# Compact development minimizes the impacts of urban growth on native mammals

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## Summary

1. Unprecedented global human population growth and rapid urbanization of rural and natural lands highlight the urgent need to integrate biodiversity conservation into planning for urban growth. A challenging question for applied ecologists to answer is: *What pattern of urban growth meets future housing demand whilst minimizing impacts on biodiversity?*

2. We quantified the consequences for mammals of meeting future housing demand under different patterns of compact and dispersed urban growth in an urbanizing forested landscape in south-eastern Australia. Using empirical data, we predicted impacts on mammals of urban growth scenarios that varied in housing density (compact versus dispersed) and location of development for four target numbers of new dwellings.

3. We predicted that compact developments (i.e. high-density housing) reduced up to 6% of the area of occupancy or abundance of five of the six mammal species examined. In contrast, dispersed developments (i.e. low-density housing) led to increased mammal abundance overall, although results varied between species: as dwellings increased, the abundance or occurrence of two species increased (up to ~100%), one species showed no change, and three species declined (up to ~39%).

4. Two ground-dwelling mammal species (*Antechinus stuartii* and *Rattus fuscipes*) and a tree-dwelling species (*Petaurus australis*) were predicted to decline considerably under dispersed rather than compact development. The strongest negative effect of dispersed development was for *Petaurus australis* (a species more abundant in forested interiors) which exhibited up to a 39% reduction in abundance due to forest loss and an extended negative edge effect from urban settlements into adjacent forests.

5. *Synthesis and applications.* Our findings demonstrate that, when aiming to meet demand for housing, any form of compact development (i.e. high-density housing) has fewer detrimental impacts on forest-dwelling mammals than dispersed development (i.e. low-density housing). This is because compact development concentrates the negative effects of housing into a small area whilst at the same time preserving large expanses of forests and the fauna they sustain. Landscape planning and urban growth policies must consider the trade-off between the intensity of the threat and area of sprawl when aiming to reduce urbanization impacts.

**Key-words:** arboreal marsupials, edge effect, forest, ground-dwelling mammals, land sharing, land sparing, residential development, spatially explicit scenarios, urban infill, urban planning

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## Introduction

Unprecedented global human population growth combined with rapid housing development in rural and natural lands world-wide highlight an urgent need to plan for

biodiversity conservation under future urbanization (Seto, Guneralp & Hutyra 2012; Lin & Fuller 2013). Currently, urbanization leads to marked environmental change, and the loss, degradation and fragmentation of habitats (Bar-Massada, Radeloff & Stewart 2014). Land modification as a result of urbanization affects biodiversity from local to global scales (McKinney 2006; Seto, Guneralp & Hutyra 2012) and threatens species with extinction world-wide (Baillie *et al.* 2010). However, planning for biodiversity conservation under future urban development is complex. This is because the impacts of urbanization on biodiversity vary with the kind of urban development (e.g. housing density and location) (Gordon *et al.* 2009; Sushinsky *et al.* 2013), as well as the species involved (McDonnell & Hahs 2015). Therefore, a challenging conservation question to answer is: *What kind of urban development meets future housing demand whilst minimizing impacts on biodiversity?*

There is a growing body of literature on the effects of urbanization on biodiversity and how to improve urban design to achieve biodiversity-sensitive cities and towns (Ikin *et al.* 2015). Yet, there is only limited evidence for how best to minimize the impacts of urban growth on regional biodiversity when first planning for future housing demand. In this context, the land sparing versus land sharing framework may provide important insights (Lin & Fuller 2013). This framework has been mainly applied to balance land for food production and biodiversity conservation in agricultural settings (Green *et al.* 2005). At the opposite ends of this framework, urban patterns may take one of two forms: compact ('land sparing') or dispersed ('land sharing'). Compact developments concentrate a high number of dwellings over a small area, leading to a high local impact on biodiversity, while other land can be set aside for conservation (Lin & Fuller 2013). In contrast, dispersed developments contain dwellings at a lower density, usually resulting in less local impact than compact development (Villaseñor *et al.* 2014), but impacts are spread over large areas of land to meet housing demands (Theobald, Miller & Hobbs 1997). Thus, dispersed development may have a higher impact on biodiversity at a landscape scale than compact developments (Gagne & Fahrig 2010a). Knowing what kind of urban development minimizes impacts on biodiversity at a landscape scale will help land planners to carry out biodiversity-sensitive land-use planning.

How species respond to patterns of urban development can be influenced by different factors. One important factor may be species' habit: small ground-dwelling species may be severely affected by increased urbanization due to the removal of ground cover vegetation (van der Ree & McCarthy 2005; Villaseñor *et al.* 2015), whereas the response of tree-dwelling species may vary according to available tree cover (Isaac *et al.* 2014; Ikin *et al.* 2015). Furthermore, species that share some life-history attributes also may exhibit different responses to urban patterns. For example, although most tree-dwelling marsupials can be found in high abundance in dispersed

developments that provide mature tree cover in south-eastern Australia, one species (the common brushtail possum *Trichosurus vulpecula*) occurs at greatest abundance in compact developments (Isaac *et al.* 2014; Villaseñor *et al.* 2014). Thus, compact developments may support high overall animal abundances underpinned by a few species adapted to urbanization (McKinney 2006; McDonnell & Hahs 2015).

Here, we present one of the few attempts to date to assess the effects on fauna of meeting future housing demand under dispersed and compact patterns of urban growth. To the best of our collective knowledge, our work is the first quantification of changes in occurrence and abundance of mammals under spatially explicit scenarios of compact and dispersed urban growth. Lin & Fuller (2013) propose that dispersed developments (land sharing) may be favoured where low-density housing allows biodiversity to persist. We tested this hypothesis in an urbanizing landscape in south-eastern Australia dominated by forested lands and urban settlements of high and low housing densities (compact and dispersed, respectively). In the study area, low-density housing developments (i.e. rural residential or exurban development) retain natural vegetation, allowing the persistence of several forest mammal species (Villaseñor *et al.* 2014). We quantified change in the: (i) occurrence of two ground-dwelling mammal species, (ii) abundance of four tree-dwelling mammal species, and (iii) summed abundance of the tree-dwelling mammals under 36 spatially explicit scenarios of urban growth that aimed to meet future demand for housing.

Scenarios varied in housing density (dispersed versus compact), location of development and number of new dwellings. Our scenarios included one dispersed and two compact forms of urban growth: (i) 'rural residential', where natural vegetation is partially cleared to develop low-density housing areas, (ii) 'residential', where natural vegetation is cleared to develop high-density housing areas (towns), and (iii) 'urban infill', where rural residential areas are changed to residential areas. Under rapid urbanization of private forests (Stein *et al.* 2012) and the rise of wildland-urban interfaces world-wide (Bar-Massada, Radeloff & Stewart 2014), urban infill may benefit biodiversity by preventing further forest loss and limiting the extent of wildlands susceptible to urban edge effects (Theobald, Miller & Hobbs 1997).

We aimed to answer the following questions: **Q1.** Do forest mammals benefit from dispersed rather than compact urban growth? **Q2.** Does urban infill benefit forest-dependent mammals? The answers to these questions will provide insights on how to minimize the impacts of future urban growth on mammals in this region. This is important because urban development has driven local mammal extinctions in south-eastern Australia (van der Ree & McCarthy 2005), a country in which a large number of endemic mammal species have already been lost (Lindenmayer 2015). Furthermore, our investigation offers important insights for mammal conservation, because most

mammal species inhabit forests (Baillie *et al.* 2010) that have experienced pervasive deforestation and fragmentation (Haddad *et al.* 2015), as well as urbanization (Stein *et al.* 2012). Our study therefore provides urgently needed insights into the impacts of alternative urban growth policies in the face of rapid urbanization of forests and rural lands.

## Materials and methods

### STUDY AREA

Our study was located in the Shoalhaven region (35·04° S, 150·6° E), on the south coast of New South Wales (NSW), southeastern Australia (Fig. 1a). The climate is mild, and an annual rainfall of ~1000 mm is distributed evenly throughout the year (www.bom.gov.au). Native vegetation (dominated by forests and woodlands of the genus *Eucalyptus*, but also including other vegetation types) and wetlands cover >80% of the terrestrial landscape, followed by urban areas (~13%) and a small percentage of other land uses (e.g. grazing, cropping, mining; ~5%) (Emery 2010). The study area is undergoing clearing of natural vegetation for residential development due to a relatively high rate of human relocation into the area and a high demand for coastal holiday houses (Shoalhaven City Council 2015). If the current rate of population growth continues, ~8000 new dwellings will be added in the next 50 years (Shoalhaven City Council 2015).

### PREDICTIVE MODELS FOR MAMMALS

We studied three ground-dwelling species: brown antechinus *Antechinus stuartii*, bush rat *Rattus fuscipes* and long-nosed bandicoot *Perameles nasuta*; and four arboreal marsupials: the common brushtail possum *Trichosurus vulpecula*, the common ringtail possum *Pseudocheirus peregrinus*, the sugar glider *Petaurus breviceps* and the yellow-bellied glider *Petaurus australis* (Table S1, Supporting Information).

### *Models for ground-dwelling mammals*

For ground-dwelling mammals, we collated presence–absence data collected during summer from two different studies. Species of ground-dwelling mammals were recorded with vertically oriented cameras placed at 77 locations (77 camera trap stations × six nights from December 2012 to March 2013) (for details, see Villaseñor *et al.* 2015) and cage trapping along 100-m transects at 97 locations (1552 cage traps × three nights during December 2013) (for details, see Lindenmayer 2014; Lindenmayer *et al.* 2016). We combined these two data sets because these methods are expected to detect ground-dwelling mammals with a high degree of confidence (De Bondi *et al.* 2010). Although presence–absence data from different sources can be used concurrently to model the distributions of species (Sardà-Palomera *et al.* 2012), we limited our inferences to the occurrence of species recorded in both studies: brown antechinus, bush rat and long-nosed bandicoot (recorded at 86, 75 and 12 locations, respectively).

We identified variables that best predicted individual species occurrences using Information Criterion model selection over a candidate set of generalized linear mixed models (GLMMs) in R (R Core Team 2013). Five adaptive Gauss–Hermite quadrature
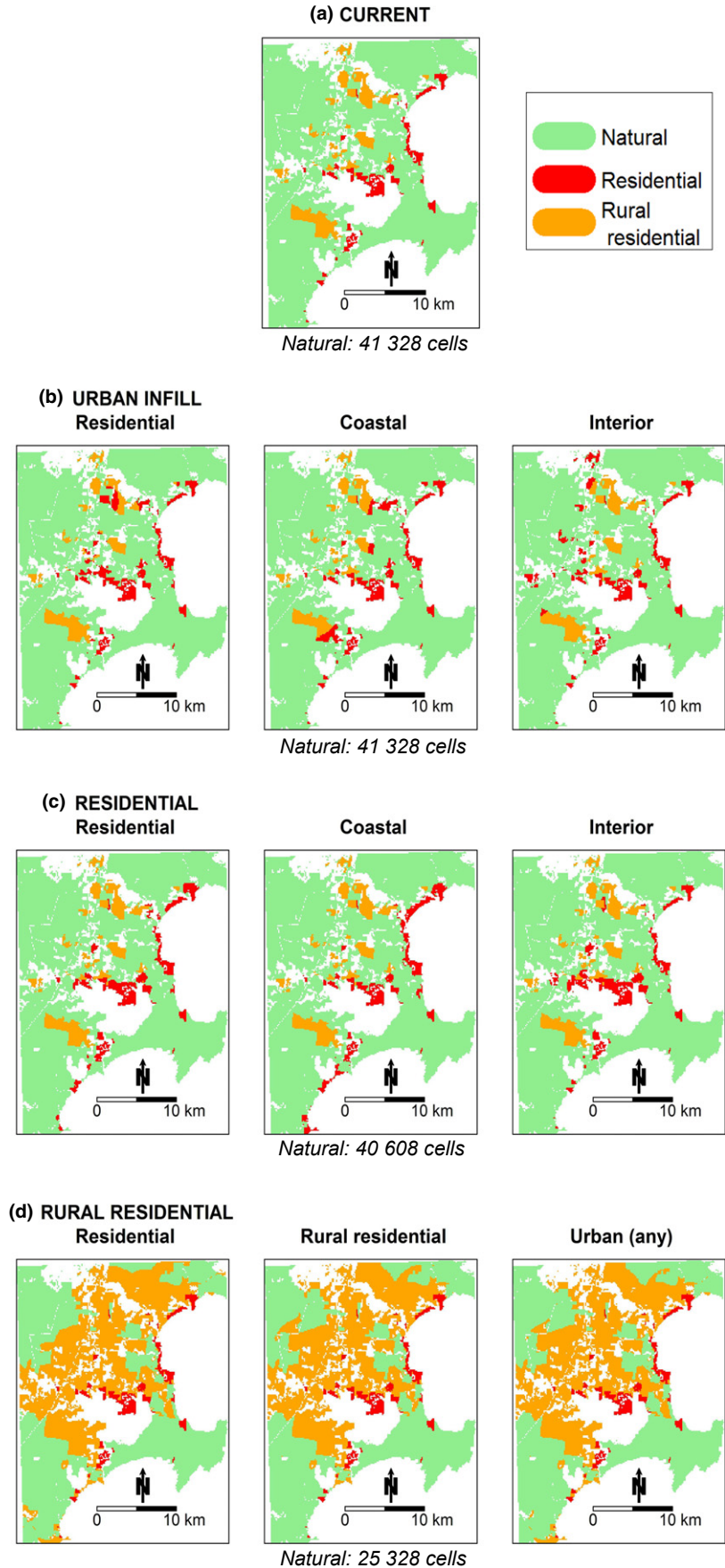
points were used to evaluate the marginal integral in the fitted GLMMs, which provides a better approximation of the integral than the Laplace approximation (Bolker 2015). We used binomial GLMMs (logit link) (package 'lme4', Bates *et al.* 2014) to fit effects on individual species occurrence of: (i) land use (categorical predictor with three levels: residential, rural residential and native vegetation − from a polygon shapefile; Emery 2010), (ii) broad vegetation type (categorical predictor with five levels: forest, woodland, shrubland, heathland and cleared vegetation − from a raster with 100 m × 100 m cell size; National Vegetation Information System (NVIS), Department of Environment), and (iii) distance to urban cover (continuous predictor− metres, calculated in ARCGIS). Distance to urban cover was transformed using a square root transformation to improve distribution of its values. The GLMMs included the effect of predictive variables in isolation and their additive effects, leading to eight models in the candidate set (including a null model). To account for spatial dependence, we grouped data from clustered locations (within a 300 m radius) in a 'site', and incorporated site ($n = 40$) as a random effect.

Because the bush rat was absent from residential areas during our sampling, we fit GLMMs with the Laplace approximation and normal priors on fixed effects (Bolker 2015). Due to the limited number of detections of the long-nosed bandicoot ($n = 12$), we restricted the inclusion of predictive variables (fixed effects) within a model to two and explored the effects of distance to the coast (continuous variable, square-root transformed) instead of broad vegetation type. Distance to the coast was chosen because this is important for a closely related species (southern brown bandicoot *Isoodon obesulus*) (Department of Environment and Conservation [NSW] 2006).

For each species, we selected the best GLMMs from each candidate model set using Akaike Information Criterion corrected by small sample size (AICc) (package 'MuMIn'; Barton 2013). We investigated whether there was evidence for spatial autocorrelation in residuals of the best GLMMs using residual variograms and calculated Morans' I index (Paradis, Claude & Strimmer 2004). Once we confirmed there was no evidence for spatial autocorrelation in model residuals (Moran's I, $P > 0·1$; Appendix S1, Table S2), we predicted variable estimates (mean ± SE) from the best models (lowest AICc).

### *Models for arboreal marsupials*

To predict the abundance of arboreal marsupials in response to different urban patterns, we used abundance data and GLMMs of individual species abundance in 100-m transects reported in Villaseñor *et al.* (2014). This earlier study described arboreal marsupial responses across urban–forest (includes forest and woodland) interfaces. Predictive variables in those models included residential density at the urban–forest interface (levels: residential, rural residential), land cover at each side of the urban boundary (levels: urban, forested) and distance to an urban boundary (50 m, 150 m and 250 m, continuous variable). Six replicates were sampled in the study area, resulting in 72 transects of 100 m length surveyed in urban–forest interfaces (for details, see Villaseñor *et al.* 2014). Because we are interested in predicting species abundances across the landscape, we incorporated data from six forested areas >400 m away from urban areas (18 transects of 100 m length − these data were only used in the previous study to predict the abundance of the yellow-bellied glider). All data (90 transects of 100 m length) were collected in the same season and year, with

**(a) CURRENT**



*Natural: 41 328 cells*

**(b) URBAN INFILL**
**Residential** **Coastal** **Interior**



*Natural: 41 328 cells*

**(c) RESIDENTIAL**
**Residential** **Coastal** **Interior**



*Natural: 40 608 cells*

**(d) RURAL RESIDENTIAL**
**Residential** **Rural residential** **Urban (any)**



*Natural: 25 328 cells*

**Fig. 1.** Distributions of land use under selected scenarios of current (a) and future (b–d) urban growth in the study area. Scenarios for urban growth included urban infill (b), residential development (c) and rural residential development (d), each occurring in one of three spatial locations (see Table 1). All scenarios for urban growth illustrated here are at the highest level of housing (8000 new dwellings). [Colour figure can be viewed at wiley-onlinelibrary.com]

the same sampling method and observers. We fitted the new GLMMs with Poisson distribution using five adaptive Gauss–Hermite quadrature points. We tested for overdispersion in these new GLMMs by comparing the sum of the squared Pearson residuals to the residual degrees of freedom (Bolker 2015). After confirming there was no evidence for overdispersion in our models ($\chi^2$, $P > 0.28$), nor spatial autocorrelation in model residuals (Moran's $I$, $P > 0.1$; Appendix S1, Table S2), we predicted variable estimates (mean ± SE) from GLMMs.

## SCENARIOS FOR URBAN GROWTH

All spatial analyses were based on rasters (Hijmans 2015) in R (R Core Team 2013). We converted our ~ 33·6 km × 26·8 km study area to a raster with 100 m × 100 m cell size (Fig. 1a), accounting for existing knowledge that some of our target mammal species respond to habitat differences at this scale (Villaseñor *et al.* 2014). The current scenario was described by multiple raster layers, each of them representing a predictive variable in our GLMMs [e.g. land use, land cover (provided by NSW Office of Environment and Heritage), vegetation type (NVIS), distance to an urban boundary]. Cells with alternative land uses (e.g. agricultural lands) for which we did not have mammal data were excluded from the analyses − thus, 46 693 cells (ha) were considered in our analysis. In addition, cells within conservation areas such as natural parks and reserves were unable to be developed and therefore did not change across urban growth scenarios (Appendix S2, Fig. S1).

We compared the biodiversity outcomes of meeting housing demands under 36 spatially explicit scenarios of urban development. These 36 scenarios included combinations of three types of urban development (urban infill, residential, rural residential, defined in the Introduction), three spatial locations per type of development (e.g. coastal, interior) and four targeted numbers for new dwellings (2000; 4000; 6000; 8000) (see Table 1 for details,

Fig. 1b–d shows scenarios for 8000 new dwellings added). In urban infill scenarios, rural residential cells were changed to residential. In contrast, in residential and rural residential development scenarios, natural cells (>90% comprised of forest and woodland, Table S3) were converted to residential and rural residential, respectively; therefore, most urban development occurred at the expense of the loss of tree-dominated vegetation (Appendix S2). To calculate the number of cells required to add the four targeted number of new dwellings (2000; 4000; 6000 and 8000) by each kind of urban development, we first calculated the number of houses per ha in residential and rural residential areas in our study area from cadastral data (residential areas: ~11·1 houses ha$^{-1}$; rural residential: ~0·5 houses ha$^{-1}$). For urban infill, the difference of houses per ha between residential and rural residential areas (~10·6) was the number of new dwellings added per rural residential cell changed to residential. Then, we divided the number of target new dwellings by the corresponding houses per ha to obtain the number of hectares (cells) required by each scenario.

To obtain raster layers that represented each predictive variable for our 36 scenarios of urban growth, we first updated the raster layer of land use for every 2000 new dwellings added (Table 1). Then, we updated all raster layers according to the new land-use layer. Raster layers for arboreal marsupials: (i) only considered urban and forested cells because we did not have abundance data for other environments, (ii) urban–forest interfaces comprised 400 m each side of an urban–forest boundary, (iii) excluded the southern peninsula because of local extinctions of arboreal marsupials registered in this area from long-term monitoring (Lindenmayer 2015) (Appendix S2).

## CHANGE IN OCCURRENCE AND ABUNDANCE UNDER FUTURE URBAN DEVELOPMENT

For each species, we used the parameter estimates for fixed effects from our GLMMs to predict presences/absences for

**Table 1.** Thirty-six spatially explicit scenarios of urban growth for south-eastern Australia (see Appendix S2 for details)

| Type of urban development | Spatial location | Dwellings added per cell changed | Description | Targeted number of new dwellings (thousands) |
|---|---|---|---|---|
| Compact: Urban infill | | | Rural residential cells change to residential and are selected according to: | |
| | Residential | 10·6 | - proximity to residential areas. | 2, 4, 6, 8 |
| | Coastal | 10·6 | - proximity to residential areas as well as their proximity to the coast. | 2, 4, 6, 8 |
| | Interior | 10·6 | - proximity to residential areas as well as distance away from the coast. | 2, 4, 6, 8 |
| Compact: Residential | | | Natural land-use cells change to residential and are selected according to: | |
| | Residential | 11·1 | - proximity to residential areas. | 2, 4, 6, 8 |
| | Coastal | 11·1 | - proximity to residential areas as well as their proximity to the coast. | 2, 4, 6, 8 |
| | Interior | 11·1 | - proximity to residential areas as well as distance away from the coast. | 2, 4, 6, 8 |
| Dispersed: Rural residential | | | Natural land-use cells change to rural residential and are selected according to: | |
| | Urban | 0·5 | - proximity to any kind of urban area (i.e. residential or rural residential) | 2, 4, 6, 8 |
| | Residential | 0·5 | - proximity to residential areas. | 2, 4, 6, 8 |
| | Rural residential | 0·5 | - proximity to rural residential areas. | 2, 4, 6, 8 |
| Total number of scenarios = 36 | | | | |

ground-dwelling mammals and abundance for arboreal marsupials across our development scenarios (including the current scenario) (Hijmans 2015). For individual species occurrence of ground-dwelling mammals, we set each cell to present or absent for a given scenario by taking a random sample of presence/absence from a binomial distribution based on parameter estimates from our binomial GLMMs (function *rbinom*, package '*stats*') (Kéry 2010). To calculate a species' *area of occupancy* (Gaston & Fuller 2009), we counted the number of cells in which a species was 'present' in a given scenario. We repeated this process 100 times to obtain 100 estimates of a species' *area of occupancy* for each scenario. For individual species abundance of arboreal marsupials, we estimated abundance in each cell for a given scenario by taking a random sample from a Poisson distribution based on parameter estimates in our Poisson GLMMs (function *rpois*, package '*stats*') (Kéry 2010). We then summed estimated abundances across cells for a given scenario. We also summed all individual species abundances to obtain *summed abundance* for all arboreal marsupials in a given scenario. We repeated this process 100 times to obtain 100 estimates of each species' *abundance* as well as *summed abundance* of all four species for each scenario.

For ground-dwelling mammals, we estimated the change in species' *area of occupancy* under the 36 development scenarios with respect to the current landscape (Sushinsky *et al.* 2013). For this, we calculated for each of the future scenarios, the percentage change in species' *area of occupancy* of the 100 estimates with respect to the species' *mean area of occupancy* in the current landscape (mean over 100 estimates). We then calculated the mean percentage change ($\pm$SE) per scenario.

For arboreal marsupials, we calculated a species' change in *abundance* as well as in *summed abundance* under the 36 scenarios with respect to the current landscape. We calculated for each of the future scenarios the mean ($\pm$SE): (i) percentage change in individual species *abundance* of the 100 estimates with respect to the *mean abundance* in the current landscape (mean over 100 estimates), and (ii) percentage change in *summed abundance* of the 100 estimates with respect to the *mean summed abundance* in the current landscape (mean over 100 estimates).

## Results

### PREDICTIVE MODELS FOR MAMMALS

The best-supported GLMM predicting the occurrence of brown antechinus and bush rat included land use only as a fixed effect (Table S4). The probability of occurrence of both species was highest in the native vegetation land-use category and lowest in residential areas (Table 2). There was no support for any of our models for long-nosed bandicoot occurrence (Table S4). We therefore could not estimate the change in its occurrence under future urban development.

Arboreal marsupials exhibited varied responses to urbanization (Table 3). The common brushtail possum was predicted to have the highest estimated abundances in residential areas and surrounding forested cover. Common ringtail possum abundance decreased from the boundary towards the interior of residential areas. Sugar glider abundance was lowest in residential areas. Yellow-bellied glider abundance was lowest in residential areas and adjacent forested cover (Table 3).

**Table 2.** Variable estimates of ground-dwelling mammal occurrence from GLMMs with a binomial distribution (logit link) from best models selected using AICc. When the variable 'Land use' is present, intercepts represent estimated occurrence (logit scale) in natural land use

| Species | Variable | Estimate | SE |
|---|---|---|---|
| Brown antechinus | Intercept | 0·18 | 0·27 |
| | Land use$_{Residential}$ | −3·04 | 1·16 |
| | Land use$_{Rural\ residential}$ | −1·14 | 0·71 |
| Bush rat | Intercept | −0·28 | 0·28 |
| | Land use$_{Residential}$ | −3·10 | 1·70 |
| | Land use$_{Rural\ residential}$ | −1·09 | 0·72 |
| Long-nosed bandicoot | Intercept | −2·60 | 0·30 |

### CHANGE IN OCCURRENCE AND ABUNDANCE UNDER FUTURE DEVELOPMENT

The estimated *areas of occupancy* for ground-dwelling mammals exhibited larger reductions under dispersed developments compared with compact developments. *Area of occupancy* for both the brown antechinus and bush rat decreased by ~5% with the addition of 2000 new dwellings and decreased by ~20% with the addition of 8000 new dwellings under dispersed developments (Fig. 2c). In contrast, in scenarios of compact development, the brown antechinus and bush rat exhibited <2% decrease in *area of occupancy* (Fig. 2a,b). The reduction in *area of occupancy* of ground-dwelling species followed the trend in the extent of clearing of native vegetation across scenarios (Fig. 2).

Arboreal marsupials exhibited varied changes in abundance within scenarios of development. Summed abundance decreased with the number of new dwellings under compact development scenarios, but increased with the new dwellings under dispersed development scenarios (Fig. 3). Compact developments had a negative effect on arboreal marsupial abundance, except for the common brushtail possum (Fig. 3a,b). Despite the negative effects of compact developments, the reduction in arboreal marsupial abundance was small (<6% change under residential development or urban infill) (Fig. 3a,b). For dispersed development scenarios, the estimated abundance of the common brushtail possum and common ringtail possum increased by ~100% and ~50%, respectively (Fig. 3c). There was a small change in the estimated abundance of the sugar glider (<1%), but the estimated abundance of the yellow-bellied glider decreased by ~39% when 8000 new dwellings were added under rural residential development scenarios.

Differences in the amount of change in the distribution and abundance of mammals among compact development scenarios were less evident. The reduction in the estimated area of occupancy for ground-dwelling mammals was <1% in urban infill scenarios and <2% in residential scenarios (Fig. 2a,b). The estimated percentage change in abundance for the common brushtail possum and common ringtail possum was slightly lower under residential development than under urban infill (~5 units difference in the percentage change for 8000 new dwellings) (Fig. 3a,b).

**Table 3.** Variable estimates from GLMMs with a Poisson distribution (log link) for arboreal marsupials. Variable 'Interface' denotes the housing density at an urban–forest interface (levels: residential, rural residential), which was combined with 'Land cover' (levels: urban, forested). Intercepts represent estimated abundance (link scale) in forested areas ≥400 m away from an urban boundary

| Species | Variable | Estimate | SE |
|---|---|---|---|
| C. brushtail possum | Intercept | −5·39 | 1·46 |
| | Interface$_{Residential}$ Land cover$_{Forested}$ | 2·79 | 1·61 |
| | Interface$_{Residential}$ Land cover$_{Urban}$ | 3·01 | 1·61 |
| | Interface$_{Rural}$ Land cover$_{Forested}$ | 0·54 | 1·75 |
| | Interface$_{Rural}$ Land cover$_{Urban}$ | 2·41 | 1·63 |
| C. ringtail possum | Intercept | −2·63 | 0·50 |
| | Interface$_{Residential}$ Land cover$_{Forested}$ | −2·53 | 2·22 |
| | Interface$_{Residential}$ Land cover$_{Urban}$ | 1·60 | 0·96 |
| | Interface$_{Rural}$ Land cover$_{Forested}$ | 0·17 | 0·95 |
| | Interface$_{Rural}$ Land cover$_{Urban}$ | 0·87 | 0·80 |
| | Interface$_{Residential}$ Land cover$_{Forested}$/dist. boundary | 0·01 | 0·01 |
| | Interface$_{Residential}$ Land cover$_{Urban}$/dist. boundary | −0·02 | 0·01 |
| | Interface$_{Rural}$ Land cover$_{Forested}$/dist. boundary | 0·002 | 0·004 |
| | Interface$_{Rural}$ Land cover$_{Urban}$/dist. boundary | 0·000 | 0·004 |
| Sugar glider | Intercept | −1·74 | 0·35 |
| | Interface$_{Residential}$ Land cover$_{Forested}$ | −0·08 | 0·50 |
| | Interface$_{Residential}$ Land cover$_{Urban}$ | −2·69 | 1·08 |
| | Interface$_{Rural}$ Land cover$_{Forested}$ | 0·20 | 0·49 |
| | Interface$_{Rural}$ Land cover$_{Urban}$ | −0·04 | 0·51 |
| Yellow-bellied glider | Intercept | −2·76 | 0·86 |
| | Interface$_{Residential}$ | −2·89 | 1·39 |
| | Interface$_{Rural}$ | −1·43 | 1·10 |

There was little variation in species' percentage change due to the spatial location of development. Species showed the same trend (i.e. positive, negative or neutral) within each kind of urban growth form irrespective of the spatial location of development (Figs 2 and 3).

## Discussion

Our study area is an example of many regions of the world where planners must facilitate human population growth. We sought to predict impacts on ground-dwelling and arboreal mammals of housing development in an urbanizing landscape of south-eastern Australia. We predicted outcomes for these species using scenarios representing different numbers of new dwellings added in one of three kinds of urban growth: two compact (urban infill, residential) and dispersed (rural residential). Mammal conservation was best achieved by avoiding dispersed (low-density housing) development and growing urban areas with any kind of compact (high-density housing) development (**Q1–Q2** in the Introduction).

### Q1. LAND SHARING OR LAND SPARING? DISPERSED VERSUS COMPACT DEVELOPMENTS

Our landscape-scale predictions of change to species occupancy and abundance demonstrated that lower local-scale impacts on mammals of low- compared with high-density housing did not compensate for the extensive modification of high-quality habitat (forested land) necessary to meet low-density housing targets. Overall, the species in our study were therefore likely to be less altered by compact rather than dispersed urban growth (Figs 2 and 3).

Our predictions for arboreal mammals revealed a variety of responses to dispersed development. Dispersed development scenarios increased summed abundance of arboreal mammals, a result consistent with earlier work on the conservation value of urban areas developed at a lower density of housing (Villaseñor *et al.* 2014; Ikin *et al.* 2015; but see Caryl *et al.* 2016). However, increased summed abundance was not reflective of increased numbers across all species of arboreal mammals, but instead was driven by two species. The common brushtail possum (a species adapted to urban environments), doubled its relative abundance, and the common ringtail possum increased by ~50% at the highest urbanization level (8000 dwellings). Both species benefited from the sprawl of dispersed development probably because of their plasticity in diet, habit and den site use (Isaac *et al.* 2014). Another arboreal mammal, the sugar glider, can inhabit disturbed forested areas (van der Ree & McCarthy 2005; Isaac *et al.* 2014) and was not affected by rural residential scenarios of dispersed development because they retained mature tree cover. In contrast, the yellow-bellied glider (a species more abundant in the forested interior) exhibited ~39% drop in abundance under dispersed development. This forest-dwelling species needs large expanses of forested land (Lindenmayer, Cunningham & McCarthy 1999). Our models predicted a decrease in its abundance not only in urban areas, but also in adjacent forested areas (urban–forest interfaces, Table 3), suggesting an extended negative edge effect from urban settlements into adjacent
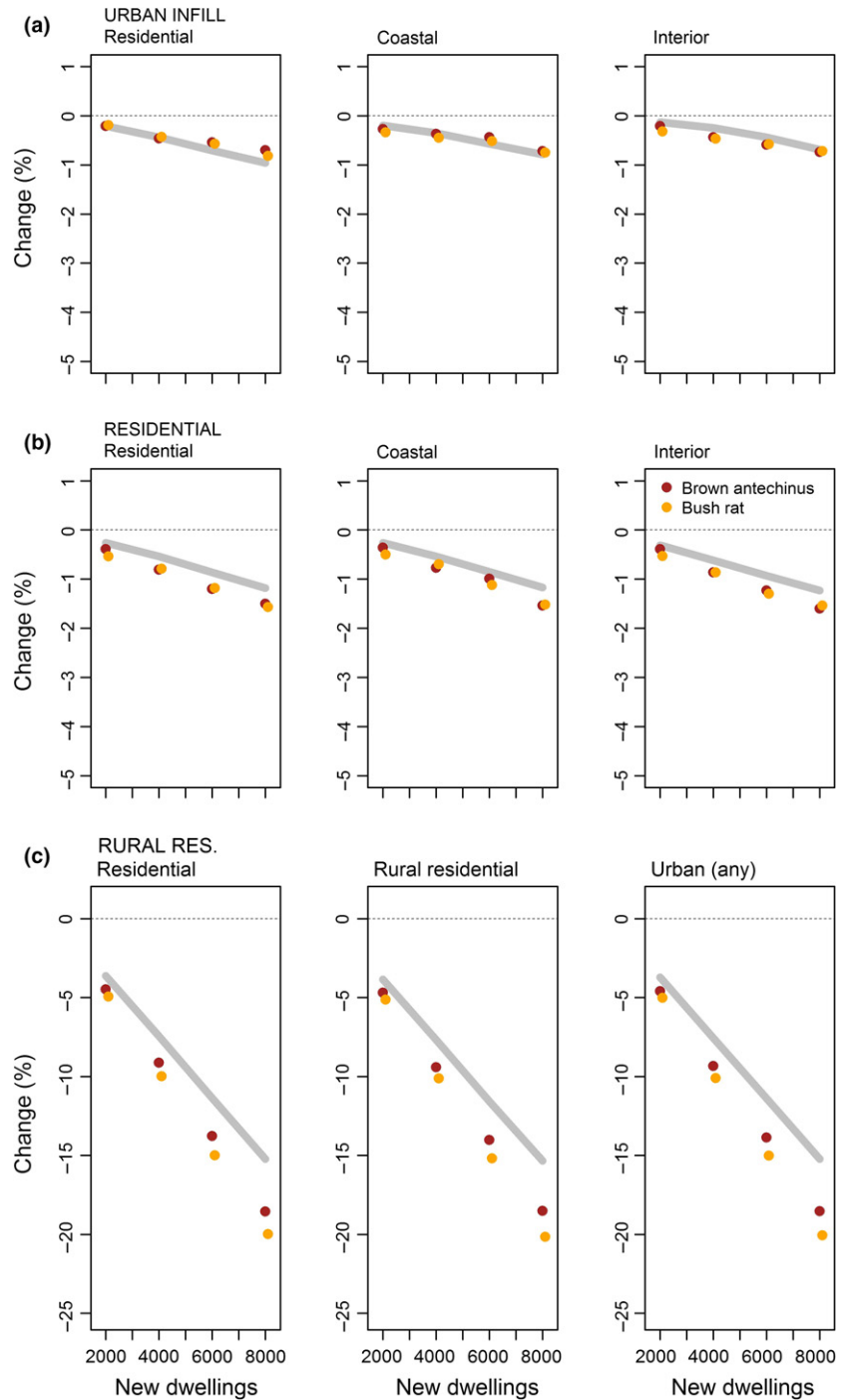
**Fig. 2.** Estimated mean percentage change of the area occupied by the brown antechinus and bush rat under scenarios of future urban growth (see Table 1 and Fig. 1). Solid grey line represents the percentage change in the amount of vegetation. Dashed horizontal line shows no change; SE is not plotted because it is smaller than the point (mean). [Colour figure can be viewed at wileyonlinelibrary.com]

forests (Villaseñor *et al.* 2014). Species that decline in urban areas and adjacent habitats are likely to be severely impacted under expansion of low-density housing.

When assessed at a landscape scale, dispersed development scenarios negatively affected ground-dwelling mammals, with up to ~20% reduction in area of occupancy expected for the brown antechinus and bush rat. Our predictive models showed that these species were more likely to occupy low- rather than high-density housing (estimated probabilities of occurrence: brown antechinus = 0·3 vs. 0·05; bush rat = 0·2 vs. 0·03) and agreed with previous studies finding that these species are more likely to persist

in less intensively developed urban areas (van der Ree & McCarthy 2005) (Table 2). However, the estimated area of occupancy for small ground-dwelling mammals was lowest in rural residential scenarios of urban growth (Fig. 2). This was because the modified forested land area was ~22 times larger under dispersed than under compact development, leading to the development of most land area outside protected areas (Fig. S1).

Land sparing may help conserve animal populations that are sensitive to landscape change because compact developments limit disturbance to a small area. Thus, forest-dependent species and species negatively affected by urban
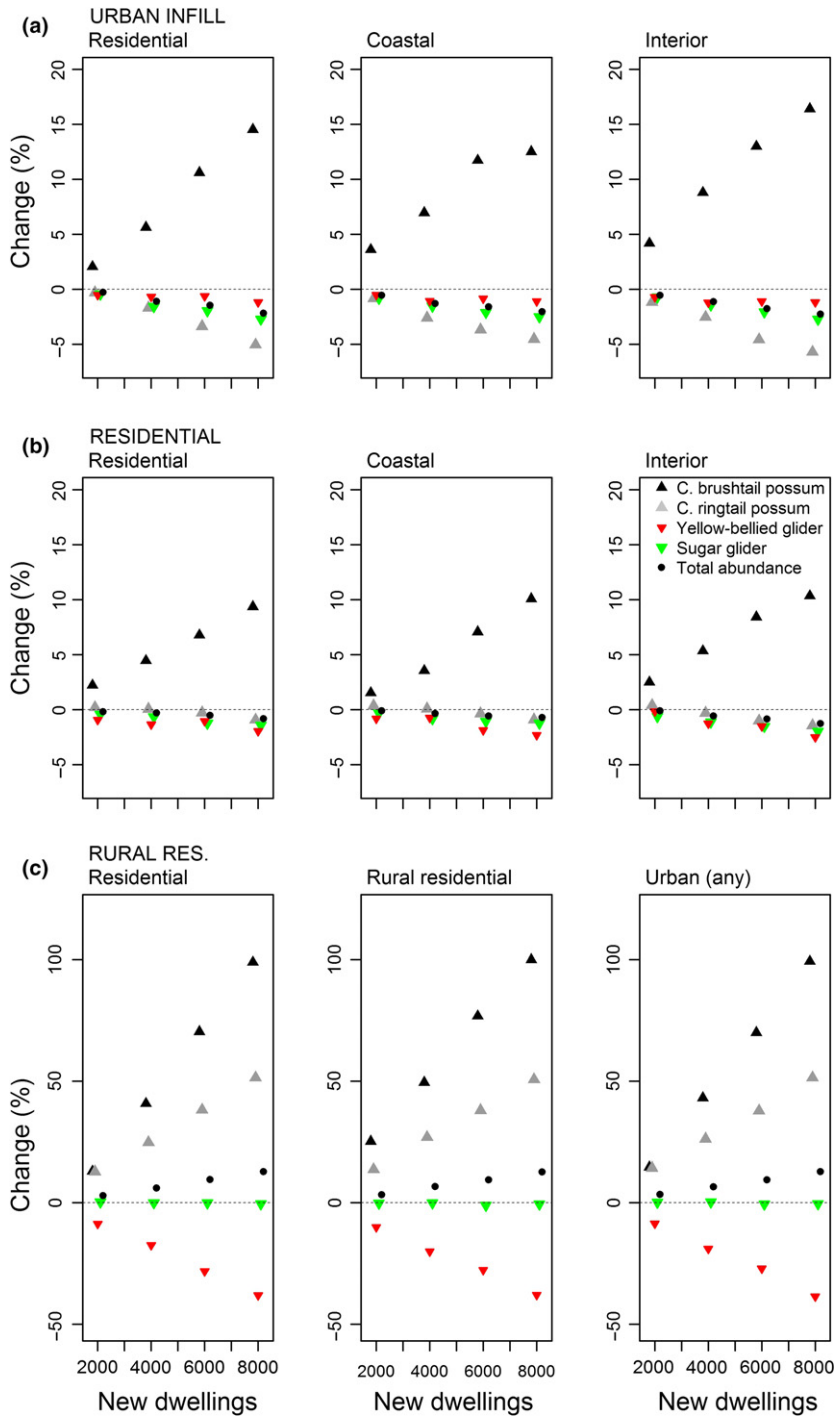
**Fig. 3.** Estimated mean percentage change for arboreal marsupial abundance under scenarios of future urban growth (see Table 1 and Fig. 1). Dashed horizontal line shows no change; SE is not plotted because it is usually smaller than point (mean). [Colour figure can be viewed at wileyonlinelibrary.com]

boundaries (e.g. forest interior) are likely to be less affected by compact rather than dispersed urban growth. Although only a few studies from around the world have predicted the fate of animals under compact versus dispersed urban growth (e.g. Gagne & Fahrig 2010b; Sushinsky *et al.* 2013), these studies have found support for land sparing rather than land sharing. For instance, hypothetical scenarios have showed that forest-dependent taxa that strongly decline with increasing housing density had the highest abundances and species richness in compact rather than dispersed scenarios of development (Gagne & Fahrig 2010a,b). In addition,

compact developments retain larger green space and are predicted to maintain larger distributions of urban-sensitive birds than dispersed developments in Brisbane, Australia (Sushinsky *et al.* 2013), as well as higher abundance of carabid beetles in Tokyo, Japan (Soga *et al.* 2014).

### Q2. COMPACT DEVELOPMENT: RESIDENTIAL VERSUS URBAN INFILL

We found similar responses (trends) in mammals under different kinds of compact developments (i.e. urban infill

and residential). The very small differences among urban infill and residential developments were driven by the scale of our analysis: a small number of cells changed under compact scenarios compared to the total number of cells in our landscape (Fig. 1), and all final responses (percentage change in species abundance and area of occupancy) were calculated at the landscape scale. Analyses within a city's limits have found that urban infill tends to have better outcomes for birds (Sushinsky *et al*. 2013) and beetles (Soga *et al*. 2014) than conversion of green spaces, but at a low number of dwellings in the landscape, urban infill may be worse for species adapted to open spaces (e.g. butterflies, Soga *et al*. 2014).

### SPATIAL LOCATION OF DEVELOPMENT

There is long-standing evidence on the effects of the spatial arrangement or configuration of landscape elements on fauna (Theobald, Miller & Hobbs 1997; Haddad *et al*. 2015; although see Fahrig 2013). However, we found that the spatial location of development had little effect on the total area of occupancy or abundance of study fauna compared with the type of development. The limited impact of different locations of development in our study may have been a result of (i) the expansive nature of urban growth (urban cells developed in proximity to current urban cells, which limited the amount of urban boundaries and their edge effects), (ii) a lack of variables in our predictive models that varied with the spatial location of development (e.g. distance to the coast), and (iii) the fact that land development mostly occurred on forested vegetation. If development occurs on vegetation types with different quality for fauna, the location of development is likely to be relevant. Furthermore, spatial configuration effects are likely to increase in importance with continued urban sprawl because a lower proportion of the original landscape will remain (Haddad *et al*. 2015).

### IMPLICATIONS FOR URBANIZING FORESTED LANDSCAPES

Our findings add support to the notion that compact development (land sparing) is less damaging for biodiversity than dispersed development (land sharing) when controlling for housing demand (Gagne & Fahrig 2010b; Sushinsky *et al*. 2013; Soga *et al*. 2014). Furthermore, dispersed (exurban) development around cities and towns can severely affect not only forest-dependent fauna (Brown *et al*. 2014) but also species that use the urban environment (Caryl *et al*. 2016). Although overall abundance increased under dispersed urban growth, we showed this measure overlooked important changes to individual species' distributions and abundances, which are likely to change ecological interactions and could lead to unexpected cascading extinctions (Lindenmayer 2015).

Due to pervasive deforestation and forest fragmentation world-wide (Haddad *et al*. 2015), there is an urgent need for land-use policies (a top-down approach to development) to limit further change of forest ecosystems. In forest-dominated landscapes, urban growth policies encouraging compact rather than dispersed development can be less detrimental for urban-sensitive biodiversity and maintain both access to nearby nature and ecosystem services provision (Stott *et al*. 2015).

### CONCLUSIONS

What is the least damaging strategy of urban growth for forest-dwelling mammals? We found that compact urban growth minimized the change in the distribution and abundance of native mammals compared to dispersed urban growth. The area of occupancy of two small ground-dwelling mammals and the abundance of a tree-dwelling species (negatively affected by urban boundaries) were reduced under any kind of urban growth. However, compact development had less impact than dispersed development on these species because the land area modified was several (~22) times smaller under compact than under dispersed development. This limited the loss of forested cover and the amount of forest subject to negative edge effects from urban areas. We showed that in the face of urban development, measures of change focused on overall abundance may overlook important changes to individual species. In addition, we found that housing density was the main driver of change of mammal distribution and abundance.

Due to increasing evidence of the detrimental effects of dispersed development on forests and the biodiversity they sustain, we recommend that urban planning and urban growth policies: focus on urban-sensitive species rather than overall abundance, encourage compact rather than dispersed urban growth and avoid expansion of low-density housing developments into forested lands.

## Acknowledgements

## Data accessibility

This article does not contain new data. Data can be found in Appendix S3 and at www.ltern.org.au (Lindenmayer 2014).

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## Supporting Information

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

**Appendix S1.** Spatial autocorrelation.

**Appendix S2.** Methodological details.

**Table S1.** Mammal species and relevant ecological information.

**Table S2.** Moran's I autocorrelation index.

**Table S3.** Cells in natural land use available for urban development by vegetation type.

**Table S4.** Model selection for ground-dwelling mammals.

**Fig. S1.** Cells in natural land use located inside and outside protected areas.

**Appendix S3.** Data.