Species diversity in urban landscapes: patterns, drivers and implications.


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Summary

In this chapter, we review studies that examine spatial and temporal patterns in species diversity [richness] across gradients of urbanization at multiple spatial and temporal scales. At broad scales (e.g. across continents), species richness for many taxonomic groups is often positively correlated with human population density – a surrogate measure for degree of urbanization. The strength of the correlation varies with the size of the sampling unit used, being stronger when sampling is conducted across regions where the distribution of people and other species appears to respond similarly to energy and/or productivity gradients. At smaller scales, studies show that species richness is generally lower in urban versus non-urban areas. Across gradients of urbanisation (e.g. spanning rural areas through to city centres), species diversity often peaks at the rural/urban interface where disturbance levels are moderate and landscape heterogeneity is high. Yet, responses vary among taxonomic groups and sub-sets of species. Plants species richness is often highest at moderate levels of urbanization, reflecting the persistence of endemic species and substantial plantings of exotics. Trends for fauna species vary across groups, although species richness (especially of natives) declines consistently from moderate to high levels of urbanization. Species responses to urbanization are dictated by interactions among species traits, tolerance to disturbance, landscape heterogeneity, and the availability of suitable resources. Within urban centres, species richness is often correlated with key socio-economic characteristics of neighbourhoods. Low density suburbs containing wealthy, well-educated residents support greater vegetation cover and more plant and animal species. Future research on urban ecology must forge ahead with integrated, interdisciplinary studies that offer the best hope for understanding the complex interactions between human behaviour and species responses.
Introduction

Spatiotemporal patterns in species diversity have intrigued ecologists for many decades (MacArthur, 1965; Brown, 1981; Gaston, 2000). These patterns occur at a variety of scales. For example, the latitudinal gradient of increasing species richness from the poles to the equator (Willig et al., 2003; Hillebrand, 2004) and altitudinal gradients across regions (Sanders, 2002; McCain, 2004). Appropriate identification and explanation of these patterns have generated enormous interest and debate among ecologists and biogeographers (Rahbek and Graves, 2001; Willig et al., 2003; Field et al., 2009). It is only logical to extend this interest to urban systems and examine species richness patterns and drivers of these patterns across gradients of urbanization at multiple spatial and temporal scales.

What sets urban studies apart is the implicit or explicit recognition of the major influence of human landscape modification on species distribution. Indeed, the effects of anthropogenic activity are virtually impossible to ignore in urban systems. Moreover, integrating social, cultural, economic, human demographic and ecological data, and exploring the role of human activities in moderating patterns in species diversity, is an exciting development that is forging new ground in interdisciplinary research.

In this chapter, we explore patterns in species diversity in urban systems across space and time, and briefly review some of the key drivers of these patterns and their implications. The chapters’ focus is on patterns in species richness, particularly native species, as variation in species abundance and density are covered in detail in Chapter 4. Much more attention is given to spatial patterns in richness and this reflects the bias in the literature. We group patterns under the headings ‘broad-scale’, ‘comparative’, ‘gradient’ and ‘urban-centric’. Broad-scale refers to patterns
that occur over large spatial extents (e.g. national, continental or global) with a large grain size (the size of the sampling unit used; e.g. 1° grid cells) where researchers have examined covariation in species richness and some measure of urbanization (e.g. human population density). Comparative studies are those that compare species richness in native habitats or rural landscapes with urban areas. A particular type of comparative study is the rural–urban or native–urban gradient, and we treat these studies separately since they are prominent in the literature. In comparative and gradient studies, spatial extent is usually much less than broad-scale studies and grain size is almost always much smaller. Urban-centric refers to patterns that occur when sampling locations are primarily nested within a single urban centre or across centres. Researchers generally compare species assemblages across different levels of urbanization, but may occasionally include direct comparisons with native or rural landscapes.

We use the terms species diversity and species richness interchangeably to describe the number of species in an area, as this is consistent with their use in the literature. However, we note that, technically, ‘diversity’ is a factor of both species richness and abundance of each species and is often encapsulated in diversity indices such as the Shannon index. Also, ‘urban’ is a term that is poorly defined across studies and is occasionally used qualitatively rather than quantitatively. Pickett and Cadenasso (2006) suggested that definitions of urban will necessarily be flexible and case specific, but nevertheless need to be defined in each study. This could be achieved by quantifying key measures such as housing density, road density or percent cover of impervious surfaces (Chapter 2). We try to avoid confusion by referring to patterns in diversity with increasing urbanization or between urban and non-urban areas (as indicated by authors). Hence, urban is used in a relative rather
than absolute sense. We make no attempt to compare levels of urbanization across studies. While this might be highly desirable, suitable data often do not exist in the literature.

Patterns in space

Broad scale

At very broad scales (national to continental), human population density (HPD) is a useful surrogate for the level of urbanization particularly in developed countries. A growing number of studies have examined correlations between HPD and species richness for a range of taxonomic groups across various spatial extents and using a diversity of grain sizes (e.g. Balmford et al., 2001; Araújo, 2003; Gaston and Evans, 2004; Luck et al., 2004; Fjeldså and Burgess, 2008). A somewhat surprising result from these studies is the consistent reporting of positive correlations between HPD and species richness; surprising because of the undoubted negative impacts of human landscape modification on the persistence of many species.

Luck (2007a) conducted a major review of the relationships between HPD and biodiversity, including a meta-analysis of studies correlating HPD with species richness. He found strong, positive population effect sizes (a population effect size is a single value combining correlation coefficients across studies using meta-analytical techniques) between HPD and the species richness of birds, mammals and plants (Figure 1). However, there was substantial variability across studies owing to, among other things, different spatial extents, grain sizes, sample sizes, habitats and approaches.

A key variable in these studies is grain size, which ranged from 100 m² plots up to countries in the research reviewed by Luck (2007a). As grain size increases, so
does the strength of the positive correlation between HPD and species richness (also see Pautasso, 2007), although this can be complicated by the fact that higher population densities may be characteristic of smaller sampling areas. At small grain sizes the correlation can be, not unexpectedly, negative rather than positive (e.g. Drake and Pereira, 2002; Urquiza-Haas et al., 2009). Moreover, broad-scale studies using alternative measures of level of urbanization may yield results that differ from those relying on HPD. Clergeau et al. (2001) conducted a biogeographical meta-analysis of 18 studies from towns in temperate and boreal climatic regions where degree of urbanization was measured as peri-urban, suburban and town centre. They found that bird species richness was negatively correlated with latitude and increasing urbanization. Lepczyk et al. (2008) found that, across the mid-western United States, native bird richness was highest where anthropogenic land cover was lowest and housing density was intermediate.

The general conclusion from the above studies is that people co-occur with a diversity of species at the regional level ($\geq 2500 \text{ km}^2$), but only a few species persist with humans at the local level particularly in highly urbanized locations. ‘Regions’ are broad enough to encompass human settlements and relatively undisturbed areas, and co-occurrence across regions seems to be driven by people and other species responding similarly to energy and/or productivity gradients moderated by human land use (see ‘Drivers’ below and Figure 7). Lower species diversity at the local level results from substantial habitat loss in highly urbanized locations. This realization helps to reconcile the apparently contradictory findings among broad-scale and local-scale studies.

Across regions, Luck (2007a) found that HPD was also positively correlated with the number of threatened species, geographically restricted species (~ local
endemics) and introduced species (especially for plants; Figure 1), although the latter has been poorly explored at broad scales. While the correlation with threatened species infers that increasing urbanization adversely affects species persistence, such spatial correlations are weak causal explanations. Stronger evidence of the negative impacts of urbanization on species persistence comes from studies that track persistence over time (e.g. Thompson and Jones, 1999; Parks and Harcourt, 2002; Tait et al., 2005). Yet, there are only a handful of these studies in the literature and there is a desperate need for long-term monitoring of species persistence in urban areas as development proceeds.

Geographically restricted species are those with small geographic ranges. The positive correlation between HPD and these species suggests their ranges occur, more often than not, close to human settlements. This presents a conservation challenge since there may be few locations within their range that are distant from human settlements and associated negative impacts. It also underscores the dire need to implement effective conservation strategies in urban areas (Schwartz et al. 2006; Lawson et al. 2008).

HPD–species richness patterns in Australia match those from other countries and continents across a range of taxonomic groups. This is true even if the effects of biased sampling effort and spatial autocorrelation are controlled for (Luck et al. unpublished data; Figure 2). However, reptiles represent an important exception to the general pattern, as there is a slightly negative correlation between HPD and reptile species richness across Australia at a grain size of 1° (although strong positive correlations between HPD and richness are recorded elsewhere, e.g. North America, Luck et al., 2004). This is because diversity patterns in reptiles, which are ecotothermic, are probably more closely related to spatiotemporal variation in solar
radiation or temperature than other Australian species (including humans) that are responding to gradients in rainfall and productivity. This results in many reptiles occurring in sparsely populated arid and semi-arid regions.

The broad-scale trends described above mask more complex patterns between species richness and urbanization occurring at local levels. Nevertheless, these studies yield important information that may guide regional management strategies. They also encourage a hierarchical approach to examining species–people relationships and demonstrate that different patterns and drivers manifest themselves at different spatial scales. A multi-scaled approach to ecological studies has gained substantial support in recent decades (Lindenmayer and Franklin, 2002) and urban ecology should continue to promote this approach.

**Comparative**

Comparisons of species richness between urban areas and those dominated by agriculture or native vegetation generally find that richness is lower in urban areas, while total species abundance is higher with a handful of species contributing the majority of individuals. There are important exceptions to this general pattern identified from studies across different taxonomic groups and sub-sets of species from a particular group (e.g. cavity-nesting birds). It is also important to note that some researchers confine their sampling entirely to patches of native vegetation (e.g. surrounded by agriculture or urbanized areas), while others sample the full range of available habitats. Taxonomic bias inevitably exists in these studies with much work conducted on birds and to a lesser extent plants, and fewer studies on other taxonomic groups. This reflects a combination of ease of sampling and the fact that a range of bird and plant species have adapted relatively well to urbanization.
Lower species diversity with increasing urbanization has been found for birds (Cam et al., 2000; Sandström et al., 2006), bats (Kurta and Teramino, 1992; De Cornulier and Clergeau, 2001), terrestrial mammals (Tait et al., 2005) and amphibians (Gagné and Fahrig, 2007; see Hamer and McDonnell, 2008 for a review of urbanization effects on amphibians), but the occasional study does not fit this trend. For example, Palomino and Carrascal (2007) found that bird species richness in native vegetation patches was not adversely affected with decreasing distance to small cities (< 15 000 people) in Central Spain, although roads had generally negative impacts. Fewer studies have been conducted on invertebrates (see McIntyre 2000 for a review), but Rickman and Connor (2003) found that the species richness and total abundance of leaf-mining Lepidoptera in habitat remnants around San Francisco Bay was not influenced by the extent of urbanization occurring in a 500 m radius around each remnant. However, increasing urban density in Melbourne, Australia had substantial negative impacts on macro-invertebrate communities of small streams, whereby metropolitan communities were dominated by a few abundant species (Walsh et al., 2001).

Variation in the results among studies can be explained in part by the varied responses of particular species groups. A number of studies have examined changes in the diversity of sub-sets of bird species with increasing urbanization, and Chace and Walsh (2006) conducted a comprehensive review of the effects of urbanization on avifaunal assemblages. Results across studies are not always consistent, but some general trends can be identified (Table 1). For example, housing density was negatively correlated with the richness of territorial species, forest interior species and Neotropical migrants in some regions of the United States (Mills et al., 1989; Friesen et al., 1995; Green and Baker, 2003), while omnivores and exotic species have been
shown to increase in urban areas in the United States and Europe (Jokimäki and Suhonen, 1998; Allen and O’Connor, 2000). Pidgeon et al., (2007) found that forest-dependent birds were mostly negatively impacted by increasing house density across the United States, although results varied for different species groups and ecoregions. Cavity-nesters, short-distance migrants and narrowly distributed species were some of the groups to show negative responses.

For bird communities in Singapore, insectivores, carnivores, shrub-nesters and primary cavity excavators were adversely affected by increasing urbanization, whereas frugivores prospered in areas of low density housing (Lim and Sodhi, 2004). Other studies support the trend of insectivore decline with increasing urbanization, while also showing that granivores may adapt well to urban environments (e.g. Allen and O’Connor, 2000; Lindsay et al., 2002). In Australia, urbanization may favour behaviourally aggressive and medium to large-bodied bird species (Garden et al., 2006). Many of these species are responding to resource availability in the urban landscape. For example, large honeyeaters are attracted to streetscapes with a high density of flowering native trees and shrubs.

In contrast to the results of Pidgeon et al., (2007) and Sandström et al., (2006), Chace and Walsh (2006) suggested that cavity-nesters are favoured by urbanization (also see Miller et al., 2003). Such apparently contradictory findings highlight the importance of acknowledging contextual and ecological differences across studies. For example, Australia has many cavity-[hollow-]nesting birds, but no species that can excavate cavities, which are formed from insect and fungal attack. Hollow-bearing trees are rare in Australia’s urban environments since most are cleared during development and hollows take many decades to form in native trees so are mostly absent from plantings post development. Hence, urban areas in Australia do not
support a high diversity of hollow-nesting species (Garden et al., 2006). It is also important to acknowledge that few studies that examine how species groups with particular traits vary in richness with urbanization simultaneously assess multiple traits or address species phylogeny.

A number of studies classify bird species into ‘urban adapted’ or ‘urban sensitive’ (e.g. Blair, 1996; Lim and Sodhi, 2004). Classifications based purely on variation in population abundance across gradients of urbanization are not particularly informative without exploration of the ecological traits that allow species to adapt to urban environments. Thankfully, a handful of studies have begun to explore this issue (e.g. Kark et al., 2007; Croci et al., 2008). Splitting species into urban adapters or urban sensitive can result in different patterns in richness. For example, Tratalos et al. (2007) found that across Britain, total bird species richness and that of urban-adapted species increased from low to moderate housing density then declined at higher density (following the hump-shaped pattern often reported in rural–urban gradient studies; see below), while the richness of urban sensitive species consistently declined with increasing density. Total species abundance and the abundance of urban-adapted species increased with housing density, declining only at the highest densities.

Richness patterns for plants often differ from those of fauna species. Urban areas have been shown to harbour more plant species than surrounding non-urban areas (Kühn et al., 2004) and species richness is positively correlated with city size (Pyšek, 1998), although this may reflect a simple species–area relationship. Positive correlations still exist even when plants are split between native and introduced species. For example, Pyšek (1998) found that, across 54 cities in central Europe, the richness of native plants, aliens, neophytes (introduced to central Europe after 1500 A.D.) and archaeophytes (introduced before 1500) increased with city area, number of
inhabitants and HPD. The increase was strongest for neophytes, the most recent introductions. An important result from this study was that the proportional representation of aliens was much higher in cities compared to their representation in the regional species pool (Figure 3). This is indicative of urban areas being highly modified landscapes, although still supporting a rich diversity of plant species.

Kühn et al. (2004) demonstrated that native and naturalized alien plant species richness were significantly higher in city grid cells compared to non-city grid cells in Germany. Native plant species richness was largely explained by the number of geological types per grid cell (130 km²) and cities were mostly settled in areas of high geological diversity. Hence, human settlers were attracted to inherently diverse locations. In contrast to Pyšek (1998), Kühn et al. (2004) found that the proportional representation of alien vs. native species was largely similar in city and non-city grid cells. Of course, contrary patterns can generally be found. For example, Roy et al. (1999) showed that total plant species richness and the richness of native plants did not increase with urbanization in Britain, although alien species richness did. Importantly, they used a much smaller grain size (2 km²) than the above studies.

In support of the results found for bird species, work on plants has also determined that species with particular traits are more likely to persist in urban environments. For example, Thompson and McCarthy (2008) demonstrated that in Sheffield and Birmingham in England, urbanization favoured plant species that were larger (based on plant height) and preferred base-rich habitats and, to some extent, dry, unshaded and moderately fertile habitats. Their results were largely consistent for both native and introduced species. Plant height also dictated the likelihood of extinction for plants in Middlesex, England, whereby short plants (mostly natives)
were more likely to suffer extinction (Preston 2000; a similar result was recorded in Auckland, New Zealand by Duncan and Young (2000)).

In an important follow up to the study by Kühn et al. (2004), Knapp et al. (2008) showed that plant species richness in German cities was not related to phylogenetic diversity. That is, high species richness mostly resulted from a greater number of more closely related, functionally similar species adapted to urban areas. This suggests functional diversity is reduced in urban vs. non-urban areas. Such a conclusion is well supported in the growing literature on biotic homogenization, whereby increasing urbanization reduces species diversity across sites and leads to greater community similarity among urban areas than among non-urban areas (Rahel, 2000; Olden and Poff, 2003; McKinney, 2006; Olden et al., 2006; Devictor et al., 2007). Homogenization of species assemblages in urban areas appears to be driven by invasions or introductions of generalist, urban-adapted species, local extinctions of specialist species (McKinney and Lockwood, 1999; Olden et al., 2004) and the promulgation of similar habitat components across urban localities. The process of homogenization raises substantial challenges for protecting diverse species assemblages within human settlements.

Gradient studies

One way to look at patterns of urbanization is to sample along a gradient of increasing settlement intensity from native habitats or rural areas to city centres. Sampling can occur at non-contiguous points in different land-use/urbanization categories along a transect running from city centre to rural/native zone, or at points located randomly throughout the entire study area. Studies of this type have been undertaken across a range of settlement sizes from major cities (population > 1 000 000) to regional towns
Grain sizes varied from < 10 ha (Sewell and Catterall, 1998; Smith and Wachob, 2006; Caula et al., 2008) to much larger plots (> 2000 ha) (Weng, 2007; Gaublomme et al., 2008). Native–urban or rural–urban gradients are generally defined by some index of urbanization using either physical (e.g. building density, land-use types, vegetation cover, density of roads or distance to the central business district; Melles et al., 2003; Clergeau et al., 2006; Pillsbury and Miller, 2008) demographic (e.g. population density or demographic indices; Rubbo and Kiesecker, 2005 Hahs and McDonnell, 2006) and/or landscape metrics (e.g. patch fragmentation, patch size, edge or land-use heterogeneity; Luck and Wu, 2002; Weng, 2007).

Studies across gradients often report species diversity peaking at moderate levels of development with reduced species richness occurring at high levels (urban) and low levels (rural and native) of development (Sewell and Catterall, 1998; Blair, 1999, 2004; Smith and Wachob, 2006). Rural–urban gradients in particular often display a hump-shaped pattern in species richness (Figure 4). This is consistent with the intermediate disturbance hypothesis, which predicts that species richness will be highest at intermediate levels of disturbance (Connell, 1978). Many studies have observed this relationship for a variety of taxonomic groups including birds (Sewell and Catterall, 1998; Blair, 2004; Chace and Walsh, 2006), bats (Gehrt and Chelsvig, 2003; Duchamp et al., 2004), and lizards (Germaine and Wakeling, 2001). This response may be the result of increased resources at moderate levels of urbanization, with gardens, parks, reserves and other land uses characterising these areas and providing habitat for particular groups of species (French et al., 2005; Gaston et al., 2007; Young et al., 2007).
McKinney (2008) conducted a comprehensive review of studies on plants, invertebrates and non-avian vertebrates (i.e. mammals, reptiles and amphibians), comparing species richness along a gradient from low (rural) to moderate (suburban) to high (urban core) levels of urbanization. He found that 64.7% of 17 plant studies recorded an increase in species richness from low to moderate urbanization, while studies of invertebrates and non-avian vertebrates were more likely to record a decrease in richness (63.8% of 57 studies and 82.4% of 31 studies, respectively; although 29.8% of invertebrate studies documented an increase in species richness from low to moderate levels of urbanization). Conversely, in the transition from moderate to high urbanization, only one study from all the groups recorded an increase in species richness, while most showed a decrease (plant species richness either decreased or remained the same – 50% of studies in each category). McKinney (2008) concluded that plant species richness tended to peak at moderate levels of urbanization, while the richness of invertebrates and non-avian vertebrates peaked at low levels of urbanization.

Species display different tolerances to urban disturbance and have been grouped as ‘exploiters’, ‘adaptors’ or ‘avoiders’ of urbanization (Blair, 1996; Kark et al., 2007; Croci et al., 2008). Species classified as adapted to moderate levels of disturbance will tend to be dominant at the rural–urban interface where landscapes are the most heterogenous (Sewell and Catterall, 1998; Melles et al., 2003; Caula et al., 2008). This is a distinct group of species able to use resources typical in this landscape, but the assemblage is very different from the species that occurred in the area prior to development (see Tait et al., 2005; McKinney, 2006).

Another recurring pattern along rural–urban gradients is the greater abundance of species at the urban centre, with a few urban exploiters contributing the majority of
individuals. This has been noted for birds and microbats (Kurta and Teramino, 1992; Lesinski et al., 2000; Blair, 2004; Palomino and Carrascal, 2007). Other taxonomic groups show a different pattern even when a few species are dominant. For example, abundance has been observed to decrease at the urban centre for amphibians (Rubbo and Kiesecker, 2005; Pillsbury and Miller, 2008), lizards (Germaine and Wakeling, 2001), butterflies (Blair, 1999) and ground beetles (Gaublomme et al., 2008).

The difference in responses of certain taxa may be related to their ability to disperse through the landscape, habitat preferences and the location of habitat along the rural–urban gradient (Niemelä et al., 2000; Atauri and De Lucio, 2001). For example, frogs are highly sensitive to habitat fragmentation and road density (Rubbo and Kiesecker, 2005; Parris, 2006; Pillsbury and Miller, 2008), which is most intense at the city centre, and often rely on ephemeral ponds for breeding, which are more likely to be found in the peri-urban and rural zone (Hamer and McDonnell, 2008). The level of urban disturbance a species is able to tolerate depends on its ecological traits and these will determine a species’ capacity to occupy niches along the gradient (see urban-centric below).

Some studies have observed seasonal variation in species richness patterns along rural–urban gradients, whereby richness generally declines with increasing building intensity during favourable seasons when resources are abundant (e.g. spring), whereas in the harshest seasons with greater resource restrictions (winter/summer) more species are recorded using urban environments of intermediate disturbance. For example in Brisbane, Australia, Sewell and Catterall (1998) found more bird species using moderately disturbed suburban environments than large vegetated remnants (> 100 ha) during summer compared to winter (summer is a harsher season for this location). In Montpelier, Southern France, Caula et al. (2008)
found more bird species using suburban environments compared to croplands and woodlands during winter than in spring. Hence, some species may be exploiting resources within moderately disturbed urban environments when harsh climactic conditions are affecting resource availability in the surrounding landscape. This suggests that urbanization may limit seasonal variation in important resources (e.g. water) and this is a crucial question for future research. Understanding the patterns of species distribution along rural–urban gradients can help to focus conservation and restoration efforts where they will be the most effective.

**Urban-centric**

Comparative studies generally show that species richness declines with increasing urbanization or that richness peaks at some intermediate level of development especially across rural–urban gradients. However, patterns vary across taxonomic groups and for species with specific ecological traits and some species can readily adapt to or exploit urban habitats. Simple comparisons of native vs. urban landscapes sometimes treat ‘urban’ as a homogeneous unit, ignoring the substantial heterogeneity that can occur within an urban environment. This heterogeneity leads to changes in species diversity and composition across neighbourhoods within cities and towns.

The species richness of fauna across neighbourhoods is often positively correlated with the cover of native and/or exotic vegetation. Studies on birds consistently report on the importance of retaining native tree canopy cover, vegetation structure and streetscape vegetation to support a higher number of species (e.g. Mills *et al.*, 1989; Fernández-Juricic, 2000; Hennings and Edge, 2003; White *et al.*, 2005; MacGregor-Fors, 2008). White *et al.* (2005) found that parks and streetscapes with native vegetation supported more bird species than recently developed streetscapes or
those with exotic vegetation in Melbourne suburbs. Hennings and Edge (2003) found that urban canopy cover promoted native bird richness in Portland, Oregon, while Green (1984), also working in Melbourne, reported that total native vegetation cover was positively correlated with native bird richness, but negatively correlated with exotic bird richness. Studies also report the importance of native remnants and riparian zones within urban environments as potential conservation reserves (Bush et al., 2003; Hennings and Edge, 2003; Hodgson et al., 2006, Pennington et al., 2008).

Surveys confined entirely within green space surrounded by urbanization (e.g. remnant vegetation or recreation parks) generally show that species richness is highest in the areas that most closely resemble the previous land cover (e.g. forest reserves) and the size of remaining vegetation patches is positively correlated with species richness, consistent with well established species–area relationships (e.g. Mörtberg, 1998; Koh and Sodhi, 2004; Palmer et al., 2008). Vegetation area seems to be particularly important for those species that are unable readily to use the surrounding urban landscape, although Antos et al. (2006) found that vegetation patch size was also positively correlated with introduced bird species richness in urban areas in Melbourne. Moreover, area might not be the most critical factor driving patterns in species richness in some taxonomic groups. Garden et al. (2007) found that habitat structural elements were the most important determinants of reptile and mammal assemblages in urban vegetation patches in Brisbane.

In sum, these results show, unsurprisingly, that native fauna species respond positively to the retention of native vegetation and richness increases with increasing vegetation cover. Hence, they demonstrate the importance of retaining vegetation in urban landscapes. Not only can this promote species conservation, vegetation offers human residents a range of additional benefits including microclimate regulation.
(Harlan et al., 2006; Jenerette et al., 2007), control of air and water pollution (Randolph, 2004), carbon storage (Nowak, 1994), recreational opportunities (Miller, 2006) and cultural and health benefits (Fuller et al., 2007; Tzoulas et al., 2007).

Some of the more interesting urban-centric work links household or neighbourhood socio-economic characteristics with vegetation cover and species diversity. This begins to tease apart some of the driving forces of neighbourhood variation in urban ecosystems and also highlights demographic groups that may be disadvantaged through lack of direct access to the benefits of nature. For example, Hope et al. (2003) found that plant species richness was positively related to, and primarily a factor of, family income and housing age across neighbourhoods in Phoenix, Arizona. Income is a key variable in studies of vegetation cover (e.g. Grove and Burch, 1997) and this suggests that people with greater financial security are either attracted to neighbourhoods with a higher level of ‘naturalness’ or promote vegetation cover and diversity through their activities. The flipside of this trend is that residents with a ‘lower’ socio-economic status often live in neighbourhoods with few species and little vegetation cover (Iverson and Cook, 2000; Pauleit et al., 2005).

Urban-centric studies are now beginning to focus on species richness patterns in household gardens and how householder behaviour may influence these patterns. For example, Thompson et al. (2003) found that a third of all plant species in gardens in Sheffield, England were native and, collectively, garden quadrats contained twice as many species as semi-natural habitats (although mean species richness per quadrat was lower in gardens). Moreover, plant species richness increased with garden area with the relationship being potentially stronger for natives than exotics (Smith et al., 2006). Householder activities such as watering and fertilising can play an important role in maintaining small plant populations and increasing the diversity of gardens,
and some potential exists for coordinating householder activities to achieve broader conservation objectives in line with incentive schemes currently used in rural landscapes.

The structure and composition of household gardens may also have a stronger influence on bird assemblages than broader landscape factors (Daniels and Kirkpatrick, 2006). Garden area has been shown to be positively related to garden bird species richness and native birds may be particularly attracted to native plants (Thompson et al., 1993; Chamberlain et al., 2004). For example, French et al. (2005) found that native nectarivores, a substantial component of Australian urban bird communities, preferred to feed on native Banksia spp and Grevillea spp than introduced Camellia spp and Hibiscus spp in Sydney, Australia.

Provision of supplementary food will generally increase bird species richness and abundance in gardens (Savard et al., 2000; Daniels and Kirkpatrick, 2006; Parsons et al., 2006). Fuller et al. (2008) documented important links between bird assemblages and bird feeding stations and the proportion of households that provide supplementary food in the neighbourhoods of Sheffield. Interestingly, they also found that species richness was higher in middle and high-income neighbourhoods, mirroring the results of Hope et al. (2003) for plants in Arizona. We have found similar results in towns (15 000 < 90 000 people) across south-eastern Australia showing that vegetation cover, bird species richness and bat activity are all higher in high income suburbs where a greater proportion of residents have completed tertiary education (Luck et al. 2009, and unpublished data) (Figure 5).

While there is much variation in the results of urban-centric studies, some general patterns are still evident such as the decline in species diversity from the edge to the interior of metropolitan areas (Green, 1984; Clergeau et al., 1998; Cam et al.,
2000; Melles et al., 2003), although it is unclear how such a pattern might be influenced by town size. The drivers of these patterns reflect complex interactions among environmental gradients, neighbourhood socio-economic characteristics, householder behaviour and species ecological traits. Potential drivers of species richness patterns in urban landscapes across scales are further explored below.

**Patterns in time**

While there are many studies on spatial patterns in diversity across urban areas there are relatively few on patterns over time. This is not unusual in ecology owing to the rarity of accurate, long-term databases. The most comprehensive work relates to temporal changes in vegetation cover in urban areas, which is relatively easy to map with satellite images or aerial photographs (e.g. Morawitz et al., 2006; DiBari, 2007). Moreover, some studies have tracked changes in urban land cover or housing development in urban and peri-urban areas and matched this with loss of vegetation (e.g. Hammer et al., 2004; Tian et al., 2005; Gonzalez-Abraham et al., 2007). Hence, we have reasonably good information on temporal patterns in urban development and changes in vegetation cover, but few data exist on changes in species diversity over time (and there are even fewer studies on changes in population size, although see, for example, Brichetti et al. 2008).

Nevertheless, a key study in this area is Tait et al. (2005). These authors tracked changes in the species richness of native and introduced plants, mammals, birds, reptiles and amphibians in Adelaide (currently a city with > 1 M people), Australia from 1836–2002. Some results were predictable, while others were quite surprising. Native species richness declined in most groups, but only marginally for reptiles (3.6% of 56 species) and not at all for amphibians. Native mammals suffered
the most, losing 50% of species \( n = 40 \); a similar result was reported by van der Ree and McCarthy (2005) for mammal species loss in Melbourne since European settlement). Interestingly, total species richness remained practically the same for birds and reptiles. That is, while 21 native bird species were lost, 20 introduced species established themselves in the city. Similarly, two native reptiles were replaced by two introduced species. The same wasn’t true for mammals (a loss of 20 species, but a gain of only nine), while there was an overall increase of 46% in the total number of plant species.

Other than for mammals, these patterns do not represent the devastating loss of species that is normally associated with urban development. However, it is important to note that Tait et al. (2005) included the entire metropolitan area in their study and this incorporates patches of native and other vegetation. Moreover, species richness is not necessarily the best measure of human’s impact on nature since many species populations can be lost, with dire implications for species persistence and ecosystem functioning, even though a species may remain extant (Hughes et al., 1997; Luck et al., 2003).

Puth and Burns (2009) also reviewed studies that examined changes in species richness over time for the metropolitan region of New York. They found that of the 26 studies documenting temporal change, 65% recorded declines in species richness (increasing to 77% when only trends in native species were considered). Only six studies found that species richness increased over time and most of these examined recolonization after disturbance. Decreasing species richness was recorded across a variety of taxonomic groups including amphibians, birds, fish, plants and reptiles. Other studies of temporal trends in New York flora concur with these findings, showing that the area has lost over 40% of its native plant species in the last 100+
years (Robinson et al., 1994; DeCandido et al., 2004). These latter studies also found that exotic plant species richness increased over the same time period.

A decline in native plants and corresponding increase in introduced species over time, sometimes leading to a net gain in plant species richness, is consistent with studies conducted over broader areas (e.g. McKinney, 2002; Pyšek et al., 2005), although site-specific results may vary from this trend (e.g. Chocholouskova and Pyšek, 2003). Parody et al. (2001) reported no change in bird species richness in moderately populated areas over a 50-year period in Michigan, while Jones and Wiencke (2000) recorded the same result for a single suburban bird community studied over 16 years in Townsville, Australia. Yet, some studies report a substantial decline in bird species richness over time for parks surrounded by urban development (e.g. Diamond et al., 1987; Corlett, 1988; Recher and Serventy, 1991), although it is unclear how much this species loss is a factor of park size and isolation (or habitat changes) and how much can be attributed to increasing urbanization.

Lane et al. (2006) estimated that, since 1819, between 33–72% of bat species have been lost from Singapore, an island that has been substantially developed (50% ‘built up’). The upper bound is based on a species assemblage inferred from a neighbouring mainland area and may be an over-estimate. The authors make the important point that many species are probably lost during initial habitat clearance prior to extensive urban development and prior to the advent of comprehensive and systematic species monitoring. Therefore, it is likely that the species richness of original assemblages used as baselines for comparing historical changes are almost always underestimated and this is problematic for detailing changes over time with increasing urbanization.
Matching spatial variation in settlement or neighbourhood age with species richness can also allude to likely temporal changes. For example, broad-scale studies by McKinney (2001, 2002) showed positive correlations between introduced plant richness or net gain in the number of plant species (i.e. introductions minus local extinctions) and HPD and time since settlement in the United States. The same was not true for fish species analysed in the same studies. Other research found that bird species richness was higher in older suburbs likely reflecting the development of urban vegetation over time (e.g. Jones, 1981; Munyenyembe et al., 1989). This probably occurs when vegetation is cleared at the time of settlement or settlement develops on previously cleared land (e.g. rural areas) and the establishment of domestic gardens increases vegetation cover and species diversity.

In sum, changes over time appear to follow these general trends (Figure 6). For plants, early human settlers clear native vegetation, but introduce many new species (for agricultural or domestic purposes) such that the number of introductions outpaces the number of local extinctions leading to a net gain in richness over time. The number of species introductions is likely to decline over time and the same is probably true for local extinctions as most urban-sensitive species have already been lost from long-established settlements. This should lead to a plateau in total species richness (although the number of exotic species will likely continue to slowly increase over time, especially for plants). A similar plateau would be reached for animal [vertebrate] species richness, but possibly through different processes. These would either be a replacement of native species with a similar number of introduced species (e.g. birds), no change in native species (e.g. reptiles), or a substantial decline in natives resulting in a new, and much lower asymptote in total species richness (e.g. mammals).
The trends in Figure 6 are, of course, simplifications and ignore the fact that rapid gains and losses in species richness can occur over short periods (Tait et al., 2005). More importantly, native species richness almost always declines with increasing urbanization and highly developed locations have substantially different species assemblages than those that existed prior to development. Spatiotemporal patterns in species diversity in urban landscapes result from a myriad of complex, interacting processes occurring over various spatial and temporal scales (Kent et al., 1999).

**Drivers**

The drivers of patterns in urban diversity vary across spatial scales (Figure 7). What drives the broad-scale congruence between species richness and HPD across regions is subject to some speculation, but little comprehensive assessment. People and other species may co-occur either because both are responding to underlying abiotic or biotic conditions (e.g. climate) or human landscape modification leads to increased species richness near human settlements (e.g. through creation of more heterogeneous landscapes). Moreover, humans are often responsible for deliberately introducing or promoting colonization of exotic species in urban environments. This is especially true for plants, but these introductions do not explain the positive HPD–species richness correlation across regions, because this correlation still exists when examining native species only (Luck 2007a).

A useful starting point is to assess whether well established drivers of biogeographic gradients in species richness also explain patterns in human distribution. Mutual drivers include potential energy and/or primary productivity, habitat heterogeneity, and evolutionary time/long-term climatic stability (Rahbek and
Graves, 2001; Willig et al., 2003). Potential energy and primary productivity are positively correlated with HPD and species richness in some locations and offer possible explanations for their co-occurrence across regions (Evans and Gaston, 2005; Luck, 2007b). Fjeldså and Rahbek (1998) suggested that historical climatic stability may have led to the spatial congruence between people and species richness.

Alternatively, human land-use policy may be solely responsible for the regional co-occurrence of human settlements and species richness through anthropogenic landscape heterogeneity (Fairbanks, 2004), increased productivity (Hugo and van Rensburg, 2008) or conservation policy (Gaston, 2005). The first two explanations suggest humans increase heterogeneity (e.g. through establishing a diversity of land uses) or productivity (e.g. through irrigated agriculture) near human settlements leading to greater species richness. The third predicts that HPD and species richness are correlated because both positively co-vary with conservation activities, or that conservation policy mediates the relationship between people and richness. The former is highly unlikely given reports of strong negative correlations between HPD and the size of conservation reserves, which likely increases the probability of species extinction inside reserves (Brashares et al., 2001; Harcourt et al., 2001; Luck, 2007b).

Hugo and van Rensburg (2008) tested each of the human land-use hypotheses for HPD and bird species correlations across South Africa at a quarter degree resolution. They found support for the anthropogenic heterogeneity and productivity hypotheses, and concluded that the co-occurrence of humans and other species is strongest in regions with greater cover of conservation land use. Extending this work, we tested the explanatory power of a range of hypotheses for both abiotic and biotic (potential energy, primary productivity, inherent habitat heterogeneity and climate
stability) and human land use (anthropogenic landscape heterogeneity, increased productivity and conservation policy) drivers of HPD and bird species richness co-occurrence across Australia at a 1° resolution (Luck et al., unpublished data). We found that potential energy (annual rainfall) and net primary productivity were the key drivers of the people–richness correlation after controlling for spatial autocorrelation and biased sampling effort. Inherent habitat heterogeneity was more strongly, positively related to species richness and HPD in low compared to high energy regions, contrary to previous findings (Kerr and Packer, 1997). Similar to Hugo and van Rensburg (2008), we found that conservation policy mediates the relationship between humans and other species, whereby the HPD–diversity correlation was strongest in areas with a greater percent cover of conservation land use and declined steadily with a reduction in conservation land use. This means that in regions where conservation land use is low, species are restricted to a few small conservation reserves that are mostly distant from human settlements. In contrast to Hugo and van Rensburg (2008), we found no support for the anthropogenic or increased productivity hypotheses.

Another potential driver of the HPD–species richness correlation that has not received adequate attention is biased sampling effort. This is particularly problematic when species lists are derived from atlas data collected by volunteer observers. Sampling effort has been shown to be greatest in regions of high HPD using such data (Luck et al., 2004) and this may lead to more species being recorded in these regions confounding relationships with other potential drivers. However, recent studies have now demonstrated that the HPD–richness correlation still exists after controlling for biased sampling effort (e.g. Evans et al., 2007; Pautasso and McKinney, 2007).
At smaller scales, the correlation between species richness and urbanization is generally negative. Therefore, the examination of potential drivers is usually focussed on the question of why more species occur in some urban areas than others. Landscape variables change considerably when moving from highly urbanized centres to peri-urban and rural areas. Vegetation patch size and density, land-use category and fragmentation show varying patterns across degrees of urbanization (Luck and Wu, 2002; Hahs and McDonnell, 2006; Weng, 2007). As urbanization intensifies, patch size generally becomes smaller and fragmentation increases (Luck and Wu, 2002; Smith and Wachob, 2006; Weng, 2007).

Across rural–urban gradients, fauna species richness may peak at intermediate locations (e.g. outer suburbs) owing to greater vegetation cover and the diversity of land uses in these locations compared to rural areas (which are largely cleared) and urban centres (Luck and Wu, 2002; Weng, 2007). Moreover, intermediate locations are areas where species that respond positively to urbanization and those more dependent on native vegetation may coexist. Landscape/habitat heterogeneity (i.e. the variety of landscape elements) plays an important role in driving faunal species richness patterns (e.g. Kerr and Packer, 1997; Atauri and de Lucio, 2001; Tratalos et al., 2007), although promotion of heterogeneity per se is unwarranted without some understanding of the key landscape elements required by particular taxonomic groups.

At various scales, bird species have been shown to respond positively to increasing vegetation cover, composition and structure (Mills et al., 1989; Munyenyembe et al., 1989; Pidgeon et al., 2007; Bino et al., 2008). Vegetation cover is often negatively correlated with housing density and the cover of impervious surfaces (e.g. roads and footpaths). The availability of anthropogenic food may also have a strong influence on bird assemblages in urban environments (e.g. Jokimäki and
Suhonen, 1998; Fuller et al., 2008), although this may increase the abundance of a few readily adaptable species rather than species richness per se. At the scale of individual streets and gardens, plant species composition has an important influence on bird assemblages. For example, Young et al. (2007) found that the presence of flowering native trees was more important in driving nectarivore assemblages in urban streets in Adelaide than the area surrounding the tree.

In sum, faunal species will respond to the availability of critical resources (e.g. for feeding and breeding) across urban landscapes and use of these resources will be dictated by their capacity to move around the landscape, interspecific interactions (e.g. competition) and species’ ecological traits. Arguably, a more interesting question then is what dictates the distribution of resources. Vegetation is an important resource for many faunal species and has been shown to vary greatly across urban areas. In contrast to fauna, plant species richness (natives and exotics) tends to be higher in urban than rural areas and increases over time with increasing urbanization (although the relationship is likely to be asymptotic). This largely reflects the introduction of new plant species for agricultural or domestic purposes (Pyšek, 1998). Moreover, humans are able to maintain very small plant populations (e.g. one to two individuals) and ensure the persistence of non-endemic species through watering, fertilization and other maintenance activities and this leads to an ‘artificially’ high diversity (i.e. many of these populations or species would go ‘extinct’ without human intervention). Also, in some regions, home gardeners have access to a huge species pool through local nurseries (Thompson et al., 2003).

While underlying heterogeneity (e.g. topographic or geological) may have an influence on plant species diversity in urban areas (Pyšek, 1998; Kühn et al., 2004), an increasing number of studies demonstrate a relationship between the socio-
economic profile of neighbourhood residents or householder behaviour and vegetation cover and plant species diversity (Hope et al., 2003; Grove et al., 2006). These studies often show that income or some other measure of social ‘status’ (e.g. education) is positively correlated with species richness or vegetation cover. Teasing apart the causal direction of this relationship will take some detailed interdisciplinary work. For example, do people with high incomes prefer to live in more vegetated suburbs (and have the financial capacity to do so) or do they increase vegetation cover through their behaviour? Some of our own work has shown that level of education may be a better predictor of vegetation cover than income (although the two are often correlated), whereby cover is positively correlated with the proportion of residents with a tertiary education (Luck et al., 2009).

If resident behaviour is important in determining levels of vegetation cover, then improving social status is a potential mechanism for increasing vegetation and subsequently plant and fauna richness in neighbourhoods. Of course, not everyone can be rich or highly educated (although income and education levels can always be improved) and local government planning is still key to improving the nature of urban environments. Moreover, more easily managed factors like housing density also have strong relationships with vegetation cover and species richness (e.g. Hope et al., 2003; Tratalos et al., 2007; Luck et al., 2009) and a lot more research is required to determine how interactions between landscape planning, socio-economic status, resident behaviour and species’ ecological traits influence flora and fauna assemblages in human settlements.

**Implications and future research**
There are two primary implications of the broad-scale congruence between people and species richness. The first is the substantial conservation challenges raised by this congruence given the negative impacts of human activities on nature. Alleviating spatial conflict between people and biodiversity has been explored in a number of studies through conservation planning strategies (e.g. Balmford et al., 2001; Araújo et al., 2002; Luck et al., 2004; O’Dea et al., 2006). These studies suggest opportunities still exist for promoting conservation in the midst of human development, but these opportunities are more restricted when conservation objectives become more demanding (e.g. protecting 20% of a species range rather than 10%).

The second implication is that there is substantial opportunity for people to experience species-rich locations near where they live if conservation close to human settlements can be improved (Schwartz et al. 2006; Lawson et al. 2008). Maintaining high diversity can be important for the production of various ecosystem services, many of which are used locally (Díaz et al., 2006). Future research should continue to focus on key drivers of spatial congruence and the development of intra- and inter-regional management strategies that ensure species persistence through appropriate settlement planning. More work is needed to assess the ecological, social and environmental (e.g. energy use) trade-offs between concentrated, high density living in increasingly large cities verses more dispersed, smaller regional centres. We know little, for example, of how rural–urban gradients vary with city size or if neighbourhoods in small towns are characterized by the same spatial variation in species richness as those in large cities. At a smaller scale, clustered development, although promoted as a tool to reduce the impacts of human settlement on nature, offered no greater conservation benefits than dispersed housing in a study in Boulder County, Colorado (Lenth et al., 2006).
Within human settlements, people living on the rural–urban fringe, in low
density housing or ‘wealthier’ neighbourhoods have the greatest opportunities to
conserve and interact with a diverse nature. However, the stark reality for most
people, particularly in large cities, is that their neighbourhood is likely to be species
poor and dominated by a handful of abundant urban exploiters (Turner et al., 2004). A
reduction in the opportunities for people to interact with nature can impact negatively
on human health and psychological well-being (Harlan et al., 2006; Tzoulas et al.,
2007) and there is some evidence to suggest that species diversity \textit{per se} is important
in promoting the latter (Fuller et al., 2007). For an increasing number of people, their
entire experience with nature may be dominated by interactions in urban
environments. Human–nature interactions can influence people’s perception of and
desire to protect nature, and may link directly with environmental activism (Dunn et
al., 2006). Since the majority of the Earth’s population now live in urban areas
(United Nations, 2008), and these people will have a substantial influence on
conservation policy through voter numbers, improving human–nature interactions in
human settlements is not only important for meeting local conservation objectives, but
could have major implications for global conservation (Dunn et al., 2006).

In the future, researchers must build on the ground-breaking interdisciplinary
studies that link ecological, socio-economic and environmental data (e.g. Hope et al.,
2003). Only through integrated research can we begin to understand the patterns of
diversity that occur in urban landscapes and tease apart the complex, interconnected
drivers of these patterns.

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Table 1. Generalized trends in species richness and abundance of sub-sets of avian species in response to increasing urbanization. A ‘?’ indicates a degree of uncertainty in likely responses, while strong conflicting trends have been reported for cavity-nesters.

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**Figure 1.** Population effect sizes (combining correlation coefficients across studies) between human population density and the species richness of birds, mammals and plants, and threatened, restricted and introduced species. Error bars are 95% confidence intervals. Data from Luck (2007a).

**Figure 2.** The distribution of bird species richness and human population density across mainland Australia. Bird data are at a resolution of 1° grid cells with equal survey effort per cell (ten random surveys). Blank (white) cells represent insufficient survey effort (< ten surveys). HPD is number of people per 0.05° grid cell (from Luck *et al.* unpublished data).

**Figure 3.** A stylized representation of broad trends in plant species richness with increasing urbanization. Introduced species generally increase in richness and in their proportional contribution to total species richness. Native species richness may either increase slightly or decline with increasing urbanization (dotted line). The relationships are asymptotic and total species richness may decline at very high levels of urbanization.

**Figure 4.** Stylized trend of species richness (synthesizing results of gradient studies) along a rural–urban gradient defined by increasing dwelling density with corresponding aerial photos of landscape types.

**Figure 5.** Suburban streetscapes in south-eastern Australia along a gradient of socio-economic ‘status’ based on income and the proportion of residents with a tertiary education. Bird and plant species richness tend to be highest in neighbourhoods with
higher status (i.e. higher income and education levels; unpublished data) (Photos: L. Smallbone).

**Figure 6.** General patterns in total species richness and the richness of native and introduced species with increasing urbanization over time (based on data reported in Tait *et al.*, 2005).

**Figure 7.** Summary of drivers across scales. (a) Across broad extents, using large grain sizes (e.g. 1°), human population density and species richness positively co-vary likely owing to mutual drivers such as available energy and primary productivity. This relationship is moderated by human land-use policy (e.g. area of conservation land near human settlements). (b) Within a region, rural–urban gradients often show peaks in species richness in fringe suburbs of metropolitan areas (intermediate disturbance) owing to greater vegetation cover and landscape heterogeneity in these locations compared to rural areas and city centres. (c) Within urban centres, the socio-economic characteristics of neighbourhoods are linked to vegetation cover and diversity and this in turn affects fauna assemblages. Neighbourhoods characterized by relatively low housing density, high income and high education levels support a greater diversity of species.