

How should we grow cities to minimize their biodiversity impacts?

JESSICA R. SUSHINSKY*, JONATHAN R. RHODES†, HUGH P. POSSINGHAM*, TONY K. GILL‡ and RICHARD A. FULLER*§

*Centre for Biodiversity and Conservation Science, School of Biological Sciences, University of Queensland, Brisbane, QLD 4072, Australia, †School of Geography, Planning and Environmental Management, University of Queensland, Brisbane, QLD 4072, Australia, ‡Joint Remote Sensing Research Program, New South Wales Office of Environment and Heritage, Dubbo, NSW 2830, Australia, §CSIRO Climate Adaptation Flagship and CSIRO Ecosystem Sciences, CSIRO, 41 Boggo Road, Dutton Park, QLD 4102, Australia

Abstract

Urbanization causes severe environmental degradation and continues to increase in scale and intensity around the world, but little is known about how we should design cities to minimize their ecological impact. With a sprawling style of urban development, low intensity impact is spread across a wide area, and with a compact form of development intense impact is concentrated over a small area; it remains unclear which of these development styles has a lower overall ecological impact. Here, we compare the consequences of compact and sprawling urban growth patterns on bird distributions across the city of Brisbane, Australia. We predicted the impact on bird populations of adding 84 642 houses to the city in either a compact or sprawling design using statistical models of bird distributions. We show that urban growth of any type reduces bird distributions overall, but compact development substantially slows these reductions at the city scale. Urban-sensitive species particularly benefited from compact development at the city scale because large green spaces were left intact, whereas the distributions of nonnative species expanded as a result of sprawling development. As well as minimizing ecological disruption, compact urban development maintains human access to public green spaces. However, backyards are smaller, which impacts opportunities for people to experience nature close to home. Our results suggest that cities built to minimize per capita ecological impact are characterized by high residential density, with large interstitial green spaces and small backyards, and that there are important trade-offs between maintaining city-wide species diversity and people's access to biodiversity in their own backyard.

Keywords: backyards, biodiversity conservation, birds, Brisbane Australia, green space, urban density, urban ecology, urban growth

Received 14 March 2012 and accepted 15 September 2012

Introduction

About half of the Earth's terrestrial surface has been cleared or otherwise dominated by human activity (Vitousek *et al.*, 1997; Lambin *et al.*, 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). Although agriculture is the most spatially extensive form of human land use (Tilman *et al.*, 2001), urbanization remains one of the most ecologically damaging and fastest growing of any land-use types globally (Antrop, 2000; Hansen *et al.*, 2005). Perhaps because of the intensely transformative nature of urbanization, there has been a recent surge of interest in quantifying the

impacts of urban development upon biodiversity (McDonnell *et al.*, 2009; Gaston, 2010a). As urbanization continues rapidly around the world a better understanding of its ecological impact is critical in informing policy and practice to help guide the construction of cities. Because urbanization is typically associated with top-down planning control, it is one of the few land uses over which policy can have direct and ongoing control of its extent and intensity at fine spatial scales (Fuller & Gaston, 2009; Dallimer *et al.*, 2011).

There are two broad approaches to minimizing the ecological impact of urbanization: (i) minimize the extent of built up areas so that the ecological impact is locally intense but spatially constrained, or (ii) minimize the intensity of urbanization so that the ecological impact is less intense locally, but spatially spread over a more extensive area. These approaches might loosely be termed compact development, in which large green

Correspondence: Jessica R. Sushinsky, fax + 504 444 2809, e-mail: jrsush@gmail.com

spaces are retained between high-density residential neighbourhoods, and sprawling development, in which residential densities are lower but spread across a larger built area with fewer interstitial green spaces for a given human population size (Davies *et al.*, 2008; Jenks & Jones, 2010).

Researchers have found that increasing urban density leads to declining ecological integrity at local scales, although the magnitude of this effect varies taxonomically and geographically (for reviews, see Chace & Walsh, 2006; McDonnell *et al.*, 2009; Fuller *et al.*, 2010; Gaston, 2010b). High-density, compact development has a severe impact on local biodiversity in built areas, and might be predicted to result (all else being equal), in a relatively high rate of local extinctions, albeit limited to a small area. Sprawling development, on the other hand, creates low-density suburbs spread over a larger area, such that one might predict fewer local extinctions within any given urbanized parcel of land. However, the ecological impact will be more spatially extensive because more land must be converted to residential uses (Hansen *et al.*, 2005; Johnson & Klemens, 2005).

The extent to which the ecological impact of an entire city differs between compact and sprawling urban growth forms is poorly understood because there are few city-scale analyses addressing the impact of urban form upon biodiversity (McDonnell *et al.*, 2009; Gaston, 2010a). Here, we model the effects of compact and sprawling urban growth strategies on distributions of bird species in Brisbane, a biodiverse, subtropical city on Australia's east coast. In common with many 'New World' cities, urban growth in Brisbane has historically been of a very low-density, sprawling character (Gaston, 2010a; Hall, 2010), but in the face of recent rapid population growth the state government has adopted a more compact urban growth strategy in an effort to reduce land conversion (Queensland Government Department of Infrastructure & Planning, 2009).

We measure the impacts of compact and sprawling urban growth patterns on bird distributions at the city scale by (i) modelling changes in the area of occupancy of bird species under compact and sprawling urban growth strategies, (ii) quantifying the magnitude of expected local extinctions, and (iii) determining the consequences for human proximity to green spaces. We show that while urban growth of any type causes overall reductions in the distributions of birds at the city scale, spatially constrained compact development substantially slows these reductions, resulting in fewer local extinctions. Averted local extinctions under compact development are most pronounced for urban-sensitive species that are dependent on large intact remnants of natural habitat or open space within the

city. However, compact development is often accompanied by smaller backyards which may limit some of the beneficial interactions between people and nature that are exclusively provided by backyards (Fuller & Irvine, 2010). Thus, while compact development may rescue the city's bird species, the venues for people to experience these rescued species may change.

Materials and methods

We began by using empirical survey data to model the current distributions of birds across the city. We then projected these models forward under two alternative urban development scenarios, using empirical relationships between bird occurrence and key features of urban form including housing density, extent of green space coverage, and primary productivity. Finally, we measured changes in people's access to public green spaces and private backyards associated with each scenario.

Study area

The city of Brisbane supports a population of 1.82 million at a mean density of 918 people per km⁻² (Australian Government Bureau of Statistics, 2006). The city is undergoing rapid population growth with a mean annual growth rate of 2.2% between 2001 and the last census in 2006 (Australian Government Bureau of Statistics, 2006). The state government plans to add 156 000 houses to the city by 2031 (Queensland Government Department of Infrastructure & Planning, 2009). Our study area covered 636 km² of the city and was defined by a series of contiguous 1 km² grid cells that were (i) within Brisbane's administrative boundary, and (ii) at least 25% urbanized (as judged by eye from aerial imagery; Fig. 1). We limited the extent of the study area to the urbanized portion of the city in this way because Brisbane's administrative boundary includes large areas of nonurban land cover. The study area allowed for adequate sampling of the target population of urban bird species across the city and ensured various land-use types and degrees of urbanization were well represented.

Bird distributions

We performed bird surveys in the urban area of Brisbane during the spring breeding season of 2009, between 25 August and 11 November. A single survey point was placed randomly within each 1 km² grid cell resulting in a total of 636 points. Each survey point was located in the field by GPS and was visited once by one of two observers (J. R. Sushinsky, 537 surveys or R. A. Fuller, 99 surveys), between 05:00 hours and 10:20 hours. Data on the presence of bird species across the city were generated by conducting five-minute point counts at each survey point during which all species encountered were listed. We used these data as presence only, and did not attempt to estimate the density of birds. Survey points were located across the urban landscape in residential and industrial areas, in public parks and gardens, along major

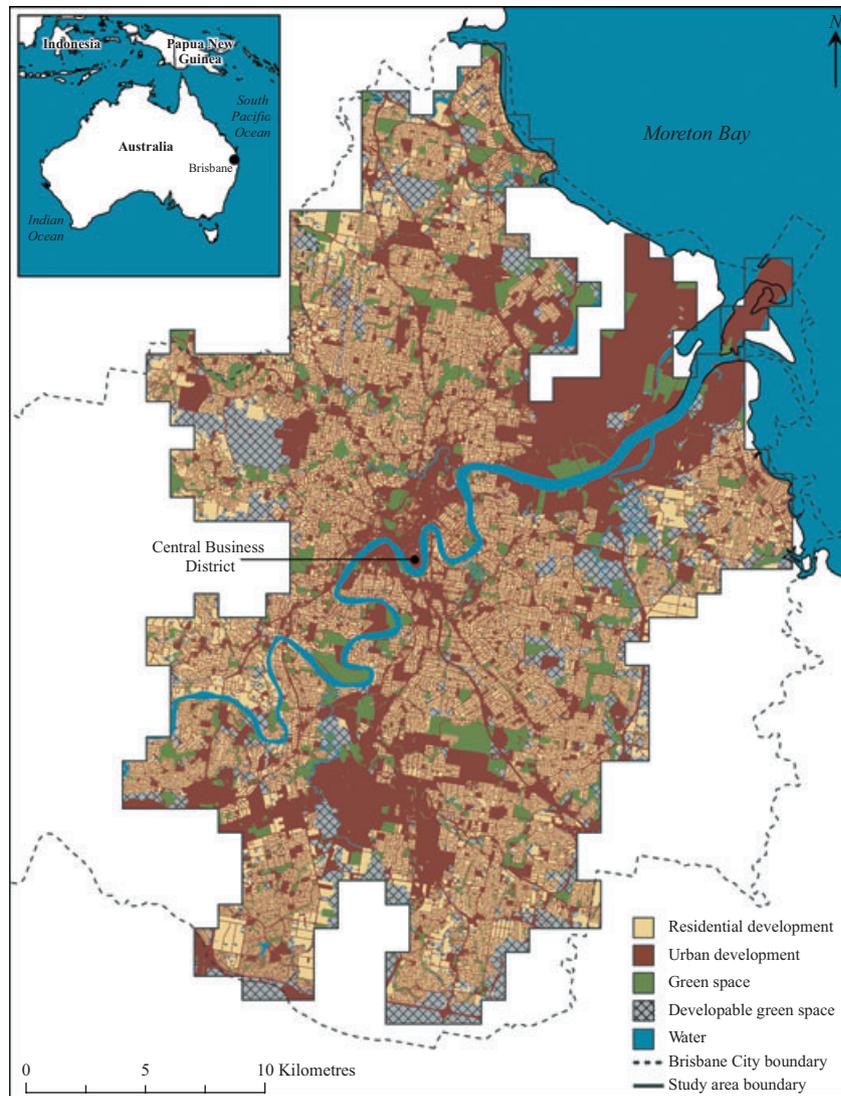


Fig. 1 The extent of the study area and the distribution of land-use types (per land parcel) used for the urban growth scenarios (see Appendix S1 for full details on development of the data layer). Residential areas (all land parcels with at least one dwelling) are coloured yellow, areas of urban development (urban infrastructure comprising impervious surfaces such as roads, commercial buildings, and shopping centres) are coloured red, green space areas (public parks and gardens and conservation reserves) are coloured green, and developable green spaces (areas covered by vegetation without any significant amenity value; used for development only in the sprawling urban growth scenario) are hatched and coloured grey.

roadways, in outdoor shopping centres, and on airport grounds. When a survey point was not accessible (e.g. located on private property, was dangerous to survey or could not be reasonably accessed on foot) a new point in similar habitat within the same grid cell was located and surveyed. The resulting dataset comprised 7986 observations of 119 species.

Based on an extensive review of the literature concerning bird and wildlife distributions in urban areas (Sandström *et al.*, 2006; Husté & Boulinier, 2007; Tratalos *et al.*, 2007; Bino *et al.*, 2008; Davies *et al.*, 2008; Catterall, 2009), we selected six environmental variables that we expected would be important in determining the distributions of bird species across the city: land use, dwelling density, vegetative cover, vegetative

heterogeneity, temperature, precipitation, and distance to the city periphery (see Appendix S1 for full details). We used our database of bird presences to model the current distributions of the 36 species each with at least 15 occurrence records, and not belonging to a group poorly sampled with our point count method (27 waterfowl and shorebird species, one nocturnal species, three migrant species and seven raptor species; Table 1). We used Maxent (Phillips *et al.*, 2006) to construct species distribution models as functions of the six selected environmental variables on a 200 m \times 200 m grid across the city. Note that although a 1 km grid was used to define the sampling for the bird surveys, all further analyses were conducted at a 200 m resolution because we expect detectability

to be approximately limited to 200 m and this resolution is fine enough to adequately capture the heterogeneity in land cover across the urban landscape. As a maximum entropy model Maxent searches for an unknown probability distribution that is the most uniform distribution, yet satisfies the envi-

ronmental constraints derived from occurrence records and environmental data (see Phillips *et al.*, 2006 for further detail). We used the default settings in Maxent (convergence threshold = 10^{-5} , maximum iterations = 500, regularization value $\beta = 10^{-4}$, and use of linear, quadratic, product, threshold, and

Table 1 Change in area of occupancy, and local extinctions and colonizations for 36 species after compact and sprawling urban growth

Species	Area of occupancy change (%)		Local extinctions and colonizations			
	Compact	Sprawling	Compact		Sprawling	
			Ext	Coln	Ext	Coln
Urban-sensitive species						
Australian Brush Turkey (<i>Alectura lathami</i>)	-0.84	-9.57	166	53	683	117
Fairy Martin (<i>Petrochelidon ariel</i>)	-10.24	0.77	82	9	124	71
Golden-headed Cisticola (<i>Cisticola exilis</i>)	-2.47	-19.74	1	0	197	0
Grey Shrike-thrush (<i>Colluricincla harmonica</i>)	-6.92	-22.79	60	4	695	11
Lewin's Honeyeater (<i>Meliphaga lewinii</i>)	-9.67	-28.27	175	11	913	108
Noisy Friarbird (<i>Philemon corniculatus</i>)	1.38	-7.57	8	120	732	22
Red-backed Fairy-wren (<i>Malurus melanocephalus</i>)	-7.59	-20.99	315	9	1,563	81
Striated Pardalote (<i>Pardalotus striatus</i>)	-6.37	-13.94	155	7	1,557	34
Superb Fairy-wren (<i>Malurus cyaneus</i>)	-7.05	-5.60	727	18	626	67
White-throated Honeyeater (<i>Melithreptus albogularis</i>)	-1.79	-20.65	60	0	1,039	1
Mean/total	-5.16	-14.84	1,749	231	8,129	512
Nonnative species						
Common Myna (<i>Sturnus tristis</i>)	2.72	9.91	141	578	60	1,212
Rock Dove (<i>Columba livia</i>)	-0.83	2.02	198	57	140	195
Spotted Turtle Dove (<i>Streptopelia chinensis</i>)	0.87	9.48	198	577	38	395
Mean/total	0.92	7.14	537	1,212	238	1,802
Urban-adapted species						
Australasian Figbird (<i>Sphecothebes vieilloti</i>)	1.33	3.46	84	334	34	582
Australian Magpie (<i>Cracticus tibicen</i>)	-0.39	2.42	178	55	130	829
Australian White Ibis (<i>Threskiornis molucca</i>)	-2.57	-1.75	161	7	350	48
Black-faced Cuckoo-shrike (<i>Coracina novaehollandiae</i>)	-2.46	-4.50	560	4	743	126
Blue-faced Honeyeater (<i>Entomyzon cyanotis</i>)	0.19	2.38	67	80	155	318
Brown Honeyeater (<i>Lichmera indistincta</i>)	-2.84	-0.95	818	184	612	291
Crested Pigeon (<i>Ocyphaps lophotes</i>)	0.22	6.09	278	389	138	962
Galah (<i>Eolophus roseicapillus</i>)	-4.98	-4.59	696	66	1,391	294
Grey Butcherbird (<i>Cracticus torquatus</i>)	0.41	0.69	210	273	249	361
Laughing Kookaburra (<i>Dacelo novaeguineae</i>)	-1.57	-2.56	251	11	459	239
Magpie-lark (<i>Grallina cyanoleuca</i>)	-3.68	5.69	135	792	53	1,146
Masked Lapwing (<i>Vanellus miles</i>)	1.37	-0.89	422	11	644	217
Noisy Miner (<i>Manorina melanocephala</i>)	0.35	0.05	146	264	254	348
Olive-backed Oriole (<i>Oriolus sagittatus</i>)	-1.45	0.10	370	7	358	276
Pied Butcherbird (<i>Cracticus nigrogularis</i>)	-1.82	1.93	890	110	254	598
Pied Currawong (<i>Strepera graculina</i>)	5.61	-1.09	47	615	461	212
Rainbow Lorikeet (<i>Trichoglossus haematodus</i>)	-0.49	-0.27	268	117	360	283
Scaly-breasted Lorikeet (<i>Trichoglossus chlorolepidotus</i>)	-3.04	-5.23	236	10	502	106
Silvereye (<i>Zosterops lateralis</i>)	-2.02	-4.74	577	36	894	92
Sulphur-crested Cockatoo (<i>Cacatua galerita</i>)	-7.51	-6.72	823	3	696	169
Torresian Crow (<i>Corvus orru</i>)	0.40	0.46	159	239	264	275
Welcome Swallow (<i>Hirundo neoxena</i>)	1.38	-0.51	94	423	488	145
Willie Wagtail (<i>Rhipidura leucophrys</i>)	-3.84	-1.97	119	43	299	69
Mean/total	-1.19	-0.54	7,589	4,073	9,788	7,986
Mean/total	-2.12	-3.87	9,875	5,516	18,155	10,300

fringe features), selecting 10 000 background points randomly from across the study area. We used the logistic output from Maxent, which equates to a probability that the species will be observed in each 200 m pixel, given the environmental conditions that exist there (Phillips & Dudík, 2008).

We checked the performance of our distribution models by comparing the observed area under the receiver-operating characteristic curve (AUC, a measure of the predictive power of the distribution model) to the AUC values based on 99 null models of randomly drawn species occurrences from surveyed locations (Raes & ter Steege, 2007). In essence, this estimates the probability that the observed AUC for each species was greater than that expected by chance. Twenty-eight of the 36 species distribution models significantly outperformed the null expectation ($P < 0.05$; see Table S1 for AUC values). There was no obvious feature uniting the eight species whose models did not perform significantly better than null expectation (mean $P = 0.287$), although a degree of difficulty in predicting species distributions at such fine scales in a heterogeneous environment is not surprising. However, for all eight of these species, the models show greater predictive power than the null model, albeit not significantly. Overall then, our models show good ($n = 28$) or adequate ($n = 8$) predictive power.

Based on a published analysis of changes in Brisbane's bird assemblages between 1994 and 2008 (Catterall *et al.*, 2010), species were categorized *a priori* into three groups: urban adapted (23), urban sensitive (10), and nonnative (3; Table 1). Native species that did not decline significantly in abundance between 1994 and 2008, and were relatively common across the urban landscape were categorized as urban adapted, whereas native species with specialized habitat requirements that experienced a significant decline in abundance between 1994 and 2008 were categorized as urban sensitive.

As a measure of distributional extent we estimated the area of occupancy (Gaston & Fuller, 2009) for each species; we multiplied the habitat suitability measure arising from the distribution models for each 200 m pixel by its area and summed these values across the study area (Wilson *et al.*, 2005). Species richness for each pixel was calculated by converting the habitat suitability measure for each species into a prediction of presence or absence. We applied a threshold that balanced omission and commission error rates (Liu *et al.*, 2005; see Table S2 for threshold values) to the habitat suitability measures for each species to determine presence or absence, and then counted the presences per pixel across all species.

Urban growth scenarios

We built spatially explicit simulations of compact and sprawling urban growth strategies. The compact scenario reflects an urban growth strategy in which housing density is increased through infill and subdivision of existing residential areas. In Brisbane, developers typically subdivide a residential property by purchasing single-dwelling plots, demolishing the existing house, and building multiple units each occupying only a portion of the original plot. The sprawling scenario reflects an urban growth strategy that directs low-density

development to areas of open space outside already developed areas, a continuation of the pattern of urban growth in Brisbane over the past few decades. In each scenario a total of 84 642 dwellings were added to the study area; this is an area-weighted proportion of the 156 000 dwellings that Brisbane City Council is expected to accommodate by 2031, according to the Southeast Queensland Regional Plan 2009 (Queensland Government Department of Infrastructure & Planning, 2009). The spatial extent of the city was not increased in either scenario because we are comparing alternative patterns of expansion within the city boundary.

To construct the compact scenario, existing single-dwelling properties with an area of at least half that of the median single-dwelling property size for each suburb were considered suitable for subdivision. Such properties were randomly selected, subdivided, and developed one at a time, rotating through all suburbs in random sequence, until 84 642 dwellings had been added to the study area. The number of subdivisions within each plot was based on the empirical relationships between plot size and the number of dwellings for all of the existing subdivided properties across Brisbane. This relationship was calculated for high-, medium-, and low-density suburbs (linear regressions: low density: $y = 0.81x - 1.67$, $r^2 = 0.674$, $P < 0.001$, medium density: $y = 0.68x - 1.3$, $r^2 = 0.632$, $P < 0.001$, high density: $y = 0.64x - 1.13$, $r^2 = 0.580$, $P < 0.001$), and plots within each suburb were subdivided according to the regression for that particular density category. For the sprawling scenario new single-dwelling properties were added through development of green spaces within the city boundary that were not designated as parks and gardens or conservation reserves (hereafter developable green spaces; Fig. 1). Developable green spaces with an area of at least half that of the median single-dwelling property within each suburb were considered suitable for development. Developable green spaces with an area greater than 1.5 times that of the median single-dwelling property size (per suburb) were prepared for development by dividing each space into rectangular plots with an area equal to that of the median single-dwelling property size within the suburb. Developable properties were then randomly selected and developed into single-dwelling properties one at a time, rotating through all suburbs in random sequence, until 84 642 dwellings were added to the study area. In practice, other factors such as flood risk, slope, or city regulations mandating that green spaces are set aside in new developments might limit the area that is developed.

Projected bird distributions

Current bird distribution models were projected forward in Maxent (Phillips *et al.*, 2006) as development progressed by updating each of the four nonconstant predictor variables (land use, dwelling density, vegetative cover, and vegetative heterogeneity) with each addition of 10 000 dwellings. Changes in land use and dwelling density were calculated directly from the urban growth simulations, whereas changes in vegetative cover and heterogeneity were estimated based on the current empirical relationships between dwelling density and vegetative cover and heterogeneity (see

Appendix S1 for methods). For each addition of 10 000 dwellings, we used the species distribution models to estimate the distributions of birds under the two development scenarios. We recalculated area of occupancy for each species with each addition of 10 000 dwellings. We ran both of the randomized urban growth scenarios six times and found negligible variation in the resulting estimates of area of occupancy for individual species (coefficients of variation less than 0.02 in all cases; see Table S3). Local species extinctions and colonizations were also determined per 200 m pixel for each species with each addition of 10 000 dwellings by applying a threshold to the model outputs for each species that balanced omission and commission error rates (Liu *et al.*, 2005) to determine presence or absence. Total local extinctions were defined as the loss of any species from a pixel, and local colonizations were defined by the presence of a species in a pixel where it was previously absent. Again, there was negligible variation among the six randomized realizations; coefficients of variation for total extinctions were 0.04 for the compact model and 0.05 for the sprawling model, and for total colonizations coefficients of variation were 0.08 for the compact model and 0.09 for the sprawling model. Consequently, we report below the results only for a single realization of the urban growth scenarios.

Access to green space

Provision of public and private green spaces was modelled under both urban growth scenarios for 1000 randomly sampled residential properties that had undergone development.

We defined access to public green space as the proportion of the area within a 1.5 km radius (approximately within 15 min' walking time), of each residential property comprising parks and public gardens, conservation reserves, or any other mostly vegetated surface. Access to private green space was represented as mean backyard size per dwelling. Because buildings are not mapped in a GIS across Brisbane we built simple linear regression models predicting backyard size from property area using random samples of 300 single-dwelling ($y = 1.2x - 0.76x, r^2 = 0.977, P < 0.001$) and 300 multidwelling properties ($y = 1.28x - 1.14, r^2 = 0.866, P < 0.001$). We then used these regression relationships to estimate backyard size from property size for each residential property in the city.

Results

Mean predicted area of occupancy across all bird species was reduced under both compact and sprawling scenarios, but the change was less pronounced and occurred more slowly under compact development (Fig. 2a; Table 1). The reductions under sprawling development were driven by urban-sensitive species, which showed a mean reduction of 15% in predicted area of occupancy (Fig. 2b). While urban-sensitive species also showed declining areas of occupancy in the compact scenario, the impact was much less severe than it was under sprawling development (Fig. 2b). Presumably, the constrained spatial extent of compact

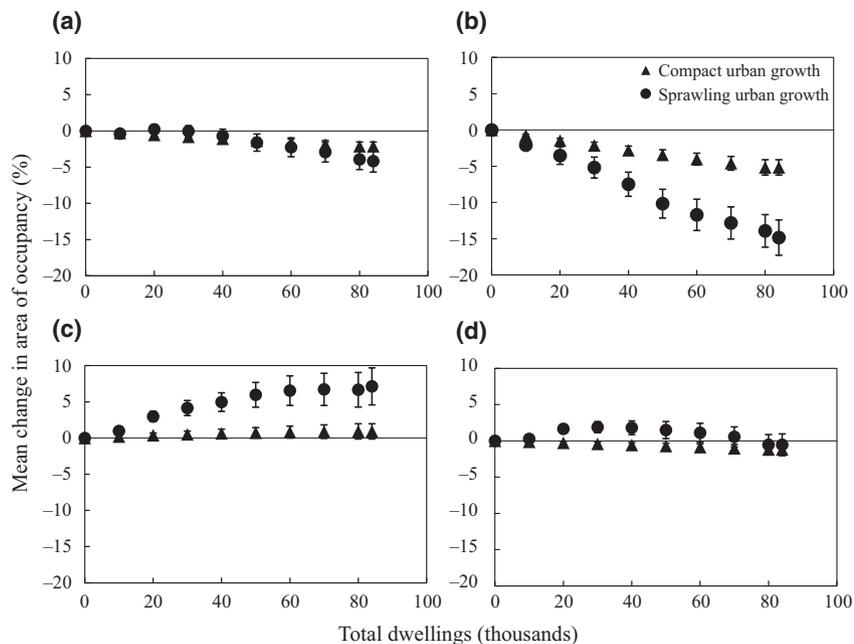


Fig. 2 Mean per cent change in species' predicted area of occupancy across the city under compact (triangles) and sprawling (circles) urban growth scenarios for (a) all species, (b) urban-sensitive species, (c) nonnative species, and (d) urban-adapted species. Error bars are standard errors of areas of occupancy across the species in each group for a single realization of the urban growth scenarios. No change is represented by a solid horizontal line.

development, and the fact that development occurred in already urbanized areas where urban-sensitive species are already rare or absent helped to minimize impacts on urban-sensitive species. Mean predicted area of occupancy of nonnative species remained relatively unchanged under compact development, but increased markedly (7%) with sprawling development (Fig. 2c). Urban-adapted species showed little change in predicted area of occupancy under either development scenario, decreasing by <1% in each case (Fig. 2d). Overall, sprawling development resulted in significant changes in predicted area of occupancy and major shifts in assemblage structure, whereas the impacts of compact development were much less pronounced.

Local extinctions, as measured by the number of disappearances of species from 200 m pixels, varied among species and between urban growth scenarios (Table 1). The species distribution models suggest that under either form of urban growth the total number of species will remain the same. However, sprawling development led to about 18 000 local extinctions, whereas compact development resulted in about 10 000 local extinctions (Table 1; Fig. 3). Extinctions under sprawling development were driven by the loss of both urban-adapted and urban-sensitive species (Fig. 3). Extinctions of both urban-adapted and urban-sensitive species outnumbered colonizations in both scenarios. However, under sprawling development there were many colonizations by urban-adapted species, compensating for the extinctions in that group, whereas there were very few colonizations and many extinctions of urban-sensitive species (Fig. 3). Compared with sprawling growth, there were relatively few extinctions of urban-sensitive species under compact development (Fig. 3). Colonizations vastly outnumbered extinctions for nonnative species under sprawling urban growth, whereas their distributions were more or less unaffected by compact growth (Fig. 3). Overall, sprawling development results in substantial local colonizations by nonnative species and urban-adapted species, but many local extinctions of urban-sensitive species.

The proximity of local biodiversity and green spaces to people also varied markedly between the two urban growth scenarios (Fig. 4). Under compact development, bird species richness in newly developed residential areas was slightly higher than under sprawling development (Fig. 4a), and people maintained greater access to public green spaces around their homes (Fig. 4b). However, compact development necessarily resulted in a smaller mean backyard size because residential density is higher in that scenario (Fig. 4c). Compact development thus has the overall effect of maintaining provision of public green spaces and proximity of local biodiversity to people, but reducing the size of private backyards.

Discussion

Urban development is proceeding rapidly around the planet. Our results show that the impacts of such urban growth on bird distributions and the proximity of people to green spaces will depend on the spatial pattern of urban growth, not just its extent. While any form of urban development reduces bird distributions, compact development better maintains species assemblages at the city scale, resulting in fewer local extinctions and much smaller reductions in species' distributions. If well planned, compact urban growth can preserve large intact green spaces, and maintain a more ecologically heterogeneous city supporting both urban-adapted and urban-sensitive species (Bryant, 2006; Sandström *et al.*, 2006). However, once residential density reaches a certain critical threshold one would expect almost all species to decline as vegetation cover reaches very low levels (Tratalos *et al.*, 2007; Evans *et al.*, 2009). Thus, the comparatively low ecological impact of compact urban growth depends crucially on maintaining high-quality interstitial green spaces between the high-density developments.

The predicted area of occupancy for urban-sensitive species decreases as development progresses regardless of urban growth form (Fig. 2a). Species such as Lewin's Honeyeater, Grey Shrike-thrush, Red-backed

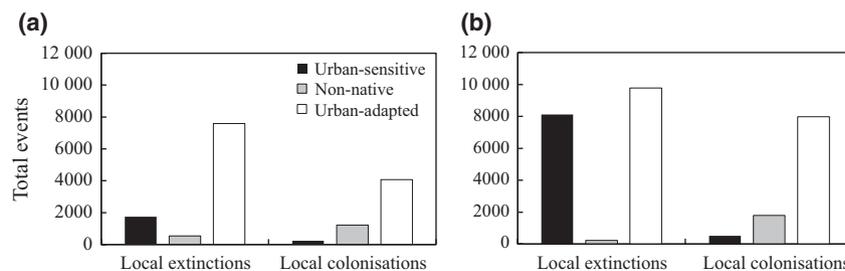


Fig. 3 The number of predicted local extinctions and colonizations for urban-sensitive (black), nonnative (grey), and urban-adapted (white) species under (a) compact and (b) sprawling urban growth scenarios. Data are the sum of extinction and colonization events for a single realization of the urban growth scenarios.

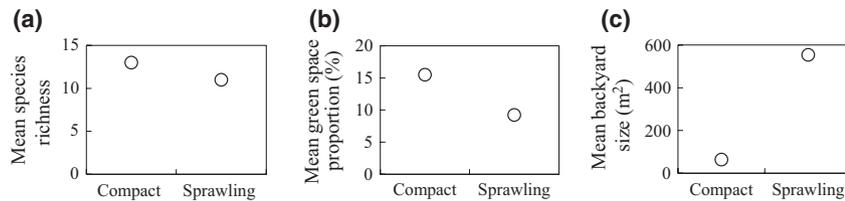


Fig. 4 Opportunities for people to experience local biodiversity under the two urban growth scenarios; (a) mean species richness per 200 m pixel in all pixels where one or more new dwellings has been added, (b) mean proportion of green space coverage within a 1.5 km radius of each residential property, and (c) mean backyard size (m²) of the newly added dwellings. Data are means for a single realization of the urban growth scenarios, and standard errors were too small to be visualized.

Fairy-wren, and Striated Pardalote show large reductions in predicted area of occupancy and high rates of local extinctions under both compact and sprawling development, albeit substantially mitigated by compact growth (Table 1). Urban-sensitive species such as these are all closely associated with remnants of natural vegetation and do not commonly persist even in low-density suburban developments (Ford *et al.*, 2001; Hepinstall *et al.*, 2008; Catterall *et al.*, 2010; Gagne & Fahrig, 2010). This suggests that compact development will be particularly beneficial where many species within a city's boundary are restricted to large green spaces or patches of remnant native habitat. Nonnative species, however, substantially increased their predicted distributions under sprawling development, but were essentially unaffected by compact growth (Fig. 2b). The two most common nonnatives (Common Myna and Spotted Turtle Dove) favour low-density suburbia (Parsons *et al.*, 2003; Blair & Johnson, 2008) and this type of land use was substantially increased under sprawling development.

In contrast to both the urban-sensitive and nonnative species, the distributions of urban-adapted species were relatively unaffected by either form of urban growth, though, there was considerable species-specific variation (Fig. 2c; Table 1). For example, Galah, Scaly-breasted Lorikeet, and Sulphur-crested Cockatoo showed some of the largest reductions in predicted area of occupancy, particularly under sprawling development (Table 1), whereas some other urban-adapted species increased under sprawling development and were relatively unaffected by compact growth, e.g. Australasian Figbird, Australian Magpie, Blue-faced Honeyeater, Crested Pigeon, Magpie-lark, and Pied Butcherbird (Table 1). These latter species are often associated with low-density suburbs containing large backyards, a habitat type that increases under sprawling development (Blair & Johnson, 2008; Catterall *et al.*, 2010).

From a biodiversity perspective, and at a city scale, compact development outperforms sprawling development, at least in a city such as Brisbane that is currently

very low density. It remains to be seen whether this pattern will generalize to other urban assemblages, given that the ecological value of retaining large green spaces depends on these sites supporting species that rarely occupy low-density suburbs. A reduction in private backyard sizes inevitably accompanies any increase in the density of residential suburbs, and despite the contribution of backyards to urban biodiversity conservation (Rudd *et al.*, 2002; Daniels & Kirkpatrick, 2006; Irvine *et al.*, 2009; Goddard *et al.*, 2010), it might be worth reducing their size if a higher residential density can be achieved. Such a reduction is already underway in Australia, as many cities respond to accelerating demand for land by allowing increased subdivision of existing residential plots (Hall, 2010). This is not without consequences for people, as smaller backyards limit beneficial interactions with species around the home, and interactions with biodiversity in public green spaces are distinct from, and not necessarily substitutable with, such interactions in backyards (Barbosa *et al.*, 2007; Forman, 2008). It has been suggested that backyard size should be maintained across the urban landscape by regulating house size (Hall, 2010), but this will necessarily limit the housing density that is achievable, thus potentially impacting biodiversity at city and regional scales. In any case, efforts to improve the ecological quality of backyards (e.g. Bryant, 2006; Smith *et al.*, 2006a,b; Gaston *et al.*, 2007; Hostetler & Drake, 2009; Goddard *et al.*, 2010) should accompany any increases in housing density to ameliorate any reduction in size.

Competition for land is intensifying as the world's population continues to increase rapidly, especially in urban areas. More efficient use of land in urban areas will be critically important in minimizing the global impact of human population growth on biodiversity (Nelson *et al.*, 2010). Our analysis suggests that such increased efficiency could be characterized by higher density residential development that retains many of the larger interstitial green spaces. However, without careful planning, increased residential density may diminish people's opportunities to interact with the local biodiversity that does persist in the face of urban growth.

Acknowledgements

We are grateful to Adrian Bannister, Margot Drewe, Scott McKinnon, and Steven Sushinsky for their assistance with data collection, and Chris Lepczyk and Paige Warren for comments and guidance. This work was funded through a University of Queensland Research Scholarship to J.R.S., a University of Queensland start-up grant to R.A.F., and an ARC Federation Fellowship to H.P.P. Additional funding support was provided by the Australian Government's National Environmental Research Program and the Australian Research Council Centre of Excellence for Environmental Decisions.

References

- Antrop M (2000) Changing patterns in the urbanized countryside of Western Europe. *Landscape Ecology*, **15**, 257–270.
- Australian Government Bureau of Statistics (2006) *2006 Australian Census*. Australian Government Bureau of Statistics, Canberra.
- Barbosa O, Tratalos JA, Armsworth PR, Davies RG, Fuller RA, Johnson P, Gaston KJ (2007) Who benefits from access to green space? A case study from Sheffield, UK. *Landscape and Urban Planning*, **83**, 187–195.
- Bino G, Levin N, Darawshi S, Van Der Hal N, Reich-Solomon A, Kark S (2008) Accurate prediction of bird species richness patterns in an urban environment using Landsat-derived NDVI and spectral unmixing. *International Journal of Remote Sensing*, **29**, 3675–3700.
- Blair RB, Johnson EM (2008) Suburban habitats and their role for birds in the urban-rural habitat network: points of local invasion and extinction? *Landscape Ecology*, **23**, 1157–1169.
- Bryant MM (2006) Urban landscape conservation and the role of ecological greenways at local and metropolitan scales. *Landscape and Urban Planning*, **76**, 23–44.
- Catterall CP (2009) Responses of faunal assemblages to urbanisation: global research paradigms and an avian case study. In: *The Ecology of Cities and Towns: A Comparative Approach* (eds McDonnell MJ, Breuste J, Hahs AK), pp. 129–155. Cambridge University Press, New York.
- Catterall CP, Cousin JA, Piper S, Johnson G (2010) Long-term dynamics of bird diversity in forest and suburb: decay, turnover or homogenization? *Diversity and Distributions*, **16**, 559–570.
- Chace JF, Walsh JJ (2006) Urban effects on native avifauna: a review. *Landscape and Urban Planning*, **74**, 46–69.
- Dallimer M, Tang Z, Bibby PR, Brindley P, Gaston KJ, Davies ZG (2011) Temporal changes in greenspace in a highly urbanized region. *Biology Letters*, **7**, 763–766.
- Daniels GD, Kirkpatrick JB (2006) Does variation in garden characteristics influence conservation of birds in suburbia? *Biological Conservation*, **133**, 326–335.
- Davies RG, Barbosa O, Fuller RA, Tratalos J, Burke N, Lewis D, Gaston KJ (2008) City-wide relationships between green spaces, urban land use and topography. *Urban Ecosystems*, **11**, 269–287.
- Evans KL, Newson SE, Gaston KJ (2009) Habitat influences on urban avian assemblages. *Ibis*, **151**, 19–39.
- Ford HA, Barrett GW, Saunders DA, Recher HF (2001) Why have birds in the woodland of Southern Australia declined? *Biological Conservation*, **97**, 71–88.
- Forman R (2008) *Urban Regions: Ecology and Planning Beyond the City*. Cambridge University Press, New York.
- Fuller RA, Gaston KJ (2009) The scaling of green space coverage in European cities. *Biology Letters*, **5**, 352–355.
- Fuller RA, Irvine KN (2010) Interactions between people and nature in urban environments. In: *Ecology Urban* (ed. Gaston KJ), pp. 134–171. Cambridge University Press, Cambridge, UK.
- Fuller RA, Tratalos J, Warren PH, Davies RG, Pepkowska A, Gaston KJ (2010) Environment and Biodiversity. In: *Dimensions of the Sustainable City* (eds Jenks M, Jones C), pp. 75–103. Springer, London.
- Gagne S, Fahrig L (2010) The trade-off between housing density and sprawl area: minimising impacts to forest breeding birds. *Basic and Applied Ecology*, **11**, 723–733.
- Gaston KJ (2010a) Urbanisation. In: *Urban Ecology* (ed. Gaston KJ), pp. 10–34. Cambridge University Press, New York.
- Gaston KJ (2010b) *Urban Ecology*. Cambridge University Press, New York.
- Gaston KJ, Fuller RA (2009) The sizes of species' geographic ranges. *Journal of Applied Ecology*, **46**, 1–9.
- Gaston KJ, Cush P, Ferguson S *et al.* (2007) Improving the contribution of urban gardens for wildlife: some guiding propositions. *British Wildlife*, **18**, 171–177.
- Goddard MA, Dougill AJ, Benton TG (2010) Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology and Evolution*, **25**, 90–98.
- Hall T (2010) *The Life and Death of the Australian Backyard*. CSIRO Publishing, Collingwood.
- Hansen AJ, Knight RL, Marzluff JM, Powell S, Brown K, Gude PH, Jones A (2005) Effects of exurban development on biodiversity: patterns, mechanisms and research needs. *Ecological Applications*, **15**, 1893–1905.
- Hepinstall JA, Alberti M, Marzluff JM (2008) Predicting land cover change and avian community responses in rapidly urbanizing environments. *Landscape Ecology*, **23**, 1257–1276.
- Hijmans RJ, Cameron SE, Parra JL, Jones PG, Jarvis A (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Hostetler M, Drake D (2009) Conservation subdivisions: a wildlife perspective. *Landscape and Urban Planning*, **90**, 95–101.
- Husté A, Boulinier T (2007) Determinants of local extinction and turnover rates in urban bird communities. *Ecological Applications*, **17**, 168–180.
- Irvine KN, Devine-Wright P, Payne SR, Fuller RA, Painter B, Gaston KJ (2009) Green space, soundscape, and urban sustainability: an interdisciplinary, empirical study. *Local Environment*, **14**, 155–172.
- Jeffrey SJ, Carter JO, Moodie KB, Beswick AR (2001) Using spatial interpolation to construct a comprehensive archive of Australian climate data. *Environmental Modelling and Software*, **16**, 309–330.
- Jenks M, Jones C (eds.) (2010) *Dimensions of the Sustainable City*. Springer, London.
- Johnson EA, Klemens MW (eds.) (2005) *Nature in Fragments: The Legacy of Sprawl*. Columbia University Press, New York City.
- Lambin EF, Geist HJ, Lepers E (2003) Dynamics of land-use and land-cover change in tropical regions. *Annual Review of Environment and Resources*, **28**, 205–241.
- Liu C, Berry PM, Dawson TP, Pearson RG (2005) Selecting thresholds or occurrence in the prediction of species distributions. *Ecography*, **28**, 385–393.
- McDonnell MJ, Hahs AH, Breuste J (eds.) (2009) *Ecology of Cities and Towns: A Comparative Approach*. Cambridge University Press, New York.
- McPeters RD, Bhartia PK, Krueger AJ *et al.* (1996) Nimbus-7 Total Ozone Mapping Spectrometer (TOMS) Data Products User's Guide. NASA reference publication 1384, Lanham, MD.
- Nelson E, Sander H, Hawthorne P *et al.* (2010) Projecting global land-use change and its effect on ecosystem service provision and biodiversity with simple models. *PLoS ONE*, **5**, e14327.
- Parsons H, French K, Major RE (2003) The influence of remnant bushland on the composition of suburban bird assemblages in Australia. *Landscape and Urban Planning*, **66**, 43–56.
- Pereira HM, Leadley PW, Proença V *et al.* (2010) Scenarios for Global Biodiversity in the 21st Century. *Science*, **330**, 1496–1501.
- Phillips SJ, Dudík M (2008) Modeling of species distributions with Maxent: new extensions and a comprehensive evaluation. *Ecography*, **31**, 161–175.
- Phillips SJ, Dudík M, Elith J, Graham CH, Lehmann A, Leathwick J, Ferrier S (2006) Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. *Ecological Applications*, **19**, 181–197.
- Pimm SL, Raven P (2000) Extinction by numbers. *Nature*, **403**, 843–845.
- Queensland Government Department of Environment and Resource Management (2006) *Digital Cadastral Database*. Queensland Government Department of Environment and Resource Management, Brisbane, QLD.
- Queensland Government Department of Infrastructure and Planning (2009) *South East Queensland Regional Plan 2009–2031*. Queensland Department of Infrastructure and Planning, Queensland, Brisbane, QLD.
- Raes N, ter Steege H (2007) A null-model for significance testing of presence-only species distribution models. *Ecography*, **30**, 727–736.
- 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 UG, 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.
- Smith RM, Gaston KJ, Warren PH, Thompson K (2006a) Urban domestic gardens (VIII): environmental correlates of invertebrate abundance. *Biodiversity and Conservation*, **15**, 2515–2545.
- Smith RM, Warren PH, Thompson K, Gaston KJ (2006b) Urban domestic gardens (VI): environmental correlates of invertebrate abundance. *Biodiversity and Conservation*, **15**, 2415–2438.

- Tilman D, Fargione J, Wolff B *et al.* (2001) Forecasting agriculturally driven global environmental change. *Science*, **292**, 281–284.
- Tratalos J, Fuller RA, Evans KL, Davies RG, Newson SE, Greenwood JJD, Gaston KJ (2007) Bird densities are associated with household densities. *Global Change Biology*, **13**, 685–1695.
- Tucker CJ (1979) Red and photo infrared linear combinations for monitoring vegetation. *Remote Sensing of Environment*, **8**, 127–150.
- Vermote EF, Tanre D, Deuze JL, Herman M, Morcrette JJ (1997) Second simulation of the satellite signal in the solar spectrum, 6S: an overview. *IEEE Transactions on Geoscience and Remote Sensing*, **35**, 675–686.
- Vitousek PM, Mooney HA, Lubchenco J, Melillo J (1997) Human Domination of the Earth's Ecosystems. *Science*, **227**, 494–499.
- Wilson KA, Westphal MI, Possingham HP, Elith J (2005) Sensitivity of conservation planning to different approaches to using predicted species distribution data. *Biological Conservation*, **122**, 99–112.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Detailed methods for the derivation and projection of the six environmental variable datasets used in species distribution models.

Table S1. The AUC values for each species' distribution model and null model as well as the total number of presence-only records used to develop the distribution models.

Table S2. The habitat suitability thresholds for each species used to determine presence or absence per species per 200 m grid pixel.

Table S3. The coefficient of variation for each species' mean area of occupancy across six randomised realisations of both the compact and sprawling urban growth scenarios.