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Continuous predictors of species distributions support categorically stronger inference than ordinal and nominal classes: an example with urban bats.

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Abstract

Understanding of how species distributions are driven by landscape-level processes has been obscured by null or inconsistent findings from poorly designed studies. We explore how differences in the way potential drivers of species distributions are defined can influence their perceived effects. Specifically, we evaluate how much statistical power is lost when continuous variables are discretised, and how the use of qualitatively defined nominal variables impacts biological interpretation of results. We fitted generalized linear models to dependent variables relating to bat distribution (species richness, diversity, relative abundance of functional groups and individual species) obtained from 36 sites across Melbourne, Australia, and independent variables that were continuous (percentage tree cover, dwelling density), ordinal (dichotomised continuous variables) or nominal (land-use, urban context). We found that models fitted with continuous predictors had better fit and explanatory power than those fitted with ordinal predictors for all response variables. Ordinal models failed to detect statistically significant effects for 4 of the 11 response variables that were successfully modelled with continuous data, suggesting Type II errors had occurred. Models fitted with nominal data explained a comparable amount of variation in some dependent variables as continuous models. However, interpretation of the mechanisms behind responses to nominal categorical levels was obscured because environmental conditions within them were confounded and not homogenous. To gain better understanding from nominal predictors would therefore require further investigation. Our findings show that careful consideration must be given to the choice of environmental variables used for species distribution modelling and how those variables are defined.

Keywords: Experimental design, functional guilds, insectivorous bats, south-east Australia, species distribution, urbanisation, variable selection.

Introduction

Understanding ecological drivers of species distributions is central to making informed management decisions and predicting the impacts of environmental change. To develop ecological generalisations, consistent effects must be confirmed across multiple analogous studies (Pickett et al. 2007). Yet despite decades of research our understanding of how species respond to many landscape-level processes remains obscured by equivocal findings (Ries et al. 2004; Eigenbrod et al. 2011; McDonnell and Hahs 2013). Some inconsistent findings can be explained biologically, where species responses are determined by functional traits or contextual factors (Ewers and Didham 2006). Many null or inconsistent findings also arise due to low statistical power, poor study design, and a pre-occupation with arbitrary statistical conventions (McCarthy and Parris 2004; Fidler et al. 2006). However, contradictory findings also occur because of inconsistencies in the way in which environmental variation is measured and represented (McGarigal and Cushman 2002; Lindegarth and Gamfeldt 2005; Raciti et al. 2012).

To determine if patterns in the effects of ecological processes are consistent among studies, those processes must be defined and compared consistently. Measures of the environment that lack quantitative definition can result in a lack of replication or pseudo-replication (*sensu* Hurlbert 1984) within studies and among them (McIntyre et al. 2001; Theobald 2004; McDonnell and Hahs 2009). Multicollinearity among environmental variables means their effects can be confounded unless they are isolated through careful design and measurement (McGarigal and Cushman 2002; Graham 2003). Our understanding of the response of organisms to their environment is further obscured when direct drivers are represented by aggregate measures, which lack specificity about which environmental gradients or ecological processes, mechanisms or constraints they represent, and typically fail to capture fine-grained heterogeneity (Theobald 2004; Shochat et al. 2006; Pickett et al.

2008). An important distinction exists between “proximal” variables which represent a direct, causal biological, ecological or physiological constraint on the distribution of the species, and “distal” variables which are weakly or indirectly related to the causal mechanisms (Austin 2002). It is almost always desirable but not always feasible to measure and incorporate proximal influences in distribution models. When forced to use distal measures in ecological analyses, it is preferable to define them such that it is clear which proximal variables or processes they are representing.

Urbanisation is a form of environmental change that involves multiple landscape-level processes (e.g., habitat loss, habitat fragmentation, increased cover by impermeable surfaces) acting across multiple spatial scales (Grimm et al. 2008; McDonnell and Hahs 2009). One of the major challenges in urban ecology is therefore to identify which processes are driving observed patterns in species distributions at different spatial scales. Despite calls for increased reproducibility among urban studies (McIntyre et al. 2001; Theobald 2004; McDonnell and Hahs 2013), studies in which urbanisation processes are neither specified nor quantified remain common and well-cited as evidence of urbanisation effects. Indeed, our understanding of how even relatively well-studied taxa respond to urbanisation lacks consensus because of inconsistencies in the way urbanisation is represented (e.g., birds: reviewed by Marzluff et al. 2001; Chace and Walsh 2006).

In this paper we examine how the way in which urban environments are represented can impact on inference about the drivers of species distributions. Specifically, we determine how representing the effects of urbanisation with independent variables that are either continuous, ordinal categorical or qualitative nominal classes might impact our understanding of what drives species distributions. We hypothesised that: (i) Models built with continuous measures of urbanisation would provide the strongest statistical inference and most direct biological interpretation; (ii) information loss from the discretisation of continuous measures into ordinal classes would result in increased Type II errors (i.e., reduced statistical power); and iii) nominal categorical variables that represent an aggregation of multiple mechanisms mediating the influence of urbanisation on biodiversity would be difficult to interpret and effectively mask the true underlying drivers of species distributions. To test our hypotheses we focus on one taxonomic group—insectivorous bats—which typically form the majority of native mammal fauna remaining in highly urbanised areas (van der Ree and McCarthy 2005). A review of studies of insectivorous bats in urban areas (n = 24) revealed that urban environments are typically represented using nominal classes, continuous gradients, continuous gradients discretised into ordinal classes or a mixture thereof (Table S1 Supplementary Material).

Methods

Study area

The study was conducted in Melbourne, Australia (37.84 °S, 144.98 °E), in a 315 km^2 area extending up to 22 km north of the central business district (CBD: Fig 1). Melbourne is the second largest city in Australia with a human population of ~4.2 million, most of whom live within an urbanised area of approximately 1940 km^2. We restricted our study area to the Victorian Volcanic Plains bioregion—an area of flat to undulating basalt plains characterised by areas of open grassland, grassy woodlands and sclerophyll forest (Oates and Taranto 2001). Urban development in this region is sprawling, with some suburbs located up to 30 km from the CBD. Only 4.5 % of the region's native vegetation remains due to extensive clearing since early European settlement (Taylor et al. 2003). To control for differences in climate within the region, which drives bat distributions at coarse spatial scales (Razgour et al. 2011), we limited site selection to areas with similar mean annual rainfall (580-780 mm) and mean annual minimum temperature (9.5-10.5 °C).

[Fig 1 here]

Experimental design

We selected 36 sites for which commonly used measures of environmental conditions and change were available (Fig 2). Percentage tree cover and dwelling density provided continuous measures of variation in a habitat resource and dwelling densification respectively. Trees provide bats with essential roosting and foraging resources (Lumsden et al. 2002; Lumsden and Bennett 2005); therefore tree cover serves as a proximal measure of resource availability. Dwelling density is an aggregated measure encompassing numerous changes associated with urbanisation, including changes to temperature, hydrological cycles, cover by impermeable surfaces, light and noise pollution and the sanitisation of ground covers (e.g., Hahs and McDonnell 2006; Grimm et al. 2008). However, it is commonly measured in urban studies because it is directly used by urban planners when designing cities. Increasing availability of resources typically has a positive effect on bats, whereas dwelling densification typically has a negative effect (Hourigan et al. 2006; Duchamp and Swihart 2008; Threlfall et al. 2011; Luck et al. 2013).

Qualitatively defined nominal categorical predictors are prevalent in urban bat ecology (Table S1 Supporting Information). Bat populations are often compared at discrete points along urban-rural gradients (e.g., “urban”, “suburban”, “rural”) or among habitats within urban areas (e.g., “residential streets”, “parks”, “old suburbs”, “open areas”). Bats are typically less abundant inside urban centres than rural areas (Gaisler et al. 1998; Russo and

Jones 2003), and riparian habitats are typically more suitable for bats than residential gardens (Gaisler et al. 1998; Bartonička and Zukal 2003). However, some studies demonstrate contrasting findings (Gehrt and Chelsvig 2003; Avila-flores and Fenton 2005; Hourigan et al. 2010; Basham et al. 2011). To look at how much variation in proximal drivers of species distribution was subsumed within categories of the nominal categories (land-use: “riparian” or “residential”; and urban context: “inner city” or “outer city”) we plotted percentage tree cover and dwelling density at sites grouped by one- and two-way categorical levels.

We allocated sampling sites equally between land-use (“residential” and “riparian”) and urban context (“inner city” and “outer city”) categories (Fig 2a). Here we use the term “city” to refer to a named and bounded locality within Melbourne’s Urban Growth Boundary. “Inner city” sites were those within inner-to-middle-ring localities in older, denser, urban areas closer to the original colonial centre of the city, and areas that were urbanised early in a city's expansion after the inner city had become established (Fig 1). “Outer city” sites were those in more recently developed urban areas that were more remote from the urban centre. Residential sites were located in rear gardens, while riparian sites were located in parkland immediately adjacent to waterways. All sites contained at least one tree (>10 cm diameter at breast height) and were located > 500 m apart. Residential sites were additionally located > 100 m from waterways to reduce any confounding influence. At each site we measured percentage tree cover and dwelling density within a 500 m radius (Fig 2b). Structural complexity (e.g., tree size, number of trees, size of gaps) at small spatial scales (i.e., tens of meters) imposes limits on bat flight manoeuvrability and prey detection, which in turn influences the distribution of bats in urban landscapes (Basham et al. 2011; Threlfall et al. 2012). A radius of 500 m (78.5 ha) therefore provided an effective landscape for bats in our study. Percentage tree cover was determined using a mapped presence/absence tree layer (defined as woody vegetation greater than 2 metres in height) derived from a combination of digital classification and visual interpretation of SPOT Panchromatic imagery with a 10 m pixel size (Department of Sustainability and Environment 2006). Dwelling density (n ha^{-1}) was calculated from census data (Australian Bureau of Statistics 2006). Continuous measures of tree cover and dwelling density were split dichotomously using median values as thresholds to class sites as “high” or ”low” tree cover and dwelling density (Fig 2c). We checked collinearity among predictor variables of each type prior to analysis which showed that continuous and discretised predictors were weakly correlated ($r = -0.28$ and $r = -0.11$ respectively), and nominal predictors were not correlated ($r = 0$).

[Fig 2 here]

Response variables

Bat echolocation calls (henceforth “passes”) were recorded with acoustic detectors (SD1: Titley Electronics, Ballina, Australia) during surveys conducted between March and April 2009. A detector was placed on the ground at each site with a microphone raised to a height of 1 m and angled up at 45° towards gaps in the surrounding vegetation. Microphone sensitivity was calibrated prior to each deployment using a Chirp Board (Nevada Bat Technology, Las Vegas, NV, USA). Detectors were left *in situ* recording from civil twilight to civil sunrise for four consecutive nights, and 9 sites were selected at random to be surveyed simultaneously. Sampling was restricted to mild nights (minimum temperature > 10 °C), with no rain, and light to moderate winds. The two nights on either side of a full moon were also avoided.

Bat passes were automatically identified to species where possible with Anascheme software (Adams et al. 2010) and regionally specific identification keys (for more details see

Lumsden and Bennett 2005). Species for which there were known identification errors with the automated system were double-checked manually (identification software, regional keys and manual identification protocols are available on request). Species identification was only attempted for passes with five or more pulses and was considered successful when $\geq$ 50 % of pulses within a pass were identified to the same species. Several congeneric species cannot be distinguished acoustically (*Nyctophilus gouldi* and *N. geoffroyi*; *Scotorepens balstoni* and *S. orion*) and so were combined into species complexes. A total of 9,156 bat passes was recorded over 142 detector-nights across 36 sites, of which 4,489 (49 %) were identified to one of 12 species (Table S2 Supplementary Material).

Studies investigating the abundance and distribution of insectivorous bats typically model one (or more) of three response types—aggregate responses, guild-level (trait-based) responses and species-specific responses. We were therefore interested in how choice and definition of predictor variables influenced understanding about key drivers of variation in each response type. Aggregate responses included species richness (total number of species), species diversity (Shannon index) and total activity of all species (total number of bat echolocation calls). Wing morphology and echolocation frequency are directly related to bat foraging and flight behaviour (Norbert & Raynor 1987) and so are often used to classify bats into functional guilds (e.g., Luck et al. 2012). Bats with short, broad wings are adapted for manoeuvrable flight within structurally complex habitats, in which high frequency (or linear) echolocation calls are needed to pick out fine detail over short distances. By contrast, bats with long, narrow wings are adapted for fast flight in open spaces, in which low frequency echolocation calls enable prey detection at greater distances. Because urbanised landscapes tend to be structurally simplified, bats with adaptations for flight in open spaces could be predicted to be “urban tolerant”, whereas those with adaptations to cluttered environments are likely to be “urban sensitive” (Table S2 Supplementary Material). We used the total numbers of echolocation calls by species with “urban tolerant” or “urban sensitive” functional traits as guild-level responses. Finally, we used the total numbers of echolocation calls of each individual bat species as species-specific responses. Five bat species occurred too infrequently (mean activity: < 1 pass / night; Table S2 Supplementary Material) to included in further analysis.

Statistical Analysis

We fitted generalised linear models (GLMs) with main and interaction effects of continuous, ordinal or nominal predictors to each response variables using R 3.0.1 (R Development Core Team 2013). Negative-binomial error distributions were fitted to all but two response variables to account for over-dispersion in the data (using the MASS package: Venables and Ripley 2013). Species richness was fitted with a Poisson error distribution and log link, and species diversity with a Gaussian error distribution and identity link. Continuous predictors were scaled and centred (mean = 0; SD = 1) and categorical predictors were effect coded (-1, 1) prior to analysis to allow direct comparison of effect size and interpretation of main effects when interactions were present (Bech and Gyrd-Hansen 2005). GLMs fitted with main and interaction effects of two factors with two levels per factor have the same number of parameters, and hence statistical power, as GLMs fitted main and interaction effects of two covariates (Cottingham et al. 2005). Model fit, explanatory power and number of responses with effects detected could therefore be directly compared between models fitted with different predictor types. A Bonferroni correction ($k = 3$; $P < 0.017$) was used to evaluate the statistical significance of parameter estimates. Akaike weights were used to rank the fit of competing predictor types to each response variable (Burnham et al. 2010). A coefficient of determination (pseudo-R-squared) was calculated for each model following Nakagawa and Schielzeth (2013):

$$R^2 = 1- (\text{model deviance}/\text{null deviance})$$

We validated models following Zuur et al. (2009). Spline correlograms with 95 % point-wise bootstrap confidence intervals confirmed deviance residuals were spatially independent (using the ncf package: Bjornstad 2013). Plots of deviance residuals against fitted values and each explanatory variable used in models confirmed the absence of any patterns in model residuals. Homoscedasticity of residuals was confirmed by plots against fitted values. QQ-plots confirmed normality of deviance residuals from species diversity models with each predictor type.

Results

Comparison of continuous and discretised models

Models were successfully fitted to 11 of the 12 response variables tested (Table 1). Although abundant and widespread, no model fitted with any predictor type explained a significant amount of variation in activity by *Chalinolobus gouldii*. Models fitted with continuous predictors explained more variance (R^2) and had a better fit (ωi) than those fitted with ordinal predictors for all eleven response variables (Fig 3). Discretising continuous data caused a loss of between 7 % and 18 % of variance explained in each response variable (mean ± SE: 13.7 ± 0.01 %). The reason for the loss in explanatory power became apparent when plots of continuous environmental gradients at sites (Fig 4a) were grouped according to ordinal categories (Fig 4b). While ordinal groups are clearly distinct from one another, a large amount of variance in tree cover and dwelling density was reduced to a single mean value.

However, there was a strong correlation in variance explained by models fitted with continuous predictors and ordinal predictors ($r = 0.98$). Both types of predictor data explained the most variance in aggregate response variables, the urban tolerant guild and individual urban-tolerant species, and relatively less variance was explained for two urban-sensitive species.

[TABLE 1 HERE]

[FIG 3 AND 4 HERE]

Models fitted with continuous predictor variables detected 17 statistically significant effects (Bonferroni corrected $p \leq 0.017$) for 11 response variables, compared with only 10 significant effects detected for seven response variables with ordinal variables (Table 1). Three further effects were marginally significant ($p \leq 0.019$) with continuous predictors, and one with ordinal predictors. All but one model fitted with continuous predictors included tree cover as a main effect, compared to only seven models fitted with ordinal predictors. Ordinal measures did not detect an effect of tree cover for four urban-sensitive species. Seven continuous models included a main effect from dwelling density, five of which were also detected by ordinal models (the effect of dwelling density on one urban-sensitive species and the urban sensitive guild were not detected). Interaction effects were detected in three continuous models but no ordinal models. The direction of effects was universal across continuous and ordinal measures: tree cover had a positive effect on bats whereas dwelling density a negative effect. Interactions implied that the negative effects of dwelling density were greater in areas of low tree cover.

Biological understanding from models based on true categorical variables

Models fitted with nominal predictor data were surprisingly powerful, with 21 statistically significant effects being detected for 11 response variables (Table 1). Eight response variables were influenced by urban context, seven by land-use type and six interactions of these factors. Riparian sites had a positive effect on bats compared to residential sites, and outer city areas were better for bats than inner city areas. Interactions indicated that the negative effect of residential land-use was greater in the inner city. Explanatory power (R^2) and fit (ωi) of models built with nominal data models were roughly equal to or greater than that of continuous models for guild-level responses and the responses of three urban sensitive species (Fig 3).

When plots of continuous environmental variables at sites (Fig 4a) were grouped according to nominal categories it became clear that, with the exception of residential sites in the inner city, nominal categories did not form discrete groups (Fig 4c-e). Residential gardens in the inner city were the only combination of land-use and urban context to differ substantially from other categories in terms of tree cover and dwelling density. However, because the effects of both environmental gradients were confounded within this category direct understanding of how either impacts bat populations was obscured, particularly given the high number of interaction effects detected.

Discussion

Our goal was to explore how differences in the way drivers of species distribution patterns are defined and modelled can alter inference about their effects. We approached this by comparing explanatory power and model-based interpretation of predictor variables defined with continuous, ordinal, or nominal measures of urbanisation. We found that continuous predictors explained up to 18 % more variance (R^2) in bat responses to urbanisation than when they were dichotomised into ordinal categories. Despite being based on the same data, models fit with ordinal predictors failed to detect effects for 4 of the 11 response variables that were successfully modelled with continuous data, suggesting that Type II errors were occurring. While the simplification of systems may be conceptually appealing, our results show that arbitrarily discretised continuous data resulted in information loss, particularly in variance explained. This provided weaker inference about how bats respond to urban change, which may result in biologically significant effects going undetected. Failure to detect a biologically significant effect because of an inappropriate choice of measure could have serious conservation implications if it is taken as evidence that a particular driver is irrelevant. For example, in agreement with other studies we found that tree cover is a significant driver of bat species distribution, particularly that by urban-sensitive species (Threlfall et al. 2011; Hanspach et al. 2012; Luck et al. 2013). However, models of the responses of four urban-sensitive species that were fitted with ordinal measures failed to detect any effect of tree cover. Similarly, continuous models detected a negative effect of dwelling density on the urban sensitive guild and one urban sensitive species that was undetected by ordinal models. Decision makers viewing these results may interpret a lack of an effect as evidence that maintaining tree cover in cities for bats is not crucial to their persistence nor increasing dwelling density a threat, despite continuous models indicating the contrary.

Models fitted with nominal predictors had reasonably high statistical power—they successfully detected effects for all response variables and explained a high proportion of variance in the responses of some (urban-sensitive) bat species. However, without further investigation into what made sites in each category more or less suitable for bats (i.e., by quantifying environmental conditions) biological understanding behind patterns in detected effects remains obscured. Environmental conditions within nominal categories are often assumed to be homogenous but seldom are unless rigorously controlled. Even where group membership is defined quantitatively, it is typically along one environmental gradient (e.g., housing density: Hourigan et al. 2010) and other confounding variables (e.g., tree cover) remain unmeasured and uncontrolled (but see Threllfall et al. 2011; Basham et al. 2011). Quantification of environmental conditions at sites we surveyed within nominal categories revealed they lacked consistency, meaning that sites within categories were not appropriately replicated. High variation and overlap in tree cover and dwelling density gradients also meant that three out of four two-way categories were indistinct from one another (i.e., assumed treatments did not differ). Additionally, the confounding influences of environmental gradients at sites in the only distinct, homogenous nominal category (residential gardens in the inner city) meant the specific drivers of negative responses at such sites were masked. Looking at these results we could not know if bat abundances were reduced because of low tree cover, or high dwelling density, the interaction of the two, or another variable not currently included in the study. We found that while nominal classes of land-use and urban context can explain some variation in the distribution and abundance of bats, they provided little specific biological understanding about how the key mechanisms underlying the urbanisation effect. An additional level of investigation (i.e., quantification of environmental conditions within categories) would therefore be required to understand why land-use categories differ in their suitability, which would defeat the object of their use for convenience and conceptual simplicity in the first place.

The studies included in our literature review (Table S1 Supporting Information) provide varying degrees of insight about the distribution patterns of bats in urban environments. The range of measures used to define urban environments demonstrates a lack of consistency among studies that makes it difficult to generalise results. Yet a high proportion of studies based on nominal (and to a lesser extent, ordinal) predictors continue to be cited as evidence of urbanisation effects. We demonstrated how a subtle change in the way we measure urbanisation processes can produce substantially different ecological understanding. Our results demonstrate that the use of nominal measures of the urban environment limit reproducibility of bat-habitat studies and obscure our understanding of specific drivers of biodiversity patterns. Inconsistent definitions of environmental predictors is hindering the development of theory not just in urban ecology (McIntyre et al., 2000; Theobald 2004; McDonnell and Hahs 2009; 2013), but in any field concerned with finding how patterns of biodiversity are driven by spatially explicit processes (e.g., McGarigal and Cushman 2002; Ries et al. 2004). Without explicit quantification of environmental conditions, measures of environmental drivers are not comparable or reproducible and evidence on the effects of urbanisation on species distribution cannot be compiled iteratively (McDonnell and Hahs 2013). We recognise that we often only have categorical data to work with because we cannot map the underlying mechanisms that cause correlations between categories of, for instance, land-use and species distributions. However, to develop a more mechanistic and robust understanding of the impacts of urbanisation on bat species distribution patterns future studies must try and characterise, map and model proximal environmental drivers in a more consistent way.

Acknowledgements

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Table 1: The number of statistically significant effects (Bonferroni corrected $P \leq 0.017$) detected by models fitted to response variables with main and interaction effects of continuous, ordinal or nominal predictor data. Non-significant effects are indicated with a dash. Continuous predictors were percentage tree cover and dwelling density. Ordinal predictors were tree cover and dwelling density dichotomised into high or low categories. Nominal predictors were land-use (residential or riparian) and urban context (inner or outer suburb).

Response variable		Continuous models			Ordinal models			Nominal models		
		Tree cover	Dwelling density	Tree * dwelling	Tree cover	Dwelling density	Tree * dwelling	Land-use	Urban context	Land-use * urban context
Aggregate	Species richness	0.00	0.00	-	0.00	0.00	-	0.00	0.01	0.01
	Diversity	0.02	-	-	0.02	-	-	-	0.01	-
	Total activity	0.00	0.00	-	0.00	0.00	-	0.00	0.00	0.00
Trait-based guild	Urban tolerant	0.01	0.01	-	0.00	0.00	-	0.00	0.00	-
	Urban sensitive	0.00	0.00	0.01	0.02	-	-	0.00	0.00	0.00
Species-specific	*Mormopterus* sp. 4	-	0.02	-	0.00	0.01	-	0.00	0.00	-
	Tadarida australis	0.00	-	-	0.00	-	-	-	0.00	-
	Vespadelus darlingtoni	0.00	0.00	0.02	-	-	-	-	-	0.00
	Chalinolobus morio	0.00	-	-	-	-	-	0.00	-	-
	Nyctophilus spp.	0.00	0.01	0.01	-	0.00	-	-	0.00	0.00
	Vespadelus vulturnus	0.01	-	-	-	-	-	0.00	-	0.00

Figure captions

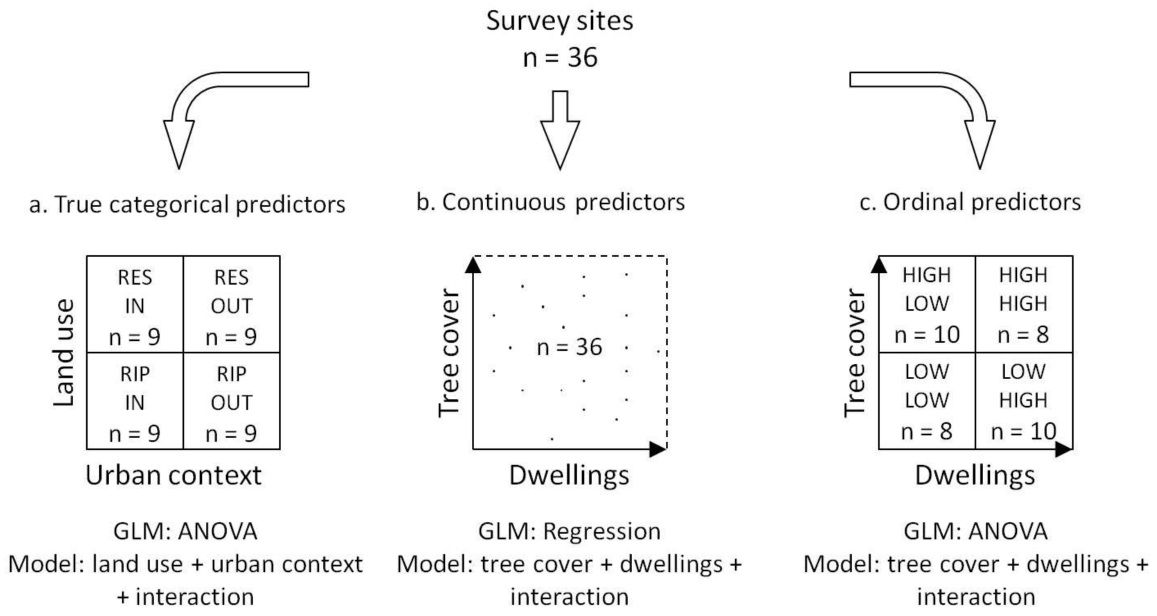
Figure 1: Location of study area in SE Australia (top left) and within the state of Victoria (bottom left). Study sites (n = 36) at which bat surveys were conducted within Melbourne (main). Circles represent residential sites, triangles represent riparian sites. The urbanised area of city is shown in grey, with darker greys representing higher dwelling densities and major roads indicated with grey lines. Melbourne's inner-to-middle ring localities are delineated by a thick black line from outer localities.

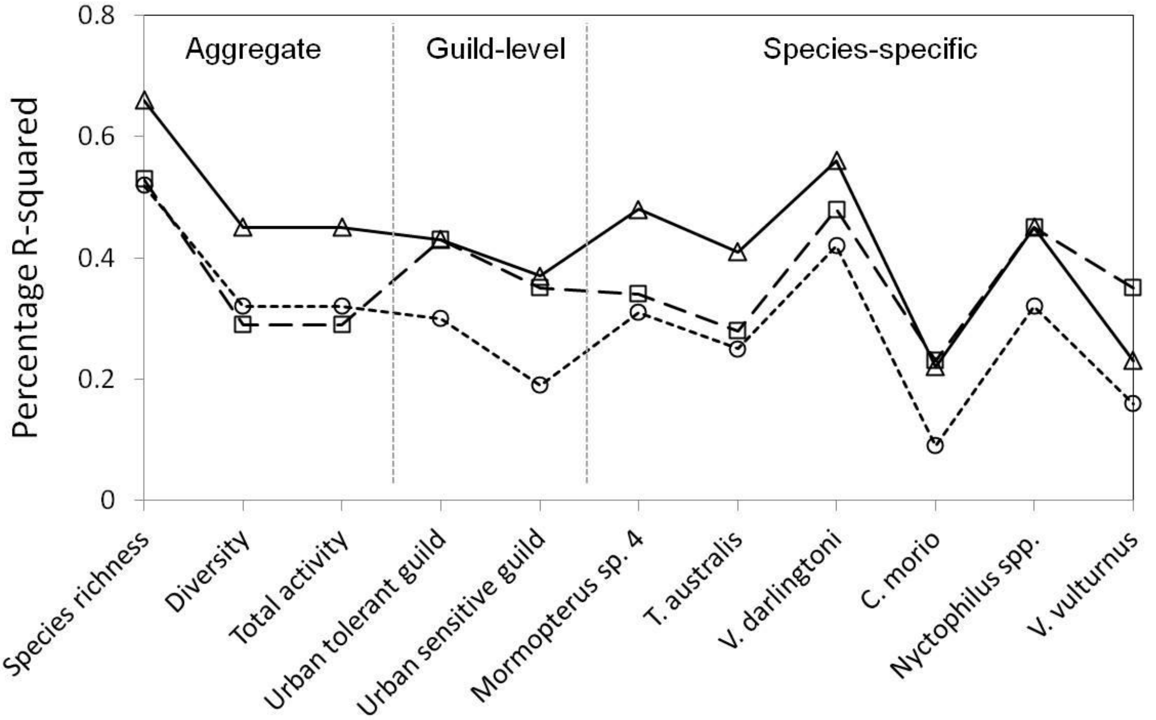
Figure 2: Illustration of how three types of predictor data were defined at the same 36 sites based on (a) qualitative nominal categories of land-use (RES = residential; RIP = riparian) and urban context (IN = inner city; OUT = outer city); (b) quantitative continuous measures of percentage tree cover and dwelling density (ha^{-1}); (c) ordinal categories formed by discretisation of percentage tree cover and dwelling density at median values into "HIGH" and "LOW" classes.

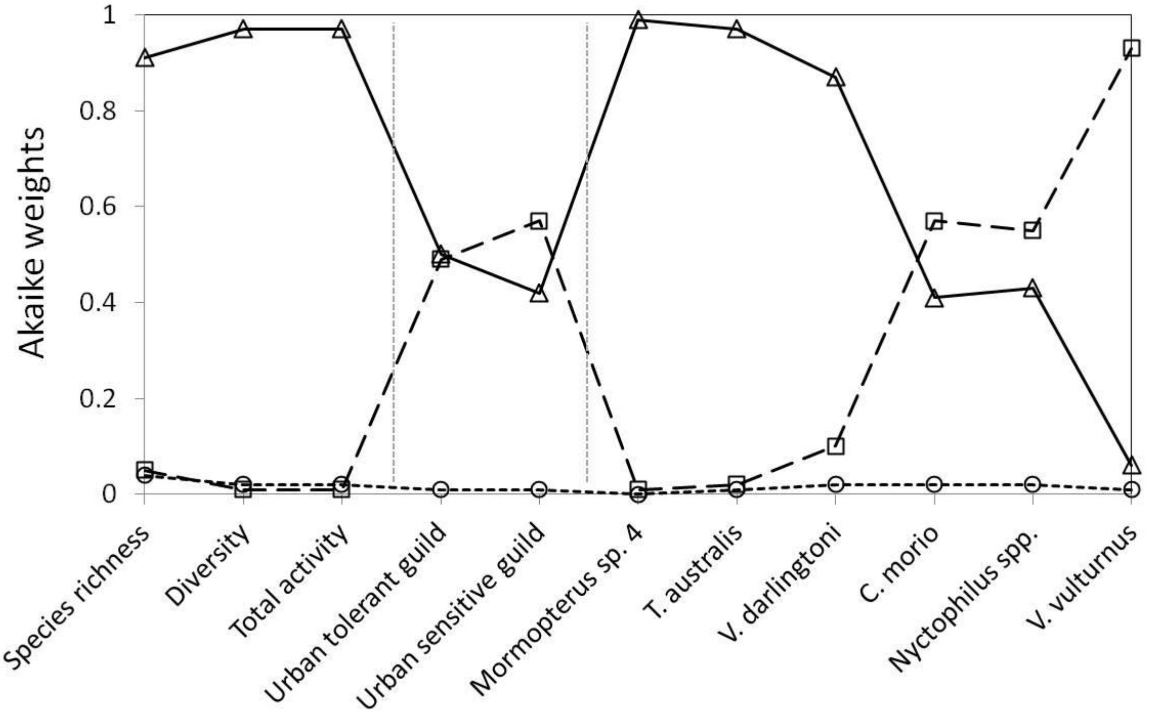
Figure 3: Percentage variance explained by (R^2) and fit of (Akaike weights; ωi) models fitted with continuous (solid line), ordinal (dotted line) or nominal (dashed line) predictors to aggregate, guild-level and species-specific responses by urban bat populations.

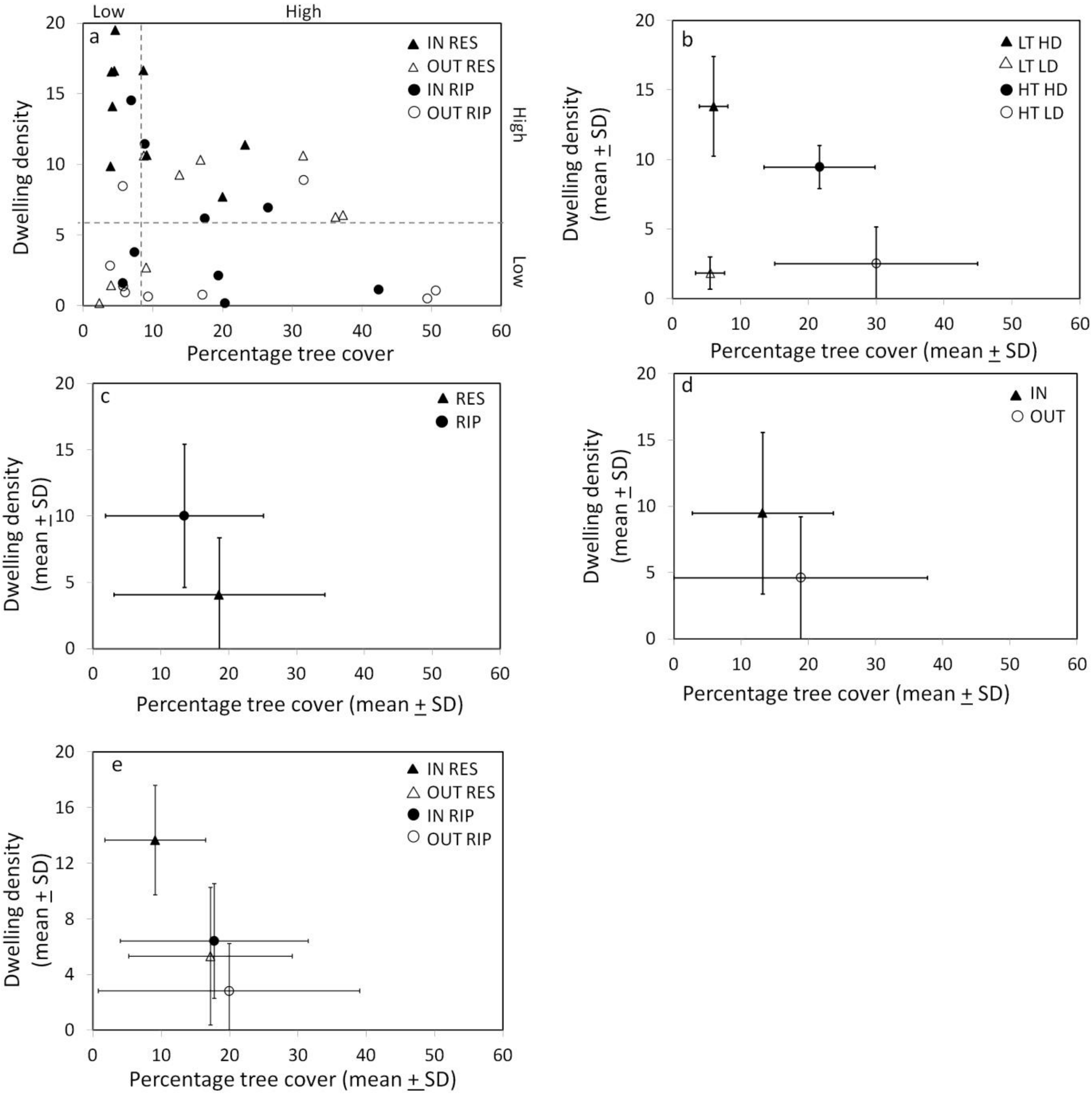
Figure 4: Variability in percentage tree cover and dwelling density within a 500 m radius of study sites (n = 36) when data are continuous (a). Vertical and horizontal dotted lines indicated the median values used to discretise data into ordinal classes (b). Mean values (± 1 SD) indicate amount of variation in continuous measures between urban context to urban centre (d: open = outer city; shaded = inner city) and their two-way interaction (e


145 °E
38 °S
20 km


Survey sites
n = 36
a. True categorical predictors
b. Continuous predictors
c. Ordinal predictors
Land use
RES IN n = 9
RES OUT n = 9
RIP IN n = 9
RIP OUT n = 9
Urban context
GLM: ANOVA
Model: land use + urban context + interaction
Tree cover
n = 36
Dwellings
GLM: Regression
Model: tree cover + dwellings + interaction
Tree cover
HIGH LOW n = 10
HIGH HIGH n = 8
LOW LOW n = 8
LOW HIGH n = 10
Dwellings
GLM: ANOVA
Model: tree cover + dwellings + interaction


Percentage R-squared
0.8
0.6
0.4
0.2
0
Aggregate
Guild-level
Species-specific
Species richness
Diversity
Total activity
Urban tolerant guild
Urban sensitive guild
Mormopterus sp. 4
T. australis
V. darlingtoni
C. morio
Nyctophilus spp.
V. vulturnus


Akaike weights
1
0.8
0.6
0.4
0.2
0
Species richness
Diversity
Total activity
Urban tolerant guild
Urban sensitive guild
Mormopterus sp. 4
T. australis
V. darlingtoni
C. morio
Nyctophilus spp.
V. vulturnus


a
Low
High
High
Low
▲ IN RES
△ OUT RES
● IN RIP
○ OUT RIP
Dwelling density
Percentage tree cover
0
5
10
15
20
0
10
20
30
40
50
60
b
▲ LT HD
△ LT LD
● HT HD
○ HT LD
Dwelling density (mean ± SD)
Percentage tree cover (mean ± SD)
c
▲ RES
● RIP
Dwelling density (mean ± SD)
Percentage tree cover (mean ± SD)
d
▲ IN
○ OUT
Dwelling density (mean ± SD)
Percentage tree cover (mean ± SD)
e
▲ IN RES
△ OUT RES
● IN RIP
○ OUT RIP
Dwelling density (mean ± SD)
Percentage tree cover (mean ± SD)
0
4
8
12
16
20

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Appendix 1 Review on studies investigating the effect or urbanisation on bats.

Methods

We searched ISI Web of Science for papers with “urban*” and “bat*” in the title, abstract or keywords from 1985 (around the time acoustic bat detectors came into popular use) to 1 April 2013. We retained papers that examined the effects of urbanisation on bat species distribution and/or abundance (e.g. species richness, diversity, activity), and excluded papers investigating bat behaviour (e.g. roost selection, home range, diet). We then used Google Scholar to see how frequently each paper had been cited.

Results

We found 24 papers matching our criteria, 11 of which (46 %) compared bat faunas at nominal points along an urban-rural gradient (e.g., “urban”, “suburban”, “rural”) or among habitats within urban areas (e.g. “residential street” versus “urban park”). Almost all of these studies provided no quantitative measures of urbanisation context. Where some level of quantification is given, it is typically along one environmental gradient (e.g., low-density housing = 1-5 dwellings ha-1; high-density housing = 10-30 dwellings ha-1: Hourigan et al., 2010) and other confounding variables (e.g., tree cover) remain unmeasured and uncontrolled (but see Threllfall et al., 2011; Basham et al., 2010). Seven papers (29 %) sampled across the entire urbanisation gradient using regression-based analysis, a trend that appears to be increasing with time (see Appendix S3), and a further five papers (21 %) presented results from both continuous and categorical analyses. However, continuous measures of urbanisation often take the form of percentage cover of urban land-use or land-cover that are not themselves quantitatively-defined (e.g., Duchamp & Swihart, 2008). Only the most recent papers measure more proximate environmental drivers (e.g. tree density: Luck et al., 2012). Despite the increased use of continuous predictors in recent years, four papers have been published since 2010 (and cited 39 times) based on qualitative categories. Overall, 62 % of citations in the urban bat literature are based on results from categorical predictors.

Table S1: Results of literature review on studies from 1985-2013 investigating the effect or urbanisation on quantitative responses by bat faunas grouped according to type of predictor data used: qualitative; discretised; continuous; mixed (both categorical and continuous predictor data used). The number of times each study was cited in Google Scholar is also given.

Study	**Description of methodological design and sample size.**	**Citations**
Nominal (qualitative)		
Geggie & Fenton 1985	Sites in three habitat types (“residential streets”, “parkland”, “open water”) found in both an urban area and a rural area. Sites were additionally sampled in the commercial zone of the urban area, and open farmland in the rural area. All habitats two replicates in each area except open water which had four.	73
Kurta & Teramino 1992	Sites within “urban riparian parkland” (n=35), and “rural riparian parkland” (n=42).	75
Gaisler et al. 1998	Sites within seven urban categories with 5-21 replicates in each e.g., city centre ("historical centre of town": n=5), old residential quarters ("streets with blocks of buildings mostly 4-5 storeys": n=15) , old suburbs ("streets of family houses with small gardens": n=18), villa quarter ("scattered villas with large gardens": n=21) , old outskirts ("old warehouses, factory premises, open areas, trees": n=10) , new housing estates ("blocks of high rise 8 storey flats, lawns and newly planted trees": n=11), river ("river and immediate surrounds": n=8).	77

Bartonička & Zukal 2003	Sites within “urban parks” (n = 2); urban areas e.g., "old and new residential buildings in suburbs and downtown" (n = 3); and at “streams and ponds” (n = 3).	24
Russo & Jones 2003	Six replicate sites in each of ten habitat types e.g., "olive groves", "arable land", "*Fagus sylvatica* woodland", "rural towns".	129
Avila-Flores & Fenton 2005	Sites (n = 12) in five habitat/land-use types e.g., "natural forest" (>11km from city), "large parks" (>100ha), "high density residential" (>10,000 people/km^2).	57
Oprea et al. 2009	Sites in “urban parks” (n=3), “streets with trees” (n=3), “streets without trees” (n=3).	14
Hourigan et al. 2010	Sites (n = 10) in each of six urban habitats: e.g., “remnant bushland” (native forest 500+ha, >50% canopy and understory present), “low-density residential” (1-5 dwellings ha^{-1}), “high-density residential” (10-30 dwellings ha^{-1}).	8
Jung & Kalko 2010	One “forest site”, one “dark urban site” (village population 500, no street lights), one “lit urban site” (same village, but street-lit area)	17
Jung & Kalko 2011	Sites in “mature secondary forest” (n=4); “urban” (city: n=2),” forest-town interface” (village population 500: n = 1).	11
Coleman & Barclay 2012	Sites ("at least nine replicates per zone") were divided between an “urban zone” (within city limits and completely bounded by human development); “rural zone” (>40 km from city limits); and a	3

	"transition zone" (located within city limits but not bounded by development or between city limits and rural zone).	
Ordinal (discretised)		
Johnson et al. 2008	National parks that were classified into equal categories as "forested" or "fragmented" according to percentage tree cover, and subdivide as "urban" or "rural" depending on distance to city and percentage cover by "urban land-uses".	29
Mixed design (categorical and continuous)		
Lesinski et al. 2000	Transects in four habitats ("wooded"; "open"; "built up area"; "riparian") in each of five urban zones: "city centre", "city outskirts", "suburbs", "non-urbanised close to city" and "non-urbanised far from the city". Also quantified percentage cover of trees; shrubs; open areas (crop fields, pasture, and wasteland); impermeable surface, and water within 60 m wide belt along transect.	3
Basham et al. 2010	Sites within five habitat types (n = 8 each), all within an study area with 11.6 people ha^{-1}, 4.2 houses ha^{-1}, and 13 % of area in parkland. At each site continuous data were measured (e.g., tree DBH, hollow cavity density etc.)	8
Threlfall et al. 2011	Sites grouped into landscape categories based on vegetation cover, dwelling density and geology:	11

	“urban” (>5 dwellings ha-1 <10% vegetation, n = 24); “suburban shale” (<5 dwellings ha-1 5-40% vegetation >80% shale, n = 24); “suburban sandstone” (<5 dwellings ha-1 5-40% vegetation >80% sandstone, n = 20); “suburban shale” (<5 dwellings ha-1 5-40% vegetation >40% shale >40% sandstone, n = 24); “vegetated” (<5 dwelling ha-1 >40% vegetation n = 24). At each site measured continuous data (e.g., amount of bushland, land cover heterogeneity and housing density within 500m, 3km, 5km; distance to water; distance to nearest native bush; landscape geology).	
Threlfall et al. 2012	Sites grouped into landscape categories based on vegetation cover, dwelling density and geology: “urban” (>5 dwellings ha-1 <10% vegetation, n = 24); “suburban shale” (<5 dwellings ha-1 5-40% vegetation >80% shale, n = 24); “suburban sandstone” (<5 dwellings ha-1 5-40% vegetation >80% sandstone, n = 20); “suburban shale” (<5 dwellings ha-1 5-40% vegetation >40% shale >40% sandstone, n = 24); “vegetated” (<5 dwelling ha-1 >40% vegetation n = 24). At each site measured continuous data (e.g., amount of bushland, land cover heterogeneity and housing density within 500m, 3km, 5km; distance to water; distance to nearest native bush; landscape geology).	4
Hale et al. 2012	Sites at “unlit ponds” stratified among five land classes (“rural”; “light suburban”; “suburban”; “dense suburban”; “dense urban”). Total area/length of land-use and land-cover variables at multiple spatial scales (14 radii between 50 m and 4 km) then measured surrounding each site.	2

Continuous		
Walsh & Harris 1996	Proportion of land classes (n = 32) within 1km^2 grid cells (n = 1030).	109
Gehrt & Chelsvig 2003	Proportion of land-use (n = 4) at 10 sites in each of 20 study areas. Also measured linear distance to urban centre; linear distance to nearest open space; streetlight density; traffic volume; human population density with 2km. Microhabitat variables also quantified.	70
Hourigan et al. 2006	Sites (n = 32) stratified between 8 habitat types (e.g. “suburb” >50 years old, “new suburb” <20 years old, “amenity parkland”), at which various continuous variables were then measured (e.g., distance to water; distance from remnant vegetation; housing density within 200m).	30
Duchamp & Swihart 2008	Proportion of land cover (n = 6) within 23km^2 landscapes (n = 27).	32
Fabianek et al. 2011	Urban green spaces (n = 24) at which various continuous variables were then measured within distance (e.g., area of forest cover; number of dwellings; length of roads).	6
Dixon 2012	Sites (n = 47) randomly located throughout metropolitan study area at which percentage land-cover (e.g., impervious surface; open water; wetland; tree cover; grassland/shrub-land/crops) within 100 m, 500 m, and 1000 m buffers.	1
Luck et al. 2012	Sites (n = 72) stratified among 18 towns and cities in SE Australia and measured local and landscape variables surrounding each site (e.g., percentage cover by woody vegetation; tree density; dwelling	0

density).

Temporal trends in types of measures used in urban bat studies.

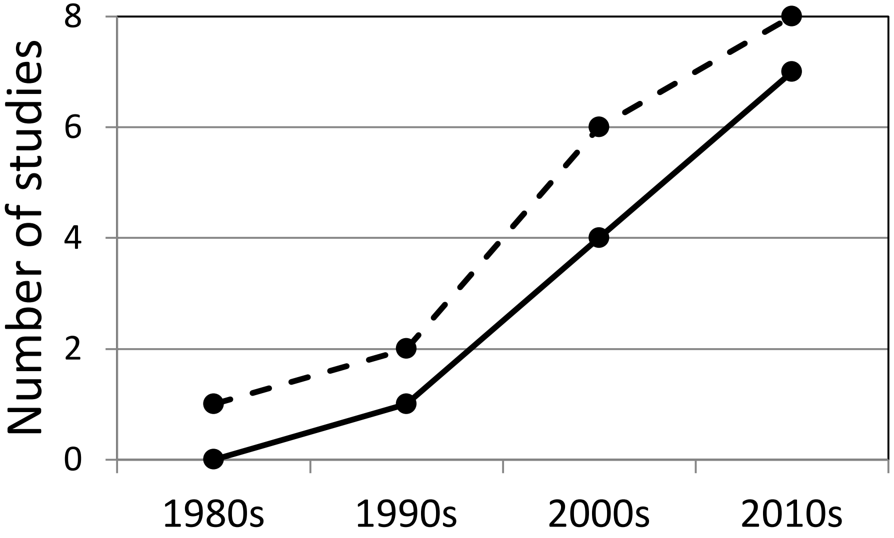

Figure : The number of studies (n = 24) investigating bat responses in urban systems published per decade (1980s = 1985-1989; 1990s = 1990-1999; 2000s = 2000-2009; 2010s = 2010-2013). Studies are grouped by their analytical approach as ANOVA with categorical data (dashed lines); regression with continuous data (solid line). Studies that employed a mix of both regression and ANOVA were included in both categories (i.e., double counted).

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Appendix 2 Summary species statistics from bat surveys

Table S2. Bat species, functional guilds, percentage of sites recorded (n = 36), percentage of total calls, and were allocated to functional guilds based on wing morphology and echolocation frequency following Threlfa that occurred too infrequently to be included in analysis.

Species	Functional guild	% sites	% calls
Chalinolobus gouldii	Urban tolerant	0.97	0.31
Chalinolobus morio	Urban sensitive	0.81	0.13
*Miniopterus schreibersii oceanensis**	Urban tolerant	0.36	0.01
Mormopterus species 4	Urban tolerant	0.86	0.24
Mormopterus species 2*	Urban tolerant	0.17	0.00
*Myotis macropus**	Urban sensitive	0.33	0.01
Nyctophilus species	Urban sensitive	0.58	0.03
Scotorepens species*	Urban tolerant	0.47	0.01
Tadarida australis	Urban tolerant	0.83	0.05
Vespadelus darlingtoni	Urban sensitive	0.39	0.05
*Vespadelus regulus**	Urban sensitive	0.31	0.00
Vespadelus vulturnus	Urban sensitive	0.61	0.15