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Butterfly richness and abundance along a gradient of imperviousness and the importance of matrix quality

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Abstract:

Heterogeneity in quantity and quality of resources provided in the urban matrix may mitigate adverse effects of urbanization intensity on the structure of biotic communities. To assess this we quantified the spatial variation in butterfly richness and abundance along an impervious surface gradient using three measures of urban matrix quality: floral resource availability and origin (native vs exotic plants), tree cover, and the occurrence of remnant habitat patches. Butterfly richness and abundance were surveyed in 100 cells (500 x 500-m), selected using a random-stratified sampling design, across a continuous gradient of imperviousness in Melbourne, Australia. Sampling occurred twice during the butterfly flight season. Occurrence data were analyzed using generalized linear models at local and meso- scales. Despite high sampling completeness we did not detect 75% of species from the regional species pool in the urban area, suggesting that urbanization has caused a large proportion of the region's butterflies to become absent or extremely rare within Melbourne's metro-area. Those species that do remain are largely very generalist in their choice of larval host plants. Butterfly species richness and abundance declined with increasing impervious surface cover and, contrary to evidence for other taxa, there was no evidence that richness peaked at intermediate levels of urbanization. Declines in abundance appeared to be more noticeable when impervious surface cover exceeded 25%, while richness declined linearly with increasing impervious surface cover. We find evidence that the quality of the urban matrix (floral resources and remnant vegetation) influenced butterfly richness and abundance although the effects were small. Total butterfly abundance responded negatively to exotic floral abundance early in the sampling season and positively to total floral abundance later in the sampling season. Butterfly species richness increased with tree cover. Negative impacts of increased urbanization intensity on butterfly species richness and abundance may be mitigated to some extent by improving the quality of the urban matrix by enhancing tree cover and the provision of floral resources – with some evidence that native plants are more effective.

Keywords – conservation, non-native plants, habitat management, habitat quality, insects, Lepidoptera, local extinction, urban woodland

Introduction:

Urban areas are amongst the fastest expanding land cover types worldwide (Seto et al. 2013). This expansion decreases ecological integrity and drives population decline and local extinctions across several species groups (Aronson et al. 2017). Native species richness and abundance of organisms generally decrease with increasing urbanization, but this trend varies among species with different ecological and life history traits (Dennis 2010, Driscoll et al. 2013), location (Norton et al. 2016) and spatial scale of analysis (Savard et al. 2000, Luck and Smallbone 2010).

When applying ecological frameworks to urban landscapes, such as the patch-matrix model (Forman 1995), large areas of green-space (e.g., parks) are often viewed as habitat patches embedded in an inhospitable environment dominated by impervious surfaces, the 'urban matrix' (Norton et al. 2016). Percent cover of impervious surfaces, hereafter referred to as 'imperviousness', is becoming a common measure of urbanization intensity within the matrix because it better reflects permanent land cover change unlike other proxies such as distance to city center, population density, road density, etc. (McDonnell and Hahs 2008). It is increasingly recognized that the urban matrix, when assessed at fine spatial scales, is highly heterogeneous in terms of its vegetation composition, structure, and management, and thus its ability to support biodiversity (Thompson et al. 2004, Norton et al. 2016, Threlfall et al. 2016). With the exception of recent studies of habitat quality in residential greenspaces (Larson et al. 2014, Lerman and Milam 2016, Narango et al. 2017, Mach and Potter 2018), urban ecology studies have largely focused on understanding factors determining the quality of large patches of green spaces whereas factors underlying fine scale variation in habitat quality within the matrix have largely been overlooked (Sadler et al. 2010, Sattler et al. 2010) - even though matrix quality is recognized as important in other habitat types (Watling and Donnelly 2006).

Butterflies can exploit small disjunct patches of habitat due to their high mobility and small body size, but they are also sensitive to spatial and temporal variation in resource availability (Lütolf et al. 2009, Ibbe et al. 2011, Pohl et al. 2011). In this way, butterflies provide an ideal taxon for investigating urbanization impacts on biodiversity, particularly the response to landscape features of the urban matrix at contrasting spatial scales (Concepción et al. 2015). Recent studies suggest that butterfly species respond negatively to increased urban development (Olivier et al. 2016, Ramírez-Restrepo and MacGregor-Fors 2017, Tzortzakaki et al. 2019). There has been a recent uptick in residential garden studies on butterflies (Burghardt et al. 2009, Fontaine et al. 2016, Olivier et al. 2016), and one recent contribution assessing the urban matrix per se (Tzortzakaki et al. 2019), but most previous studies have primarily focused on butterfly community responses within large patches of green space (Williams 2009, Lizée et al. 2011, Chong et al. 2014, Sing et al. 2016, Aguilera et al. 2019). Consequently, understanding of which habitat features of the matrix influence urban butterfly communities is very limited.

Nectar availability is a key resource that can determine butterfly abundance, as it a common adult food resource (Dennis 2010, Curtis et al. 2015). Urban areas contain a wide range of planted and spontaneous exotic plant species, which can be locally abundant (Loram et al. 2008, Threlfall et al. 2016, Ward and Amatangelo 2018). Butterflies readily use flowers from both native and exotic species (Bergerot et al. 2010, Dennis 2010, Jain et al. 2016). Other than a recent study showing that butterfly richness and abundance in gardens were not influenced by whether plants were native or exotic (Majewska et al. 2018), there is little comprehensive evidence on whether plant origin influences urban butterfly communities. Such effects, though, have been documented for other insect groups that use floral resources, especially some bee guilds (Hanley et al. 2014, Pardee and Philpott 2014, Threlfall et al. 2015). Further, larval host plants are another key resource that can affect butterfly communities and their responses to environmental change (Curtis et al. 2015, Soga et al. 2015). Remnant native vegetation patches can support diverse butterfly assemblages through provision of habitat resources, including larval host plants, shade trees (Williams 2011), and native floral resources - the benefits of which could facilitate spillover effects to influence butterfly communities within the urban matrix (Spear et al. 2018). Further, most butterflies have known habitat affinities (e.g., grassland or woodland; Dennis 2010) and will use a matrix that is structurally similar (i.e. woodland butterflies may key-in on trees in the matrix), particularly if food plants are available (Lütolf et al. 2009, Ibbe et al. 2011, Öckinger et al. 2012, Soga and Koike 2012). It is important to understand the potential mitigating effects of the availability of these features within the urban matrix when assessing the impacts of urbanization on butterfly communities.

Here, we quantify how butterfly species richness and abundance vary along a gradient of imperviousness, in Melbourne, Australia. Our aim is to measure the effects of imperviousness on the butterfly community and to investigate whether attributes that determine matrix quality can mitigate those effects. Specifically, we pose the following questions: 1) does spatial scale influence the butterfly community's response to a gradient of impervious surface cover (used as a metric of urbanization intensity)?, 2) does the provision of native and exotic floral resources have additional effects on the butterfly community?, and 3) do vegetation characteristics, i.e. tree cover and presence of remnant vegetation affect butterfly richness and abundance? Our expectations based on the literature are that both butterfly richness and abundance should decrease with increasing urbanization (i.e., impervious-surface cover) and that impacts will be greater at the local scale. The provision of floral resources is expected to increase butterfly abundance, while we expect that tree cover and the presence of native remnant vegetation will provide a wide range of resources (including larval host plants within remnant vegetation), thus increasing species richness.

Methods:

Study Area:

We conducted this study within the eastern suburbs of Melbourne, Australia's second largest city with approximately 4.5 million residents. Melbourne's greater metropolitan area lies across four bioregions. To minimize variation in biophysical properties (e.g., soil type, climate) and vegetation communities, the study area was restricted to the Gippsland Plain Bioregion which is dominated by a variety of grassy woodland and heathland vegetation types (Hahs et al. 2009). The 28 km-diameter study area, centered in the Boroondara local government area (latitude = -37.829967° S, longitude = 145.071481° E), contains a representative mosaic of residential areas with small to large residential parcels, several local urban centers with higher human population densities, intensively managed sports fields, small pocket parks, and mixed-use woodland reserves, areas of remnant vegetation, and parklands along the Yarra River. Melbourne has a temperate oceanic climate with mild winters and warm summers. The annual mean maximum temperature is 19.9°C, while the mean minimum temperature is 10.2°C. Rain falls throughout the year, but less so in summer, historically averaging 648 mm/year (from 1855 and 2015; Bureau of Meteorology 2020).

Site Selection:

Using ArcMap 10.2 (ESRI, Redlands, CA), a grid of 500 x 500-m cells was generated over the study area. Grid cell imperviousness was calculated using the total impervious surface cover data from a GIS dataset supplied by Melbourne Water (Grace Detailed-GIS Services 2012). This dataset maps all the impervious surfaces (e.g., roads, roofs, sidewalks) within Melbourne's greater metropolitan area using infrared aerial imagery at a 0.5 m resolution. Imperviousness within the grid cells ranged from 2% to 97% across the study area. Twenty cells from each of five imperviousness categories: (0-20%, 20-40%, 40-60%, 60-80%, and 80-100%) were randomly selected giving a total of 100 cells (Fig. 1), in which imperviousness ranged from 2% to 94% and thus closely matched the variation in the wider study area.

#Insert Figure 1 here#

Butterfly Sampling:

We surveyed butterfly abundance and species richness (i.e., butterfly community structure) within each 500 x 500-m cell along a 1-km transect using a modified Pollard Walk, a standard butterfly surveying technique (5 x 5-m sampling box, 50-m/min walking pace; Pollard 1977, Collier et al. 2006). Transect routes were selected along accessible streets, trails or footpaths (sidewalks) and were selected to cover all major land uses within each cell (e.g., industrial, residential, and greenspace) in relation to their relative coverage. Transects were kept as continuous as possible within cells, though 32 cells had a break to cross a busy road and 19 cells had breaks to maneuver around an obstacle or restriction such as waterways, fences, or lack of access between land-uses within the grid cell. All butterflies seen within the sampling box along each transect were recorded and identified to species when possible (using photographs or capture and release with a hand net). All identifications followed Field (2013) and were conducted by a single trained observer (JK) to allow consistency in identifications and avoid double counts. In limited cases (0.03%), butterflies crossed the transect too quickly to be correctly identified to species and were classified to family level (i.e., blues (*Lycaenidae*), darts (*Hesperiidae*), whites (*Pieridae*), or browns (*Nymphalidae*)). These individuals were included in abundance calculations, but only contributed to the species richness counts when no other species of that family were identified on that transect.

Butterfly surveys were conducted between 09:00 and 17:30 when weather conditions were most favorable for butterfly activity, i.e., air temperatures between 13 and 34°C, wind speed <10 km/hr, and cloud cover <60%. Surveys were conducted twice during the austral butterfly flight season to account for seasonal variation in the butterfly community (Appendix S1: Table S1; round 1: 8 November 2014 to 22 January 2015 (late spring into mid-summer); round 2: 23 January to 22

March 2015 (mid-summer into early fall); Williams 2011, Field 2013). At each transect, the first and second survey rounds were conducted at least 50-days apart to avoid counting the same individuals (most individual butterflies live for less than 30-days (Pyle 1992, Orr and Kitching 2010)). To ensure sample completeness we obtained non-parametric chao 1 species richness estimates (based on abundance data) using the 'SpadeR' package (Chao et al. 2016) R 3.5.2 (R Development Core Team 2015). We do so using our combined dataset (to assess the number of species that our survey may have failed to record) and separately for each urbanization category and sampling round (to assess if insufficient sampling completeness could influence our inference regarding spatial and seasonal patterns).

Environmental variables:

Three of four environmental variables of interest (percent cover of impervious surfaces, remnant vegetation, and tree cover) were calculated at two scales, the local scale (500 x 500-m cell, i.e.; the spatial resolution that butterflies were sampled at) and a larger meso-scale (a 750-m radius circular buffer around the center point of each sampling cell) that samples an area which is seven times larger than the local scale, to assess how butterfly response varied between the two spatial extents. The fourth environmental variable, floral resource abundance, was only calculated at the local scale due to logistical constraints on conducting additional fieldwork at our larger spatial scale. Many published studies of multi-scale ecological patterns use arbitrarily chosen scales; such an approach can be informative but it is preferable to select scales that reflect the known ecology of the system, for example based on home range or movement data (Wheatley and Johnson 2009). Daily movement data for Australian butterflies is largely unknown, but our local scale is within the daily movement distance of the non-native Small White (a.k.a., cabbage white; *Pieris rapae*) (250-600-m/day; Jones et al. 1980), and the larger meso-scale is outside the maximum daily distance movement. The contrast in our spatial scales thus fits the recommendation of Wheatley and Johnson (2009) to consider movement distances to choose contrasting and biologically relevant spatial scales in ecological studies. Meso-scale variables are thus likely to influence the structure of butterfly communities by influencing the quality of the habitat through which butterflies could move, while local scale variables are more likely to influence butterfly community structure by determining local resource availability.

Percent tree cover was obtained from a GIS layer which mapped tree cover at a 0.5 x 0.5-m pixel resolution across our focal region using LiDAR data obtained in 2009 ('High_Res_Landcover_2009' supplied by Grace GIS Services). Most of the butterfly species detected in our sampling prefer open woodland/savannah like habitats (Field 2013), thus this variable was included to investigate the influence of tree cover. This tree cover data layer was derived from remotely-sensed data, and as such, it includes vegetation over-hanging impervious surfaces such as roofs, sidewalks, and roads, but was designed to exclude grasslands and large lawns in maintained parks and playing fields. Thus, values obtained from it do not represent a directly inverse value to impervious surface cover.

The amount (ha) of remnant natural vegetation was calculated from a native vegetation GIS layer ('Native Vegetation – Modelled Extent 2005 supplied by Department of Environment, Land, Water & Planning) mapped at a resolution of 12.5 x 12.5-m based on existing maps, ground truthing, and expert validation. Despite being 10 years old, this is the most recent map of remnant native vegetation of the study area. During fieldwork, it became apparent that a number of these mapped remnants had been lost to urban development. Thus, we conducted additional validation using Google Earth aerial imagery taken within five years of our sampling and ground truthing to subsequently remove remnant vegetation polygons that were no longer present.

Most studies sample only a small portion of a site for floral abundance (e.g., median percent of site assessed = 0.69%; Szigeti et al. 2016), but unlike more rural or natural settings, the spatial variability of vegetation within the urban matrix is large (Thompson et al. 2004). Thus, to address relationships between floral abundance and butterflies we measured floral abundance along the entire transect within the same butterfly sampling box (covering approximately 2% of the grid cell plus the vertical extent up to 5 m). Floral surveys were completed within two days of the butterfly surveys, with 90% of them being completed on the same day. Flowering forbs, shrubs, and trees along the transect route were identified to species where possible (otherwise to genus or family); we did not try to identify cultivars or varieties (Thompson et al. 2004). Grasses were excluded *a priori* since they do not produce nectar. Of the 546 taxa of flowering forbs, shrubs, and trees recorded in the study area 404 were identified to species and 142 to genus.

The number of floral units on each flowering plant, i.e., raceme, umbel, capitulum, etc., were recorded in seven categories (<25, 25-50, 51-100, 101-200, 201-500, 501-2000, and 2001-4000 floral units) adapting methods from Feber et al. (1996) and Carvell et al. (2006). These data were used to calculate the abundance of floral resources available to foraging butterflies by using the mid-values of each category to calculate the total number of floral units using only data from species that produce nectar or have nectaries. We did this as nectar is the dominant food source for adult individuals of all the butterfly species detected during our surveys (Orr and Kitching 2010, Field 2013). Plant species were classified as producing nectar based on data for that species or genus obtained through extensive literature searches in Web of Science and Google Scholar (conducted in August and September 2016; Appendix S1: Table S2). We then calculated total floral abundance and that of native and exotic species, defining exotic species as those with known origins outside Australia and its islands. Collecting these data in close association with the butterfly data and then calculating floral abundance values for each sampling round allows for a closer look at the relationship between the butterfly community and available adult food resource.

Data analysis:

Butterfly species richness and abundance, and floral abundance for each cell were compared between sampling rounds 1 and 2 using a Wilcoxon signed rank test in R 3.5.2 (R Development Core Team 2015); a non-parametric test was used because the differences between sampling rounds were not normally distributed. Butterfly species richness and abundance was then modelled as a function of environmental variables by constructing separate models for the two sampling rounds. Two butterfly species – Common Grass Blue (*Zizina otis*) (GB) and the exotic Small White (SW) – were very widespread (occurring in 95% of all cells in both sampling rounds) and were, often by an order of magnitude, the two most common butterfly species within a sampling cell. We thus calculated total species richness and abundance with and without these two species. Species richness including and excluding GB and SW were highly correlated with each other (round 1: Spearman's r = 0.89; round 2: Spearman's r = 0.82), so we constructed statistical models for three response variables: total species richness, total abundance, and abundance excluding GB and SW. Prior to modelling, all data were checked for spatial autocorrelation using the package 'ape' ver. 4.0 (Paradis et al. 2004) in R 3.2.1 (R Core Development Team 2015). For most response variables there was no evidence of spatial autocorrelation, and in all other cases Moran's I values were extremely small and negative (richness round 2: Moran's I = -0.042; abundance of less common species round 1: Moran's I = -0.038 and round 2 = -0.057) indicating negligible spatial autocorrelation.

Butterfly species richness in sampling round 1 was normally distributed, but richness in round 2 had a non-Gaussian distribution and was modelled as a Poisson distribution using a generalized linear model with a log link. Total butterfly abundance, from both sampling rounds, had a Gaussian distribution following logarithmic transformation. Abundance of the less common species (i.e., excluding GB and SW) was highly skewed and therefore modelled as a negative binomial distribution using a generalized linear model with a log link. All modelling was run in R 3.2.1 (R Development Core Team 2015) using the 'Mass' package (Venables and Ripley 2002).

Our set of predictor variables were: i) sampling conditions, i.e., sampling date (with 21 June (austral winter equinox) as day one), time of day (minutes after sun-rise - defined as civil dawn) and air temperature (°C) – these are included as potential confounding variables that could influence butterfly activity, ii) floral abundance (i.e., total, native, and exotic floral abundance), all of which were square root transformed to reduce the skew in their distributions, iii) impervious surface (percentage cover at the local (500 x 500-m grid cell) and meso-scales (750-m buffer), iv) tree cover (percentage cover at the same scales as impervious surface cover) and v) to account for the massive variation in spatial extent of the native vegetation mapping (local: present in 37 of 100 cells, ranging from 525 to 208,522m^2; meso-scale: present in 62 of 100 cells, ranging from 801 to 1,168,500m^2), we opted to include presence/absence of native remnant vegetation (at local and meso-scales). Given the disparity in the range of values across predictor variables these were all, except the presence/absence of remnant vegetation, standardized prior to analysis by centering and scaling using the 'scale' function in R 3.2.1 (R Core Development Team 2015). Data used in modeling are provided in DataS1: 100CellData, while their descriptive statistics can be found in Appendix S1: Table S3.

We used an information theoretic approach to enable multi-model inference (Burnham and Anderson 2002). All possible models were constructed for each of our three key research questions (for model sets see Appendix S1: Table S4). Due to the strong collinearity between imperviousness at the local and meso-scales (Spearman's r = 0.82) we did not include both variables in the same model. Similarly, total floral abundance and exotic abundance were highly correlated in both sampling rounds (round 1 = 0.89, round 2 = 0.97); total floral abundance was also correlated with native abundance in round 1 = 0.79 and hence, these were not included in the same models. Lastly, imperviousness and tree cover were also highly negatively correlated within our study area (cell level = -0.80; buffer level = -0.75; cell level imperviousness with buffer level tree = -0.76; buffer level imperviousness with cell level tree = -0.74) and therefore were not included in the same model. Linear and quadratic terms for each of our key predictor variables were used to account for non-linear relationships (Appendix S1: Table S4).

Question 1 focused on butterfly community responses to urbanization intensity and was addressed by modelling butterfly species richness and abundance as a function of impervious surface cover, whilst taking sampling conditions into account. Question 2 assessed if the availability of floral resources had additional influences on butterfly communities. We thus retained all the best performing models from question 1 (i.e. those with ΔAICc <2 relative to the model with the lowest AICc value) as a series of base models to which all possible combination of additional predictors that measure the amount of floral resources (distinguishing between those from native and exotic plants) were added. Question 3 assessed if the presence/absence of remnant vegetation or percentage tree cover had additional influences on butterfly communities. For the presence/absence of remnant vegetation we again took the base models from question one and then added all combinations of additional predictors that captured information on remnant vegetation. Due to strong collinearity between imperviousness and tree cover, we could not use the same approach as above to address the effect of tree cover on the butterfly community. Thus, the model set was designed to compare the effects of imperviousness and tree cover on the butterfly community structure. (Appendix S1: Table S4). For each question we ranked models using the Akaike Information Criterion corrected for small sample size (AICc) generated using the 'AICcmodavg' R package (Mazerolle 2016). In cases where there was more than one model within two ΔAICc points of the best performing model (i.e. that with the lowest AICc value) we conducted model averaging over all models within two AICc points of the best model. We calculated model-averaged parameter estimates, their associated unconditional standard errors, and model-averaged partial r^2 values. Model averaging was conducted by setting a parameter estimate and partial r^2 for a predictor as zero if it was not present in a given model.

Results:

In total 14 butterfly species were detected during the butterfly surveys, with 10 found in both sampling rounds. One of these species (Small White, SW, *Pieris rapae*) is not native to Australia, and, in addition, two Australian species are not native to Victoria: Orange Palm Dart (*Cephrenes augiades*) and Dainty Swallowtail (*Papilio anactus*). Two of the 14 species detected could be considered larval host plant specialists within Victoria (Appendix S1: Table S5; Field 2013). Species richness estimates (Appendix S1: Table S6) indicate overall our sampling was close to completion with non-parametric Chao 1 species richness estimates suggesting that just 3 species were missed from our surveys. During the floral surveys two additional species were detected - Imperial Jezabel (*Delias harpalyce*) (a tree top dwelling species) and one sighting of either a Blotched (*Candalides acasta*) or Varied Dusky-blue (*C. hyacinthinus*). When comparing observed and estimated species richness within each set of samples (each category of urbanization intensity in each of the two sampling rounds representing early and later parts of the season) sampling completeness was consistently high (Appendix S1: Table S6) although in the first sampling round sampling efficiency was lowest in the least urbanized category – suggesting that our results may slightly underestimate the adverse impacts of urbanization on local species richness earlier in the season. When restricting the regional species pool to those butterflies that do not mainly occur in tree canopies (which are poorly sampled by our pollard walk methodology; Appendix S1: Table S1) during all our fieldwork we detected 15 (24.6%) of the 61 species in the total regional species pool, and 12 (20.7%) of the 58 species native to Victoria.

Mean total species richness per cell (± standard error) was 2.67 ± 0.12 (round 1) and 2.70 ± 0.17 (round 2). These differences were not statistically significant (Z= 1.31, P = 0.91). The most abundant species were GB and SW which comprised 91.00% of the 3037 individual butterflies counted in round 1, and 91.80% of the 1834 individuals counted in round 2. Butterfly abundance excluding GB and SW was higher in the earlier sampling round (round 1: 2.72 ± 0.50, round 2: 1.50 ± 0.27, Z = -2.50, P = 0.006), as was total butterfly abundance (mean abundance round 1: 30.37 ± 3.26 individuals, round 2: 18.34 ± 1.86, Z = -4.85, P < 0.001). Floral abundance was significantly higher in round 1 (mean total floral abundance round 1: 8031.06 ± 653.79, round 2: 3163.66 ± 226.50, Z = -8.34, P < 0.001; mean native floral abundance round 1: 2947.55 ± 393.01, round 2: 564.86 ± 58.7, Z = -7.07, P < 0.001; mean exotic floral abundance round 1: 5083.51 ± 361.53, round 2: 2598.80 ± 196.26, Z = -8.00, P < 0.001).

Question 1: Effects of impervious surfaces and spatial scale dependency

We found consistent evidence that increased imperviousness at local and meso-scales reduced butterfly species richness and abundance in both sampling rounds. These effects had a greater explanatory power than the sampling conditions, i.e., date, time of day, and temperature

(Appendix S1: Table S7). The relative strength of local and meso-scale effects was not consistent between rounds, except with regards to abundance excluding GB and SW in which case local scale effects consistently had greater explanatory power (Appendix S1: Table S7). Species richness declined linearly as local or meso-scale impervious surface increased (Appendix S1: Table S7; Fig. 2). There was evidence for a quadratic relationship between abundance and percentage impervious cover, especially in sampling round 1, with limited variance in abundance when impervious cover was less than 25%, but strong declines in abundance above this threshold (Appendix S1: Table S7; Fig. 2).

Question 2: Effects of floral resources

Incorporating floral abundance measures improved the fit of species richness and abundance models compared to that achieved when only using impervious surface cover, especially when modelling total abundance (cf. Appendix S1: Tables S7 & S8). Butterfly species richness increased with total and native floral abundances in both rounds (Appendix S1: Table S8). In round 1, exotic floral abundance was also positively associated with species richness, but explanatory power was consistently limited (Appendix S1: Table S8).

Total butterfly abundance was negatively associated with exotic floral abundance in sampling round 1 (Fig. 3b), and positively associated with total floral abundance in round 2 (Appendix S1: Table S8; Fig. 3d). Abundance of butterflies excluding GB and SW was negatively correlated with exotic floral abundance in round 1, but all floral abundance metrics had negligible influence on this abundance measure in round 2 (Appendix S1: Table S8). When taking floral abundance into account, the effects of impervious surface cover on butterfly richness and abundance remained similar to those measured when floral abundance was not accounted for, although there were some small reductions in explanatory power (cf. Appendix S1: Tables S7 & S8; Fig. 3a,c).

Question 3: Effects of tree cover and remnant vegetation

Butterfly species richness was positively associated with percentage tree cover in both sampling rounds (Appendix S1: Table S9). Tree cover was not, however, associated with butterfly abundance when taking the percentage impervious surface cover into account.

The presence of remnant vegetation at the local scale slightly increased butterfly species richness in sampling round 2, but had little or no effect on species richness in round 1 or the butterfly abundance measures (Appendix S1: Table S10).

#Insert Figures 2-3 here#

Discussion:

When pooling data across sampling rounds, chao species richness estimates suggest that we detected the majority (82%) of species present in the survey area (Appendix S1: Table S6). Species that are part of the regional species pool but that were not detected in our surveys have flight periods that overlap our survey dates by at least a month (Appendix S1: Table S1) and are thus likely to be extremely rare or genuinely absent from the survey area. We detected approximately one quarter of the butterfly species from the regional species pool, and one fifth of the species native to the state of Victoria. Our study thus suggests that urbanization has caused a substantial reduction in butterfly species richness within the greater Melbourne area. Studies conducted in urban parks find substantial variation in the retention of butterfly species following urbanization, ranging from 5% of regional species (60 species detected during one year in 10 parks in Kuala Lumpur compared to 793 species in peninsular Malaysia; Sing et al. 2016), to 49% of regional species in Adelaide, Australia (surveyed 4 parks over 2 years; Collier et al. 2006) to 89% (35 of 39 species detected in 46 urban and peri-urban remnants over 5 years in Perth, Australia; Williams 2009). Additionally, a long-term study found at least 45% decline in butterfly species in Rome, Italy (Fattorini 2011). The proportion of regional species that we detected in our study area is at the low end of the range reported in these studies, and while most studies had multiple years of data, our chao species richness estimates clearly indicate that our sampling was close to complete. Consequently, while increased sampling intensity or additional field seasons may increase the number of species found in our focal urban area (Westphal et al. 2008, Hughes et al. 2017) it is clear that urbanization has driven a substantial reduction in butterfly species richness within the greater Melbourne area.

Spatial autocorrelation and dispersal barriers

The western part of our study area is delimited by a hard ocean boundary, Port Phillip Bay, contrasting with the eastern end of the study area, which is delimited by the edge of the Gippsland Plain bioregion but contains much green-space. Dispersal of butterflies across the bioregion boundaries could thus have elevated species richness on the eastern boundary, whilst the lack of dispersal at the western boundary could have constrained species richness in those cells, thus driving spatial structure in species richness. Such spatial structure was not, however, detected by our spatial autocorrelation analysis.

Butterfly response to imperviousness

Our results demonstrate that some butterfly species, including native (GB) and exotic (SW) species, can occur at relatively high densities in the urban matrix, despite most species occurring at very low densities. Urban butterfly studies typically, but not invariably, find that species richness and total abundance decline with increasing urbanization intensity (Ramirez-Restrepo and MacGregor-Fors 2017, Tzortzakaki et al. 2019). Results from this study are similar, but extend much of this earlier work by considering whether butterflies respond to urbanization intensity in a non-linear fashion at both local and meso-scales. No evidence was found for a strong unimodal pattern in which species richness peaked at intermediate levels of urbanization. Such unimodal peaks have been documented for various taxa, especially birds, and is thought to be driven by greater habitat diversity or enhanced habitat quality in suburban areas as compared to more developed areas (Marzluff 2005). Within the urban matrix, butterfly abundance did not decline until impervious surface cover increased above 25%. This should not be considered evidence that low levels of urban development do not adversely influence butterfly communities (as evidenced by the large number of regionally occurring species that were not detected), but it does suggest that there is a threshold of development intensity above which urban butterfly abundance may substantially decline. The lack of a unimodal response, whereby richness peaks in suburban areas along the urbanization gradient, also suggests that any increase in habitat diversity in suburban areas that does occur within our study area probably provides might provide limited benefits to butterflies.

Our local-scale urbanization metric relates to a spatial extent that appears to be within butterflies' daily movement distances, and seven times smaller than the extent of our meso-scale urbanization metric. Meso-scale variables are thus likely to influence the structure of butterfly communities by influencing the quality of the habitat through which butterflies could move, while local scale variables are more likely to influence butterfly community structure by determining local resource availability (on the importance of picking appropriate scales, see Wheatly and Johnson 2009).

Species richness and total abundance were negatively associated with local and meso- scale urbanization intensity, with the most influential spatial scale varying between sampling rounds for richness and total abundance. This concurs with Concepción et al. (2015) who found that butterfly communities declined in richness with increasing urbanization intensity, and that such responses were detected at variable spatial scales. The lack of a clear distinction in responses at local and meso-scales suggests that urbanization is likely to impact butterfly communities by reducing local resource availability, and movement capacity through the wider landscape. Notably, however, the abundance of the less common species (excluding GB and SW) was most strongly and consistently influenced by local-scale urbanization intensity. This suggests that even localized efforts to increase habitat quality for butterflies could benefit species that already occur in urban areas. These less common species may also be the least mobile ones as Concepción et al. (2015) found that such species tend to only respond to urbanization at the smallest spatial scales. Urbanization and habitat fragmentation affect rare and specialist species more than generalist species (Kitahara and Fujii 1994, Clark et al. 2007, Lizée et al. 2011, Tzortzakaki et al. 2019), with specialists tending to be less abundant than generalists and more spatially restricted (Kitahara and Fujii 1994). Indeed, all of the species we detected in our dedicated butterfly surveys are classified as generalist based on their wide selection of larval host plants (Appendix 1: Table S5). It thus seems likely that a substantial proportion of the species within the regional species pool that are missing from or very rare within our focal urban area are specialists (either restricted by habitat, mobility, or food resource use), as is the case for the two additional species we detected during the floral surveys, i.e. in Victoria Jezebels use just two genera of mistletoes as larval host plants, which are no longer common within Melbourne's suburbs, and Blotched and Dusky Blues only use two *Cassytha* species as larval host plants (Field 2013).

Butterfly response to floral resources

The abundance of floral resources influenced butterfly species richness and abundance, with the strongest effects being on total butterfly abundance. While much of the work assessing impacts of floral abundance on urban pollinators has focused on taxa other than butterflies (Blackmore et al. 2014, Pardee and Philpott 2014, Lerman and Milam 2016), there is a small literature that similarly highlights the importance of floral abundance to butterflies in urban (Fontaine et al. 2016) and especially non-urban settings (Clausen et al. 2001, Pywell et al. 2004, Kitahara et al. 2008, Curtis et al. 2015). However, it is important to note that, after taking into account the urban gradient and floral abundance, much of the spatial variation in butterfly species richness and abundance remains unexplained by our statistical models. This suggests that other factors, such as availability of larval host plants (Kurylo 2018), anthropogenic disturbance (particularly regular or intensive management), climatic factors and potentially stochastic variation also contribute to the spatial patterning of butterfly community structure along urbanization gradients (Sattler et al. 2010, Lerman and Milam 2016, Aguilera et al. 2019).

While most butterflies are nectar generalists, some species show greater specialization in their floral nectar selection (Stefanescu and Traveset 2009, Dennis 2010), which could limit survival of some butterfly species unable to adapt to new food sources in urban areas (Jain et al. 2016). Native floral abundance had a small positive influence on butterfly richness across the whole season. At the same time, while exotic floral abundance had a negative effect on total butterfly abundance early in the season, total floral abundance had a positive effect later in the season. Regardless, the less common butterflies (i.e. species other than grass-blue and small white), were consistently negatively affected by exotic floral abundance. These two general patterns, native plants increasing butterfly richness and exotic plants having negative effects on butterfly abundance, are compatible with previous research indicating that invertebrate richness and abundance is higher in urban settings with more native plants and their taxonomically close relatives than settings with more exotic plants (Burghardt et al. 2009, Salisbury et al. 2015, Narango et al. 2017). However, we are cautious and do not interpret our results as compelling evidence that exotic plants are unlikely to provide useful nectar resources for butterflies. Our results are correlative. Without behavioral data on which flowers butterflies actually use as nectar sources it would be inappropriate to suggest our results refute literature suggesting that some exotic flowering species can provide beneficial supplementary adult nectar sources within the urban matrix (Bergerot et al. 2010, Dennis 2010, Jain et al. 2016, Majewska et al. 2018, Nagase et al. 2019). There are likely several confounding factors. Indeed, the three most common and abundant plant species found during our surveys are exotic, e.g. *Medicago polymorpha*, *Taraxacum* spp., and *Trifolium repens* and these ubiquitous yard weeds are known to be regularly visited and used by insects in North American urban areas where they are also non-native (Larson et al. 2014, Lerman and Milam 2016). Relative flowering phenology of native versus exotic species and its impact on nectar resource availability could also be key as between the two sampling periods there was a much larger reduction in native floral resource abundance (80% drop; round 1: 2947.55 ± 3930.11, round 2: 564.86 ± 587.66) than exotic floral resource abundance (49% drop; round 1: 5083.51 ± 3615.26, round 2: 2598.80 ± 1962.61). Consequently, and similar to our later season results for total butterfly abundance, exotic plant species may be particularly important at maintaining provision of adult food resources later in the season (Koyama et al. 2018, Mach and Potter 2018). It is also plausible that the apparent negative relationship between butterfly abundance and exotic floral abundance is spurious. It may arise because cells with higher exotic floral abundance are those with more intensively managed gardens or other landscapes that adversely impact butterflies due to other factors associated with high management intensity, such as chemical use, mowing, or reduced abundance of larval host plants. Our results do, however, suggest that butterfly species richness would benefit from planting native floral nectar species within the urban matrix, but more evidence is needed to tease apart the mechanisms driving urban butterfly responses to floral resource availability, especially those provided by exotic plants.

Butterfly response to tree-cover and remnant vegetation

Tree cover had a positive and larger effect on total butterfly richness, particularly at the local scale, than did imperviousness. Importantly, early in the season this effect was more pronounced for the less abundant butterflies (excluding SW and GB), and later in the season was exclusively exhibited by these rarer species. This larger effect of tree cover was unexpected given the pronounced negative effects of imperviousness on butterfly richness that we also found and may suggest that tree cover mediates its negative effects. It could be argued tree cover is a proxy for green space, especially given its negative correlation with imperviousness, but one would have then expected tree cover to also have a relationship with butterfly abundance – which is not the case. Similarly, in reference to a lack of relationship between tree cover and butterfly abundance, the trees within the urban matrix, in general, may not be acting as a substantial nectar resource despite the presence of floriferous native street trees such as Broad-leaved Paperbark (*Melaleuca quinquenervia*). While none of the butterflies in our sampling wholly depend on tree species as either a larval or adult food plant (Field 2013), butterflies are known to use urban matrices that are structurally similar to their known natural habitat (Lütolf et al. 2009, Ibbe et al. 2011, Öckinger et al. 2012, Soga and Koike 2012). Thus, urban tree cover could be providing habitat structures suitable for some butterfly species, particularly those from non-open grassland habitats.

There was negligible evidence that the presence of remnant vegetation increased butterfly abundance, and while remnant vegetation explained little of the variation in species richness in the earlier part of the flight season there was some evidence that remnant vegetation increased species richness in the later part of the flight season (Burghardt et al. 2009, Chong et al. 2013). A number of factors may have contributed to these patterns. First, our analysis was not able to consider the size (from a single pre-settlement tree to several thousand m^2) or quality of patches of remnant vegetation (ranging from restored to degraded). Second, most of the butterfly species detected (12 of 14) in our surveys use a wide range of larval host plants, with nine of those known to readily use exotic plant species (Appendix S1: Table S5; Field 2013); many of which can be readily found, as planted or spontaneous vegetation, within the urban matrix. For instance, the most abundant butterfly species in our surveys, Common Grass Blues (GB), readily use the introduced white clover (*Trifolium repens*) – one of the three most abundant species in our floral abundance surveys - as a larval host plant. In terms of adult food resources, the primarily native flowering plants in remnants and natural areas tend to have a short flowering periods in contrast to the much longer flowering periods of the mostly ornamental plants found in suburban and urban areas (Neil and Wu 2006, Leong and Roderick 2015, Davis et al. 2016). This can perhaps limit the importance of remnant habitats because some of the resources they provide occur elsewhere within the urban environment. Notably, though during the later phase of the flight season, when the abundance of all types of floral resources is lower than earlier in the flight season, we did detect slightly more butterfly species in cells that contained remnant vegetation. It is thus plausible that remnants slightly enhance butterfly richness in the late part of the flight season by providing some resources at this time of year that are relatively rare in the wider urban landscape. More generally though it seems plausible that the loss of more specialized butterfly species following urbanization has reduced the importance of remnant vegetation patches in determining the richness and abundance of those butterfly species that remain in urban environments. Enhancing the diversity of the urban butterfly fauna may well, however, require restoration and expansion of remnant vegetation patches.

Conclusions

We found that impervious surfaces have a negative influence on the butterfly community regardless of the spatial scale of analysis. The vast majority of butterfly species occurring within the regional species pool appear to be excluded from the urban matrix. Tree cover had a positive influence on butterfly richness, but the presence of urban remnant habitats currently does little to bolster butterfly richness or abundance. Only one native butterfly species is abundant within the urban matrix and the community as a whole exhibits further declines in abundance when impervious surface cover exceeds approximately 25%. The less common butterfly species within our community (i.e., all species except GB and SW) are more responsive to local scale environmental variables than those at the larger meso-scale, as suggested for numerous other taxa (Beninde et al. 2015). Our study thus provides evidence that some features of the urban matrix, for example provision of native nectar sources, can be managed to enhance butterfly communities. This study further demonstrates that butterfly richness and abundance respond to different landscape attributes and at different scales within the urban matrix. Further, it also shows that the response is not constant from the earlier and later periods of the flight season. Similar to other taxa, it is important to understand these differential responses when making management suggestions across the urban matrix either for biodiversity restoration, enhancement or conservation (Kudavidanage et al. 2012, Burgio et al. 2015).

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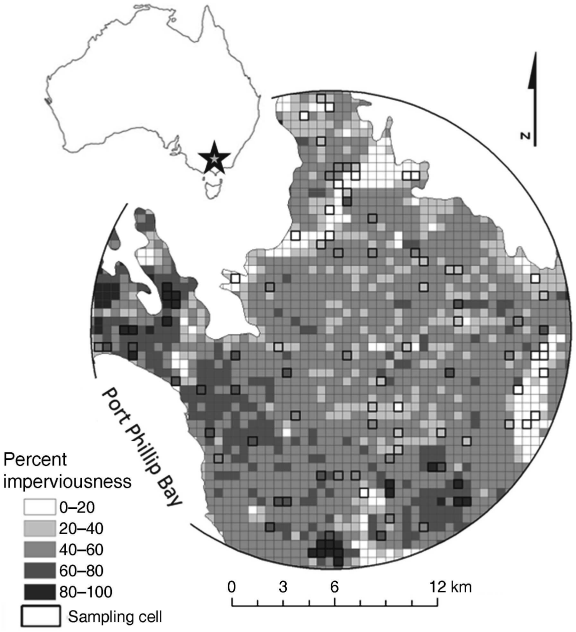
Figure 1 – Percentage cover of impervious surfaces and the location of the sampling cells across the 28-km diameter study area in Melbourne, Australia. Impervious surface cover was measured by using a GIS dataset supplied by Melbourne Water (Grace 2012).

Figure 2 – Predicted relationships between imperviousness and butterfly species richness and butterfly abundance during spring to early-summer (round 1) (a and b) and early-summer to early fall (round 2) (c and d). The weighted model average models in Appendix S1: Table S7 were used to fit the line for each response variable in panels a and b, while weighted model average models in Appendix S1: Table S8 were used to fit the line for panels c and d. Three data points from panels a and b (abundance of 288 at 9.44% imperviousness; abundance of 108 at 43.24% imperviousness; abundance of 84 at 25.25% imperviousness) and two points from panels c and d (richness of 8 at 32.93% and 6 at 11.38% imperviousness; abundance of 110 at 10.42% and 96 at 50.95% imperviousness) have been excluded to improve figure clarity.

Figure 3 – Predicted relationship between butterfly abundance and imperviousness when floral resources are included in the model during the spring to mid-summer (round 1) (a and b) and mid-summer to fall (round 2) (c and d). The weighted model average models in Appendix S1: Table S7 were used to fit the line for each response variable in panels a and b, while weighted model average models in Appendix S1: Table S8 were used to fit the line for panels c and d. Due to unusually high butterfly abundances three data points have been excluded from panels a and b (abundance of 288 at 9.44% imperviousness, 2237 exotic floral abundance (EFA); abundance of 108 at 43.24% imperviousness, 6379 EFA; abundance of 84 at 25.25% imperviousness, 6127 EFA) and two points from panels c and d (abundance of 110 at 9.44% imperviousness, 4719 total floral abundance; abundance (TFA) of 96 at 44.49% imperviousness, 3694 TFA) to improve figure clarity.



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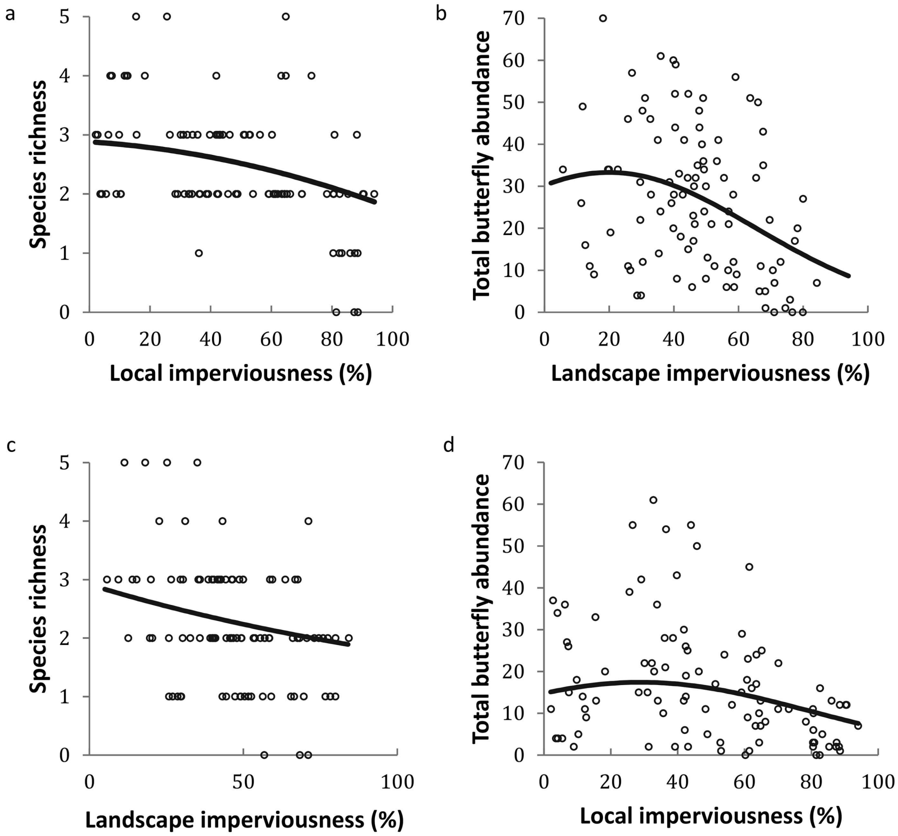

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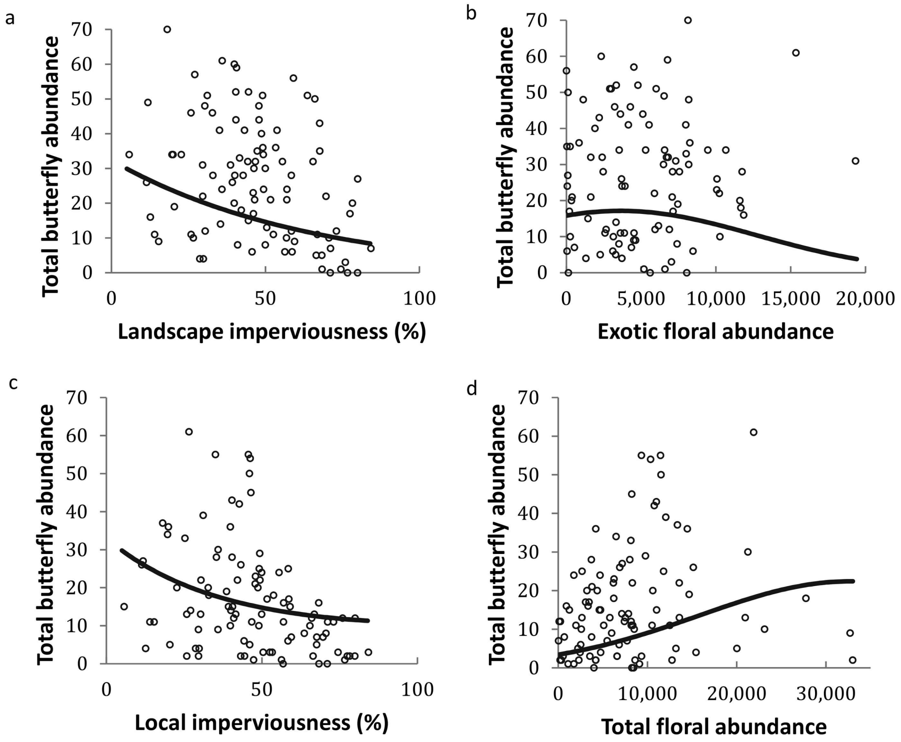

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