (idiosyncratic) land uses and plant cultivation choices at small spatial scales (Savard et al. 2000; Thompson et al. 2003). This spatial heterogeneity can produce very high levels of beta diversity (Niemelä 1999) and greater species richness than surrounding rural areas (Wania et al. 2006) especially in groups with that require relatively small areas to support viable populations (e.g., plants and insects). In addition, urban habitats often have much greater primary productivity than surrounding areas, due to the importation of water, fertilizers and other limiting factors. A typical sub-urban lawn is a good example (Falk 1976). At least up to a point, increasing productivity often increases biodiversity (Shochat et al. 2006). This productivity effect is enhanced by the importation of vast amounts of processed foods, ranging from garbage to birdseed, that provide food for many urban species (Adams 1994). Yet another factor that can increase urban biodiversity is the very high rate of dispersal of species, especially nonnative species, into urban areas. Human settlements import species (often nonnative species) for several reasons, ranging from the accidental importation by traffic (trucks, planes and ships) associated with centers of commerce to the intentional importation of species for cultivation, pets, and other human uses (Mack and Lonsdale 2001).

A key question in urban ecology is whether the addition of nonnative species associated with urbanization exceeds the loss of native species to produce a net gain in species richness with urbanization. One way to examine this would be to analyze temporal data, e.g., changes in species inventories of a city over time. For example, Tait et al. (2005) show that in the city of Adelaide, Australia, plant species richness has increased by 46% from 1836 to 2002 because plant species introductions have outpaced plant species extinctions. On the other hand, mammals in Adelaide show a net species loss (Tait et al. 2005).

However, such temporal studies in urban areas are rare in the literature, probably because accurate detailed urban inventories are unavailable for long periods. But there are many studies of urban-rural gradients, describing the spatial effects of urbanization on species-richness by examining changes along an intensity gradient (McKinney 2002). Marzluff (2001) compiled a list of urban-rural gradient studies for birds, to examine the effects of urbanization on bird species-richness. Of 51 studies, 31 of the studies (61%) showed lower species richness in urban areas, when compared to more natural rural areas. The remaining 20 studies reported either an increase or no change in species richness with increasing human settlement. A more recent review by Chace and Walsh (2006) concludes that bird species richness generally decreases with urbanization, across a wide range of habitats.

In this paper, I expand the view of urban impacts beyond birds, and review studies on urbanization impacts on the species richness of terrestrial organisms including: plants, mammals, reptiles, amphibians and terrestrial arthropods (mainly insects). Specifically, I will seek to answer three questions. (1) Is there a general pattern of monotonic decrease in species richness with increasing urbanization? (2) Or is there evidence of intermediate disturbance effect whereby species-richness often increases at intermediate levels of urbanization. This latter effect has often been reported for birds (Marzluff 2001), including recent studies by Marzluff (2005) and Leveau and Leveau (2005). (3) Do either of these potential species richness patterns, monotonic decline or intermediate peak with urbanization, vary among taxa? Do plants, for example, show the same pattern as mammals?

Methods

Several search engines were used to identify articles with abstracts containing the words "urban*", "species" and "diversity" or "richness". These search engines included: Web of Science, Biological Abstracts, Zoological Record Plus, and Wildlife & Ecology Studies Worldwide. This search identified over 2,000 articles that were subsequently examined to see if they contained information about changes in species richness with urbanization. Because species richness is by far the most common method of measuring biodiversity in urban ecosystems (as reviewed in many listed papers below), I will focus on species richness here even though it is an incomplete metric of biodiversity that omits species abundance (Magurran 2004). However, in the few studies where abundance is included in diversity metrics, they tend to yield the same patterns as species richness metrics (e.g., Germaine and Wakeling 2001).

For each study, species richness changes were reported along a spatial gradient denoted by three points, representing low, moderate, and high levels of urbanization, as described in each study. My designation of low, moderate and high levels of urbanization was based on the following criteria (following McKinney 2002, Fig. 2). A high level of urbanization was assigned for habitats that represented the urban core. These are mainly "hardscapes" with an area of over 50% impervious surfaces. A moderate level of urbanization was assigned for habitats in suburban areas, i.e., outside the urban core but not including undeveloped or rural areas, usually having 20–50% impervious surface area (McKinney 2002, Fig. 2). A low level of urbanization represented rural or undeveloped areas beyond the suburban fringe, with less than 20% impervious surface area.

For each of the three urbanization levels (low, moderate and high), the corresponding species richness at that intensity is reported as based on the richness values of the original studies. The lowest species richness along the spatial gradient was assigned an ordinal value of "1" and the highest species richness along the gradient was assigned a value of "3". In some cases, species richness at only two points along the gradient are reported in the study so some data are shown as missing. Also, some studies found no significant change in species richness along the gradient so these are shown by the same ordinal value. For example, 1,2,2 indicates that species richness increased going from low to moderate levels of urbanization, with moderate and high levels of urbanization showing about the same species richness.

Statistical analysis of the tabulated data used chi-square tests to examine differences among plants, vertebrates and invertebrates. These looked at differences in the frequencies

Table 1 Low-mid urbanization change

	Increase	Decrease	Same
Plants	+11 (64.7%)	−1 (5.9%)	5 (29.4%)
Vertebrates	+2 (11.8%)	−14 (82.4%)	1 (5.9%)
Invertebrates	+14 (29.8%)	−30 (63.8%)	3 (6.4%)

Number (and percentage) of studies showing increase (+), decrease (−) or no change in species richness going from low to middle levels of urbanization

of reported species richness patterns, such as whether similar proportions of studies reported that plants and vertebrates both tended to increase in species richness at moderate levels of urbanization (=2) relative to low levels of urbanization (=3). Deviations in the chi-square value from the expected null hypothesis therefore indicate that taxa respond differently to urbanization. This statistical test was used because it has the benefit of being nonparametric and therefore does not require the data to be normally distributed and other assumptions of parametric statistics.

Results

I found 105 studies that reported species richness data along a gradient of urbanization. This included: 17 studies for plants, 31 studies for mammals, reptiles and amphibians, and 57 studies for invertebrates. These are tabulated in Appendix as Tables 7, 8, and 9. These studies span a very wide geographic spectrum including urban environments of Asia, North and South America, Europe and Australia.

Summarizing species richness changes along the urban–rural gradient for the three groups indicates that some differences apparently exist among the groups. For the transition from low to moderate urbanization (Table 1), 11 plant studies show an increase in species richness, one study shows a decrease and five show no change in species richness. In contrast, for (non-avian) vertebrates, in the transition from low to moderate urbanization (Table 1), only two studies show an increase in species richness, whereas 14 show a decrease and one shows no change in species richness. Among invertebrates (Table 1), 14 studies show an increase in species richness, 30 show a decrease and three show no change in species richness. Put another way, 64.7% of plant studies show an increase in species richness going from low to moderate levels whereas vertebrates show this for only 11.8% and invertebrates for 29.8% of the studies.

A chi-square analysis of these species richness changes from low to moderate urbanization among the groups (Table 2) indicates highly significant differences among the three groups (χ^2=24.38, 4 *df*, *p* is less than or equal to 0.001). However, if plants are omitted, the distribution is not significant (χ^2=2.25; Table 2), indicating that vertebrates and invertebrates have similar patterns. In contrast, any pairwise comparison that includes

Table 2 Low-mid urbanization change

Taxa	*df*	χ^2	*p*
P,V,I	4	24.38	0.001
P,V	2	20.16	0.001
P,I	2	17.85	0.001
V,I	2	2.25	0.32

Chi-square results of Table 1

P Plants, *V* vertebrates, *I* invertebrates

Table 3 Mid-high urbanization change

	Increase	Decrease	Same
Plants	+0 (0.0%)	−7 (50.0%)	7 (50.0%)
Vertebrates	+0 (0.0%)	−21(100%)	(0.0%)
Invertebrates	+1 (2.6%)	−29 (79.3%)	8 (21.0%)

Number of studies showing increase, decrease or no change in species richness going from middle to low levels of urbanization

plants (plant-vertebrate; plant-invertebrate) produces a chi-square result that is highly significant (p<0.01), indicating a distinct pattern for plants (Table 2).

In the transition from moderate to high urbanization, very few studies show an increase in species richness (Table 3). No plant studies show increasing species richness; seven studies show decreasing species richness and seven show no change. For vertebrates, no studies show increasing species richness, 21 studies show decreasing species richness and 0 show no change. For invertebrates, 1 study shows increasing species richness, 29 studies show decreasing species richness and eight show no change. A Chi-square analysis of these species richness changes from moderate to high urbanization among the groups (Table 4) indicates highly significant differences among the three groups (χ^2=13.87, 4 *df*, *p* is less than or equal to 0.001). However, some of the pairwise comparisons (plants-invertebrates, vertebrates-invertebrates) indicate no significant difference.

For studies that included species-richness data at all three points along the gradient, it was possible to tabulate species-richness "peaks", defined as a point which is higher or lower than other points on the gradient (Table 5). In cases where two points on the gradient are equally high relative to a third point, such as 2,2,1, then these were both designated as "peaks". Plants show a tendency to peak at intermediate levels of urbanization (69.2% of studies) whereas most vertebrate (66.6%) and invertebrate (72.4%) studies tend to show the highest species richness at low levels of urbanization (Table 5, Fig. 1). Chi-square tests of these patterns (Table 6) support the hypothesis of significant differences (χ^2=16.60, 4 *df*, *p* is less than or equal to 0.02). However, if plants are omitted, the distribution is not significant (χ^2=1.11; 2 *df*, *p* is less than or equal to 0.57), indicating that vertebrates and invertebrates have similar patterns (Table 6). Any pairwise comparison that includes plants (plant-vertebrate; plant-invertebrate) produces a chi-square result that is highly significant (p<0.01), indicating a distinct pattern for plants.

Discussion

Any conclusions reached here must have the caveat that urban-rural gradient studies are clearly a simplification of the complex patterns produced by urbanization (Alberti et al. 2001; Hahs and McDonnell 2006). The specific impacts of urbanization on species richness

Table 4 Mid-high urbanization change

Taxa	*df*	χ^2	*p*
P,V,I	4	13.87	0.001
P,V	1	12.59	0.001
P,I	2	4.14	0.13
V,I	2	6.05	0.05

Chi-square results of Table 3

P Plants, *V* vertebrates, *I* invertebrates

Table 5 Number of studies showing a peak in species richness at low, middle and high levels of urbanization

	Low	Mid	High
Plants	1 (7.7%)	9 (69.2%)	3 (23.1%)
Vertebrates	6 (66.6%)	3 (33.3%)	0 (0.00%)
Invertebrates	21 (72.4%)	6 (20.7%)	2 (6.9%)

will vary, depending on such variables as the geographic location of the city (including its natural ecological matrix) and many historical and economic factors that are unique to each city. Also, spatial scale is a factor. Pautasso (2007) showed that human population density is negatively correlated with species richness in studies done at fine spatial scales, but richness is positively correlated with species richness in studies analyzing coarse spatial scales.

A likely cause of this scaling relationship is that, at small (local) spatial scales, increasing human population size (e.g., in highly populated urban core areas) tends to eliminate species via extreme human disturbances in the local vicinity. However, at coarser spatial scales, people have preferentially settled in areas of high biodiversity and have enhanced beta diversity even further with many species introductions and increasing habitat heterogeneity via complex land use patterns (Pautasso 2007). For example, Hogsden and Hutchinson (2004) found that butterfly species richness peaked at moderately disturbed sites when spatial scale was larger (6 ha) and peaked at the least disturbed sites when the scale was smaller (0.75 ha).

Because of the drastic environmental changes produced by urbanization, it is probably expected that many studies, especially those focusing on smaller spatial scales, indicate a tendency to decline in species richness with increasing urbanization. The animal studies examined here (invertebrates and non-avian vertebrates) indicate the most consistent decline with urbanization. This agrees with the review by Marzluff (2001) which showed that most bird studies (61%) indicated a species-richness decline with urbanization intensity (see also Chace and Walsh 2006).

A simple species-area model would predict that the replacement of vegetation by impervious surfaces will reduce animal diversity by the loss of habitable area. Many studies of several taxa confirm that species-area relationships do apply to urban habitats (e.g., Helden and Leather 2004; Cornelis and Hermy 2004). This loss of habitable area for animals is probably enhanced because increasing urbanization also reduces the habitat quality of remaining vegetation. Urbanization intensity correlates with increased disturbance and the structural simplification of remaining vegetation by landscaping practices

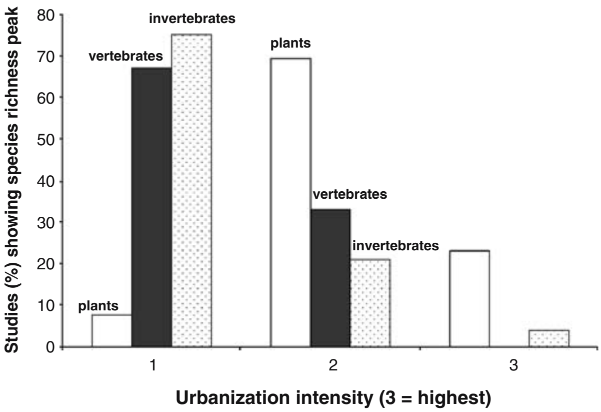

Fig. 1 Percentage of studies, by group, showing species richness peaks at three levels of urbanization (1=lowest level, 3=highest level of urbanization)

Table 6 Species richness peak

Taxa	*df*	χ^2	*p*
P,V,I	4	16.60	0.002
P,V	2	9.15	0.010
P,I	2	15.07	0.001
V,I	2	1.11	0.57

Chi-square results of Table 5

P Plants, *V* vertebrates, *I* invertebrates

that remove woody plants, leaf litter and other microhabitats of natural communities (Marzluff and Ewing 2001). All of these factors combine to reduce habitat area and quality for animals, and these factors tend to increase with urbanization intensity (Alberti et al. 2001; Hahs and McDonnell 2006).

Some studies compiled herein indicate that urbanization sometimes increases species richness, especially at intermediate levels of development. This is especially true with plants (about two thirds of studies show this) but is also significant in invertebrates (about 30% of studies) and a small minority of vertebrates (about 12% of studies). It has been suggested that such increases in species-richness at moderate levels of urbanization are related to the intermediate disturbance hypothesis (Blair and Launer 1997; Germaine and Wakeling 2001). This hypothesis asserts that moderate levels of human disturbance promote the coexistence of many types of species, including early successional native species as well as introduced species. For example, in Berlin, Germany, Zerbe et al. (2003) found that the greatest variety of land uses and plant species richness is in the transition zone between the city center and the outskirts. They suggested that the mosaic of land use patterns in the transition zone, with moderate intensities of disturbance, increases species diversity by increasing habitat diversity. Several other studies showing high plant diversity in European studies have suggested that high urban plant diversity is caused by the extensive habitat heterogeneity found in urban areas produced by variations in land use (Kowarik 1995, Kühn et al. 2004).

Porter et al. (2001) proposed that the disturbance heterogeneity model (DHM) may also explain some of the high biodiversity of moderate urbanization levels. The DHM is similar to the intermediate disturbance hypothesis but specifically incorporates spatial (as opposed to temporal) disturbances to account for increased habitat diversity. In their reviews of urban ecology, Rebele (1994) and Niemelä (1999) discuss (with examples) how the spatial diversity of urban habitats promotes higher beta diversity (spatial turnover) in plants and insects.

It is notable that nearly all of these studies discussing urban habitat diversity as a cause of increased biodiversity are focused on plant species richness. As found here, vertebrates are much less likely than plants to show increased species richness in urban habitats. One reason for this disparity may be related to the spatial scale required to maintain viable population sizes. As reviewed by Gaston et al. (1998) for Britain, plants tend to have much smaller geographic ranges than mammals and birds, indicating that smaller areas are required to sustain viable populations of plants relative to vertebrates. Put another way, isolated fragments of unpaved habitat in urban areas often sustain different plant communities but are likely typically visited by individuals of many of the same wide-ranging bird and mammal species. Also, most of the invertebrates analyzed by Gaston et al. (1998) have geographic ranges that are intermediate between plants and vertebrates which also conforms to the findings here, with invertebrates having a value intermediate between plants and invertebrates. The percentages of studies showing increasing species richness with urbanization are: plants 65%, invertebrates 30%, and vertebrates 12%.

In addition to high habitat diversity produced by spatial heterogeneity, a second factor that could promote increased urban species richness is human-aided dispersal of introduced (nonnative) species into urban areas. While urbanization removes habitats for many native species, nonnative species are able to occupy urbanized habitats via many kinds of preadaptations (McKinney 2006a). For example, the proportion of nonnative plant species rises from 6% in nature preserves outside the city of Berlin, Germany to 25% in the suburbs to 54% in the most intensively urbanized central areas (Kowarik 1995). This trend of increasing proportion of nonnative species toward the urban core is also found in birds (Marzluff 2001), mammals (Mackin-Rogalska et al. 1988), and insects (McIntyre 2000). Pysek (1998) found a significant increase in nonnative plant species richness with European city size (and human population). Kowarik (1990) discusses data showing that Polish villages have an average of 30% nonnative plant species, medium-sized towns average 40–50%, and cities average 50–70% nonnatives.

Humans import a diverse array of nonnative plants into cities for landscaping and other horticultural goals (Reichard and White 2001) so it may be that human importation of nonnative plants is also a main factor for the increased species richness of plants in urban habitats. In contrast, there seems to be no parallel for this in animals, including invertebrates and vertebrates. While a few nonnative species, such as pet mammals and birds, are imported into cities, it seems likely that far fewer species and individuals are imported compared to nonnative plants. Indeed, this effect can be seen at larger spatial scales, which show that nonnative plant species generally constitute a much larger percentage of total species. A recent compilation of studies at several spatial scales showed that nonnative species generally comprise a much higher percentage of total species for plants compared to birds, mammals, reptiles and amphibians (McKinney 2006b).

Putting these findings into a larger context, Sax et al. (2005) review evidence that, across several spatial scales in many kinds of habitats, humans have almost always increased the total species richness of plants because introductions have outpaced native species extinctions. They also report a tendency for humans to increase species richness of mammals, although the tendency is less consistent. For birds, the pattern is even less clear, with little or no general increase in species richness from human activities (Sax et al. 2005). The findings here, focusing on urbanization impacts, agree with their results in that plants are the group that most consistently increases in species richness. This also agrees with at least one study that analyzed temporal data. In Adelaide, Australia, plant species richness has increased by 46% from 1836 to 2002 because plant species introductions have outpaced plant species extinctions whereas mammals in Adelaide show a net species loss during that period (Tait et al. 2005).

In conclusion, this paper has sought to address three basic questions. (1) Is there a general pattern of monotonic decrease in species-richness with increasing urbanization? (2) Or is there evidence of intermediate disturbance effect whereby species-richness often increases at intermediate levels of urbanization, as reported in some studies of birds (reviewed by Marzluff 2001; Chace and Walsh 2006). (3) Do either of these potential species richness patterns, monotonic decline or intermediate peak with urbanization, vary among taxa?

My results, based on 105 studies of the effects of urbanization on the species-richness of mammals, reptiles, amphibians, invertebrates and plants, indicated that, for all groups extreme urbanization (as found in urban core areas) almost always reduces species-richness. Much of this is predictable by a species-area effect via the loss of habitable area (impervious surface), and the degradation of remaining habitat by pollution, traffic and other human disturbances. However, the effects of moderate levels of urbanization (i.e., suburban areas) vary significantly among groups, showing a less consistent tendency to reduce species richness. Most of the plant studies (about 65%) indicate increasing species richness with moderate urbanization whereas only a minority of invertebrate studies (about 30%) and a very small minority of non-avian vertebrate studies (about 12%) show increasing species-richness. Further research may determine the possible explanations for cases where species richness is increased by moderate levels of urbanization. Potential factors to be examined would include the relative roles of: nonnative species importation, spatial scale, spatial heterogeneity, and intermediate disturbance dynamics.

Appendix. Studies used as data for this paper

Table 7 Plant species richness changes along the urban–rural gradient

Group	Urban intensity			Location	References
	Low	Mid	High		
Plants	1	2	–	Belgium	Honnay et al. 2003
Plants	2	3	1	Belgium	Godefroid and Koedam 2003
Plants	2	3	1	Germany	Zerbe et al. 2003
Plants	2	3	1	Germany	Kleyer 2002
Plants	2	3	1	Germany	Kowarik 1995
Plants	2	3	1	Germany	Deutschewitz et al. 2003
Plants	1	1	1	U.K.	Thompson et al. 2003
Plants	1	2	2	Finland	Tonteri and Haila 1990
Plants	1	2	–	Arizona	Hope et al. 2003
Plants	3	2	1	S. Korea	Kim and Pauleit 2005
Woody	2	3	1	Ohio	Porter et al. 2001
Woody	1	1	1	Georgia	Burton et al. 2005
Understory	1	1	1	Georgia	Loewenstein and Loewenstein 2005
Understory	1	1	1	Wisconsin	Guntenspergen and Levenson 1997
Plants	1	2	2	USA	McKinney 2006a
Plants	1	2	2	Germany	Kühn et al. 2004
Wetland plants	1	1	–	New Jersey	Ehrenfeld 2005

3=relative maximum richness, 1=relative minimum richness found in study cited

Table 8 Non-avian vertebrate species richness changes along the urban–rural gradient

Group	Urban intensity			Location	References
	Low	Mid	High		
Mammals	2	3	1	Canada	Racey and Euler 1982
Mammals	–	2	1	U.K.	Dickman 1987
Mammals	–	2	1	Poland	Andrzejewski 1982
Mammals	–	2	1	Poland	Goszczynski 1979
Mammals	2	2	1	Pennsylvania	Mahan and O'Connell 2005
Mammals	–	2	1	Russia	Tikhova et al. 2006
Rodents	2	1	–	Arizona	Germaine et al. 2001
Rodents	–	2	1	Poland	Andrzejewski et al. 1978

Table 8 (continued)

Group	Urban intensity			Location	References
	Low	Mid	High		
Bats	–	2	1	Michigan	Kurta and Teramino 1992
Lizards	2	3	1	Arizona	Germaine and Wakeling 2001
Reptile	2	1	–	Belize	Henderson 1976
Snakes	–	2	1	Ohio	Collins and McDuffie 1972
Snakes	2	1	–	Nigeria	Luiselli and Akani 2002
Amphibians	–	2	1	Poland	Mazgajska 1996
Amphibians	3	2	1	Minnesota	Lehtinen et al. 1999
Amphibians	2	1	–	Pennsylvania	Rubbo and Kiesecker 2005
Amphibians	–	2	1	Russia	Semenov et al. 2000
Amphibians	2	1	–	California	Riley et al. 2005
Amphibians	3	2	1	Australia	Parris 2006
Amphibians	–	2	1	U.K.	Beebee 1979
Frogs	2	1	–	Florida	Delis et al. 1996
Frogs	3	2	1	Wisconsin	Knutson et al. 1999
Frogs	3	2	1	Ontario	Findlay et al. 2001
Frogs	–	2	1	Argentina	Acosta et al. 2005
Herptiles	2	1	–	Italy	Scali and Zuffi 1994
Herptiles	2	1	–	New York	Schlauch 1980
Herptiles	3	2	1	Czech Republic	Kral et al. 1983
Herptiles	2	1	–	Slovakia	Kminiak 2000
Herptiles	2	1	–	Australia	Maryan 1993
Herptiles	–	2	1	Indiana	Minton 1968
Herptiles	–	2	1	California	Banta and Morafka 1966

3=relative maximum richness, 1=relative minimum richness found in study cited

Table 9 Arthropod species richness changes along the urban–rural gradient

Group	Urban intensity			Location	References
	Low	Mid	High		
Invertbrates	2	–	1	France	Czechowski 1979
Arthropods	1	2	–	Arizona	McIntyre et al. 2001
Arthropods	2	–	1	Arizona	Rango 2005
Arthropods	3	2	1	Japan	Kitazawa 1986
Insects	–	2	1	Germany	Denys and Schmidt 1998
Insects	3	2	1	UK	Davis 1978
Insects	3	2	1	California	Pouyat et al. 1994
Insects	2	1	1	Many	Frankie and Ehler 1978
Insects	–	2	1	Germany	Klausnitzer et al. 1980
Butterflies	–	2	1	UK	Hardy and Dennis 1999
Butterflies	2	3	1	Ontario	Hogsden and Hutchinson 2004
Butterflies	2	1	–	Colorado	Nelson and Nelson 2001
Butterflies	3	2	1	Brazil	Ruszczyk and De Araujo 1992
Butterflies	3	2	1	Brazil	Fortunato and Ruszczyk 1997
Butterflies	2	3	1	California	Blair and Launer 1997
Butterflies	2	3	1	Ohio	Blair 2001
Butterflies	–	2	1	New York	Shapiro and Shapiro 1973

Table 9 (continued)

Group	Urban intensity			Location	References
	Low	Mid	High		
Butterflies	3	2	1	Phillipines	Posa and Sodhi 2006
Butterflies	–	2	1	Japan	Yamamoto 1977
Butterflies	2	1	–	Pennsylvania	Yahner 2001
Butterflies	3	2	1	Spain	Stefanescu et al. 2004
Butterflies	3	2	1	Massachusetts	Clark et al. 2007
Moths	3	2	1	S. Africa	Rosch et al 2001
Moths	1	–	2	Russia	Kozlov 1996
Moths	3	2	1	U.K.	McGeoch and Chown 1997
Bumblebees	1	3	2	Poland	Pawlikowski and Pokorniecka 1990
Bees	2	1	–	Arizona	McIntyre and Hostetler 2001
Bees	1	2	–	Malaysia	Liow et al. 2001
Bees	1	2	–	California	Frankie et al. 2005
Bees	1	2	2	New Jersey	Winfree et al. 2007
Social bees	3	2	1	Brazil	Zanette et al. 2005
Beetles	2	1	–	New York	Gibbs and Stanton 2001
Beetles	3	2	1	several	Niemelä et al. 2002
Beetles	3	2	1	Japan	Ishitani et al. 2003
Beetles	3	2	1	Finland	Venn et al. 2003
Beetles	2	1	2	Hungary	Magura et al. 2004
Beetles	–	2	1	Germany	Weller and Ganzhorn 2004
Beetles	2	1	–	Sweden	Lundkvist et al. 2002
Beetles	1	1	1	Germany	Deichsel 2006
Beetles	2	1	1	U.K.	Sadler et al. 2006
Beetles	1	2	1	Finland	Alaruikka et al. 2002
Flies	1	1	1	Ohio	Avondet et al. 2003
Flies	2	1	1	Argentina	Centeno et al. 2004
Hoverflies	1	2	–	U.K.	Owen 1981
Ants	–	2	1	Mexico	Lopez-Moreno et al. 2003
Ants	1	2	–	Florida	Forys and Allen 2005
Ants	1	2	–	Quebec	Lessard and Buddle 2005
Ants	2	1	–	China	Zheng-hui et al. 1999
Ants	2	1	–	Australia	Majer and Brown 1986
Spiders	1	2	–	Zimbabwe	Cumming and Wesolowska 2004
Spiders	2	1	1	Arizona	Shochat et al. 2004
Spiders	2	1	–	Texas	Vincent and Frankie 1985
Spiders	2	1	–	Brazil	Fowler and Venticinque 1995
Spiders	1	2	–	California	Fraser and Frankie 1986
Spiders	1	1	1	Finland	Alaruikka et al. 2002
Termites	–	2	1	Thailand	Klangkaew et al. 2002
Mosquitoes	3	2	1	Brazil	Montes 2005
Grasshoppers	3	2	1	Poland	Nagy 1997

3=relative maximum richness, 1=relative minimum richness found in study cited

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