The relationship between wealth and biodiversity: A test of the Luxury Effect on bird species richness in the developing world

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Abstract

The Luxury Effect hypothesizes a positive relationship between wealth and biodiversity within urban areas. Understanding how urban development, both in terms of socioeconomic status and the built environment, affects biodiversity can contribute to the sustainable development of cities, and may be especially important in the developing world where current growth in urban populations is most rapid. We tested the Luxury Effect by analysing bird species richness in relation to income levels, as well as human population density and urban cover, in landscapes along an urbanization gradient in South Africa. The Luxury Effect was supported in landscapes with lower urbanization levels in that species richness was positively correlated with income level where urban cover was relatively low. However, the effect was reversed in highly urbanized landscapes, where species richness was negatively associated with income level. Tree cover was also positively correlated with species richness, although it could not explain the Luxury Effect. Species richness was negatively related to urban cover, but there was no association with human population density. Our model suggests that maintaining green space in at least an equal proportion to the built environment is likely to provide a development strategy that will enhance urban biodiversity, and with it, the positive benefits that are manifest for urban dwellers. Our findings can form a key contribution to a wider strategy to expand urban settlements in a sustainable way to provide for the growing urban population in South Africa, including addressing imbalances in environmental justice across income levels and racial groups.

KEYWORDS

detectability, income, population growth, socioeconomic development, South Africa, tree cover, urbanization

1 | INTRODUCTION

The proportion of the world's human population that lives in urban areas is now greater than that which lives in rural areas, a trend that is expected to continue (United Nations, 2015). Sustainable development of cities is one of the United Nations' key development goals for 2030 (United Nations, 2018a). Urban development can be considered both with respect to physical changes, in terms of the built environment, and to socio-economic advancement, in terms of the wealth of citizens. Usually urban and socioeconomic development increase in tandem (Sanderson et al., 2018). Generally, the development of the physical built environment that characterises urbanization is likely to conflict with biodiversity conservation (Czech, 2008). However, within urban areas there is actually considerable evidence that biodiversity measures correlate positively with socioeconomic status (e.g. Hope et al., 2003; Martin et al., 2004; Luck et al., 2009; Shanahan et al., 2014; Leong et al., 2016, 2018). This has been termed the 'Luxury Effect' (Hope et al., 2003), which posits that areas of greater wealth have relatively enhanced biodiversity compared to poorer areas in urban landscapes. Studies of biodiversity across spatial gradients in socioeconomic conditions may therefore give insights into how development may affect biodiversity through space-for-time substitutions, a common approach in urban ecological studies (McDonnell & Pickett, 1990; Bàtary et al., 2018).

Urbanization represents one of the most severe and irreversible forms of human impact (Grimm et al., 2008; Aronson et al., 2014; Sol et al., 2014). Paradoxically, however, increasing urbanization may also represent opportunities for environmental improvement due to positive influences of social progress. For example, greater social mobility, wealth creation and female empowerment may lower population growth rates, thus relieving pressure on resources, and increase educational standards, raising environmental consciousness in the urban human population (Sanderson et al., 2018). To fulfil this potential, urban areas need to grow sustainably, minimising harmful impacts before the future benefits can be realised (Sanderson et al., 2018). Urban biodiversity can provide a means by which the human population, often detached from everyday experiences of nature, can connect with and appreciate the wider benefits of biodiversity (Dunn et al., 2006), which include cultural (e.g. Fuller et al., 2007; Dearborn & Kark, 2009; Belaire et al., 2015) and environmental (e.g. Bolund & Hunhammar, 1999; Niemelä et al., 2010) ecosystem services. However, the opportunity to derive such benefits may vary according to socioeconomic status, typically leading to environmental injustice, when access to urban biodiversity is not equal across all social, economic and

cultural levels of the urban human population (e.g. Kinzig et al., 2005; Shanahan et al., 2014). There is therefore a need to understand how development (both physical and socioeconomic) impacts biodiversity in order to plan and manage sustainable urban landscapes in line with key development goals, including environmental justice for all urban dwellers.

The factors that affect urban biodiversity are complex and numerous (Faeth et al., 2011). However, many studies have found that socioeconomic variables are closely correlated with important habitat variables that likely drive urban biodiversity patterns, and that socioeconomic variables can be at least as good as habitat variables in explaining species diversity across urbanization gradients (Kinzig et al., 2005; Luck et al., 2009; Ackley et al., 2015; Magle et al., 2016). Whilst several studies have assessed variations in biodiversity patterns (mostly plants and birds) in relation to socioeconomic factors in urban areas, they have been almost exclusively conducted in single large cities within developed countries (e.g. Australia [Shanahan et al., 2014; Zivinovic & Luck, 2016], USA [Hope et al., 2003; Loss et al., 2009] and UK [Pauliet et al., 2005; Tratalos et al., 2007]). The evidence base is therefore overwhelmingly derived from relatively short socioeconomic gradients in single large cities that are also highly biased towards higher levels of socioeconomic development relative to the global range of conditions. No studies have considered animal biodiversity in relation to socioeconomic gradients in Africa (further details on the geographic context of the study are given in Appendix S1), even though it has the highest levels of people living in poverty (World Bank, 2018). Given that population growth rates are highest in the developing world, that 95% of urban expansion in the next decades will take place in the developing world (United Nations, 2018b), and that these regions hold the highest levels of biodiversity and poverty (Fisher & Christopher, 2007), it is essential that such studies exploring the influence of urbanization on biodiversity are undertaken in poorer, rapidly urbanizing areas where they are most needed. Furthermore, urbanization in terms of both expansion of the built environment and of human populations is as much linked to smaller towns and suburbs as it is to large cities (Christiaensen et al., 2013), hence a broader landscape-scale approach is needed to fully assess the link between socioeconomic development and biodiversity.

We analysed native bird species richness as an indicator of wider impacts of urbanization on biodiversity (Blair, 1999; Alberti, 2005) across gradients characterized by different levels of physical and socioeconomic development in a large sample of landscapes representing a gradient of urbanization across

South Africa. South Africa is considered a developing economy (IMF, 2017) and has amongst the highest levels of income inequality in the world (Leibbrandt et al., 2010), from rich 'westernized' urban areas with highly developed infrastructure to slum areas subject to extreme poverty (Appendix S1). This range of conditions therefore presents an opportunity to assess the link between socioeconomic levels and biodiversity across a gradient of urban development at a landscape scale. Furthermore, we consider three potential development measures, socioeconomic status, urbanization and population density, in order to test their independent effects on biodiversity along the gradient considered, as well as any interactions between them.

There were two specific objectives: (i) to test for the Luxury Effect by analysing the relationship between native bird species richness and income level in urbanized landscapes in South Africa (Fig. 1), and how this relationship is mediated by other key components of development, specifically human population density and level of urbanization; (ii) to assess a potential biological driver of any such Luxury Effect by analysing the relationship between vegetation cover and species richness, and vegetation cover and development variables. In particular, we expect that the Luxury Effect should be explained, at least in part, by greater tree cover in wealthier areas, as found in a number of other studies (Gerrish & Watkins; 2018). Our work improves our understanding of how development can affect urban biodiversity and associated environmental justice. Such an understanding can help to develop strategies that contribute to the successful achievement of development goals.

2 | MATERIALS AND METHODS

2.1 | Bird data

Bird species richness estimates were derived using data from the second South African Bird Atlas Project (SABAP2; http://sabap2.adu.org.za/), an ongoing citizen science programme whereby volunteer observers record the presence of all species detected during timed visits to 5 min longitude x 5 min latitude grid cells ('pentads' of approximately 9 x 9 km). We did not include exotic species as they can show different responses to socio-economic status (Loss et al., 2009), and because it was questionable whether many exotic species (especially wildfowl which made up a large proportion of non-natives) could be considered as being in a wild state. Furthermore, native species are considered the priority (compared to exotic species) in terms

of retaining the biological distinctiveness of urban areas, and of promoting wider conservation goals (McKinney 2006). We therefore consider only native species richness (although for brevity, we henceforth refer to this as species richness). Multiple visits are usually carried out to each pentad, hence the species recorded are based on a variable effort in terms of both time spent per visit (mean ± SD = 160 ± 90 min) and in terms of the number of atlas cards (a species list made on each visit) per pentad (further details in Appendix S2). Observers are given specific instructions to visit as many habitats as possible, in order that the bird data are representative of the whole pentad. Eleven specific habitats are listed in the instructions that should be particularly targeted, including urban and suburban environments (Harebottle et al., 2008).

2.2 | Selection of study areas

Urban areas were identified using the South African National Land-Cover Dataset from 2013-14 (Department of Environmental Affairs, 2015), which categorizes 30m x 30m raster grid cells into dominant land-cover classes ("parent" classes) and several land cover types using multi-seasonal Landsat 8 imagery. We focussed on the "urban" parent class, which was defined as the following land use types: industrial, commercial, informal settlement, residential, schools & sports, small-holding, sports/golf, township, village and city. The total area of urban land was calculated by summing the area of urban parent class grid cells (i.e. the aforementioned land use types) for each pentad. This value was then divided by the total land area in a pentad to give the proportion covered by urban land (henceforth referred to as 'urban cover'). This was used to select pentads for analysis (as a categorical variable – see below), and to model effects of urbanization on native bird species richness.

To select pentads for the analysis, three urbanized land-cover subclasses were defined based on the urban cover: peri-urban (5-20% urban), suburban (21-50% urban) and urban (>50% urban). Pentads with < 5% urban cover were not included. The focus of the study was on larger urban landscapes which showed a degree of variation in the level of urbanization. Within our classification, we therefore selected peri-urban pentads that were adjacent to at least one other pentad of a different urban land-cover sub-class (i.e. either suburban or urban; Fig. 1 and Fig. S1) to ensure that pentads were sampled from larger urban landscapes, rather than small, relatively isolated rural settlements.

FIG1XXX

2.3 | Quantifying development

Household income levels are commonly used in studies of socioeconomic data and provide the most direct test of the Luxury Effect (Leong et al., 2018). We derived our socioeconomic measures of median annual household income (in South African Rands, where 1R was equivalent to c. US$0.15 in 2011; http://www.x-rates.com/historical/?from=USD&amount=1&date=2011-06-01), and population density from the 2011 South African National Population Census (Statistics South Africa, 2012), in which approximately 15 million households were surveyed (data available at www.statssa.gov.za). These data were selected to match the time period as closely as possible to the bird data (2013-14). The lowest spatial resolution of the data was a small area unit (85 907 polygons for South Africa, where a polygon was a variable sized small area unit containing c. 200 households), and median household income per pentad was derived as the median proxy income value for all small area units with their polygon centroid located within a pentad. Median income was closely associated with a range of other socioeconomic variables derived from the same census data (Fig. S3) and can be considered as a proxy measure for socioeconomic status. Human population density, which was also obtained from the 2011 census data (Statistics South Africa, 2012), was the total number of individuals across all small area units within a pentad. It was included in our analysis to account for those urban pentads that were mostly associated with commercial and industrial properties (i.e. with few residents). Median income across the pentads varied between R14 010 and R443 500 (between US$2 102 and US$66 525, median = R27874, US$4182), and population density between 1 and 6885 inhabitants per km^2 (median = 337). Both variables were log-transformed prior to analysis. Urban cover (i.e. proportion of land in the urban parent class) was used as our measure of urbanization (as per Suri et al., 2017) in the analysis to account for effects of urbanization on biodiversity and varied across the pentads from 6% to 82% (median = 24.6%).

2.4 | Vegetation data

Vegetation cover has been shown to significantly influence bird communities in urban landscapes (Fernández-Juricic, 2004; Nielsen et al., 2014). The percentage tree cover was used as a proxy for general

vegetation cover as it was strongly correlated with NDVI, a measure of general 'greenness' ($r_{383} = 0.86$, $p < 0.0001$), it is an element that can be managed (e.g. planting and maintenance of street trees; Kuruneri-Chipeto & Shackleton, 2011), and it has been shown to be positively correlated with socioeconomic status in urban areas (e.g. Kardan et al., 2015; Gerrish & Watkins, 2018), including in South Africa (Gwedla & Shackleton, 2017). Tree cover was therefore assumed a likely driver of bird communities and a potential mechanism for the Luxury Effect. Tree cover was extracted from the Global Land Cover Facility – Landsat Tree Cover dataset at a 30m resolution (Sexton et al., 2013) and was summed for each pentad.

2.5 | Analytical approach

Citizen-science data are challenging to analyse because the observation process has to be taken into account in order to minimize bias (Altwegg & Nichols, 2019). In addition to carefully designed methods, the analysis should include adequate data screening and use of analytical techniques such as occupancy modelling in order to reduce biases typical of citizen-science surveys (Isaac et al., 2014; Altwegg & Nichols, 2019). To screen the data, we first removed pentads that only had single visit atlas cards, pentads without corresponding socioeconomic or land cover data, and pentads that had land cover estimates for <75% of the total area (e.g. to remove those with large areas of unknown land cover), leaving a final sample size of 3233 atlas cards for analysis from 385 pentads (180 peri-urban, 144 suburban, 61 urban) from 22 metropolitan areas (Table S1). In order to avoid bias towards hyper-sampled sites (the range of atlas cards considered was from 2 – 650 per pentad) and to minimize the likelihood of the closure assumption being violated in occupancy models (see below), we first limited the number of atlas cards analysed per pentad by randomly selecting a maximum of 11 atlas cards (equal to the median number) per pentad (Appendix S3). This step was necessary to avoid bias in overall likelihood estimates of detection and occupancy probabilities (and hence species richness) which may be strongly weighted towards hyper-sampled pentads. Within the range considered (i.e. 2 to 11 cards), there was no obvious relationship between estimates of species richness and number of cards used in the analysis, so although uncertainty around species richness was generally lower with more cards, it is unlikely that the variable number of surveys introduced substantial bias into our quantification of mean species richness for each pentad (Appendix 3, Fig. S4).

We then used a two-step approach to explore the relationship between avian species richness and socioeconomic variables across a landscape gradient ranging from highly urbanized areas to peri-urban areas with a relatively low urban cover. First, we used a multi-species occupancy model in a Bayesian framework to estimate species richness on the pentad scale while accounting for imperfect detection in the atlas data (Dorazio & Royle, 2005; Dorazio *et al*., 2006; Kéry & Royle, 2016). In a separate model, we then analysed the relationship between the derived species richness from the first model and a set of covariates in order to test for an association with income (i.e. the Luxury Effect), and of urban cover and population density.

We jointly estimated detection and occupancy probability of each species in a hierarchical manner. The description of the ecological process underlying the latent state of occurrence (presence or absence) z_{ik} of species *k* in pentad *i* is modelled as a Bernoulli random variable,

$$z_{ik} \sim \text{Bernoulli}(\psi_{ik}),$$

where ψ_{ik} is the occupancy probability of species *k* in pentad *i*. The observation process is modelled as another Bernoulli random variable such that the observed detection/non-detection data, y_{ijk}, given the true presence or absence of a species z_{ik} is represented as

$$y_{ijk}|z_{ik} \sim \text{Bernoulli}(z_{ik} * p_{ijk}),$$

where p_{ijk} is the probability of detecting species *k* in pentad *i* during atlas card *j*. We sought to model species-specific relationships of both occupancy and detection and so included species identity as a random effect.

We modelled detection probability as a function of two covariates associated with each atlas card (Julian day and survey duration) and one pentad level covariate, road density (as mean number km/pentad derived in ArcMap 10.4 from gRoadsV1, 2013), which is an important predictor of sampling effort (Hugo & Altwegg, 2017). Given that Julian day is a circular variable (i.e. values of 1 and 365 are more similar than 180), we converted this variable to radians. First, we created an angle equal to Julian day/365*360. We then took that angle and converted to radians by applying the formula cos(π*Julian day angle/180). This gave a

value between 1 and – 1 where positive values corresponded to summer months and negative values to winter months. We used species random effects for both the intercept and slope parameters (β) yielding the equation:

$$\text{logit}(p_{ijk}) = \text{lp}_\text{k} + \beta_{1\text{k}} * \text{JulianDay} + \beta_{2\text{k}} * \text{RoadDensity} + \beta_{3\text{k}} * \text{SurveyDuration}$$

To calculate species richness in a pentad, we summed the z_{ik} values for each pentad. After running the occupancy models, we extracted the estimated species richness and associated measure of uncertainty for each pentad. We used the Bayesian modelling software JAGS 4.2.0 (Plummer, 2003) called through the *jagsUI* R package (Kellner, 2016). We ran 3 chains of 10 000 Markov Chain Monte Carlo (MCMC) iterations, each with a burn-in period of 2 000 iterations. Samples where thinned at a rate of 2. We used uninformative priors from the uniform distribution bounded by 0 and 1 for all occupancy parameters and normal distributions for covariate parameters. Initial values for parameters were chosen at random. In order to assess MCMC chain convergence, we used a combination of diagnostic traceplots and the Gelman-Rubin statistic (Gelman &Hill, 2007), where values < 1.1. indicate convergence. Covariates were standardised prior to input into models.

South Africa shows marked geographical trends in species richness, which is likely a consequence of a range of environmental variables (e.g. climate, topography, altitude and vegetation). Regional species pools are therefore likely to vary in composition and richness according to geographic location, resulting in spatial autocorrelation among sample pentads. We accounted for this background geographical effect by using distance-based Moran's eigenvector maps (MEMs; Dray et al., 2006, 2012), representing spatial structures at multiple scales, to generate spatial predictor variables across the selection of pentads. The MEMs provide a decomposition of the spatial structure and relationships between each of the sample pentads. MEMs were modelled in a separate step prior to the main model, following which, four MEMs representing the broad-scale variation were included in the final modelling procedure to account for spatial effects (see Appendix S3 for derivation of spatial variables).

We then fitted a linear regression to model the effects of median income (IncMed), urban cover (UrbCov), population density (PopDen), spatial structure (MEMs 1- 4) and the interaction between income

and urban cover on estimated species richness. The full model estimating species richness (*N*) included all single-term covariates and the interaction between income and urban cover and can be written as

$$N = \beta_0 + \beta_1 * \text{IncMed} + \beta_2 * \text{UrbCov} + \beta_3 * \text{PopDen} + \beta_4 * \text{MEM1} + \beta_5 * \text{MEM2} + \beta_6 * \text{MEM3} + \beta_7 * \text{MEM4} + \beta_8 * \text{IncMed} * \text{UrbCov}$$

We confined the analyses to linear covariate effects. There was no evidence that non-linear covariates or more complex interactions provided a better model fit (Appendix 3), hence we adopted a parsimonious approach and based our inference on the simplest model possible. Potential effects of collinearity amongst predictor variables were examined by calculating Variance Inflation Factors (VIFs) using the AED package (Zuur et al., 2009). There was no evidence of strong collinearity (VIFs < 3.0). Inspection of diagnostic plots indicated that the species richness models had a good fit in that residuals were normally distributed with fairly constant variance across the range.

We used an AIC model selection approach (Burnham & Anderson, 2002) to evaluate the strength of several candidate models based on different combinations of socioeconomic covariates in the full model. The best model set was defined as those models within 2 AIC units of the best ranked model (i.e. ΔAIC $\leq$ 2). Spatial variables accounting for large-scale geographical patterns and hence spatial autocorrelation were included as constant in all models. We then carried out the same approach substituting tree cover for socioeconomic variables and their interactions to explore which variable has most explanatory power with respect to species richness. Finally, we added tree cover to the full socioeconomic model (above) to determine whether it had additive effects (hence decreasing ΔAIC).

3 | RESULTS

3.1 | Evidence for a Luxury Effect in South African birds

There was a single best model (ΔAIC = 7.38) that accounted for 95% of the total model weight (Table1), and which included population density, median income, urban cover, and the interaction between median income and urban cover (Table 1). Bird species richness was negatively associated with urban cover , but there was no evidence for an association with human population density (Fig. 2). There was no strong evidence of the

Luxury Effect when considering median income alone – the beta coefficient was positive, but confidence limits overlapped zero (Fig. 2). Importantly, however, the significant interaction showed that species richness increased with income level in less urbanized areas (i.e. when urban cover was relatively low), but that the opposite occurred in highly urbanized areas (Fig. 3). In other words, high income, relatively less urbanized, areas had the highest species richness, whilst similarly wealthy, but highly urbanized, areas had the lowest species richness. In contrast, species richness was less markedly affected by urbanization in poorer areas, which showed relatively little variation in species richness, and which was generally low compared to richer areas in all but the most urbanized pentads (Fig. S6). There were also significant spatial effects, indicating that species richness was spatially structured at very broad scales (Appendix S3). This makes sense given that the broad scale geographic gradients cover several different biomes with different avifaunal communities (Fig. 1, Fig. S5). The model with only spatial effects and median income performed poorly (ΔAIC = 25.74), showing that effects of income are not strongly evident without accounting for urbanization level in South African urban landscapes.

FIG2XXX

FIG3XXX

An alternative representation of the significant interaction between urbanization level and median income is given in Fig. 4, which shows the linear effect of median income on species richness at four different levels of urban cover. At low levels of urbanization, species richness increases with median income, but increasing urbanization affects this relationship. There is no relationship (i.e. slope = 0) at approximately 38% urban cover (see also Fig. S5), after which the relationship becomes negative, hence the Luxury Effect is only supported below this threshold.

FIG4XXX

3.2 | The effect of tree cover on urban bird species richness

Tree cover had similar effects to median income when substituted for it in the best ranked model in Table 1, i.e. a positive effect (albeit significant this time) and a significant interaction with urban cover (Fig. S7). This model was equivalent to that for median income (ΔAIC = 0.40). Moreover, adding tree cover to the other variables in Table 1 resulted in an improved model fit (ΔAIC = 3.64; Table S4, Fig. S8), suggesting that both the interactive effect of median income and urban cover, and tree cover, are important predictors of bird species richness across our sample of pentads. This model explained 16% of variation in the data. Notably, there was a negative (though relatively weak) correlation between median income and tree cover (r = -0.14, p < 0.01), and VIFs in this model were low (< 3.0). There was no correlation between tree cover and either urban cover (r = -0.08, p = 0.12) or population density (r = -0.02, p = 0.63). The result in Fig. 3 therefore cannot therefore be explained by a relationship between income and tree cover – rather, tree cover has independent additive effects on species richness. A Luxury Effect mediated through an interaction with urban cover is therefore still supported when accounting for a key potential ecological driver of urban biodiversity.

4 | DISCUSSION

At the landscape scale considered (*c*. 9km X 9km), there was no strong support for a Luxury Effect on native South African bird species richness when considering effects of median income alone. However, there was evidence that the Luxury Effect was mediated by an interaction with the level of urbanization: species richness increased as income level increased, but only in areas with relatively low levels of urbanization. As landscapes became more urbanized, the effect became negative; the lowest species richness was in highly urbanized, rich areas.

Our findings imply that within South Africa, socioeconomic development will increase biodiversity initially, but as urbanization increases, the effect of socioeconomic development flips and becomes negative. Our model suggests that the point at which development of the built environment has negative impacts on biodiversity is 38% urban cover (Fig. 4). In our sample, these more urbanized areas comprised a total of 100 out of 385 pentads (26%; Fig. S2). Thus, for 74% of the sampled sites in this study, there was broad support

for the Luxury Effect. Nevertheless, the results show that continued urbanization is likely to negate any positive effects of socioeconomic status on biodiversity due to effects of increasing urban cover. Our third measure of development, population density, did not have any effect on biodiversity. If urbanization increases without concomitant increases in socioeconomic status, then the richest areas will only experience negative effects, whereas the poorest areas will see little change in biodiversity, which will remain relatively low. On average, therefore, there is evidence of environmental injustice in urban South Africa in that poor areas have lower average biodiversity. Furthermore, within South Africa, this is also divided along racial grounds – poorer areas, with a higher proportion of black households and a lower proportion of white households (Fig. S3), had lower bird diversity.

The lack of a clear effect of urbanization in poorer areas is surprising, but may be related to more intensive management of non-urban land for subsistence in poor rural areas (i.e. management to maximize production and minimise impacts of weeds and herbivorous invertebrates), and possibly even localised hunting of wild birds for food (e.g. McGarry 2008). Within South Africa, there is support for a Luxury Effect on vegetation species richness, but this is largely driven by an increase in alien and often ornamental species in affluent, white racial group-dominated areas (Kuruneri-Chipeto & Shackleton, 2011; Davoren et al., 2016; Gwedla & Shackleton, 2018). In contrast, utilitarian plants that provide food and medicine predominate in poorer areas that are mainly populated by African and Coloured racial groups (Lubbe et al., 2010; Davoren et al., 2016). Given the investment in utilitarian plants as a means to provide sustenance and additional income to households in conditions of high job insecurity (Lubbe et al., 2010), allied with possible cultural differences in vegetation management (as found elsewhere; Clarke & Jenerette 2015), it seems likely that vegetation will be managed more intensively and hence has the potential to be less species rich compared to that in wealthier areas which may be largely managed for aesthetic reasons. This in turn may have effects on higher trophic levels, including birds.

Two of the main mechanisms proposed to explain the Luxury Effect are: a greater investment in management of vegetation (both public and private) in richer areas; and, a greater demand for housing in greener and more biodiverse areas which thus increases property prices (Leong *et al*. 2018). These are not mutually exclusive. In both cases, the Luxury Effect for birds would be driven by a cascading effect of enhanced plant communities in wealthier areas (e.g. Lermann & Warren, 2011; Luck et al., 2013). However,

although tree cover was significantly related to bird species richness, we found no evidence to suggest that this was underpinning the Luxury Effect observed for South African birds: our income-urban cover interaction term still contributed to variation in species richness, even after accounting for tree cover. We had limited data at our disposal to fully test the mechanisms that might underpin the Luxury Effect. Nevertheless, this result is interesting given the importance of trees for urban biodiversity in general. Furthermore, the fact that there are additive effects of wealth and tree cover suggests that enhancing tree cover in urban areas can have additional effects to other benefits of socioeconomic development on biodiversity.

We have used a large sample of urbanized South African landscapes to provide the first test of the Luxury Effect on African bird species richness. Whilst we believe our results provide important insights into potential impacts of socioeconomic and physical development, there are nevertheless some caveats on the interpretation of the results. First, in common with the vast majority of Citizen Science-based atlas data, we do not know the precise locations surveyed for any given visit within a pentad, so the extent to which systematic biases in observer behaviours may have affected the results remains unknown. However, we know that urban areas were amongst the habitat specifically targeted (Harebottle et al., 2008) and that there is a general bias in coverage towards urban areas (Hugo & Altwegg, 2017), so we believe that even in peri-urban pentads, urban coverage is likely to have been adequate. Furthermore, although we cannot control for spatial effort, we did control for the effort in terms of the number of cards submitted and the time spent surveying. Second, our measure of human population density was based on where people were resident, so industrial but highly urbanized areas would likely have had a low population density. However, such areas may be temporarily highly populated during working periods, so potential effects of high human population density may not be fully taken into account by considering residential areas only. Nevertheless, we expect a more constant disturbance in residential areas. Furthermore, high urban – low population density pentads were uncommon (n = 24 in both the lower 25% quartile of population density and the upper 25% quartile of urban cover), hence we do not believe that this potential bias is likely to have greatly affected our outcomes.

We assessed spatial associations between bird species richness, and socioeconomic and physical variables, at a landscape scale. To what extent can this information be used to assess potential impacts of future development? It is often assumed that such inferences can be drawn using the gradient approach (i.e.

space-for-time substitution; McDonnell & Pickett, 1990). However, in terms of the two key development variables considered here, income and urban cover, there is as yet limited evidence that such gradient approaches can really be used as a basis for assessing future scenarios of urban and/or socioeconomic development. For example, we are unaware of any study that has explicitly tested the Luxury Effect over time in birds. However, in plants, there is evidence of a temporal Luxury Effect in terms of species richness peaking in periods of economic prosperity (Ripplinger et al., 2017), and also evidence that the strength of the relationship between income levels and vegetation cover increases over time (Jenerette et al., 2011). We believe that our results give sound general guidelines on how to introduce new settlements into urbanizing landscapes, and how such guidelines may be influenced by differing socioeconomic trends. However, we acknowledge that further research is needed, both in terms of long-term monitoring, and in terms of finer-scale studies, rather than the relatively large landscape scale (c. 9 x 9 km) used here. Furthermore, such studies should be replicated in other areas of the developing world in order to assess the extent to which the effects of socioeconomic status on biodiversity are evident in different geographical contexts.

Our findings have important implications in terms of designing new, sustainable, settlements for growing populations in developing countries. Indeed, sustainable cities and communities comprise one of the United Nations' key development goals for 2030 (United Nations, 2018a), which includes reduction of environmental impacts of cities, sustainable urbanization through planning and management, provision of affordable housing and upgrading slums, and provision of access to urban green space, all within the overall goal of universal and sustainable economic growth. Assuming development goals relating to improving poverty levels can be met (leading to increased socio-economic status), then to minimise harmful impacts on biodiversity, urban planning should maintain the level of urban cover below a level at which negative associations were seen. Using our threshold of 38% as a general guide, we suggest that development should strive to maintain an urban cover of lower than 50% at the landscape scale considered here in order to achieve sustainable urban development. Given that population density did not have negative effects in our analyses (but see above), this could be achieved by high density housing (e.g. apartment blocks) within a matrix of green space that could enhance opportunities for improvement of the social and environmental quality of the urban environment (e.g. recreation areas, communal gardens, urban nature reserves). It seems likely that initiatives such as increasing tree cover (Fernández-Juricic, 2004; Nielsen et al., 2014) and the

proportion of native rather than exotic plants (Dures & Cumming, 2010) would improve the value of any such green spaces in an urban context. Whilst the variation in avian species richness explained by our model was relatively high for a large-scale ecological study, it also suggests much unexplained variation that may, at least in part, have been caused by fine-scale habitat features other than tree cover within our urban landscapes which we were unable to measure.

We acknowledge that planning new urban development needs to take into account the biodiversity value of the land on which development takes place (e.g. Geschke et al., 2018), as well as social aspects that can benefit local communities and hence further address additional key development goals for Sustainable Cities and Communities. However, given the widely acknowledged benefits of green space for urban dwellers (Fuller et al., 2007; Dearborn & Kark, 2009; Belaire et al., 2015), we see our findings as a key part of any wider strategy to plan expanding urban settlements in a sustainable way, including addressing imbalances in environmental justice across income levels and racial groups.

ACKNOWLEDGEMENTS

We thank the Animal Demographic Unit and UCT for coordinating the SABAP surveys and data collection. We also thank all the volunteer citizen scientists who contributed data to SABAP. We are grateful to Res Altwegg for statistical discussions, to Péter Bàtary and Simon Gillings who provided constructive criticisms on an earlier version of this manuscript, and to Marta Szulkin and three anonymous referees for their suggested revisions. Finally, we are grateful to Dr James Waters for supplying the image in Fig. 3c.

REFERENCES

Ackley J.W., Jianguo Wu J., Angilletta M.J. Jr., Myint S.W., Sullivan, B. (2015). Rich lizards: How affluence and land cover influence the diversity and abundance of desert reptiles persisting in an urban landscape. Biological Conservation, 182, 87–92.

Alberti M. (2005). The effects of urban patterns on ecosystem function. International Regional Science Review, 28, 168-192.

Altwegg R., Nichols J.D. (2019). Occupancy models for citizen-science data. Methods in Ecology and Evolution in press. DOI: 10.1111/2041-210X.13090

Aronson M.F.J., La Sorte F.A., Nilon C.H., Katti M., Goddard M.A., Lepczyk C.A., Warren P.S., Williams N.S.G, Cilliers S., Clarkson B., Dobbs C., Dolan R., Hedblom M., Klotz S., Kooijmans J.L., Kühn I., MacGregor-Fors I., McDonnell M., Mörtberg U., Pyšek P., Siebert S., Sushinsky J., Werner P., Winter, M. (2014). A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proceedings of the Royal Society of London B, 281, 20133330.

Bàtary P., Kurucz K., Suarez-Rubio M., Chamberlain D. (2017). Non-linearities in bird responses across urbanization gradients: A meta-analysis. Global Change Biology, 24, 1046-1054.

Belaire J.A., Westphal L.M., Whelan C.J., Minor E.S. (2015). Urban residents' perceptions of birds in the neighborhood: Biodiversity, cultural ecosystem services, and disservices. Condor, 117, 192-202.

Blair R.B. (1999). Birds and butterflies along an urban gradient: Surrogate taxa for assessing biodiversity? Ecological Applications, 9, 164-170.

Bolund P., Hunhammar S. (1999). Ecosystem services in urban areas. Ecological Economics, 29, 293-301.

Burnham, K.P. & Anderson, D.R. (2002). Model Selection and Multimodel Inference. A Practical Information-theoretic Approach, 2nd edn. New York: Springer-Verlag.

Christiaensen L., De Weerdt J., Todo Y. (2013). Urbanization and poverty reduction: The role of rural diversification and secondary towns. Agricultural Economics, 44, 435-447.

Clarke L.W., Jenerette G.D. (2015). Biodiversity and direct ecosystem service regulation in the community gardens of Los Angeles, CA. Landscape Ecology, 30, 637–53.

Czech B. (2008). Prospects for reconciling the conflict between economic growth and biodiversity conservation with technological progress. Conservation Biology, 22, 1389-1398.

Davoren E., Siebert S., Cilliers S., Du Toit M.J. (2016). Influence of socioeconomic status on design of Batswana home gardens and associated plant diversity patterns in northern South Africa. Landscape and Ecological Engineering, 12, 129–139.

Dearborn D.C., Kark, S. (2009). Motivations for conserving urban biodiversity. Conservation Biology, 24: 432-440.

Department of Environmental Affairs (2015). 2013-14 National Land-Cover -72 Classes. Pretoria, South Africa: Department of Environmental Affairs.

Dorazio R.M., Royle J.A. (2005). Estimating size and composition of biological communities by modeling the occurrence of species. Journal of the American Statistical Association, 100, 389–398.

Dorazio R.M., Royle J.A., Söderström B., Glimskär A. (2006). Estimating species richness and accumulation by

modeling species occurrence and detectability. Ecology, 87, 842–854.

Dray S., Legendre P., Peres-Neto, P.R. (2006). Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). Ecological Modelling, 196, 483–493.

Dray S., Pélissier R., Couteron P., Fortin M.J., Legendre P., Peres-Neto P.R., Bellier E., Bivand R., Blanchet F.G., De Cáceres M., Dufour A.B. (2012). Community ecology in the age of multivariate multiscale spatial analysis. Ecological Monographs, 82, 257-275.

Dunn R.R., Gavin M.C., Sanchez M.C., Solomon J.N. (2006). The Pigeon Paradox: Dependence of global conservation on urban nature. Conservation Biology, 6, 1814-1816.

Dures S.G., Cumming G. S. (2010). The confounding influence of homogenising invasive species in a globally endangered and largely urban biome: Does habitat quality dominate avian biodiversity? Biological Conservation, 143, 768-777.

Gelman A., Hill, J. (2007). Data Analysis using Regression and Multilevel Hierarchical Models. New York: Cambridge University Press.

Gerrish E., Watkins S.L. (2018). The relationship between urban forests and income: A meta-analysis. Landscape and Urban Planning, 170, 293-308.

Geschke A., James S., Bennet A.F., Nimmo, D.G. (2018). Compact cities or sprawling suburbs? Optimising the distribution of people in cities to maximise species diversity. Journal of Applied Ecology, 55, 2320-2331.

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.

Gwedla N., Shackleton C.M. (2017). Population size and development history determine street tree distribution and composition within and between Eastern Cape towns, South Africa. Urban Forestry and Urban Greening, 25, 11-18.

Faeth S.H., Bang C., Saari, S. (2011). Urban biodiversity: patterns and mechanisms. Annals of the New York Academy of Sciences, 1223, 69–81.

Fernández-Juricic E. (2004). Spatial and temporal analysis of the distribution of forest specialists in an urban-fragmented landscape (Madrid, Spain): Implications for local and regional bird conservation. Landscape and Urban Planning, 69, 17-23.

Fisher B., Christopher, T. (2007). Poverty and biodiversity: Measuring the overlap of human poverty and the biodiversity hotspots. Ecological Economics, 62, 93-101.

Fuller R.M., Irvine K.M., Devine-Wright P., Warren P.H., Gaston K.J. (2007). Psychological benefits of greenspace increase with biodiversity. Biology Letters, 3, 390-394.

gRoadsV1 Center for International Earth Science Information Network (CIESIN)/Columbia University, and Information Technology Outreach Services (ITOS)/University of Georgia. 2013. Global Roads Open Access Data Set, Version 1 (gROADSv1). Palisades, NY: NASA Socioeconomic Data and Applications Center (SEDAC). Downloaded from http://sedac.ciesin.columbia.edu/data/set/groads-global-roads-open-access-v1

Harebottle D., Smith N., Underhill L.G., Brooks D. (2008). Southern African Bird Atlas Project 2. Instruction Manual. 1st Edition, updated. BirdLife South African, Animal Demography Unit, and South African National Biodivresity Unit.

Hope D., Gries C., Zhu W., Fagan W.F., Redman C.L., Grimm N.B., Nelson A.L., Martin C., Kinzig A. (2003). Socioeconomics drives urban plant biodiversity. Proceedings of the National Academy of Science USA, 100, 8788-8792.

Hugo, S. & Altwegg, R. (2017). The second Southern African Birds Atlas Project: Causes and consequences of geographical sampling bias. *Ecol. Evol.* 7, 6839-6849.

IMF (2017). https://www.imf.org/en/Publications/WEO/Issues/2017/04/04/world-economic-outlook-april 2017# Statistical Appendix Accessed 28/2/2018

Isaac N., van Strien A.J., August T.A., de Zeeuw M.P., Roy D.B. (2014). Statistics for citizen science: extracting signals of change from noisy ecological data. Methods in Ecology and Evolution 2014, 1052–1060.

Jenerette, G.D., Harlan, S.L., Stefanov, W.L., Martin, C.A. (2011). Ecosystem services and urban heat riskscape moderation: water, green spaces, and social inequality in Phoenix, USA. Ecological Applications, 21, 2637-2651.

Kardan O., Gozdyra P., Misic B., Moola F., Palmer L.J., Paus T., Berman M.G. (2015). Neighborhood greenspace and health in a large urban center. Scientific Reports, 5, 11610.

Kellner K. (2016). jagsUI: A Wrapper Around “rjags” to Streamline “JAGS” Analyses. R package version 1.4.4. https://cran.r-project.org/package=jagsUI. in press.

Kéry, M., Royle, J. A. (2016). Hierarchical Models for Communities. In: M.J. Kéry & J.A. Royle (Eds.), Applied Hierarchical Modeling in Ecology (pp. 631–728). New York: Academic Press,

Kinzig A., Warren P., Martin C., Hope D., Katti, M. (2005). The effects of human socioeconomic status and cultural characteristics on urban patterns of biodiversity. Ecology and Society, 10: 23.

Kureneri-Chitepo C., Shackleton C.M. (2011). The distribution, abundance and composition of street trees in selected towns of the Eastern Cape, South Africa. Urban Forestry and Urban Greening, 10, 247-254.

Leibbrandt M., Woolard I., Finn A., Argent, J. (2010). Trends in South African Income Distribution and Poverty since the Fall of Apartheid, OECD Social, Employment and Migration Working Papers, No. 101. Paris, France: OECD Publishing.

Leong M., Bertone M.A., Bayless K.M., Dunn R.R., Trautwein M.D. (2016) Exoskeletons and economics: indoor arthropod diversity increases in affluent neighbourhoods. Biology Lettres, 12: 20160322.

Leong M., Dunn R.R., Trautwein M.D. (2018). Biodiversity and socioeconomics in the city: A review of the Luxury Effect. Biology Letters, 14: 20180082.

Lerman S.B., Warren P.S. (2011). The conservation value of residential yards: linking birds and people. Ecological Applications, 21, 1327–1339.

Loss S.R., Ruiz M.O., Brawn J.D. (2009). Relationships between avian diversity, neighborhood age, income, and environmental characteristics of an urban landscape. Biological Conservation, 142, 2578-2585.

Lubbe C.S., Siebert S.J., Cilliers S.S. (2010). Political legacy of South Africa affects the plant diversity patterns of urban domestic gardens along a socio-economic gradient. Scientific Research and Essays, 5, 2900-2910.

Luck G.W., Smallbone L.T., O'Brien R. (2009). Socioeconomics and vegetation change in urban ecosystems: patterns in space and time. Ecosystems 12, 604-620.

Luck, G.W., Smallbone, L.T. & Sheffield, K.J. (2013). Environmental and socio-economic factors related to urban bird communities. Austral Ecology, 38, 111-120.

Magle S.B., Lehrer E.W., Fidino, M. (2016). Urban mesopredator distribution: examining the relative effects of landscape and socioeconomic factors. Animal Conservation, 19, 163-175.

Martin C.A., Warren P.S., Kinzig A.P. (2004). Neighborhood socioeconomic status is a useful predictor of perennial landscape vegetation in residential neighborhoods and embedded small parks of Phoenix, AZ. Landscape and Urban Planning, 69, 355-368.

McDonnell M.J., Pickett S.T.A. (1990) Ecosystem structure and function along urban-rural gradients: an unexploited opportunity for ecology. Ecology, 71, 232-1237.

McGarry D. (2008). The impact of HIV/AIDS on rural children's reliance on natural resources within the Eastern Cape, South Africa. Doctoral dissertation, Rhodes University, South Africa.

McKinney M.L. (2006). Urbanization as a major cause of biotic homogenization. Biological Conservation, 127, 247–260.

Nielsen A.B., van den Bosch M., Maruthaveeren S., van den Bosch C.K. (2014). Species richness in urban parks and its drivers: A review of empirical evidence. Urban Ecosystems, 17, 305-327.

Niemelä J., Saarela S.-R., Söderman T., Kopperoinen L., Yli-Pelkonen V., Väre S., Kotze D.J. (2010). Using the ecosystem services approach for better planning and conservation of urban green spaces: a Finland case study. Biodiversity and Conservation, 19, 3225–3243.

Pauliet S., Ennos R., Golding Y. (2005). Modeling the environmental impacts of urban land use and land cover change—a study in Merseyside, UK. Landscape and Urban Planning, 71, 295-310.

Plummer M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. Proceedings of the 3rd International Workshop on Distributed Statistical Computing, 124.

Ripplinger J., Collins S.L., York A.M., Franklin J. (2017). Boom–bust economics and vegetation dynamics in a desert city: How strong is the link? Ecosphere, 8, e01826.

Sanderson E.W., Walston J., Robinson J.G. (2018). From bottleneck to breakthrough: Urbanization and the future of biodiversity conservation. BioScience, 68, 412-426.

Sexton J.O., Song X.-P., Feng M., Noojipady P., Anand A., Huang C., Kim D.-H., Collins K.M., Channan S., DiMiceli C., Townshend J.R.G. (2013). Global, 30-m resolution continuous fields of tree cover: Landsat-based rescaling of MODIS Vegetation Continuous Fields with lidar-based estimates of error. International Journal of Digital Earth, 130321031236007.

Shanahan D.F., Lin B.B., Gaston K.J., Bush R., Fuller, R.A. (2014). Socio-economic inequalities in access to nature on public and private lands: A case study from Brisbane, Australia. Landscape and Urban Planning, 130, 14-23.

Sol D., González-Lagos C., Moreira D., Maspons J., Lapiedra O. (2014) Urbanization tolerance and the loss of avian diversity. Ecology Letters, 17, 942–950.

Statistics South Africa (2012). www.statssa.gov.za Accessed 22/2/2018

Suri J., Sumasgutner P., Hellard E., Koeslag A., Amar A. (2017). Stability in prey abundance may buffer Black Sparrowhawks *Accipiter melanoleucus* from health impacts of urbanization. Ibis, 159, 38-54.

Tratalos J., Fuller R.A., Evans K.L., Davies R.G., Newson S.E., Greenwood J.J.D. et al. (2007) Bird densities are associated with household densities. Global Change Biology, 13, 1685–1695.

United Nations (2015) World Urbanization Prospects: The 2014 Revision. United Nations, New York.

United Nations (2018a). www.un.org/sustainabledevelopment/sustainable-development-goals/). Accessed 25/7/2018

United Nations (2018b). www.un.org/sustainabledevelopment/cities/ Accessed 25/7/2018

World Bank (2018). https://commons.wikimedia.org/wiki/File:Countries_by_poverty_rate_world_bank_data.png#/media/File:Countries_by_poverty_rate_world_bank_data.png (accessed 25/7/2018).

Zivanovic A.J., Luck G.W. (2016). Social and environmental factors drive variation in plant and bird communities across urban greenspace in Sydney, Australian Journal of Environmental Management, 169, 210-222.

Zuur A.F., Ieno E.N., Walker N.J., Saveliev A.A., Smith G.M. (2009) Mixed Effects Models and Extensions in Ecology with R. Springer, New York.

TABLE 1 Results of the model selection procedure showing the top five best performing models, and the null model. Models are ranked in terms of AIC. The best model set was considered as those where ΔAIC < 2. Model weights (AICWt), cumulative model weights (Cum.Wt) and the number of estimable parameters (K) are also given. Spatial variables are represented in the table as 'MEM', comprising four separate variables (MEM1-4) which were included to capture large-scale geographic variation in bird species richness (Fig. S5). These were held constant in all models. MedInc = median income, PopDen = human population density, UrbCov = urban cover.

Model	**K**	**ΔAIC**	**AICWt**	**Cum.Wt**
MEM1 + MEM2 + MEM3 + MEM4 + UrbCov + PopDen + MedInc + UrbCov* MedInc	10	0.00	0.95	0.95
MEM1 + MEM2 + MEM3 + MEM4 + UrbCov	7	7.38	0.02	0.97
MEM1 + MEM2 + MEM3 + MEM4 + UrbCov + MedInc	8	8.59	0.01	0.98
MEM1 + MEM2 + MEM3 + MEM4 + UrbCov + PopDen	8	8.82	0.01	0.99
MEM1 + MEM2 + MEM3 + MEM4 + UrbCov + PopDen + MedInc	9	10.06	0.1	1.00
Null	2	44.02	0.00	1.00

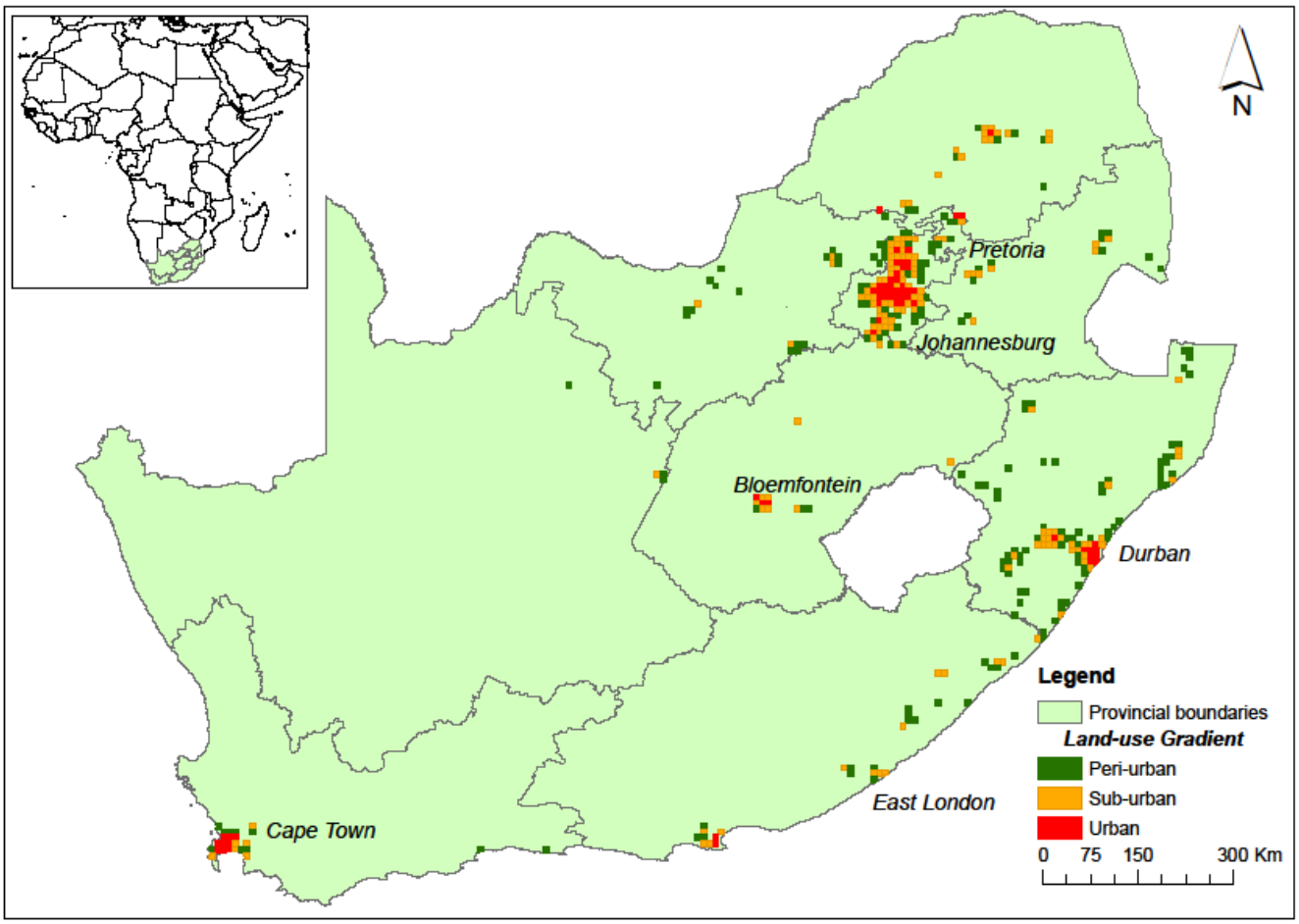
FIGURE CAPTIONS

FIGURE 1 Location of pentads contributing bird data to the analysis in South Africa (see inset top-left for geographical location within Africa). Pentads were defined into three subclasses: peri-urban (green, 5-20% urban cover), suburban (orange, 21-50% urban cover) and urban (red, >50% urban cover). See Fig. S1 for more detailed examples. Major cities (human population > 250,000 inhabitants) are also indicated.

FIGURE 2 Model outputs for the effects of median income (MedInc) human population density (PopDen), urban cover (UrbCov) and spatial structure (MEM1-4) on model-derived parameter estimates of bird species richness in South African urban landscapes. Beta coefficients and 95% Bayesian credible intervals for estimating the associations between bird species richness and median income, urban cover and their interaction, human population density, and spatial effects, are presented. Effects were considered significant when credible intervals of the estimate did not overlap zero.

FIGURE 3 Interactive effects of median income and urban cover on bird species richness (central panel), and examples of representative landscapes (outer panels). Estimated species richness was derived from the parameter estimates presented in Fig. 2, and incorporates detectability of individual species. Urban cover was expressed as the proportion of a pentad with land-cover types within the urban parent class. Median income is the log-transformed median household income, in Rands, at the pentad level. Note that analysis was performed on centred and scaled predictor variables, but they are presented here as unscaled, uncentred values to aid interpretation. Illustrated landscapes were high income, low urban cover (a), high income, high urban cover (b), low income, low urban cover (c), and low income, high urban cover (d). Italicised letters on the graph indicate approximate income and urban cover values that correspond to the images in the outer panels. Images supplied by Chevonne Reynolds (a, b and d) and Dr James Waters (c).

FIGURE 4 Alternative representation of the interactive effect of median income and urban cover on species richness, showing the response of species richness to income at different levels of urban cover. Median income is the log-transformed median household income, in Rands, at the pentad level. Note that analysis was performed on centred and scaled predictor variables, but they are presented here as unscaled, uncentred values to aid interpretation. The point at which the effect of urban cover on species richness switches from positive to negative (i.e. a slope of 0, indicated by the thin horizontal line) was 38%.



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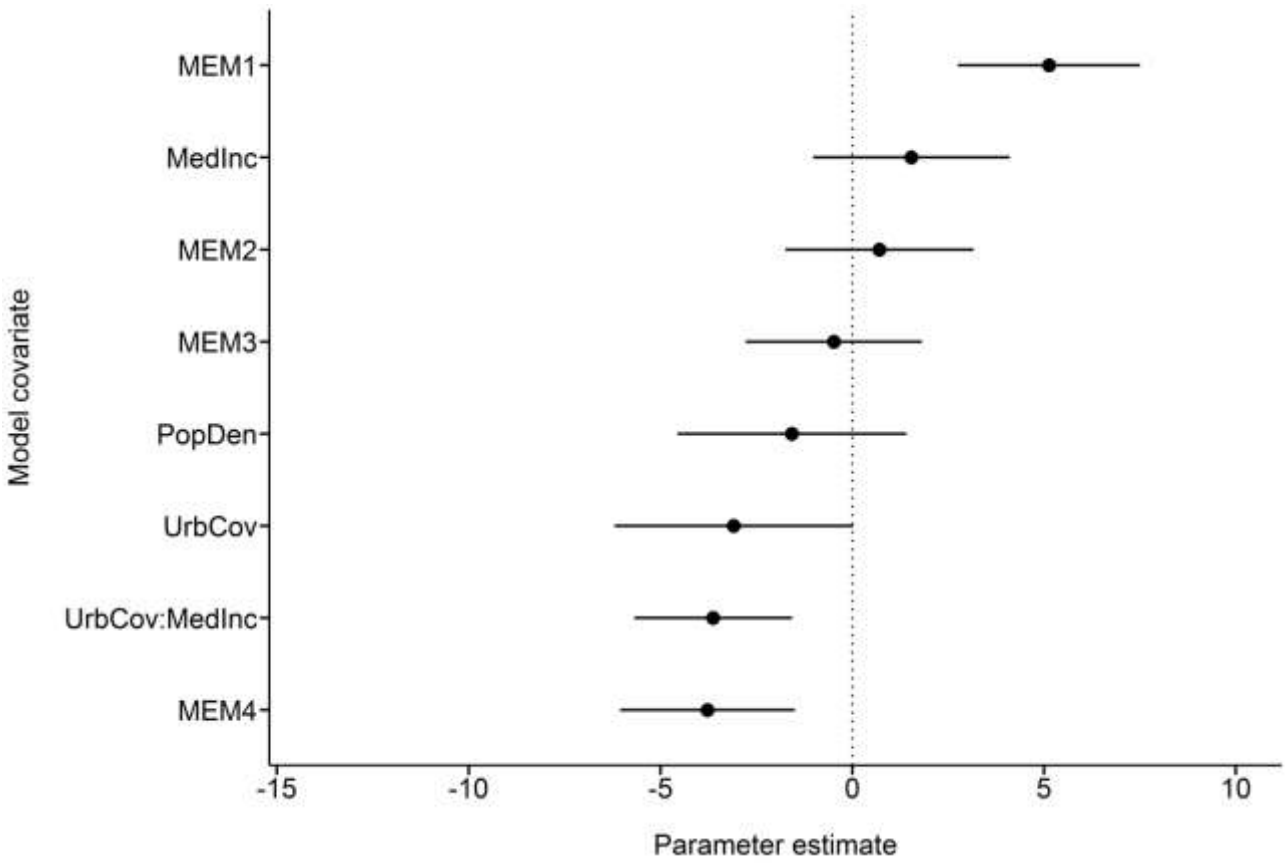

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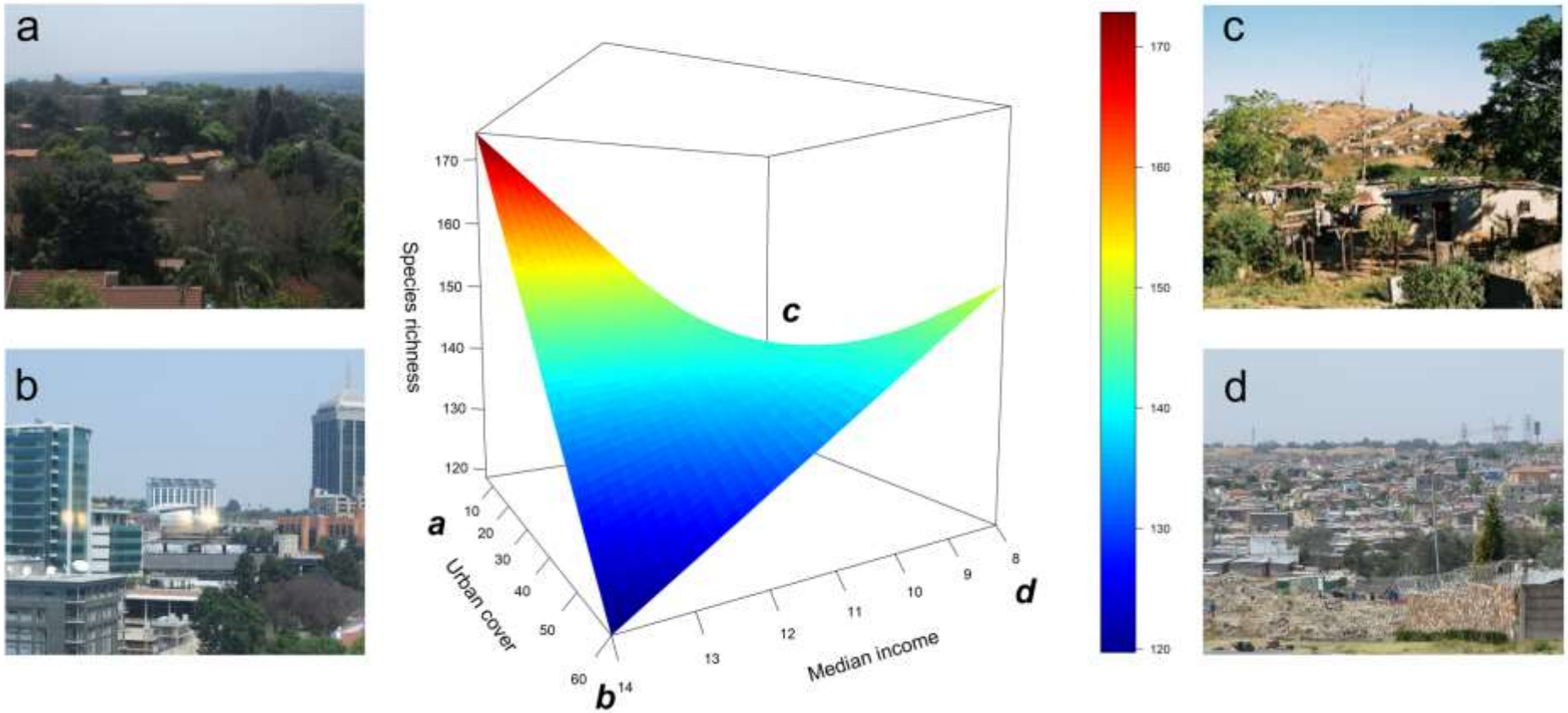

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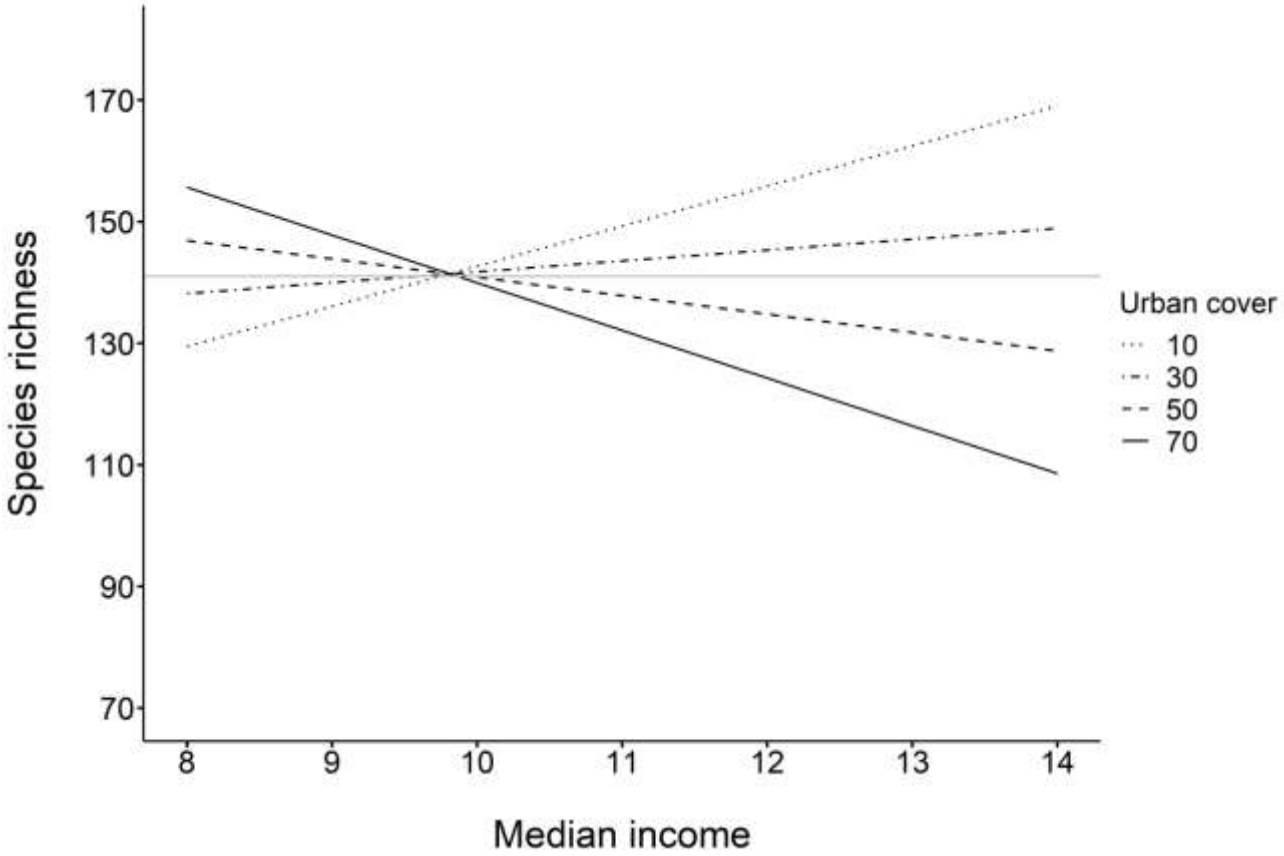

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