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Urbanization as a major cause of biotic homogenization

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ABSTRACT

When measured by extent and intensity, urbanization is one of the most homogenizing of all major human activities. Cities homogenize the physical environment because they are built to meet the relatively narrow needs of just one species, our own. Also, cities are maintained for centuries in a disequilibrium state from the local natural environment by the importation of vast resources of energy and materials. Consequently, as cities expand across the planet, biological homogenization increases because the same “urban-adaptable” species become increasingly widespread and locally abundant in cities across the planet. As urbanization often produces a local gradient of disturbance, one can also observe a gradient of homogenization. Synanthropic species adapted to intensely modified built habitats at the urban core are “global homogenizers”, found in cities worldwide. However, many suburban and urban fringe habitats are occupied by native species that become regionally widespread. These suburban adapters typically consist of early successional plants and “edge” animal species such as mesopredator mammals, and ground-foraging, omnivorous and frugivorous birds that can utilize gardens, forest fragments and many other habitats available in the suburbs. A basic conservation challenge is that urban biota is often quite diverse and very abundant. The intentional and unintentional importation of species adapted to urban habitats, combined with many food resources imported for human use, often produces local species diversity and abundance that is often equal to or greater than the surrounding landscape. With the important exception of low-income areas, urban human populations often inhabit richly cultivated suburban habitats with a relatively high local floral and faunal diversity and/or abundance without awareness of the global impoverishment caused by urbanization. Equally challenging is that, because so many urban species are immigrants adapting to city habitats, urbanites of all income levels become increasingly disconnected from local indigenous species and their natural ecosystems. Urban conservation should therefore focus on promoting preservation and restoration of local indigenous species.

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1. Introduction

Urbanization is one of the leading causes of species extinction. In the United States, for example, urbanization endangers more species and is more geographically ubiquitous in the mainland United States than any other human activity

(Czech et al., 2000). The reason is that habitat alteration from urbanization is both drastic and increasingly widespread. Large parcels of land are devegetated, paved and dramatically modified in ways that often greatly exceed habitat changes that occur from logging, traditional farming and many other land uses (Marzluff and Ewing, 2001). Also, land modifications

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during urban growth are usually long-term and indeed often intensify with time so that there is no opportunity for successional recovery.

Furthermore, cities are expanding worldwide in almost every locality. The world's population is projected to increase by more than one-third over the next 30 years, adding 2 billion people with almost all expected growth in the world's population is concentrated in urban areas (United Nations, 2004). In the US, about 80% of the population lives in or near cities: 50% of the population lives in the suburbs and another 30% lives in metropolitan urban areas (USCB, 2005). Over 5% of the total surface area of the United States is covered by urban and other built-up areas (USCB, 2005). This is more land than is covered by the combined total of national and state parks and areas preserved by private groups, and the growth rate of urban land use is accelerating much faster than land preserved as parks or conservation areas (McKinney, 2002). In the next 25 years, US developed area is projected to increase by 79%, raising the proportion of the total land base that is developed from 5.2% to 9.2% (Alig et al., 2004). Much of this urban growth is expected in areas already stressed in human–environment interactions, such as coastal counties, increasing potential impacts on sensitive watersheds, riparian areas, wildlife habitat, and water supplies.

The goal of this paper is to describe how urbanization not only extirpates native species from an area but also promotes the establishment of non-native species. The massive disturbances created by city growth not only destroy the habitat of native species but they create habitat for a relatively few species that are adapting to urban and suburban conditions. This process of replacing localized native species with increasingly widespread non-native species promotes biotic homogenization on several spatial scales (McKinney and Lockwood, 1999, 2001; Rahel, 2002; Olden and Poff, 2003). A major consequence for conservation is that non-native species may often enrich local biodiversity (Sax and Gaines, 2003) but global diversity is decreased by the subsequent extinction of unique local species that are lost to the global species pool.

Although many human activities promote biotic homogenization, urbanization is one the most homogenizing activities of all. One reason is their exceptionally uniform nature: cities are habitats constructed almost exclusively to meet the relatively narrow demands of just one species, *Homo sapiens*. As a result, cities are physically very similar throughout the world: roads, skyscrapers, and residential housing in the suburbs are almost indistinguishable. Also, cities typically grow by accretion and their homogenizing influence expands as land-use alteration intensifies.

Urban biotic homogenization is a huge challenge to conservation for at least two fundamentally different but important reasons. One challenge already mentioned is its dominant role in the loss of native species and the consequent homogenization of the world's biota. But another reason is the impact of urbanization on human perceptions of nature. Because so many people live in cities, and because so many urban flora and fauna are not indigenous to the local urban environment, the human species is becoming increasingly unfamiliar, some would say disconnected, from their native biological environment. This has disconcerting impli-

cations for the conservation of native species. Trying to educate and persuade public opinion to promote conservation of native species may be that much more difficult when so many people have no factual knowledge of, experience with or emotional connection to indigenous species in their own area (McKinney, 2002; Turner et al., 2004; Miller, 2005a).

2. Documenting replace of native with non-native species in cities

Many studies show that the construction and expansion of towns and cities promote the loss of native species and their replacement by non-native species. (In this paper, non-native species refers to a species that did not occur in a specified area before recent importation by humans.) These studies can be grouped into two basic categories. One category documents the process through time in a single location. For example, detailed comparisons of plant inventories made at different times show that, for 13 towns and cities representing several continents, native plant species richness declined between 3% and 46% in a span of 50–150 years (Bertin, 2002).

Conversely, the proportion of non-native plant species in human settlements always increases through time. New York City has lost 578 native species (a loss of roughly 43% of the original native species) while gaining 411 non-native species (DeCandido et al., 2004). Similarly, in the last century, Needham, Massachusetts has lost over 330 native plant species (about 44% of its native richness) while gaining over 200 non-native species (Standley, 2003). European and Australian cities show this too. In the last 120 years, the city of Plzen in the Czech Republic lost 368 native species (about 31%) while gaining 238 non-native species (Chocholouskova and Pysek, 2003). In Adelaide, Australia between 1836 and 2002, at least 89 species of native plants disappeared and 613 non-native species were added (Tait et al., 2005).

A second category of studies to show the replacement of native with non-native species examines spatial patterns. These studies are more common than temporal studies because the data are more readily available. Such analyses almost always show that, for many taxa, increasing intensity of urban activity causes non-native species to increase in abundance and species richness while native species decline. For example, the proportion of non-native 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 non-native species toward the urban core is also found in birds (Marzluff, 2001), mammals (Mackin-Rogalska et al., 1988), and insects (McIntyre, 2000). Other kinds of spatial studies have examined the relationship between city size and non-native species establishment. Pysek (1998) found a significant increase in non-native plant species richness with European city size (and human population). McKinney (2001) found a similar pattern in non-native plants and population of US states. Kowarik (1990) discusses data showing that Polish villages have an average of 30% non-native plant species, medium-sized towns average 40–50%, and cities average 50–70% non-natives.

3. Why urbanization promotes non-native species establishment

Urbanization is closely associated with two basic factors that increase non-native species richness: (1) increasing importation of non-native individuals and (2) favorable habitat for the establishment of non-native species. Human settlements import non-native 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).

Human settlements also provide the environmental conditions that allow many of the imported non-native species to become established. Much evidence indicates that disturbance promotes the establishment of non-native species (D'Antonio and Meyerson, 2002, for review). Disturbance alters the natural selection regime, often putting native species at a competitive disadvantage (Byers, 2002). However, as Simberloff (1997) has noted, many habitats classified as “disturbed” could equally be termed “new” and “human-produced” and it is these features rather than the disturbance per se that often renders them vulnerable to invasion. Certainly, many such novel habitats are created by the complex physical alterations of the local environment caused by urbanization.

Shea and Chesson (2002) offer a useful framework for understanding urban disturbance and invasion by focusing on “niche opportunity”. This defines conditions that promote species invasions in terms of three key variables: resources, natural enemies, and the physical environment. An invasion-promoting disturbance thus increases the population growth of an invading species by: providing resources, reducing the threat of natural enemies and/or altering the physical environment (e.g., temperature) to improve habitability for the invader.

The growing literature of urban impacts on biological communities documents many specific examples of all three variables providing niche opportunities for non-native species. Synanthropic species, those that are most strongly associated with humans and highly urbanized areas. Examples include the rock dove (*Columbia livia*), house mouse (*Mus musculus*) and feral house cats (*Felis catus*), all being very dependent on food resources provided humans. As these food subsidies are imported from outlying areas in large amounts, such “subsidized species” are not only able to colonize cities but they can attain population densities far above those found under natural conditions (Buijs and Van Wijnen, 2001).

Humans also provide niche opportunities by reducing (and often eliminating) natural enemies. For example, the elimination of large carnivores in many parts of the US has led to the rapid population growth (Crooks and Soulé, 1999) and geographic expansion of raccoons and other mesopredators (Byers, 2002, for review). Conversely, aggressive competitors, such as European starlings (*Sturnus vulgaris*) and house sparrows (*Passer domesticus*), have spread to flourish in many cities of the world (Marzluff, 2001) contributing to urban homogenization. Finally, human alteration of the

environment can create physical conditions allowing a non-native species to thrive in an area, where it would otherwise not survive. Conversely, these changes may render the physical environment unlivable for native species. Perhaps the most obvious example is the urban heat island effect, i.e., the universal tendency for cities to have higher ambient temperatures than the surrounding natural matrix. As a result, plants are able to inhabit cities at colder latitudes and altitudes where they are not naturally found (Kowarik, 1990). Another example is soil chemistry, such as the high alkalinity of many urban soils (from concrete and other lime-based materials), which promotes the growth of plants that require high-pH soils (Gilbert, 1989). Sukopp (2004) summarizes the effects of eutrophication, sulfur oxides and other physical changes in urban habitats that create habitat for non-native species.

4. Homogenization is extensive because cities are homeostatic systems

Simply increasing non-native species richness (and abundance) in urban habitats does not guarantee biological homogenization. If different non-native species colonize different cities, then the opposite of homogenization, or biological differentiation, can occur (Olden and Poff, 2003; McKinney, 2004a). However, as shown using data below, biological homogenization is indeed what typically occurs from urbanization because the same non-native species tend to become established in many cities. While the exact cause of this pattern remains to be rigorously investigated, it seems likely that the high numbers of shared urban species are related to the two factors noted above, transportation and habitat. Where humans tend to favor many of the same non-native species, e.g., the same ornamental plants and pets, they tend to transport the same ones into many settlements (Mack and Lonsdale, 2001).

Also, urban habitats tend to be very similar. As noted by Clergeau et al. (2001, p. 1123): “In general, human activities have produced similar ecological structures in urban areas even in different biogeographical areas”. Savard et al. (2000, p. 136) also emphasize this: “Urban ecosystems are quite similar worldwide in terms of structure, functions, and constraints”.

Perhaps the best way to understand the physical similarity among cities is to acknowledge that, wherever they occur, cities are human habitats that are constructed and maintained in a state that is usually far out of equilibrium from the natural ecosystem. All aspects of a city's physical environment, ranging from gross structural features through their hydrological and chemical characteristics, are built and maintained only by the infusion of huge resources (of energy and materials) imported from outlying areas (Wackernagel and Rees, 1996). For example, cities import at least 10,000 times the kilocalories of energy per square meter than is utilized by natural ecosystems (Collins et al., 2000). This large input of natural resources is used to maintain the urban habitat in a homeostatic condition that is designed to meet a relatively narrow set of human needs. As a result, urban habitats across the

globe are similar regardless of the very different natural matrices in which they occur.

An excellent example of homeostatic nature of cities is found in studies of urban forest cover. In cities located in the eastern US, about 31% of the urban area is covered by trees (Nowak et al., 1996). This occurs because the urban habitat is deforested compared to nearly 100% cover in the forested areas where they are located. In contrast, for cities located in prairies, grassland and desert ecosystems of the more western US, tree cover is significantly greater than those natural ecosystems because of tree cultivation by humans. In other words, city-dwellers in the US have traditionally preferred a moderately forested habitat (Henderson et al., 1998), creating what has been aptly called an “urban savanna” perhaps because of human aesthetics evolved from our African savanna origins (Gobster, 1994). Therefore, in heavily forested natural regions of the US city-dwellers *remove* trees but in unforested regions they *add* trees. Of course many other environmental parameters show this homeostatic process of buffering against the natural context. Perhaps most notable are temperature and water resources. The urban heat island effect produces a microclimate that is much warmer than the surrounding landscape (Collins et al., 2000), whereas massive irrigation projects provide water for desert cities in much greater amounts than would naturally occur.

As a result of such homeostatic buffering processes, cities are much more similar as a physical habitat than are the habitats that surround them. For example, the habitats available to birds, plants and other species found in the urban environments of Sydney, Australia and Berlin, Germany are likely to be much more similar than the natural environments outside of those cities. Thus, Clergeau et al. (2001) found that urban bird communities are independent of the bird diversity of adjacent landscapes.

Biological homogenization is promoted by this homogenization of the physical environment if the same urban-adapted species are able to become established in cities and thereby become shared between those cities. Evidence for this was found by McClure (1989) who noted that of 848 bird species in Malaysia, Thailand, Japan and the United States, only 70 species (about 8%) could be considered as urban birds. Using somewhat broader criteria, Johnston (2001) tabulates that about 25% of North American birds can be considered as species able to adapt to human settlements.

In a test of these ideas, when Blair (2001) compared the bird communities of cities in California and Ohio, he found that the communities of highly urbanized areas were more similar than the more natural communities adjacent to those cities. Even waste products associated with urbanization create physical conditions promoting homogenization. In the state of Georgia (USA), increased sediment volume from urbanization has homogenized fish assemblages in creek and river watersheds (Walters et al., 2003).

5. Documenting biotic homogenization among cities

Thus far, this paper has discussed general reasons why urbanization should promote biological homogenization,

especially the role of cities in creating habitat for widespread non-native and native species. I now present direct evidence that urbanization does promote homogenization. I will also show evidence on the specific role of range-expanding native species in homogenization, and the extreme homogenization in areas of intensive urbanization.

To document that cities promote biological homogenization, I analyzed the community similarity index (Jaccard's Index) of urban localities and of more natural, park localities. For the urban localities, I analyzed data from recently published plant inventories of native and non-native species for eight United States cities, compiled by Clemants and Moore (2003). These cities are: Boston, New York City, Philadelphia, Minneapolis, Chicago, Washington, DC, Detroit and St. Louis. For the more natural localities, I analyzed relatively complete plant inventory data from 18 natural areas in state and national parks, described detail in McKinney (2002, 2004a,b). As is generally true of many “natural areas” in the US today, they are far from pristine, and all of them contain at least a few species of non-native plants. However, these natural areas are far less modified than the urban areas in this study.

To measure the similarity of species composition among localities, I calculated Jaccard's Index (henceforth called JI) for all possible combinations of pairwise site comparisons for the urban, and the more natural, localities. There are many indices for measuring similarity of species composition between sites but, as reviewed by Olden and Poff (2003) and McKinney (2004a,b), most previous studies on homogenization have used Jaccard's Index.

To show homogenization, one needs to account for the role of distance among sites being compared. Basic biogeographic principles imply that increasing proximity among two sites will tend to increase community similarity among native species because, among other things, they share more similar physical parameters and species immigration pools. Two studies have documented an exponential decline in Jaccard's similarity index among communities of native plants (Nekola and White, 1999) and animals (Poulin, 2003). Also, McKinney (2004a,b) showed that Jaccard's Index (JI) for both native and non-native plants in natural areas had an exponential decline with increasing distance between sites.

When JI for urban and more natural areas are compared as a function of distance, it is evident that community similarity in both urban and more natural areas decline with distance (Fig. 1). But plant community similarity among cities is initially much higher and it continues to remain higher with distance. It seems that cities have consistently more similar plant communities than more natural areas.

6. Increasing homogenization with urbanization intensity

A common approach to analyzing urban impacts on natural systems uses the urban–rural gradient. This analyzes changes in physical or biological parameters along a transect across various parts of the urban to rural environment (McDonnell et al., 1993). Physical changes along the gradient strongly influence available habitat for species. These physical

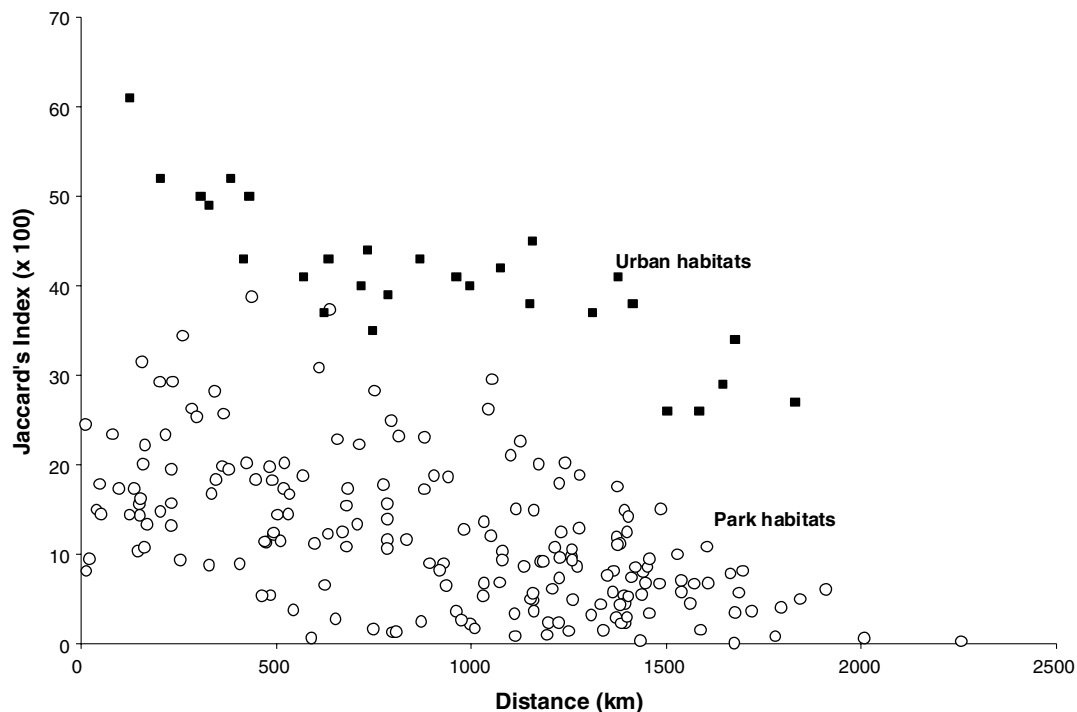


Fig. 1 – Jaccard's Index for plant communities in park habitats compared to urban habitats. Parks refers to relatively undisturbed state and national wildlands.

changes include exponential increases toward the urban core in: human population density, road density, fragmentation of natural vegetation, air and soil pollution, average ambient temperature, average annual rainfall, soil compaction, soil alkalinity, and other metrics of anthropogenic disturbance (McKinney, 2002). The percentage of area that is impervious sealed surface (pavement, asphalt and buildings) ranges from well over 50% at the urban core to less than 20% at the fringe of urban expansion.

Such a linear gradient is an obvious simplification of the more complex dynamics of urban habitats. As noted by Alberti et al. (2001), modern metropolitan areas are not simple concentric rings but are often polycentric entities that have variable density concentrations in several directions. While keeping this caveat in mind, I focus on the urban–rural gradient here for the practical reason that it is the basic approach of many studies analyzing urban impacts on natural ecosystems.

Species vary widely in their ability to adapt to the drastic physical changes along the urban–rural gradient. However, perhaps surprisingly, species do not occur in random combinations along the gradient but tend to assemble into coherent communities. As Sukopp (1990) noted, early urban ecologists soon found that “even in man-made sites, characteristic combinations of organisms could be found under similar conditions”. Rebele (1994) and Niemela (1999) discuss how urban biotic assemblages (communities) reflect adaptations to the physical environment as well as the biotic interactions (such as predation and competition) that occur in those environments. While it is probably possible to discern many communities along the gradient, many urban–rural studies of several

taxa have concluded that, for convenience, species along the gradient can be classified into three distinct categories reflecting their response to urbanization. Following the terminology of Blair (2001, and earlier works cited therein), these three responses are: avoidance, adaptation and exploitation. Examples that show evidence of these three responses along the urban–rural gradient include studies of birds (e.g., Maeda and Maruyama, 1991; Blair, 2001), mammals (Nilon and Van-Druff, 1987), insects (McIntyre, 2000), and plants (Witte et al., 1985).

That so many workers have utilized a threefold grouping of species along the urban–rural gradient probably reflects the empirical observation that, wherever urbanization occurs, some species are extremely sensitive and disappear quickly (avoidance), some species thrive as urban commensals to the point that they become dependent on urban resources (exploitation), and some species can adapt to urban habitats but also utilize natural resources (adapters). These three categories have also been used for butterflies (Blair and Launer, 1997) and lizards (Germaine and Wakeling, 2001) in urban–rural gradient studies. Witte et al. (1985) use the terms urbanophobes and urbanophiles to describe negative and positive responses to urbanization, respectively. Kühn et al. (2004a) have expanded Witte et al. (1985) scheme to include moderately urbanophilic species that are most abundant in suburban areas. Exploiters (urbanophiles) are probably most commonly termed synanthropes. Johnston (2001) distinguishes full synanthropes (exploiters and urbanophiles) from casual synanthropes (adapters and moderately urbanophilic) and non-synanthropes (avoiders and urbanophobes).

I discuss exploiters (full urbanophiles and synanthropes) and adapters (moderate urbanophiles) in more detail below because they are the species producing most biological homogenization. First however, a few general observations about community assembly across the urban-rural gradient are warranted. Many species will occur all along the gradient, or parts of it, but often in low numbers. A species occurrence in a category reflects its abundance peak and its location along the gradient. Exploiters, for example, peak in the urban core, whereas avoiders peak at the other extreme outside the city. Adapters have peak abundance in the suburbs. Also, one of the most important traits separating the three categories is the extent to which species depend on human subsidized resources to exist in an area. As subsidized resources increase toward the urban core, there is a concurrent increase in species that utilize them, ranging from exploiters (most usage) to avoiders (little or no usage). For animals, another key factor is vegetation, which becomes less common, with more non-native species toward the urban core (Kowarik, 1995). Exploiters are often inversely correlated with vegetation (McKinney, 2002). In contrast, adapters require considerable vegetation for shelter and food but can typically utilize both native and non-native plant species (Reichard et al., 2001), as both are common in the suburbs (Porter et al., 2001). Avoiders tend to require native vegetation.

Several general biological trends along the urban-rural gradient have been discerned. What follows is a simplified compilation distilled from: Adams (1994), Rebele (1994), Niemela (1999), McIntyre (2000), Marzluff (2001), McKinney (2002). Going from the rural end toward the urban core, these trends are as follows. Decrease in: species-richness, biotic interactions, ecosystem complexity. Increase in: biomass, total abundance, abiotic influences on species abundance, ecosystem reliance on imported resource subsidies. While most of these trends are not directly related to the topic of homogenization, there is one important aspect, that of functional homogenization. As discussed by Olden and Poff (2003), functional homogenization occurs when the same kind of ecosystem becomes more uniformly widespread. As indicated by the trends noted above, intensively urbanized ecosystems are sometimes relatively simple, with uncomplicated food webs and dominated by abiotic controls and imported food subsidies (Rebele, 1994). Thus, it seems likely that the spread of similar species and similar physical conditions in the intensively modified core (“hardscape”) urban habitats will tend to produce an increase in functional homogenization.

7. Regional homogenization: species adapting to suburban habitats

Many of the species that adapt to low-moderate levels of urbanization are native species in the sense that they were not transported from other nations. Instead, many of these are plant and animal species that immigrate from the surrounding areas to take advantage of human-created habitat. Using the terms above, this includes mostly species in the categories of adapters, moderate urbanophiles and casual synanthropes.

One of the challenges in using a simple (but convenient) category such as “adapters” is that it we need to remind ourselves that these each species actually has its own unique way of adapting to suburban areas. Furthermore, the biotic and abiotic factors that determine the population abundance of each species along the urban-rural gradient are often complex, and will also vary among adapter species. For example, in southwestern Florida, the burrowing owl (*Athene cunicularia*) has its greatest population density at moderate levels of urbanization because residential landscaping enhances vegetative cover which, in turn, increases availability of lizard and insect prey (Wesemann and Rowe, 1986). On the other hand, in areas of very intense urbanization, owl abundance declines because vegetative cover declines, human interactions increase, and probably several other negative influences as well. The adaptations of many species to urban life are discussed in Garber's (1987) *Urban Naturalist*, about the plants and animals living in New York City.

While keeping such species-specific adaptations in mind, it is still useful to try and make some theoretical generalizations about adapter species. Among animals, urban adapters typically include species often referred to as “edge species”, adapted to forest edges and surrounding open areas (Adams, 1994; Marzluff, 2001). For birds, the best-studied suburban animal, urban adapters includes a high proportion of certain feeding guilds (see reviews in Marzluff, 2001; Chace and Walsh, 2005). In North American and European cities, these guilds include: insectivorous and omnivorous ground foragers, seed eaters, and aerial sweepers. Each of these three guilds seems to be responding to different aspects of human impacts. The highly productive (i.e., fertilized) lawn and ornamental plant ecosystem provides a rich source of invertebrate and plant foods (Falk, 1976) for ground gleaners, while seed eaters are favored by bird feeding stations and many ornamental plants that produce seeds (Adams, 1994). Tree and shrub nesters, and cavity nesters are also common among urban adapters. Most avian urban adapters are non-migratory. Some small raptors thrive on plentiful rodents, songbirds and other small prey (Chace and Walsh, 2005). In some tropical cities, frugivores are adapting to suburbs with low-density housing and feeding on fruit-bearing ornamental plants. These species originate from mangrove and coastal scrub forests (Lim and Sodhi, 2004).

For mammals, life in suburban environments poses different challenges from birds. However, mammalian urban adapters are able to find shelter from intensive human activity as well as exploit rich sources of food provided by humans (Nilon and VanDruff, 1987). Although, less well studied than birds and mammals, some native herptiles (amphibians and reptiles) and insects are also clearly adapting to urbanization in low-moderately urbanized locations around the world. Even some large reptiles such as the carpet python can adapt, by avoiding human contact and feeding on abundant non-native prey (Shine and Fitzgerald, 1996). Insects in suburban landscapes tend to be generalists, trophically adapted to early successional habitats (McIntyre, 2000). Carabid beetles are a commonly occurring urban insect and studies show that, globally, native suburban species tend to be smaller, and

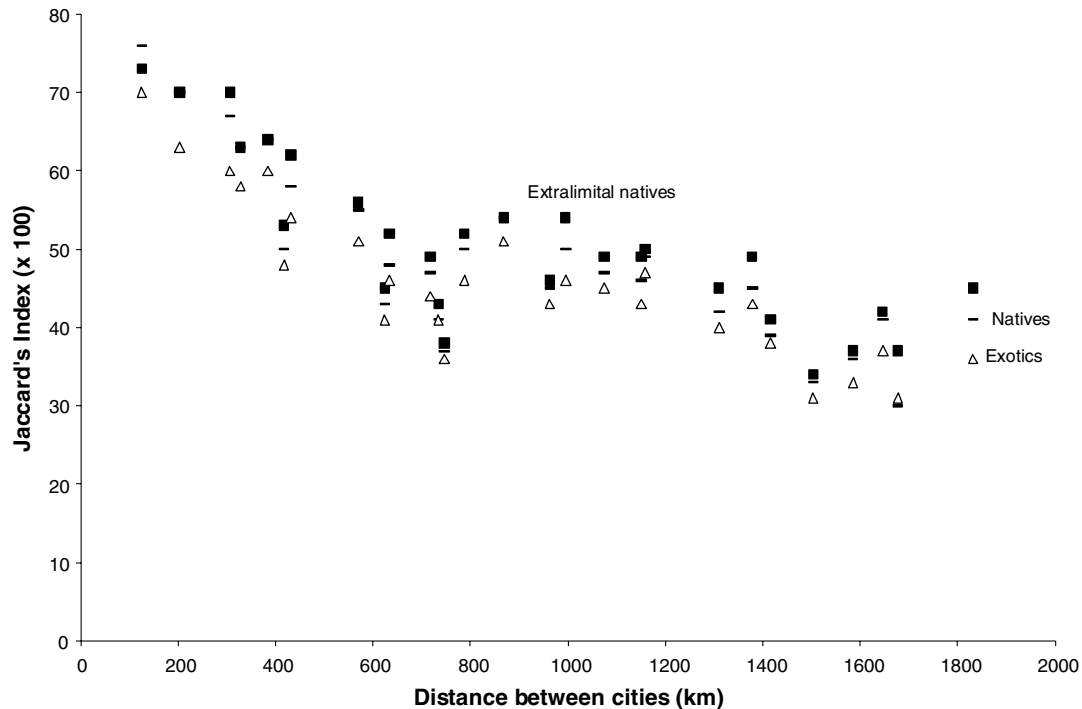


Fig. 2 – Jaccard's Index for plant communities between cities, for extralimital natives (natives outside natural range), exotic and non-extralimital native plant species.

trophically more generalized than species in fully natural habitats (Ishitani et al., 2003).

Regarding plants, landscapes in suburban, or periurban, areas often retain substantial amounts of vegetation, in the form of remnant fragments of native vegetation and as cultivated plots (Whitney, 1985; McKinney, 2002). Many of these are early successional plants including many native and non-native species (Garber, 1987; Sukopp, 1990; Kowarik, 1995). Some are purposely dispersed by humans (e.g., turfgrass, fast-growing ornamental shrubs and trees) and some are weedy species that are self-dispersing. The most common weedy species are wind dispersed lawn weeds, e.g., dandelion (*Taraxacum officinale*) and bird dispersed invasive shrubs, e.g., Chinese privet (*Ligustrum sinense*) that commonly grow on cleared, untended landscapes (Crowe, 1979).

In contrast to ecosystems in intensely urban ("hardscape") habitats, biotic interactions in suburban areas are often quite complex (Faeth et al., 2005). It is thus unclear if suburban ecosystems undergo the same degree of functional homogenization seen in more urbanized ones.

8. Documenting regional homogenization by native species

As most urban adapters are native species taking advantage of low to moderate levels of urbanization in the suburban and rural-fringe (i.e., periurban) habitats, it seems likely that range-expanding native species play a significant role in biological homogenization by cities. Indeed, one might expect that native species introductions from less distant areas

would be more numerous than from foreign areas due to simple dispersal logistics: increasing proximity would seemingly improve the probability of immigration, either human-assisted or self-dispersing.

To examine this idea, I again analyzed the data set on eight United States cities compiled by Clemants and Moore (2003). These data distinguish between exotic non-native plant species (from outside the US) and extralimital non-native species (US species but not native to the region where the city is located). I calculated Jaccard's Index (JI) for all possible pairwise comparisons ($n = 28$) for: native species, native species plus exotic non-native species, and native species plus extralimital non-native species. The results showed that for all three groups, similarity declines with distance (Fig. 2). However, the JI including extralimital non-native species is typically higher than the JI for native species, indicating a homogenizing effect for extralimitals. In contrast, JI including foreign exotic is typically below native species only, indicating that exotic plants often have the opposite effect from homogenization, that of differentiating the flora among cities.

9. Exploiters of highly urbanized habitats

Urban exploiters (i.e., full synanthropes and urbanophiles) inhabit intensively urbanized "hardscapes" near the urban core. Unlike urban avoiders and adapters, the diversity and abundance of urban exploiters is usually not dependent upon vegetation (Mackin-Rogalska et al., 1988; Nilon and VanDruff, 1987). Instead, exploiters rely on foods imported by humans and shelter provided by humans. The combination of preda-

tor release, strong competitive abilities, and the ability to exploit abundant food subsidies and other resources allows them to attain enormous population densities (Adams, 1994; Marzluff, 2001).

As with urban adapters, each urban exploiter species uses a unique opportunity niche, among a variety of potential microhabitats. For animals, one useful way of categorizing these urban exploiter niches is to denote whether the species lives most of its life outside or inside of buildings. Among those that utilize habitat on the outside of structures, are those species evolutionarily adapted to rocky areas, and therefore preadapted to the devegetated concrete edifices of very urbanized areas (Lancaster and Rees, 1979; Garber, 1987; Adams, 1994). Common avian examples include the rock dove (*Columbia livia*) and peregrine falcon (*Falco peregrinus*). There are many other microhabitats for nesting birds around human buildings, as described in their common names such as: house sparrow (*Passer domesticus*), barn owl (*Tyto alba*), and chimney swift (*Chaetura pelagica*). Trophically, avian urban exploiters tend to be ground foraging seed eaters or omnivores (Lancaster and Rees, 1979; Adams, 1994).

Other urban exploiters find habitat mainly inside of buildings. Some of these are mammals, including the house mouse (*Mus musculus*) and Norway rat (*Rattus norvegicus*). A few reptiles, such as the house gecko (*Hemidactylus mabouia*), have exploited this habitat, as have many insects such as the house cricket (*Acheta domestica*; Garber, 1987). The term “domiciliary” is sometimes applied to such a house-dwelling species (Ezequiel et al., 2001). A third groups of urban exploiters are able to inhabit both the inside and outside of buildings, including many lizards which are described as “edificarian” in the scientific literature (Howard et al., 2001). It is notable that only some of the species commonly found in buildings require them for breeding. A review of the house spiders of Kansas shows that only 15 species are true synanthropes that establish breeding populations in houses. Another 26 species are commonly found in houses, but breed in natural habitats outside (Guarisco, 1999).

Among plants, some urban exploiters are ruderal species, especially grasses and annuals, that can tolerate high levels of disturbance (reviews in Whitney, 1985; Kowarik, 1995). Examples include wind-dispersed weeds that colonize abandoned industrial and commercial properties and plants that can grow in and around pavement. Adaptive traits typical of urban exploiting plants include tolerance to high levels of: air pollution (especially smog and acidic fog), trampling, and alkaline, compacted and nitrogenous soils. Another category of plant urban exploiters is the cultivated street tree population. Although these are probably not what many ecologists would consider as exploiters in the usual sense, these tree species certainly thrive in urban settings. Furthermore, they are typically drawn from a relatively small pool of commonly planted, often non-native, tree species (Galvin, 1999) so that street trees contribute to the biological homogenization of urban flora.

The urban core habitat typically has more in common with other cities than with adjacent natural ecosystems

(Sukopp and Werner, 1982), so urban exploiters are often not native to a region (Adams, 1994; Kowarik, 1995; Blair, 2001). Instead, they leapfrog from city to city. Thus, rock doves, starlings, house sparrows, Norway rats, and the house mouse are common to all cities from Europe (Mackin-Rogalska et al., 1988) to North America (Adams, 1994). This is also true for urban plants (Whitney, 1985). Erz (1966) suggested that bird species do not colonize urban areas from the surrounding countryside but immigrate from already urbanized populations.

In a wide-ranging review, Clergeau et al. (2001) find that urban bird communities are independent of the bird diversity of adjacent landscapes. Local features, such as quantity and quality of urban vegetation, are more important determinants of bird diversity than landscape factors. Likewise, Hruska (1989) showed that the flora of the Italian countryside was more visible in the city suburbs, whereas urban centers contained floras distinct from the countryside. Many domiciliary (house-dwelling) arthropods have apparently been transported all over the world by “house to house” jump dispersal as humans move. Examples include the house cricket, cockroaches and houseflies (Garber, 1987) and the black widow spider (Garb et al., 2004).

10. Documenting extreme homogenization in intensely urbanized habitats

An implication of community assembly along the urban-rural gradient is that highly urbanized (hardscape or downtown) areas at the urban core should show the greatest degree of biological homogenization of any habitat along the gradient, and perhaps of any habitat on Earth. As noted above, cities are homeostatic ecosystems maintained out of their natural equilibrium by huge resource inputs. As a consequence, highly urbanized habitats should be very similar across the planet, even more similar than suburban and other slightly urbanized habitats. Therefore, exploiter species that can inhabit highly urbanized habitats could, in theory, produce very similar urban core communities.

To test this hypothesis, I utilized the approach of Blair (2001) who calculated Jaccard's Index to show that the bird community of downtown Palo Alto, California was very similar to the downtown community of Oxford, Ohio. In contrast, the bird communities of less urbanized areas of those cities were less similar. To expand on this approach, I compiled a data set from studies of birds in several cities across the globe. These studies contained lists of birds living in downtown, suburban and relatively natural habitats outside the city. Jaccard's Index (JI) was then calculated among cities for each of these habitats. The data sources, cities, and calculations are shown in Appendix.

When JI for the three habitat types is plotted as a function of distance between the cities, bird community similarity among natural habitats declines rapidly (Fig. 3). JI for suburban habitats also declines with distance, although at a slower rate. In contrast, JI for downtown habitats remains fairly constant, between 0.10 and 0.20, at all distances above

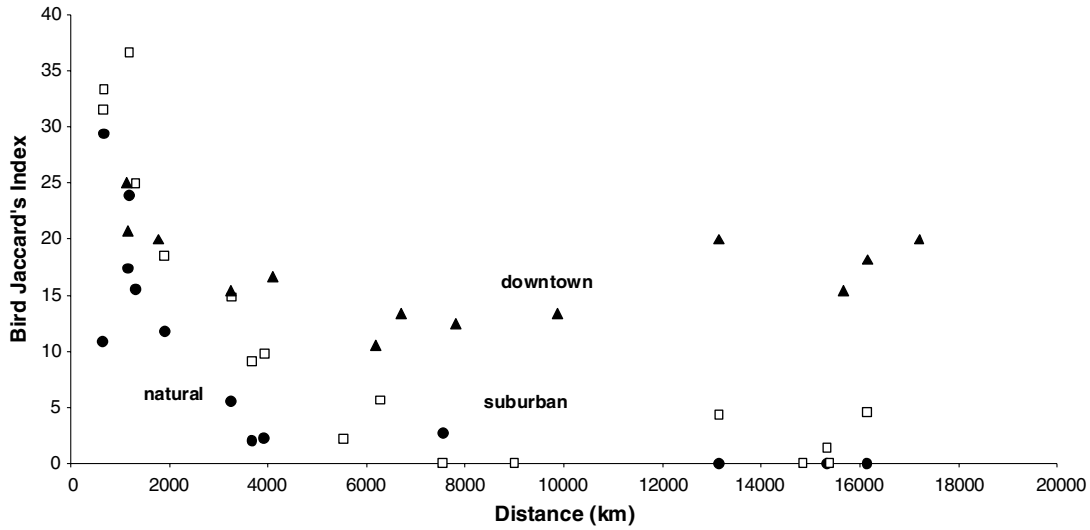


Fig. 3 – Jaccard's Index for bird communities in three kinds of habitats: natural, suburban, and downtown. Data for these points are in Appendix.

2000 km including cities on nearly opposite sides of the globe (Fig. 3).

11. The conservation challenge of rich but homogenizing urban biodiversity

A major challenge for native species conservation is that, despite the homogenizing effects of urbanization, cities

often have high species richness. Sax and Gaines (2003) have reviewed the literature to document that local and regional species richness is often increased by exotic species establishment, especially plants and freshwater fishes. This process has the effect of increasing local biodiversity but reducing global biodiversity because the rich local biota becomes increasingly enriched in species that are spreading to many parts of the biosphere to replace many locally

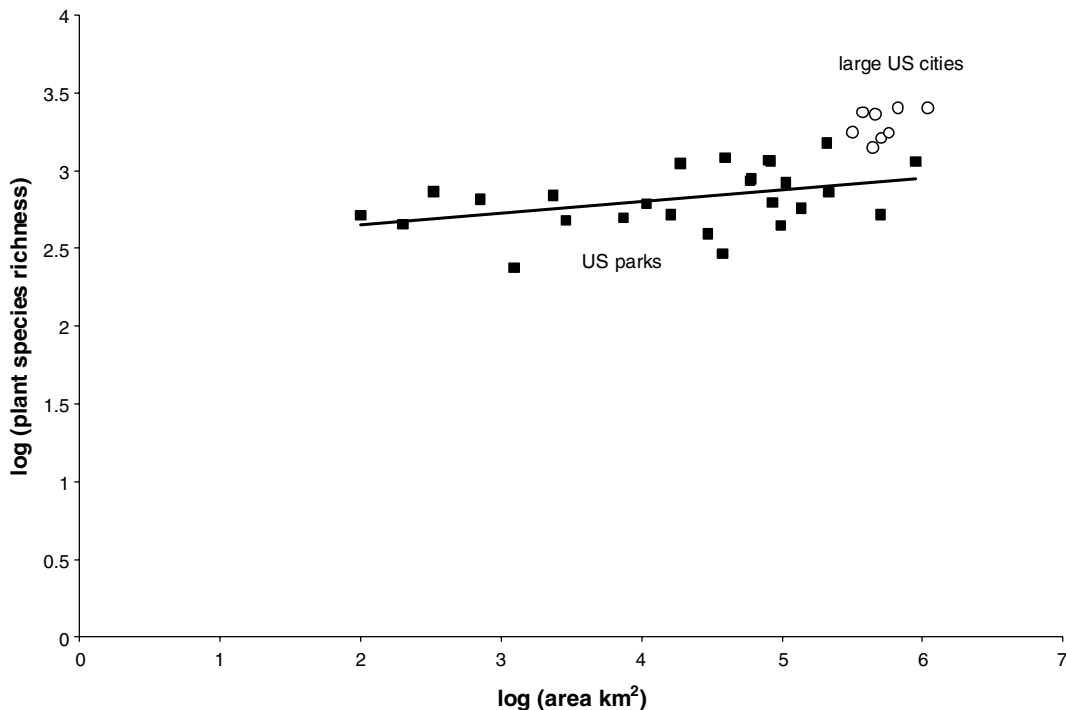


Fig. 4 – Species-area curve (log-log) for plant species richness in larger US national parks compared to plant species richness in eight major US cities.

unique, endemic native species (McKinney and Lockwood, 1999). In the case of cities, plant species richness is often greater than that of surrounding areas (Kuhn et al., 2004b). This is illustrated by plotting total plant species richness (native and exotic species) of the eight US cities used above on a species-area curve, and comparing it to a species-area curve for total plant richness of US state and national parks from many geographic locations (park data from McKinney, 2004a). This shows that the same non-native plants that homogenize urban flora (Figs. 1 and 2) also increase the total plant species richness of those cities relative to parks (Fig. 4). In the context of the urbanization gradient noted above, most of this high floristic diversity is found in suburban habitats where parks, gardens and residential landscapes contain many native and non-native plants species (Kowarik, 1995; McKinney, 2002). Thompson et al. (2003) found that private gardens contain twice as many plant species than any other habitats in Sheffield, United Kingdom. Although this number includes many cultivated species not capable of self-sustaining populations, it does illustrate the very high floral diversity experienced by the urbanized public.

It is unclear if urban animal diversity is generally enriched relative to surrounding natural habitats but it is often diverse. Italian cities have been shown to contain almost 50% of all species of the total Italian avifauna (Dinetti et al., 1996). Although most studies show a decline in animal species richness toward the urban core, richness is still quite high in suburban habitats relative to more natural areas (reviews in Marzluff, 2001; McKinney, 2002). A few studies even indicate that mammal, bird and butterfly species richness peaks in suburban areas, at intermediate levels of human disturbance along the gradient (Racey and Euler, 1982; Blair and Launer, 1997). At coarser scales, Vazquez and Gaston (2005) cite many studies that have documented a strong positive relationship between species richness of many animals groups and human population density, which includes highly urbanized landscapes.

The problem for biodiversity conservation is that despite this high species richness in urbanizing areas, including the importation of non-native species, global biodiversity continues to decline. This pattern of local enrichment but global decline is a crucial one for conservation biology because it may divert public attention away from the more global problem of global species decline. This is illustrated by the fact that, while people often value species diversity, most of the general public cannot identify whether a local species is exotic (McKinney, 2002). Even when they do know it is exotic, they still place a high value on that species if it is aesthetically pleasing (Reichard and White, 2001), good for sport or has some other utilitarian value (McKinney, 2002).

12. Conclusions: slowing homogenization

Simply encouraging the preservation and restoration of biodiversity in urban habitats is insufficient. As just noted, biodiversity in many urban (especially suburban) areas is often already quite high, in terms of species richness, beta and alpha diversity.

The central insight provided by biotic homogenization studies is that the preservation and restoration of local indigenous species biodiversity must be emphasized if we are to slow the loss of regional biotic uniqueness. There is a parallel here with suggestions that the solution to “globalization” and the consequent homogenization of culture is for nations to move toward more localized economies and the preservation of local cultures (Goldsmith and Mander, 2001).

The preservation of indigenous species in urban habitats is important for more than retaining the biological distinctiveness of urban areas. For conservation goals, it is also important as a way of educating the large numbers of people who inhabit cities about local indigenous biodiversity. Educating the urban public could be the most important method of promoting effective conservation of native species (Kendle and Forbes, 1997; Miller and Hobbs, 2002). Because most people live in or near urban areas, there are many opportunities for creating an informed public that can wield enormous economic and political pressure to promote conservation policies. People who live in urban environments often have a great appreciation of many urban species, such as birds (Clergeau et al., 2001). Residents of urban areas tend to place a much higher value on species conservation than those living in rural areas (Kellert, 1996). In the US, legislators from highly urbanized states and districts tend to be more supportive of strengthening the Endangered Species Act (Mehmood and Zhang, 2001). Ironically, most urban dwellers are concentrated into urban habitats with the least amount of biodiversity (Turner et al., 2004). This pattern is influenced by economic factors such that residents with higher incomes tend to occupy urban areas that have greater species diversity (Kinzig et al., 2005).

Finding practical ways to actually preserve local native species in urbanizing habitats, and giving the urban public more direct experience with native species, will obviously be a challenge. For thousands of years, cities have been constructed with the needs of only one species in mind. This has increasingly produced what Miller (2005a) has aptly described as the “extinction of experience”. Accommodating the needs of other species on a large scale, and creating a deeper appreciation of local native species in the urban public, will require a revolutionary rethinking in urban design. Examples of such designs are provided in this journal issue by Miller (2005b) and Snep et al. (2005).

These efforts to preserve native species in urban areas, and increase their exposure to the public, not only promote conservation by educating the public but can preserve native species that are listed as threatened and have high conservation values. For example, Schwartz et al. (2002) document how many rare and endangered plant species occur near and within cities in the US. They also note that there is great potential for preservation of these rare species with relatively little cost or effort. For example, in San Francisco most rare species have at least one population on publicly owned land or on land protected by the Nature Conservancy (Schwartz et al., 2002).

Appendix. Data for Fig. 3

Locality	Kilometer	Sites	N1	N2	C	Jaccard	References
Natural	7545.1613	Florida–Finland	27	11	1	2.7027027	Woolfenden and Rohwer (1969)–Huhtalo and Jarvinen (1977)
Natural	1158.0645	England–Finland	67	14	12	17.391304	Batten (1972)–Huhtalo and Jarvinen (1977)
Natural	1904.8387	Massachusetts–Florida	29	28	6	11.764706	Walcott (1974)–Woolfenden and Rohwer (1969)
Natural	654.83871	Massachusetts–Virginia	28	23	5	10.869565	Walcott (1974)–Aldrich and Coffin (1980)
Natural	1191.9355	Ohio–Massachusetts	29	28	11	23.913043	Beissinger and Osborne (1982)–Walcott (1974)
Natural	3674.1935	Arizona–Massachusetts	29	22	1	2	Emlen (1974)–Walcott (1974)
Natural	672.58065	Ohio–Virginia	29	15	10	29.411765	Blair (2001)–Aldrich and Coffin (1980)
Natural	1317.7419	Virginia–Florida	29	23	7	15.555556	Aldrich and Coffin (1980)–Woolfenden and Rohwer (1969)
Natural	3258.0645	California–Ohio	21	17	2	5.5555556	Blair (2001)–Blair (2001)
Natural	3909.6774	California–Virginia	24	21	1	2.2727273	Blair (2001)–Aldrich and Coffin (1980)
Natural	13137.097	Tasmania–California	21	10	0	0	Maeda and Maruyama (1991)–Blair (2001)
Natural	16141.935	Tasmania–Ohio	17	10	0	0	Maeda and Maruyama (1991)–Blair (2001)
Natural	15329.032	Queensland–Virginia	48	31	0	0	Jones (1983)–Aldrich and Coffin (1980)
Suburban	6275.8065	Virginia–Finland	29	27	3	5.6603774	Aldrich and Coffin (1980)–Huhtalo and Jarvinen (1977)
Suburban	7545.1613	Florida–Finland	27	11	0	0	Woolfenden and Rohwer (1969)–Huhtalo and Jarvinen (1977)
Suburban	1904.8387	Massachusetts–Florida	21	11	5	18.518519	Walcott (1974)–Woolfenden and Rohwer (1969)
Suburban	654.83871	Massachusetts–Virginia	29	21	12	31.578947	Walcott (1974)–Aldrich and Coffin (1980)
Suburban	1191.9355	Ohio–Massachusetts	21	20	11	36.666667	Beissinger and Osborne (1982)–Walcott (1974)
Suburban	3674.1935	Arizona–Massachusetts	21	15	3	9.0909091	Emlen (1974)–Walcott (1974)
Suburban	672.58065	Ohio–Virginia	29	15	11	33.333333	Blair (2001)–Aldrich and Coffin (1980)
Suburban	1317.7419	Virginia–Florida	29	11	8	25	Aldrich and Coffin (1980)–Woolfenden and Rohwer (1969)
Suburban	3258.0645	California–Ohio	16	15	4	14.814815	Blair (2001)–Blair (2001)
Suburban	3925.8065	California–Virginia	29	16	4	9.7560976	Blair (2001)–Aldrich and Coffin (1980)
Suburban	13137.097	Tasmania–California	16	8	1	4.3478261	Maeda and Maruyama (1991)–Blair (2001)
Suburban	16141.935	Tasmania–Ohio	15	8	1	4.5454545	Maeda and Maruyama (1991)–Blair (2001)
Suburban	15329.032	Queensland–Virginia	45	29	1	1.369863	Jones (1983)–Aldrich and Coffin (1980)
Suburban	8996.7742	Singapore–Finland	48	27	0	0	Maeda and Maruyama (1991)–Huhtalo and Jarvinen (1977)
Suburban	5529.0323	Singapore–Queensland	48	45	2	2.1978022	Maeda and Maruyama (1991)–Huhtalo and Jarvinen (1977)
Suburban	14840.323	Singapore–Arizona	48	15	0	0	Maeda and Maruyama (1991)–Huhtalo and Jarvinen (1977)
Suburban	15382.258	Singapore–Virginia	48	29	0	0	Maeda and Maruyama (1991)–Huhtalo and Jarvinen (1977)
Urban	1158.0645	England–Finland	56	14	12	20.689655	Batten (1972)–Huhtalo and Jarvinen (1977)
Urban	3258.0645	California–Ohio	7	8	2	15.384615	Blair (2001)–Blair (2001)
Urban	13137.097	Tasmania–California	5	7	2	20	Maeda and Maruyama (1991)–Blair (2001)
Urban	16141.935	Tasmania–Ohio	5	8	2	18.181818	Maeda and Maruyama (1991)–Blair (2001)
Urban	1780.6452	Hungary–Finland	10	14	4	20	Sasvari (1984)–Huhtalo and Jarvinen (1977)
Urban	7819.3548	Hungary–Ohio	10	8	2	12.5	Sasvari (1984)–Blair (2001)
Urban	9879.0323	Hungary–California	10	7	2	13.333333	Sasvari (1984)–Blair (2001)
Urban	15651.613	Hungary–Tasmania	10	5	2	15.384615	Sasvari (1984)–Maeda and Maruyama (1991)
Urban	6195.1613	Quebec–Finland	7	14	2	10.526316	Clergeau et al. (1998)–Huhtalo and Jarvinen (1977)
Urban	17196.774	Quebec–Tasmania	7	5	2	20	Clergeau et al. (1998)–Maeda and Maruyama (1991)
Urban	6691.9355	Quebec–Hungary	7	10	2	13.333333	Clergeau et al. (1998)–Sasvari (1984)
Urban	1135.4839	Quebec–Ohio	7	8	3	25	Clergeau et al. (1998)–Blair (2001)
Urban	4100	Quebec–California	7	7	2	16.666667	Clergeau et al. (1998)–Blair (2001)

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