

## FORUM

# Sharing or sparing? How should we grow the world's cities?

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## Summary

1. There has long been a debate amongst conservation biologists about how agricultural land use should be distributed spatially. Advocates of land sparing argue that high-intensity food production on small units of land will conserve more natural habitat than low-intensity farming spread across larger areas. Others argue that less intensive production over a greater area of land will reduce the overall load of human stressors upon ecosystems.

2. Although agricultural and urban systems have traditionally been considered as different fields of research, there are strong parallels between the two landscapes in the patterns of their spatial configuration and the trade-offs associated with their development. Continued and rapid urbanization, with associated losses in vegetation, highlights the need for a uniting spatial framework to assess the ecological impacts of urbanization. Here, we apply some of the thinking emerging from the agricultural land-sparing debate to urbanization, review the similarities and differences between the two systems and set out a research agenda.

3. Intensification of urban systems to increase housing density leads to buildings being interspersed with small tracts of natural or semi-natural habitat patches (e.g. forest patches, parks). Urban extensification, on the other hand, is characterized by sprawling suburbanization with less concentrated, more distributed green space, often predominantly in the form of backyard or streetscape vegetation. We argue that regional scale analyses are urgently needed to determine which of these patterns of urban growth has a lower overall impact on biodiversity and to explore the geographical and taxonomic variation in the most ecologically appropriate city layout.

4. *Synthesis and applications.* The spatial pattern of urban development will affect biodiversity conservation within and beyond a city's borders. We chart the early progress of empirical work on the land-sparing debate in an urban context and suggest that to yield development patterns that minimize overall ecological impact, urban planners must work at the scale of at least the entire city rather than on a case-by-case basis.

**Key-words:** biodiversity, ecosystem services, landscape configuration, land-use transformation, mosaics, spatial models, urban densification

## Introduction

About half of the Earth's terrestrial surface has been cleared or otherwise dominated by human activity (Vitousek *et al.* 1997; Lambin 2003), precipitating a global biodiversity crisis in which the rate of species extinction

far exceeds the background expectation (Pimm & Raven 2000; Pereira *et al.* 2010). While agriculture is by far the most spatially extensive form of human land use, one of the most ecologically destructive forms of global change is urbanization, currently the fastest growing of any land-use type globally (Antrop & Van Eetvelde 2000; Hansen *et al.* 2005). Net human population growth is now occurring almost entirely within towns and cities, and by 2050, urban areas will need to accommodate an additional 2.6

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billion people (United Nations 2011). Urban development results in rapid local extinctions, frequently eliminating most native species (Marzluff, Bowman & Donnelly 2001), and so it is critical that future urban growth is planned in a way that minimizes ecological harm.

Although the impact of anthropogenic land use is often measured by its spatial extent, land uses vary markedly in intensity from pressures that barely modify a natural ecosystem, such as selective harvesting of nontimber products from a forest to intensive transformation that results in complete ecological degradation, such as intensive wheat production (Matson *et al.* 1997; Tschardt *et al.* 2005). As land-use intensity increases, extinctions accumulate (Radford, Bennett & Cheers 2005; Maron *et al.* 2012) and ecological function is compromised (Flynn *et al.* 2009). This has led to a vigorous debate about how we should arrange damaging land uses across landscapes.

Within agricultural landscapes, this debate has been well characterized. At one end of the spectrum is recognition that low-intensity forms of agriculture will deliver lower local impacts upon biodiversity and ecosystem function than more intensive transformations (Fischer *et al.* 2008). However, low-intensity land uses often cover a larger area than high-intensity land uses to deliver a similar overall yield. At the other end of the spectrum is a recognition that although intensive land use leads to greater local ecological impacts, it might be efficient to construct a landscape in which some parts are given over to intensive land use, while others are spared from direct ecological degradation to maintain the ecosystem services valuable to society (Fischer *et al.* 2008; Phalan *et al.* 2011).

This debate, thus far, has focused primarily upon agricultural land uses. In principle, we believe that many of the same arguments apply to any form of land use that can vary in intensity. Habitat conversion due to rapid human population growth (8–10 billion by 2050) and the increasing urbanization of society highlight the need to understand biodiversity loss in and around cities (Grimm *et al.* 2008). However, the intensity of human settlement can vary enormously from low-density residential plots in which much of the original vegetation is left intact to complete coverage by high-density built form and total destruction of the original vegetation (Fuller & Gaston 2009; Jenks & Jones 2010). The pattern of spatial fragmentation of vegetation will significantly affect conservation at local and regional scales, and this behoves us to characterize the patterns of development that have the least overall impact on ecological systems. Here, we (i) chart the history of the agricultural land-use debate, (ii) consider how this way of thinking might usefully be applied in the context of urbanization and (iii) outline a research prospectus.

### History of the land-use debate in agricultural development

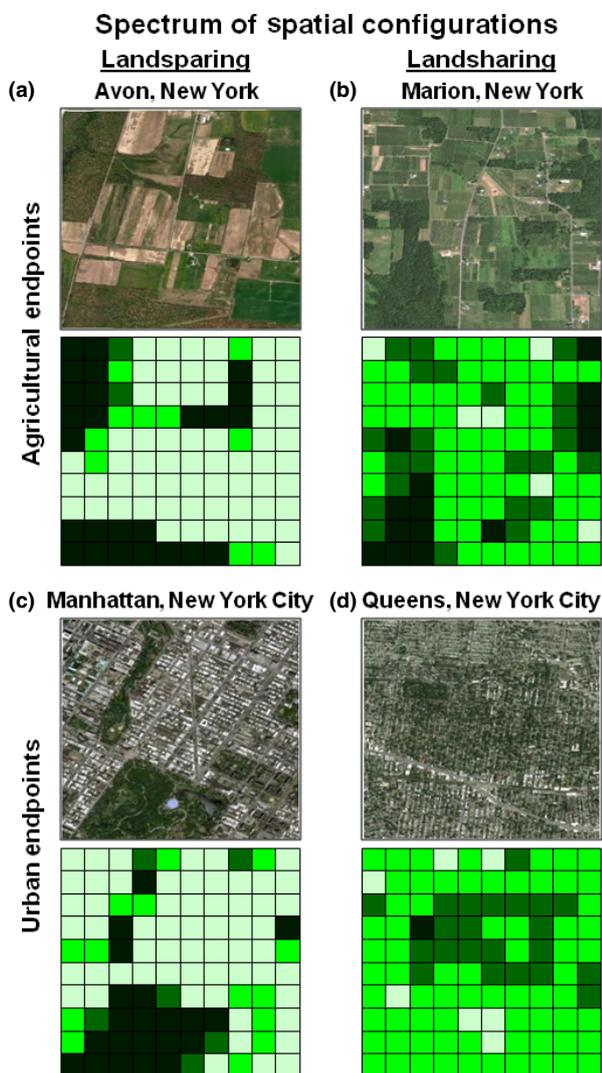
Crop production, as the primary goal of agricultural landscapes, has significantly increased through intensification

(Matson *et al.* 1997). Increasing demand for food and fuel has expanded and intensified agricultural systems around the world (Millennium Ecosystem Assessment, 2005), providing a growing global per capita food supply (United Nations 2011).

Although there have been tremendous gains in production from land-use conversion and management intensification, it remains a major challenge to meet the ever-growing demand for agricultural products while conserving biodiversity, providing crucial ecosystem services and maintaining rural livelihoods (Harvey *et al.* 2008). There are many examples of native species declines from agricultural land-use intensification (Aebischer 1991; Sotherton 1998; Benton *et al.* 2002), and there is often a corresponding loss in functional diversity (Flynn *et al.* 2009). For example, in postwar Europe, reductions in farmland bird populations followed soon after the onset of agricultural intensification, with reductions closely associated with increased cereal yield and fertilizer use (Donald, Green & Heath 2001). Land-use changes have also been linked to losses of ecosystem services because simplified landscapes disrupt many natural processes such as pest management, carbon sequestration, and water and soil conservation (Tschardt *et al.* 2005).

There are two major agricultural land-use policy models that attempt to maintain agricultural production while minimizing ecological damage. Although the goals are similar, the outcomes are structurally and spatially quite different. The first model is that of land sparing where agricultural land is farmed as intensively as possible in order to maximize food production, while other land is set aside purely for conservation (Phalan *et al.* 2011). Here, we term these remnants biodiversity-supporting vegetation. In this model, agricultural systems become intensified through mechanization, concentrated water use and the application of agrochemicals, and often result in large increases in the production of goods per unit area of farmed land (Matson *et al.* 1997). In theory, land sparing allows for the retention of large, albeit isolated, patches of habitat across the landscape that contribute to conservation goals. Conservation areas emerge as islands within the otherwise intensive landscape and are spatially separated from agricultural systems (Fig. 1a).

The second model is that of land sharing, also known as nature or wildlife farming, where greater areas of land are used for agriculture, but the landscape is managed at a lower intensity to allow the coexistence of biodiversity-supporting vegetation and production in a mosaic across the landscape (Fischer *et al.* 2008). Typically, such systems yield lower levels of production per unit of farmed area, but because the ecological quality of the landscape is more evenly degraded at a lesser extent, ecosystem services are supported and biodiversity is not restricted entirely to interstitial habitat patches (Fischer *et al.* 2008). In this system, farmland and conservation land are integrated across the landscape as a continuous unit (Fig. 1b).



**Fig. 1.** Spatial patterns of land-use intensity for (a, b) agricultural landscapes and (c, d) urban landscapes. For all grids, a cell size of  $200 \times 200$  m is used, and the green shading darkens with increasing extent of tree cover, which we consider to be the key biodiversity-supporting vegetation in these landscapes. The figures highlight two ends of the land-use spectrum from the isolated patches of vegetation cover associated with a land-sparing model to the spatial continuity of a mosaic of low-intensity land uses associated with land sharing. Many intermediates exist between these endpoints yielding great variation in ecological impacts.

These two models represent endpoints of a continuum of land-use strategies, with a spectrum of land-use compositions in between corresponding to various resolutions of the trade-off between conservation and production (Fischer *et al.* 2008). Arguments for and against both models have been made based on divergent beliefs about how best to design landscapes that support high levels of biodiversity per unit production. Crucially though, both aim to optimize the production landscape in a manner that allows for conservation while permitting the necessary production.

Although the debate has not yet reached consensus, an obvious benefit of having sparing-sharing models to

underpin discussion is that they provide a spatial framework in which to evaluate trade-offs between production and conservation across the agricultural landscape. Considering the extent of urbanization in recent history and the expected acceleration of change in the near future, an equivalent spatial framework for urban land use would be useful to assess how changes in landscape design and infrastructure may affect natural system persistence and ecosystem service provision in cities. Certainly, there are clear parallels between the two environments in terms of their potential spatial configurations (Fig. 1).

### Applying a spatial framework to the urban land-use context

A dramatic shift to urbanization with more people and resources concentrating in cities has formed economies of scale that accelerate innovation and wealth creation (Bettencourt *et al.* 2007; Batty 2008). Productive values in urban systems include the ability to create efficiencies, knowledge and economic output through the focusing of information and skills (Carlino, Chatterjee & Hunt 2007). Urban dwellers now exceed 50% of the global population, and by 2050, there will be 2.6 billion more town and city-dwellers on the planet (United Nations 2011). Individual cities are growing to unprecedented sizes with many megacities of greater than 10 million people emerging in the developing world (Grimm *et al.* 2008). The responsibility for planning future urban development is spread inequitably across the world, and it may be in these rapidly growing population epicentres that the opportunity for a land-sparing debate to influence future urban development is greatest, and where potential for averting poor outcomes for biodiversity still remains. There may also be a case for exploring how more affluent countries can assist if any mitigation measures are required as a result of more biodiversity conscious urban development. Clearly, urbanized land will have to provide both environmental and human well-being needs under increasing land-use constraints (Grimm *et al.* 2008) and incentivizing urban forms that support a wide range of socio-ecological functions will be increasingly important to future cities.

Maintaining natural systems within the urban boundary yields a number of benefits for human society. Urban ecosystems (e.g. street trees, lawns, parks, forests, wetlands) provide microclimate regulation of urban heat stress through increased vegetation, with benefits for both human health and biodiversity (McPherson 1994). Vegetation buffers residential areas from urban noise pollution, and green spaces reduce peak flood discharge by allowing greater levels of infiltration and recharge within the urban system (Bolund & Hunhammar 1999). Less tangible services such as increased psychological well-being result from exposure to urban green spaces (Ulrich 1984; Fuller *et al.* 2007) and opportunities to experience nature close to where people live and work (Pyle 2003; Miller 2005).

There is increasing interest in the ecological consequences of alternative patterns of urbanization, not least because the most dense, populous and fastest growing cities are in areas where species richness is naturally the highest (Cincotta 2000; Luck 2007). Although agricultural and urban systems have traditionally been considered as different fields of research, there are strong parallels between the two landscapes in their spatial configuration and the trade-offs associated with their development (Fig. 1). We believe that the sparing–sharing framework developed to understand the ecological impacts of agriculture could be usefully applied to urban systems to characterize and better understand the trade-offs in urban settings, and many similarities in land-use change patterns and spatial structure will allow for the transfer of this framework to urban systems.

Urban growth and intensification, like agricultural intensification, drive extinctions and ecosystem service degradation in and around cities, and biodiversity impacts vary depending on the degree of conversion (McDonald, Kareiva & Forman 2008; Hahs *et al.* 2009; Nelson *et al.* 2009). Urbanization and suburbanization have been shown to affect biodiversity and ecological integrity at local scales across most biotic communities, disrupting both species richness and evenness (McKinney 2002), although the magnitude of these effects varies taxonomically and geographically (Chace & Walsh 2006; Gaston 2010). For example, moderate levels of urbanization (e.g. suburbanization) more severely affect nonavian vertebrate and invertebrate taxonomic groups than plants (McKinney 2008). There are some observations of increases in the abundance and biomass of birds (Chace & Walsh 2006) and arthropods (Faeth *et al.* 2005) as a result of urbanization, but mammals can be greatly affected when patch connectivity is degraded (FitzGibbon, Putland & Goldizen 2007).

Cities, like agricultural systems, are also large homogenizing forces selecting for a small range of ‘urban-adapted’ species, although a subset of native species (usually species adapted to edges) can become locally abundant at the expense of other indigenous species (McKinney 2006). Bird communities often shift to more granivorous species at the expense of insectivorous species (Chace & Walsh 2006), and arthropod communities may shift from specialist to generalist (McIntyre *et al.* 2001). The transformation of land cover also favours organisms that are capable of rapid colonization (Alberti *et al.* 2003), and homogenization of species proceeds at different rates in different geographical areas depending on human population growth and species composition (Olden 2006).

It has been argued that well-planned urban growth can preserve large intact green spaces and maintain ecologically heterogeneous cities that support both urban-adapted and urban-sensitive species (Bryant 2006; Sandström, Angelstam & Mikusiński 2006). However, it is difficult to envision the overall result of such a pattern of development without a spatial model that structurally analyses the

effects of different spatial configurations on biodiversity. On the one hand, high-density, compact, bounded development may have a severe impact on local biodiversity in those built areas and might be predicted to result in a relatively high rate of local extinctions if high-quality interstitial green space is not maintained. However, the loss of biodiversity-supporting vegetation would be limited to a small area. Sprawling development, on the other hand, creates low-density cities with moderately degraded biodiversity-supporting vegetation spread over a much larger area, such that one may predict fewer local extinctions within any given built area. However, the ecological impact will be more spatially extensive because more green space must be converted to urban land use (Rudd, Vala & Schaefer 2002; Goddard, Dougill & Benton 2010).

Some attempts have been made to estimate the consequences of these alternatives. Species distribution modelling of Brisbane’s birds suggests that high residential densities with large interstitial green spaces and small backyards will minimize the overall ecological impact of that city in the future (Sushinsky *et al.* 2013). Another study from Stockholm found that urban and suburban areas with a sufficient number of mature and decaying trees within the landscape allowed for habitat connectivity and the maintenance of green corridors important for the several red-listed bird species (Mörtberg & Wallentinus 2000). Because of the large amount of variation observed in urban development patterns, there remain many questions regarding best practice in designing biodiversity friendly cities. The resolution of this central trade-off in urban design thus mirrors that of the land sparing–sharing debate in agricultural systems (Fig. 1).

Another key similarity between agricultural and urban landscapes is the huge spatial variation in land-use intensity exhibited across both systems. The urban landscape, like the agricultural landscape, represents a diverse mosaic of human and ecological land uses, with a wide range of density and development variability within and between cities (Karathodorou, Graham & Noland 2010). Urban areas have a rich spatial and temporal heterogeneity and a complex mosaic of biological and physical patches managed by social institutions, leading to continual changes in the urban form (Machlis, Force & Burch 1997). Housing density and green space provision vary by several orders of magnitude amongst cities (Fuller & Gaston 2009) providing substantial opportunity for urban design management. Such diversity means that neighbourhoods will exhibit varying levels of development intensity and potentially allow for pockets of conservation lands that can be distributed across the urban landscape. While this complex matrix may help in minimizing the impact that urban development has on the natural system by creating diverse disturbance regimes, it may also thwart conservation and ecosystem services that are in the midst of being rehabilitated within the system.

Finally, both agricultural and urban landscapes are subject to local and regional planning controls that help

define patterns of development and conservation across the landscape. The pattern of agricultural intensification is largely controlled through regulatory mechanisms that regulate crop production and management (Dowd, Press & Huertos 2008; Matt *et al.* 2011), although many planning regulations and incentives are also aimed at biodiversity conservation. For example, nearly four billion Euros are paid annually in agri-environmental schemes to farmers in Europe and North America to maintain environmental improvements to their land, and such schemes have reversed declines in farmland wildlife populations and provided beneficial effects over large areas when appropriately designed (Donald & Evans 2006). In the Conservation Reserve Program scheme in the USA, nearly 75% of participants reported increases in wildlife populations from environmental improvements (Donald & Evans 2006). Similar types of policies that incentivize the greening of urban areas could be worthwhile. In urban environments, planning controls may modify how the conservation-production trade-off is resolved, yet just as in agriculture, a complex array of social, economic and political factors affect how such planning controls play out. While there is some empirical evidence that policies controlling urban form are effective in Europe (Dallimer *et al.* 2011), this might not be true in many other parts of the world, and because urban environments are characterized by many small landholders, the biodiversity quality of an urban landscape is affected by many thousands of individual management decisions rather than a few high-level policy instruments. Such bottom-up processes can also be important in agricultural settings, where land transformation models suggest that in the absence of direct planning control, changes in farm management can lead to farmland abandonment with subsequent increases in biodiversity (Pijanowski *et al.* 2002; Lakes, Muller & Kruger 2009).

While our understanding of the ecological impact of urbanization has improved in recent decades, it has not kept pace with the rapid and widespread growth of cities (Dye 2008; Zang *et al.* 2011). Improving our knowledge of the trade-offs associated with particular urban spatial configurations is crucial for managing environmental health and ecosystem service delivery in expanding cities. Like agricultural ecosystems, urban ecosystems must be considered from a landscape perspective to minimize overall biodiversity impacts. For example, are regional or national conservation targets best served by a concentrated pattern of urbanization that limits the spatial extent of cities or by lower-density development that minimizes its local impact albeit over a larger area of a nation? The answer to this fundamental question is likely to vary depending on the land-use history of a region, and the extent to which its biodiversity is progressively degraded as urbanization unfolds. A spatial framework such as that developed for agricultural environments would help urban planners to balance conservation trade-offs over the whole landscape, not just that area within city boundaries.

## Future research directions

Although the commonalities between the two landscapes permit a relatively straightforward application of the sharing-sparing paradigm to urban environments, there are some key areas in which research effort could usefully be focused.

First, it is crucial to improve our understanding of how biodiversity responds to urbanization intensity, particularly at the low-intensity end of the spectrum. Land sharing is more likely to be favoured in situations where low-density housing allows a substantial component of biodiversity to persist, yet the evidence on this issue is scattered and somewhat contradictory. Some studies have found substantial biodiversity persistence in low-density exurban development (e.g. Maestas, Knight & Gilgert 2003; Williams *et al.* 2005; Daniels 2011), while others identify rapid ecological perturbation as a result of low-density sprawling development (Nilon, Long & Zipperer 1995; Bock *et al.* 2007; Sushinsky *et al.* 2012). We urgently need to understand under what conditions biodiversity can persist within low-density urban development, and how this changes amongst ecosystem types.

Second, we need to understand how the arrangement and size of remaining fragments of habitat influences the extinction probabilities of urban populations (Vandermeer & Lin 2008; Shanahan *et al.* 2011). Extinction probabilities increase as (i) intact habitat patches are made smaller, (ii) patches become more isolated from one another and (iii) the degree to which the matrix between habitat patches traversed by organisms becomes increasingly disturbed (Saunders, Hobbs & Margules 1991). Therefore, patterns of direct and indirect loss may synergistically have greater impacts on biodiversity than would be expected if only direct loss was measured, yet these are poorly understood.

Third, we need to better understand which urban ecosystems and designs are especially useful in supporting biodiversity, population persistence and ecosystem services in fragmented urban landscapes. Increasing fragmentation in agricultural landscapes has led to changes in biodiversity (Goheen *et al.* 2003), and interfragment movement has become increasingly important as a way to manage local extinctions (Vandermeer & Perfecto 2007). Species will be incapable of persisting in landscapes where fragmentation and matrix degradation has reduced the carrying capacity below that necessary to sustain a metapopulation (Honnay *et al.* 2002; Opdam & Wascher 2004). The challenge has therefore been to develop matrix systems that allow for movement between fragments and create pathways compatible with the land use (Cullen, Alger & Rambaldi 2005). Urban systems comprise many different types of built form (e.g. residential, commercial, industrial) and green spaces (e.g. parks, urban gardens, urban forests, vacant lots) which in combination create a huge array of varying matrix and fragment quality. Future work to identify landscape configurations that

support interfragment movement could provide clearer guidance on landscape level urban planning for minimum biodiversity impact. ‘Softening’ the matrix in urban systems to facilitate interfragment movement, such as restoring riparian and aquatic habitat (Bernhardt & Palmer 2007) or maintaining natural drainage systems, can increase the provision of ecosystem services to the urban population (Chocat *et al.* 2001). The range of built form and green space configurations that can exist within the urban landscape will lead to a range of different ecological outcomes. However, this range also presents an opportunity to investigate which configurations can provide for both high urban production and minimum biodiversity harm.

Fourth, there is an urgent need for whole-of-city analyses of ecological impact if we are to understand how urban development affects biodiversity at the landscape scale. Assessing biodiversity effects at a housing or development unit scale individually throughout an urban landscape will likely underestimate the effect of land-use change on biodiversity persistence. Only by understanding the overall effects over a landscape can decisions be made effectively to protect biodiversity and ecosystem services. It is only possible to resolve a sharing–sparing decision for a particular landscape if both alternatives can be evaluated at a scale that is broad enough to be meaningful. Information about the response of biodiversity to urbanization at fine scales is not necessarily generalizable to larger-scale analyses and will not be helpful for determining how a range of land used should be arranged across a landscape (Polasky *et al.* 2008). The extent to which the ecological impact of a city differs between a compact, high-density growth form and a low-density sprawling growth form is poorly understood because there are few city-scale analyses addressing the impact of urban form upon biodiversity (McDonnell, Hahs & Breuste 2009; Gaston 2010). A related issue in making a sparing–sharing judgment is the question of whether the peri-urban fringes into which cities might expand are already degraded as a result of agricultural land uses. In some cases, peri-urban areas are critically important habitat, for example 50% of Australia’s threatened species occur within the urban fringe (Yencken & Wilkinson 2000).

Lastly, we currently know little about how the wider ecological footprint of a city depends on its urban form. The density and concentration of cities require them to draw resources (food, water, materials) from outside their boundaries, such that the ecological footprint of a city is far greater than the actual city extent. For example, urban inhabitants within the Baltic Sea drainage depend on forest, agriculture, wetland, lake and marine systems that constitute an area about 1000 times larger than that of the urban area proper (Folke *et al.* 1997). However, in the context of spatial configuration of land-use intensity, the appropriate measure of the ecological footprint of a city should be calculated as a per capita value, rather than an area multiplier to accurately compare the consequences

of shared and spared urban configurations. An efficient, highly compact city could have a large area multiplier, but a relatively low per capita ecological footprint beyond its boundaries. Thorough analysis of these issues is urgently required to better understand the potential positive and negative consequences of designing cities with reduced ecological footprints within and beyond city boundaries.

## Closing remarks

Competition for land is becoming increasingly intense as the world’s population continues to urbanize. Decades of research in agriculture have generated a useful paradigm for exploring the trade-offs associated with how different types of land use are organized spatially, and we encourage their adoption by those studying the ecological consequences of urbanization. Only through clear analyses of the impacts of alternative urban designs both within cities and beyond their borders will we understand how best to grow our cities in a way that correctly balances environmental harm with all the benefits that cities bring to society.

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## References

- Aebischer, N. (1991) Twenty years of monitoring invertebrates and weeds in cereal fields in Sussex. *The Ecology of Temperate Cereal Fields* (eds L.G. Firbank, N. Carter, J. Darbyshire & G. Potts), pp. 305–331. Blackwell Scientific Publications, Oxford.
- Alberti, M., Marzluff, J.M., Shulenberg, E., Bradley, G., Ryan, C. & Zumbunnen, C. (2003) Integrating humans into ecology: opportunities and challenges for studying urban ecosystems. *BioScience*, **53**, 1169–1179.
- Antrop, M. & Van Eetvelde, V. (2000) Holistic aspects of suburban landscapes: visual image interpretation and landscape metrics. *Landscape and Urban Planning*, **50**, 43–58.
- Batty, M. (2008) The size, scale, and shape of cities. *Science*, **319**, 769–771.
- Benton, T.G., Bryant, D.M., Cole, L. & Crick, H.Q.P. (2002) Linking agricultural practice to insect and bird populations: a historical study over three decades. *Journal of Applied Ecology*, **39**, 673–687.
- Bernhardt, E.S. & Palmer, M.A. (2007) Restoring streams in an urbanizing world. *Freshwater Biology*, **52**, 738–751.
- Bettencourt, L.M.A., Lobo, J., Helbing, D., Kühnert, C. & West, G.B. (2007) Growth, innovation, scaling, and the pace of life in cities. *Proceedings of the National Academy of Sciences*, **104**, 7301–7306.
- Bock, C.E., Bailowitz, R.A., Danforth, D.W., Jones, Z.F. & Bock, J.H. (2007) Butterflies and exurban development in southeastern Arizona. *Landscape and Urban Planning*, **80**, 34–44.
- Bolund, P. & Hunhammar, S. (1999) Ecosystem services in urban areas. *Ecological Economics*, **29**, 293–301.
- Bryant, M.M. (2006) Urban landscape conservation and the role of ecological greenways at local and metropolitan scales. *Landscape and Urban Planning*, **76**, 23–44.
- Carlino, G.A., Chatterjee, S. & Hunt, R.M. (2007) Urban density and the rate of invention. *Journal of Urban Economics*, **61**, 389–419.
- Chace, J.F. & Walsh, J.J. (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning*, **74**, 46–69.

- Chocat, B., Krebs, P., Marsalek, J., Rauch, W. & Schilling, W. (2001) Urban drainage redefined: from stormwater removal to integrated management. *Water Science and Technology*, **43**, 61–68.
- Cincotta, R.P. (2000) Human population in the biodiversity hotspots. *Nature*, **404**, 990.
- Cullen, L., Alger, K. & Rambaldi, D.M. (2005) Land reform and biodiversity conservation in Brazil in the 1990s: conflict and the articulation of mutual interests. *Conservation Biology*, **19**, 747–755.
- Dallimer, M., Tang, Z., Bibby, P.R., Brindley, P., Gaston, K.J. & Davies, Z.G. (2011) Temporal changes in greenspace in a highly urbanised region. *Biology Letters*, **7**, 763–766.
- Daniels, G. (2011) Ecological implications of exurban development: The effects of people, pets and paddocks on avian and mammalian wildlife. PhD thesis, University of Tasmania.
- Donald, P.F. & Evans, A.D. (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. *Journal of Applied Ecology*, **43**, 209–218.
- Donald, P.F., Green, R.E. & Heath, M.F. (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proceedings Biological Sciences*, **268**, 25–29.
- Dowd, B.M., Press, D. & Huertos, M.L. (2008) Agricultural nonpoint source water pollution policy: the case of California's Central Coast. *Agriculture, Ecosystems and Environment*, **128**, 151–161.
- Dye, C. (2008) Health and urban living. *Science*, **319**, 766–769.
- Faeth, S.H., Warren, P.S., Shochat, E. & Marussich, W.A. (2005) Trophic dynamics in urban communities. *BioScience*, **55**, 399–407.
- Fischer, J., Brosi, B., Daily, G.C., Ehrlich, P.R., Goldman, R., Goldstein, J., *et al.* (2008) Should agricultural policies encourage land sparing or wildlife-friendly farming? *Frontiers in Ecology and the Environment*, **6**, 380–385.
- FitzGibbon, S., Putland, D. & Goldizen, A. (2007) The importance of functional connectivity in the conservation of a ground-dwelling mammal in an urban Australian landscape. *Landscape Ecology*, **22**, 1513–1525.
- Flynn, D.F.B., Gogol-Prokurat, M., Nogeire, T., Molinari, N., Richers, B.T., Lin, B.B., *et al.* (2009) Loss of functional diversity under land use intensification across multiple taxa. *Ecology Letters*, **12**, 22–33.
- Folke, C., Jansson, A., Larsson, J. & Costanza, R. (1997) Ecosystem appropriation by cities. *Ambio*, **26**, 167–172.
- Fuller, R.A. & Gaston, K.J. (2009) The scaling of green space coverage in European cities. *Biology Letters*, **5**, 352–355.
- Fuller, R.A., Irvine, K.N., Devine-Wright, P., Warren, P.H. & Gaston, K.J. (2007) Psychological benefits of greenspace increase with biodiversity. *Biology Letters*, **3**, 390–394.
- Gaston, K.J. (2010) *Urban Ecology*. Cambridge University Press, New York.
- Goddard, M.A., Dougill, A.J. & Benton, T.G. (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology and Evolution*, **25**, 90–98.
- Goheen, J.R., Swihart, R.K., Gehring, T.M. & Miller, M.S. (2003) Forces structuring tree squirrel communities in landscapes fragmented by agriculture: species differences in perceptions of forest connectivity and carrying capacity. *Oikos*, **102**, 95–103.
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X., *et al.* (2008) Global change and the ecology of cities. *Science*, **319**, 756–760.
- Hahs, A.K., McDonnell, M.J., McCarthy, M.A., Vesik, P.A., Corlett, R.T., Norton, B.A., *et al.* (2009) A global synthesis of plant extinction rates in urban areas. *Ecology Letters*, **12**, 1165–1173.
- Hansen, A.J., Knight, R.L., Marzluff, J.M., Powell, S., Brown, K., Gude, P.H. & Jones, K. (2005) Effects of exurban development on biodiversity: patterns, mechanisms, and research needs. *Ecological Applications*, **15**, 1893–1905.
- Harvey, C.A., Komar, O., Chazdon, R., Ferguson, B.G., Finegan, B., Griffith, D.M., *et al.* (2008) Integrating agricultural landscapes with biodiversity conservation in the Mesoamerican hotspot. *Conservation Biology*, **22**, 8–15.
- Honnay, O., Verheyen, K., Butaye, J., Jacquemyn, H., Bossuyt, B. & Hermy, M. (2002) Possible effects of habitat fragmentation and climate change on the range of forest plant species. *Ecology Letters*, **5**, 525–530.
- Jenks, M. & Jones, C. (2010) *Dimensions of the Sustainable City*. Springer, London.
- Karathodorou, N., Graham, D.J. & Noland, R.B. (2010) Estimating the effect of urban density on fuel demand. *Energy Economics*, **32**, 86–92.
- Lakes, T., Muller, D. & Kruger, C. (2009) Cropland change in southern Romania: a comparison of logistic regressions and artificial neural networks. *Landscape Ecology*, **24**, 1195–1206.
- Lambin, E.F. (2003) Dynamics of land-use and land-cover change in tropical regions. *Annual Review of Environment and Resources*, **28**, 205–241.
- Luck, G.W. (2007) A review of the relationships between human population density and biodiversity. *Biological Reviews*, **82**, 607–645.
- Machlis, G.E., Force, J.E. & Burch, W.R. (1997) The human ecosystem Part I: the human ecosystem as an organizing concept in ecosystem management. *Society and Natural Resources*, **10**, 347–367.
- Maestas, J.D., Knight, R.L. & Gilgert, W.C. (2003) Biodiversity across a rural land-use gradient. *Conservation Biology*, **17**, 1425–1434.
- Maron, M., Bowen, M., Fuller, R.A., Smith, G.C., Eyre, T.J., Mathieson, M., *et al.* (2012) Spurious thresholds in the relationship between species richness and vegetation cover. *Global Ecology and Biogeography*, **21**, 682–692.
- Marzluff, J.M., Bowman, R. & Donnelly, R. (2001) *Avian Ecology and Conservation in an Urbanizing World*. Kluwer Academic Publishers, Norwell, MA.
- Matson, P.A., Parton, W.J., Power, A.G. & Swift, M.J. (1997) Agricultural intensification and ecosystem properties. *Science*, **277**, 504–509.
- Matt, J., Licker, R., Foley, J., Holloway, T., Mueller, N.D., Barford, C., *et al.* (2011) Closing the gap: global potential for increasing biofuel production through agricultural intensification. *Environmental Research Letters*, **6**, 034028.
- McDonald, R.L., Kareiva, P. & Forman, R.T.T. (2008) The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation*, **141**, 1695–1703.
- McDonnell, M.J., Hahs, A.K. & Breuste, J. (2009) *Ecology of Cities and Towns: A Comparative Approach*. Cambridge University Press, New York.
- McIntyre, N.E., Rango, J., Fagan, W.F. & Faeth, S.H. (2001) Ground arthropod community structure in a heterogeneous urban environment. *Landscape and Urban Planning*, **52**, 257–274.
- McKinney, M.L. (2002) Urbanization, biodiversity, and conservation. *BioScience*, **52**, 883–890.
- McKinney, M.L. (2006) Urbanization as a major cause of biotic homogenization. *Biological Conservation*, **127**, 247–260.
- McKinney, M. (2008) Effects of urbanization on species richness: a review of plants and animals. *Urban Ecosystems*, **11**, 161–176.
- McPherson, E. (1994) Cooling urban heat islands with sustainable landscapes. *The Ecological City: Preserving and Restoring Urban Biodiversity* (eds R.H. Platt, R.A. Rowntree & P.C. Muick), pp. 151–171. University of Massachusetts Press, Amherst, MA.
- Millennium Ecosystem Assessment (2005) *Ecosystems and human well-being: synthesis report*. Washington DC.
- Miller, J.R. (2005) Biodiversity conservation and the extinction of experience. *Trends in Ecology and Evolution*, **20**, 430–434.
- Mörtberg, U. & Wallentinus, H.-G. (2000) Red-listed forest bird species in an urban environment — assessment of green space corridors. *Landscape and Urban Planning*, **50**, 215–226.
- Nelson, E., Mendoza, G., Regetz, J., Polasky, S., Tallis, H., Cameron, D., *et al.* (2009) Modeling multiple ecosystem services, biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Frontiers in Ecology and the Environment*, **7**, 4–11.
- Nilon, C.H., Long, C.N. & Zipperer, W.C. (1995) Effects of wildland development on forest bird communities. *Landscape and Urban Planning*, **32**, 81–92.
- Olden, J.D. (2006) Biotic homogenization: a new research agenda for conservation biogeography. *Journal of Biogeography*, **33**, 2027–2039.
- Opdam, P. & Wascher, D. (2004) Climate change meets habitat fragmentation: linking landscape and biogeographical scale levels in research and conservation. *Biological Conservation*, **117**, 285–297.
- Pereira, H.M., Leadley, P.W., Proença, V., Alkemade, R., Scharlemann, J.P.W., Fernandez-Manjarrés, J.F., *et al.* (2010) Scenarios for global biodiversity in the 21st century. *Science*, **330**, 1496–1501.
- Phalan, B., Onial, M., Balmford, A. & Green, R.E. (2011) Reconciling food production and biodiversity conservation: land sharing and land sparing compared. *Science*, **333**, 1289–1291.
- Pijanowski, B.C., Brown, D.G., Shellito, B.A. & Manik, G.A. (2002) Using neural networks and GIS to forecast land use changes: a Land Transformation Model. *Computers, Environment and Urban Systems*, **26**, 553–575.
- Pimm, S.L. & Raven, P. (2000) Biodiversity: extinction by numbers. *Nature*, **403**, 843–845.

- Polasky, S., Nelson, E., Camm, J., Csuti, B., Fackler, P., Lonsdorf, E., *et al.* (2008) Where to put things? Spatial land management to sustain biodiversity and economic returns. *Biological Conservation*, **141**, 1505–1524.
- Pyle, R.M. (2003) Nature matrix: reconnecting people and nature. *Oryx*, **37**, 206–214.
- Radford, J.Q., Bennett, A.F. & Cheers, G.J. (2005) Landscape-level thresholds of habitat cover for woodland-dependent birds. *Biological Conservation*, **124**, 317–337.
- Rudd, H., Vala, J. & Schaefer, V. (2002) Importance of backyard habitat in a comprehensive biodiversity conservation strategy: a connectivity analysis of urban green spaces. *Restoration Ecology*, **10**, 368–375.
- Sandström, U.G., Angelstam, P. & Mikusiński, G. (2006) Ecological diversity of birds in relation to the structure of urban green space. *Landscape and Urban Planning*, **77**, 39–53.
- Saunders, D.A., Hobbs, R.J. & Margules, C.R. (1991) Biological consequences of ecosystem fragmentation: a review. *Conservation Biology*, **5**, 18–32.
- Shanahan, D.F., Miller, C., Possingham, H.P. & Fuller, R.A. (2011) The influence of patch area and connectivity on avian communities in urban revegetation. *Biological Conservation*, **144**, 722–729.
- Sotherton, N.W. (1998) Land use changes and the decline of farmland wildlife: an appraisal of the set-aside approach. *Biological Conservation*, **83**, 259–268.
- Sushinsky, J.R., Rhodes, J.R., Possingham, H.P., Gill, T.K. & Fuller, R.A. (2013) How should we grow our cities to minimize biodiversity impacts? *Global Change Biology*, **19**, 401–410.
- Tscharntke, T., Klein, A.M., Kruess, A., Steffan-Dewenter, I. & Thies, C. (2005) Landscape perspectives on agricultural intensification and biodiversity – ecosystem service management. *Ecology Letters*, **8**, 857–874.
- Ulrich, R.S. (1984) View through a window may influence recovery from surgery. *Science*, **224**, 420–421.
- United Nations (2011) *World Urbanization Prospects: The 2011 Revision*. United Nations, New York.
- Vandermeer, J. & Lin, B.B. (2008) The importance of matrix quality in fragmented landscapes: understanding ecosystem collapse through a combination of deterministic and stochastic forces. *Ecological Complexity*, **5**, 222–227.
- Vandermeer, J. & Perfecto, I. (2007) The agricultural matrix and a future paradigm for conservation. *Conservation Biology*, **21**, 274–277.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. & Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science*, **277**, 494–499.
- Williams, N.S.G., Morgan, J.W., McDonnell, M.J. & McCarthy, M.A. (2005) Plant traits and local extinctions in natural grasslands along an urban–rural gradient. *Journal of Ecology*, **93**, 1203–1213.
- Yencken, D. & Wilkinson, D. (2000) *Resetting the Compass: Australia's Journey Towards Sustainability*. CSIRO Publishing, New Melbourne.
- Zang, S., Wu, C., Liu, H. & Na, X. (2011) Impact of urbanization on natural ecosystem service values: a comparative study. *Environmental Monitoring and Assessment*, **179**, 575–588.

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