Low-intensity urbanisation alters community composition across multiple trophic levels on Lipsi Island, Greece

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Abstract

Urbanisation has reduced the abundance and diversity of many taxonomic groups, and the effects may be more pronounced on islands, which have a smaller regional species pool to compensate. Green spaces within urban environments may help to safeguard wildlife assemblages, and the associated habitat heterogeneity can even increase species diversity. Here, total abundance and species diversity of butterflies, birds, and vegetation at nine rural and nine urban locations were quantified on Lipsi Island, Greece. Sites were assessed using Pollard walks for butterflies, point-count surveys for birds, and quadrats for vegetation. There was no significant difference in the abundance or species diversity of butterflies or vegetation among rural and urban locations, which could pertain to the low building density within urbanised areas and the minimal extent of urbanisation on the island. However, urban areas hosted a significantly greater abundance and richness of birds compared to rural sites. The community composition of butterflies, birds, and vegetation also differed significantly between urban and rural locations, highlighting the impact of urbanisation on species across a broad range of trophic groups. This study contributes to ecological knowledge on the impacts of urbanisation across multiple trophic levels in island ecosystems, with comparisons across a gradient of island size and urbanisation intensity needed in future research.

Introduction:

In the debate regarding global biodiversity decline, urban areas have sometimes been suggested to promote diversity (Cardinale et al., 2018). Urbanisation involves changes in the landscape, soil modifications, climates changes, and biodiversity loss, resulting in a distinct ecosystem (Rodrigues et al., 2018). Fragments of semi-natural spaces such as parks, gardens, and other green areas may provide a diverse plant composition and fulfil ecosystem functions needed to maintain urban wildlife (Townsend, 2008). But they also host ornamental or non-native plants which fail to support native wildlife. Urban habitats place stronger environmental constraints on plant and animal communities than rural ecosystems and may disrupt ecological interactions between plants and pollinators via habitat fragmentation (Hennig and Ghazoul, 2011). Impacts on species richness in urban areas are dependent on the specific taxonomic group, the spatial scale of analysis, and the intensity of urbanisation (McKinney, 2008). A greater species richness in urban areas may be due to the increased number of both native and non-native species, due to the larger species pools that urban areas maintain (Dolan et al., 2011). Moderate levels of urbanisation lead to varying patterns of species diversity across taxonomic groups, particularly when there are sufficient corridors of green space to allow colonisation from the regional species pool (Rega-Brodsky, et al., 2022). Effects of urbanisation on top-down control (e.g., altering predation by birds) or bottom-up control (e.g., altering vegetation structure) could also lead to indirect effects on abundance, species diversity, or community composition throughout the food web (Theodorou, 2022).

Urban areas can be characterised as a spatial assemblage of people whose lives are structured around non-agricultural activities, with rural areas defined as any place that is not classified as urban (Weeks, 2010). Urban areas can also be classified as land that is built over, while rural areas consist of land that is not built over and with a much smaller population size (Bibby and Shepherd, 2004). Rapid urban development and expansion in recent years have altered many wildlife assemblages, especially invertebrates (Van Swaay and Warren., 1999). Perhaps the most well studied group is butterflies, as they are popular, easy to identify, and have been used as model insects for many years (Warren et al., 2021). But butterflies are also in decline due to severe habitat loss and climate change (Zografou et al., 2009). More generally, butterflies are important indicators of ecosystem health due to their susceptibility and sensitivity to changes in the environment (Ghazanfar et al., 2016). Butterflies have a high reproductive rate and occupy low trophic levels; thus, they respond quickly to environmental stressors and could be utilised as a proxy for general reductions in wildlife (Ghazanfar et al., 2016). Here, we focus on butterflies as indicator taxa, whilst considering the impact of urbanisation on their predators and resources.

Urbanisation has been shown to degrade bird communities through species decline and functional homogenisation (Tzortzakaki et al., 2018). The main factors affecting bird species assemblages are green space availability and noise pollution (Rodrigues., 2018). Collisions with buildings in urban areas also heavily affects bird populations, including species of conservation concern (Hager et al., 2017). Vincze et al. (2017) found that in urbanised areas there was an increase in predation of bird nests by urban exploiters such as crows (Corvus spp), magpies (*Pica pica*), and cats (*Felis silvestris catus*). However, it is also suggested that prey populations of birds thrive in urban areas as these habitats are low in abundance of larger predators (Vincze et al., 2017). Cities and towns have variability in terms of the activity or usage of areas, thus bird species distribution in urban areas is related to the degree of urbanisation and habitat features such as tree and shrub cover and the density of buildings (Rodrigues et al., 2018). Moreover, human landscape characteristics favour species that can exploit novel resources and adapt to new habitats, such as hooded crows (*Corvus cornix*), house sparrows (*Passer domesticus*), and pigeons (*Columbidae spp*) (Kark et al., 2007).

The high abundance of adaptive birds in urban environments could thus have negative impacts on invertebrates, specifically butterfly populations compared to rural habitats. However, butterflies have developed various defensive traits against birds, such as chemical cues and aposematic or cryptic colouration, i.e., bright colours in conspicuous patterns on the wings (Paladini et al., 2018). Additionally, many butterflies have adopted fast, unpredictable flight and weak, fragile wings that allow escape by tearing when pecked by birds (Pinheiro and Cintra, 2017). Brighter colouration signals are commonly associated with potent defence and greater reproductive success, as predators are naturally deterred, within-species rivals are more cautious, and potential mates are more interested (Yeager and Barnett, 2021). Due to the high frequency of beak marks on the wings of butterflies, birds are likely their most significant predator (Pinheiro and Cintra, 2017). Nonetheless, small mammals, toads, and lizards also feed on adult butterflies, and there may be significant predation by a variety of invertebrates (Londt, 1999).

Changes in the patterns of vegetation composition and structure in urban areas, can lead to a reduction of bird species richness and selection for omnivores, carnivores, and species which nest in cavities (de Toledo et al., 2012). But native vegetation diversity within green spaces can strengthen the abundance and richness of specialist and insectivorous bird species (Silva et al., 2021). Furthermore, urban vegetation is necessary for mitigating urban heat islands, floods, increasing carbon storage, improving biodiversity, and benefitting human health (Chen et al., 2022). Plant biodiversity is greatly affected in urban areas by the introduction of exotic, non-native species, changes in microhabitat availability, and altered landscape patterns (Peng and Liu, 2007). The introduction of non-native plant species in urban areas degrades habitats and shifts community composition, which can influence ecosystem services and habitat resilience (Dolen et al., 2011). Urbanisation also alters the timing of important reoccurring plant phenology events, such as flowering and leaf-out, leading to cascading consequences on the species within a community and disturbing important interactions such as pollination and herbivory (Li et al., 2019). The gross primary productivity of vegetation also decreases with increasing levels of urbanisation from loss of green land and changing macro-environment (Chen et al., 2022). While habitat enhancements of exotic species may increase ecosystem resilience and integrity, restoration of native communities in urban areas may increase connectivity to surrounding rural landscapes and support native ecosystems (de Carvalho et al., 2022).

There is a mutual and historical co-evolution in operation between plants and invertebrates (Ghazanfar et al., 2016). Co-evolutionary traits include adaptive radiation of plants that evolved to have chemical protection from herbivores, followed by adaptive radiation in herbivores who developed characteristics to counter this defence (Feeny, 1975). For example, the butterfly proboscis attachment has adapted to reach the nectar at the base of long-tubed flowers (Ghazanfar et al., 2016). Alternatively, some skippers (Hesperiidae) are only capable of utilising shallow blossoms, such as flowers in the myrtle family (Myrtaceae) (Ghazanfar et al., 2016). Smaller plant patches found in urban environments tend to receive fewer pollinator visits and suffer pollen limitation (Barker, 2018). This reduces genetic exchange and flowering plant diversity, and consequently, supports fewer pollinator species. Yet, low building density and the presence of green space within urban areas, may drive pollinator movement and thus gene flow between patches (Hennig and Ghazoul, 2011).

Whilst anthropogenic disturbances are fostering negative impacts on butterfly species, human practices have created agricultural and woodland management systems such as hay meadows and coppicing that assist the growth of butterfly populations (Dover and Settele, 2009). The Mediterranean is one of the world's 25 biodiversity hotspots, mainly due to the abundance of endemic species within this area (Lopez-Villalta et al., 2010). The Aegean Sea is located within the Mediterranean where butterfly species vary between the islands. In this area, Haahtela et al. (2019) recorded the highest levels of diversity on Samos Island (64 species) and Lesbos Island (63 species) (Haahtela et al., 2019). The evolution, extinction, and species migration of animals and plant species over archipelago islands are reflected in the pattern of species diversity (Dennis et al., 2000). Therefore, a distinct and endemic species assemblage of butterflies may be present across the Aegean islands. This highlights the importance of green space within Mediterranean urban areas and a demand to assess the butterfly species within this environment. The study of butterflies within the Aegean region is severely lacking and mainly focuses on biogeographical studies (e.g., Dennis et al., 2000; Hammoud et al., 2021; Hausdorf and Hennig, 2005), thus, the specific habitat types that butterflies utilise is not known. When studying Tuz Lake in Turkey, Seven (2017) compared habitat preferences of butterflies and observed the highest species diversity within the steppe habitat (defined as semi-arid grassland) and the lowest diversity in the stony and rocky area (poorly vegetated areas dominated by rocks), indicating that species may prefer vegetated and shaded areas. Due to the global decline of butterflies, the exploration of urban green space as a possible diversity hotspot is crucial and contributes to current research. As butterfly ecology has been seldom studied within the Aegean, an investigation of the urban and rural habitats adopted by butterflies in island ecosystems is of high ecological importance.

This study aims to compare the ecological communities found in rural areas and urban green spaces on Lipsi Island, Greece. It is hypothesised that total abundance, species richness, and Shannon diversity of (1) butterflies, (2) birds, and (3) vegetation will be higher in rural compared to urban sites and that (4) urbanisation will have an impact on community composition of each trophic group.

Methodology:

Study sites

The study was conducted during the months of May and June 2021 on Lipsi Island, Greece (approximate area: 17 km^2), which is located within the eastern Aegean Sea (37° 17' 44.7" N, 26° 46' 45.5" E) and used as a model small island ecosystem. Nine urban and nine rural sites with clear separation were selected (Figure 1). The minimum distance between study sites in urban areas was 75.3 m, which limited the double counting of individuals. Due to the lack of trees, shade is restricted on Lipsi Island, thus, locations with high light intensity and low shade were utilised to give an accurate representation of the urban and rural habitats used by butterfly species. Sites were chosen to represent the predominant land-use types utilised by butterflies during one or several stages of their life cycle (Grill and Cleary, 2003). The chosen rural habitats were shrubland, olive groves, and meadows, while the urban habitats included agricultural meadows, abandoned land, parks, roadsides, and olive groves. The sites were similar in size to keep the sampling effort consistent.

Butterfly sampling

The sampling technique implemented was the butterfly census method, which is widely used by the UK Butterfly Monitoring Scheme (UKBMS). Developed in 1973 by Ernest Pollard (Sevilleja et al., 2019), this method uses W- or M-shaped transects to cover heterogeneity within the sampling area. The key variables to standardise with this method are the transect length, walking speed, time of day, and weather (Wheater et al., 2011). The implemented method was adapted from Zografou et al. (2009). The four corners of each site were located using QGIS to create a square shaped plot for one Pollard transect, ranging from 40 – 70 m. The average site size for both urban and rural plots was 583.2 ± 55.1 m^2 (mean ± standard error). Butterflies observed 5 m in front and on either side of the transect were recorded and identified. According to Wheater et al. (2011), butterfly surveys should be performed between 10:00 and 16:00, but preliminary surveys indicated that butterflies on Lipsi were very sensitive to changes in temperature during these hours and the highest abundance of butterflies was found before 10:00. Therefore, butterfly surveys were undertaken between 07:00 and 10:00 with temperatures $<$ 27 °C and wind conditions $<$ 25 km h^{-1}. The "*Butterflies of Britain and Europe: A photographic guide* " was used for species identification (Haahtela et al., 2019). One transect was conducted at each site in both May and June for a total sample size of $n = 36$.

Bird sampling

Point-counts were also implemented to quantify the degree to which birds affect butterfly populations in urban and rural habitats (Huff et al., 2000). Using binoculars, two people recorded species and number of individuals in point-count surveys for 5 minutes in each compass direction, starting with North, and rotating through East, South, and West. The total survey time was 20 minutes, whereby five minutes in each direction within a small sampling site helps to avoid counting the same individuals twice (Lee and Marsden, 2008). The start and end times were recorded, as well as the species and number of individuals. Bird distance to the habitat was also estimated and assigned one of the four categories: (1) 0 to 50 m from the station centre point: birds up to top of vegetation or canopy; (2) $>$ 50 m from the station centre point: birds up to top of vegetation or canopy; (3) Fly-over associated with the habitat: birds above the top of the canopy; (4) Fly-over independent of the habitats: birds above the top of the canopy, which do not seem to be interacting with the environment (Huff et al., 2000). Observations took place between 05:30 and 10:00 with wind $<$ 30 km h^{-1} and when there was no rain or fog. The "*Birds of Greece* " was used for species identification (Nason, 2020). This sampling method was conducted at each site in May and June for a total sample size of $n = 36$.

Vegetation sampling

On the first visit to each site, the percentage cover of shrubs and bare ground were recorded using the same quadrats for percentage cover of plants, and the percentage cover of trees was later recorded using Google Maps. Plant surveys were conducted following Tzortzakaki et al. (2019), with four 0.5 m^2 quadrats established at even distances along the butterfly transects. The small quadrat size was due to the limited spatial extent of the sites. The percentage cover of each plant species was recorded for each quadrat, with vegetation surveys conducted at each site in May and June for a total sample size of$n = 144$. The app "PictureThis" was used alongside local taxonomic expertise for species identification (Glority Global Group Limited, 2020).

Data analysis

The abundance, species richness, and species diversity of vegetation, butterflies, and birds found at each site were quantified as the number of individuals, number of unique species, and Shannon index, respectively. The butterfly, bird, and vegetation data were tested for normality using the Shapiro-Wilk test and Q-Q plots, and tested for homogeneity of variance using the Bartlett test and boxplots. If the data met the parametric assumptions of normality and homogeneity, then the Student's t-test was used to compare urban and rural sites, otherwise the Wilcoxon rank-sum test was used. Non-metric multidimensional scaling (NMDS) was used to explore the differences in community composition between rural and urban sites, with significant differences tested using PERMANOVA. All analyses were performed using R 3.5.2 (R Core Team, 2021). Data were organised using the '*tidyr* ' package (Wickham et al., 2019), graphs were created using '*ggplot2* ' (Wickham et al., 2019), '*cowplot* ' (Wilke, 2019), and '*gridExtra* ' (Auguie, 2017), and diversity and ordination analysis were performed with the '*vegan* ' package (Oksanen et al., 2019).

Results:

A total of 156 butterfly individuals (85 rural and 71 urban) from 14 species, 1,668 bird individuals (511 rural and 1157 urban) from 12 species and a 15 ± 0.9% (mean ± standard error) percentage cover of plants from 115 species (220 rural and 189 urban) were recorded across the 18 study sites. The most abundant butterfly species were Freyer's grayling (*Hipparchia fatua* ; 49 individuals, 7 in urban, 42 in rural), Scarce swallowtail (*Iphiclides podalirius* ; 21 individuals, 20 in urban, 1 in rural), and Mallow skipper (*Carcharodus alceae* ; 21 individuals, all in urban). The most abundant bird species were House sparrow (*Passer domesticus* ; 588 individuals, 559 in urban, 29 in rural), Yellow-legged gull (*Larus michahellis* ; 452 individuals, 277 in urban, 152 in rural), and Hooded crow (*Corvus cornix* ; 395 individuals, 152 in urban, 243 in rural). The most abundant vegetation species were Desert saltgrass (*Distichlis spicata* ; present in 37 quadrats, 5 in urban, 32 in rural), Slender wild oat (*Avena barbata* ; present in 24 quadrats, 10 in urban, 14 in rural), and Mastic shrub (*Pistacia lentiscus* ; present in 19 quadrats, 6 in urban, 13 in rural).

Butterflies

The abundance of butterflies was greater at rural (2.43 ± 0.44; mean ± standard error) compared to urban sites (2.09 ± 0.31), but there was no significant difference between the two locations (Wilcoxon rank-sum test: W = 603.0, p = 0.92; Figure 2A). The species richness of butterflies was greater at urban (2.83 ± 0.44) compared to rural sites (1.94 ± 0.27), but there was no significant difference between locations (Wilcoxon rank-sum test: W = 71.5, p = 0.11; Figure 2B). The Shannon diversity of butterflies was also greater at urban (0.74 ± 0.15) compared to rural sites (0.45 ± 0.11), however the two locations did not differ significantly (Wilcoxon rank-sum test: W = 78.0, p = 0.20; Figure 2C). These results conclusively reject our first hypothesis.

Birds

The abundance of birds was greater at urban (6.06 ± 0.56; mean ± standard error) compared to rural sites (4.56 ± 0.55), and there was a significant difference between the two locations (Wilcoxon rank-sum test: W = 8842, p = 0.010; Figure 3A). The species richness of birds was greater at urban (2.85 ± 0.18) compared to rural sites (2.19 ± 0.18), and both locations differed significantly (Wilcoxon rank-sum test: W = 1277, p = 0.016; Figure 3B). The species diversity of birds was greater at urban (0.67 ± 0.06) compared to rural sites (0.51 ± 0.07), but there was no significant difference between the two locations (Wilcoxon rank-sum test: W = 1409, p = 0.09; Figure 3C). These results conclusively reject our second hypothesis, with evidence for a greater abundance and species richness of birds in urban, not rural habitats.

Vegetation

The percentage cover of bare ground was greater at urban (53.6 ± 20.0; mean ± standard error) compared to rural (41.3 ± 26.6) sites, and there was a significant difference between the two locations (Wilcoxon rank-sum test: W = 2055.5; p = 0.035; Figure 4A). The percentage cover of shrubs was lower at urban (5.28 ± 7.41) compared to rural (15.1 ± 14.2) sites, and both locations differed significantly (Wilcoxon rank-sum test: W = 3050; p = 0.017; Figure 4B). The percentage cover of trees was greater in urban (23.9 ± 22.0) compared to rural sites (14.4 ± 21.7), but the two locations were not significantly different (Wilcoxon rank-sum test: W = 28; p = 0.279; Figure 4C). The percentage cover of vegetation was greater at rural (17.5 ± 1.31) compared to urban (15.9 ± 1.24) sites, but there was no significant difference between the two locations (Wilcoxon rank-sum test: W = 19968;p = 0.47; Figure 4D). The species richness of vegetation was greater at rural (rural = 3.10 ± 0.19) compared to urban sites (3.00 ± 0.18), but there was no significant difference between locations (Wilcoxon rank-sum test: W = 2270.5; p = 0.88; Figure 4E). The Shannon diversity of vegetation was greater at urban (0.81 ± 0.06) compared to rural sites (0.77 ± 0.06), but the two locations were not significantly different (Student's t-test: $t_{131.8}$= -0.41; p = 0.68; Figure 4F). These results conclusively reject our third hypothesis.

Community composition

There was a significant effect of urbanisation on butterfly community composition (PERMANOVA: $F_{8,1}$ = 2.96; p = 0.013), with a clear separation between urban and rural sites in NMDS space (Figure 5A). There was also a significant effect of urbanisation on bird community composition (PERMANOVA: $F_{8,1}$ = 11.46, p = 0.001), with a clear separation between rural and urban sites in NMDS space (Figure 5B). Finally, there was a significant effect of urbanisation on vegetation community composition (PERMANOVA: $F_{8,1}$ = 5.93, p = 0.001), with a clear separation between urban and rural sites in NMDS space (Figure 5C). These results conclusively support our fourth hypothesis.

Discussion:

Butterflies

Surprisingly, urbanisation had no effect on the abundance, richness, or diversity of butterfly species on Lipsi Island (Figure 2). Habitat connectivity may be amplified due to the small spatial extent of the island, enabling butterflies to utilise both rural and urban habitats. The low building density and development of ecological corridors on Lipsi may also increase movement between urban and rural areas (Hennig and Ghazoul., 2011). Nonetheless, there was a significant change in butterfly community composition between urban and rural habitats (Figure 5a), as found in several other locations (Numa et al., 2016, Stefanescu et al., 2004, Tzortzakaki et al., 2019). Butterfly species respond differently to the environmental constraints encountered along an urbanisation gradient due to variation in tolerance levels associated with life history and distribution (Pignataro et al., 2020). For example, a study in Patras city, Greece, showed that specialist butterfly species with specific feeding requirements were often absent from urban environments, whereas generalists exhibited a greater abundance in urban areas (Tzortzakaki et al. 2019). Habitat fragmentation and reduced connectivity due to urbanisation may lead to a decline in specialist species within these areas (Kuussaari et al., 2021; Brückmann et al., 2010), however, the Geranium Bronze (*Cacyreus marshalli*) and Mallow Skipper (*Carcharodus alceae*) were more abundant in urban areas on Lipsi, despite being specialists. Geranium Bronze is highly associated with cultivated geranium plants (*Pelargonium*) found in gardens and parks, whilst the Mallow Skipper caterpillar feeds on mallow plants (Malvaceae) which are weeds found in urban waste ground, roadsides, and gardens (Tzortzakaki et al., 2019). Therefore, the presence of cultivated plants within urban locations could mitigate the loss of natural vegetation and support certain specialist species (Chong et al., 2014), whilst generalist or opportunistic butterflies may be able to exploit the resources found in both urban and rural locations (Pignataro et al., 2020).

Birds

Urban sites had a greater abundance and species richness of birds compared to rural sites (Figure 3), which could be attributed to the addition of species accustomed to urban environments, termed "urban exploiters" (Crooks et al., 2004). For example, Rock Doves (*Columba livia*), and House Sparrows (*Passer domesticus*) are dexterous at exploiting discarded food, utilising human made nesting sites (roofs) and other resources in urban environments, and consequently achieving higher densities in developed areas (Blair et al., 1996). Indeed, sparrows were abundant in urban locations in our study (559 individuals) and were much less common in rural areas (29 individuals), echoing the finding of Belinsky et al, (2019). This dominance of adaptable bird species in urban locations underpinned the disparity in community composition compared to rural habitats (Figure 5b), with urban areas usually supporting fewer species from ecologically sensitive groups, e.g., ground nesters, migratory birds, and dietary specialists (Dale, 2018; Blair et al., 1996). Our findings differ from prior research suggesting that species richness is lower in urban areas due to the prevalence of buildings over vegetation (Kark et al., 2007, Tzortzakaki et al., 2018). Several studies have found that species richness peaks with intermediate levels of urbanisation which resonates with the low-intensity urbanisation found on Lipsi Island (Crooks et al., 2004, Blair et al., 1996). Indeed, eight of our nine urban sites are naturally vegetated and underdeveloped, consistent with the findings from White et al. (2005), showing that underdeveloped areas had a greater abundance and species richness of birds compared to recently developed locations.

Nevertheless, the greater abundance and species richness of birds in urban areas did not seem to elevate the predation pressure on butterflies, which had similar abundance and diversity in urban and rural environments. This could be due to increased dominance of non-predatory functional groups of birds, with Nason et al. (2021) finding a greater abundance of granivorous and omnivorous birds rather than insectivores in urban areas, perhaps due to the abundance of discarded food available there, causing a decline in overall bird attacks on animal prey. Indeed, urban dominance by omnivorous House Sparrows, Hooded Crows, and Yellow-Legged Gulls on Lipsi may have reduced predation pressure on butterflies in urban areas. However, the insectivorous Barn Swallows and Common House Martins were more abundant in urban (93 individuals) compared to rural (32 individuals) sites, suggesting complex effects of urbanisation on food web interactions that would require dietary studies to disentangle.

Changes in predation pressure are further complicated by responses of non-avian predators to urbanisation. For example, robber flies (Asilidae spp), which are important predators of butterflies (Londt, 1999; Lehr et al., 2007), were seen in almost every shrubland site, but rarely in urban areas. Aposematism defence (use of vibrant colours) acts as a warning for predators (Pinheiro and Cintra, 2017), and butterflies with intricate camouflage such as meadow brown and graylings were observed to be more abundant in rural habitats (63 individuals) compared to urban locations (13 individuals). This may point to the greater predation pressure experienced by butterflies in rural areas and could help to explain the surprising similarity in abundance and diversity of butterflies in rural compared to urban environments.

Vegetation

The lack of significant differences in the abundance, richness, and diversity of plants between urban and rural sites (Figure 4d-f) could be due to the limited spatial extent of habitat patches and the prevalence of native, unmanaged vegetation within urban green spaces on Lipsi. Whilst rural areas had significantly more shrubs and less bare ground than urban sites, there was no difference in the cover of trees, which are scarce on Lipsi, negating the possibility for greater tree cover to promote butterfly species richness (Kurylo et al. 2020). The lack of a marked difference in vegetation structure between urban and rural areas could thus be a key factor in explaining the similarity in butterfly abundance and diversity across habitats. A prevalence of non-native plant species in urban areas may prevent larval development of butterflies (Dylewski et al., 2019), but exotic species were only present at three urban sites and in low abundance, limiting their potentially negative effects on butterflies. Furthermore, butterfly abundance responds negatively to non-native plants in late spring and positively by mid-summer (Kurylo et al., 2020), highlighting the importance of greater temporal resolution of sampling to characterise vegetation effects on butterflies.

Urbanisation altered vegetation community composition (Figure 5c), with cultivated barley (*Hordeum vulgare*), castor bean (*Ricinus communis*), and scutch grass (*Cynodon dactylon*) prevalent in urban environments, while natural Mastic shrubs (*Pistacia lentiscus*), wild oats (*Avena barbata*), and desert saltgrass (*Distichlis spicata*) dominated in rural environments. This may have contributed to the observed differences in butterfly community composition, with cultivated patches hosting different butterfly assemblages than natural forests and scrub (Chong et al., 2014). Thus, whilst we did not detect any effect of urbanisation on the abundance or diversity of the vegetation and butterfly assemblages, the observed changes in taxonomic identity could have major implications for ecosystem functioning, which should be quantified in future studies.

Conclusion:

There remains a pressing concern of global declining butterfly populations, mainly due to anthropogenic pressure from urban development (Van Swaay and Warren., 1999). Green spaces within urban locations may help to maintain total abundance and species diversity (Hennig and Ghazoul, 2011), but habitat fragmentation and smaller size and quality of habitat patches will alter community composition (Belinsky et al., 2019). The structural similarities between urban and rural habitats and the limited extent of urbanisation on Lipsi Island may have driven the overlap in abundance and diversity of butterflies and vegetation, whilst the greater habitat heterogeneity and discarded food in urban environments could have promoted the abundance and species richness of generalist and opportunistic birds. Thus, metrics other than simple counts of individuals and species are needed to characterise the impacts of urbanisation on community composition across multiple trophic levels. Future research should aim to characterise changes in community structure along a gradient of urban development and island size and the implications for ecosystem functioning. Whilst butterflies were considered as important indicator species here, follow-up studies should quantify effects of urbanisation on other pollinators and arthropod assemblages for a more complete understanding of changes throughout the food web. Finally, dietary characterisation is required to quantify changes in the strength and diversity of ecological interactions, which could help elucidate impacts of urbanisation on the flow of energy through ecological networks.

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Authors contributions

ERH, NC, and EOG conceptualised the study. ERH and EOG designed the methodology. ERH performed the investigation, data curation, visualisation, analysis, and preparation of the first draft. LM, AMM, and EOG supervised the project. AM provided resources and project administration. All authors reviewed and edited the manuscript and agreed to the final version.

Data availability statement

The data that supports this study are available in Supporting Information.

Conflicts of interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

References:

Aguilera, G., Ekroos, J., Persson, A.S., Pettersson, L.B. and Öckinger, E., 2019. Intensive management reduces butterfly diversity over time in urban green spaces. Urban Ecosystems, 22(2), pp.335-344. https://doi.org/10.1007/s11252-018-0818-y

Auguie, B., 2017. gridExtra: Miscellaneous Functions for "Grid" Graphics. R package version 2.3. https://CRAN.R-project.org/package=gridExtra

Barker, C., 2018. Impacts of an urbanization gradient on pollination services to a bee-pollinated plant (Doctoral dissertation, Université d'Ottawa/University of Ottawa). http://dx.doi.org/10.20381/ruor-22563

Belinsky, K., Ellick, T. and LaDeau, S., 2019. Using a birdfeeder network to explore the effects of suburban design on invasive and native birds. Avian Conservation and Ecology, 14(2). https://doi.org/10.5751/ACE-01408-140202

Bibby, P. and Shepherd, J., 2004. Developing a new classification of urban and rural areas for policy purposes–the methodology. *London: Defra* .

Blair, R.B., 1996. Land use and avian species diversity along an urban gradient. Ecological applications, 6(2), pp.506-519. https://doi.org/10.2307/2269387

Brückmann, S.V., Krauss, J. and Steffan-Dewenter, I., 2010. Butterfly and plant specialists suffer from reduced connectivity in fragmented landscapes. Journal of Applied Ecology, 47(4), pp.799-809. https://doi.org/10.1111/j.1365-2664.2010.01828.x

Cardinale, B.J., Gonzalez, A., Allington, G.R. and Loreau, M., 2018. Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. Biological Conservation, 219, pp.175-183. https://doi.org/10.1016/j.biocon.2017.12.021

Carvalho, C.A., Raposo, M., Pinto-Gomes, C. and Matos, R., 2022. Native or Exotic: A Bibliographical Review of the Debate on Ecological Science Methodologies: Valuable Lessons for Urban Green Space Design. *Land* , *11* (8), pp.1201. https://doi.org/10.3390/land11081201

Chen, Y., Huang, B. and Zeng, H., 2022. How does urbanization affect vegetation productivity in the coastal cities of eastern China? Science of The Total Environment, 811, p.152356. https://doi.org/10.1016/j.scitotenv.2021.152356

Chong, K.Y., Teo, S., Kurukulasuriya, B., Chung, Y.F., Rajathurai, S. and Tan, H.T.W., 2014. Not all green is as good: Different effects of the natural and cultivated components of urban vegetation on bird and butterfly diversity. Biological Conservation, 171, pp.299-309. https://doi.org/10.1016/j.biocon.2014.01.037

Connell, J.H., 1978. Diversity in tropical rain forests and coral reefs. Science, 199(4335), pp.1302-1310. https://doi.org/10.1126/science.199.4335.1302

Crooks, K.R., Suarez, A.V. and Bolger, D.T., 2004. Avian assemblages along a gradient of urbanisation in a highly fragmented landscape. Biological conservation, 115(3), pp.451-462. https://doi.org/10.1016/S0006-3207(03)00162-9

Dale, S., 2018. Urban bird community composition influenced by size of urban green spaces, presence of native forest, and urbanisation. Urban Ecosystems, 21(1), pp.1-14. https://doi.org/10.1007/s11252-017-0706-x

Dennis, R.L., Shreeve, T.G., Olivier, A. and Coutsis, J.G., 2000. Contemporary geography dominates butterfly diversity gradients within the Aegean archipelago (Lepidoptera: Papilionoidea, Hesperioidea). Journal of Biogeography, 27(6), pp.1365-1383. https://doi.org/10.1046/j.1365-2699.2000.00514.x

Dover, J. and Settele, J., 2009. The influences of landscape structure on butterfly distribution and movement: a review. Journal of Insect Conservation, 13(1), pp.3-27. https://doi.org/10.1007/s10841-008-9135-8

Dylewski, Ł., Maćkowiak, Ł. and Banaszak-Cibicka, W., 2019. Are all urban green spaces a favourable habitat for pollinator communities? Bees, butterflies and hoverflies in different urban green areas. Ecological Entomology, 44(5), pp.678-689. https://doi.org/10.1111/een.12744

Feeny, P., 1975. Biochemical coevolution between plants and their insect herbivores. Coevolution of Animals and Plants. https://doi.org/10.7560/710313-002

Frentiu, F.D., 2010. The colorful visual world of butterflies.*Encyclopedia of the Eye* , pp.326-333. https://doi.org/10.1016/B978-0-12-374203-2.00163-9

Getis, A., 2005. Spatial pattern analysis. pp.627-632. https://doi.org/10.1016/B0-12-369398-5/00336-4

Ghazanfar, M., Malik, M.F., Hussain, M., Iqbal, R. and Younas, M., 2016. Butterflies and their contribution in ecosystem: A review. Journal of Entomology and Zoology Studies, 4(2), pp.115-118.

Glority Global Group Limited (2020) *Picture This* (Version 3.18.1) [Mobile app]. Available at: App store (Downloaded: October 2020)

Grill, A. and Cleary, D.F., 2003. Diversity patterns in butterfly communities of the Greek nature reserve Dadia.Biological Conservation, 114(3), pp.427-436. https://doi.org/10.1016/S0006-3207(03)00070-3

Haahtela, T., Saarinen, K., Ojalainen, P., Aarnio, H., 2019. Butterflies of Britain and Europe: A photographic guide. Bloomsbury Publishing. ISBN: 9781472960559, 1472960556

Hager, S.B., Cosentino, B.J., Aguilar-Gómez, M.A., Anderson, M.L., Bakermans, M., Boves, T.J., Brandes, D., Butler, M.W., Butler, E.M., Cagle, N.L. and Calderón-Parra, R., 2017. Continent-wide analysis of how urbanization affects bird-window collision mortality in North America. Biological Conservation, 212, pp.209-215.

Hammoud, C., Kougioumoutzis, K., Rijsdijk, K.F., Simaiakis, S.M., Norder, S.J., Foufopoulos, J., Georgopoulou, E. and Van Loon, E.E., 2021. Past connections with the mainland structure patterns of insular species richness in a continental-shelf archipelago (Aegean Sea, Greece). Ecology and Evolution. https://doi.org/10.1002/ece3.7438

Hausdorf, B. and Hennig, C., 2005. The influence of recent geography, palaeogeography and climate on the composition of the fauna of the central Aegean Islands. Biological Journal of the Linnean Society, 84(4), pp.785-795. https://doi.org/10.1111/j.1095-8312.2005.00467.x

Hennig, E.I. and Ghazoul, J., 2011. Plant–pollinator interactions within the urban environment. Perspectives in Plant Ecology, Evolution and Systematics, 13(2), pp.137-150. doi:10.1016/j.ppees.2011.03.003

Hogsden, K.L. and Hutchinson, T.C., 2004. Butterfly assemblages along a human disturbance gradient in Ontario, Canada. Canadian Journal of Zoology, 82(5), pp.739-748. https://doi.org/10.1139/z04-048

Huff, M.H. Bettinger, K.A. Ferguson, H.L. Brown, M.J. Altman, B., 2000. A habitat-based point-count protocol for terrestrial birds, emphasizing Washington and Oregon (Vol. 501). US Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Kark, S., Iwaniuk, A., Schalimtzek, A. and Banker, E., 2007. Living in the city: can anyone become an 'urban exploiter'? Journal of Biogeography, 34(4), pp.638-651. https://doi.org/10.1111/j.1365-2699.2006.01638.x

Kurylo, J.S., Threlfall, C.G., Parris, K.M., Ossola, A., Williams, N.S.G. and Evans, K.L., 2020. Butterfly richness and abundance along a gradient of imperviousness and the importance of matrix quality. Ecological Applications, 30(7), p.e02144. https://doi.org/10.1002/eap.2144

Kuussaari, M., Toivonen, M., Heliola, J., Poyry, J., Mellado, J., Ekroos, J., Hyyrylainen, V., Vaha-Piikkio, I. and Tiainen, J., 2021. Butterfly species' responses to urbanisation: differing effects of human population density and built-up area. Urban Ecosystems, 24(3), pp.515-527. https://doi.org/10.1007/s11252-020-01055-6

Lee, D.C. and Marsden, S.J., 2008. Adjusting count period strategies to improve the accuracy of forest bird abundance estimates from point transect distance sampling surveys. Ibis, 150(2), pp.315-325. https://doi.org/10.1111/j.1474-919X.2007.00790.x

Lehr, P.A., Ghahari, H. and Ostovan, H., 2007. A contribution to the robber flies of subfamilies Stenopogoninae and Asilidae (Diptera: Asilidae) from Iran. Far Eastern Entomologist, 173(1.14). ISSN: 1026-051X

Lev-Yadun, S., 2018. Mullerian and Batesian mimicry out, Darwinian and Wallacian mimicry in, for rewarding/rewardless flowers. Plant signaling & behavior, 13(6), p.e1480846. https://doi.org/10.1080/15592324.2018.1480846

Li, D., Stucky, B.J., Deck, J., Baiser, B. and Guralnick, R.P., 2019. The effect of urbanization on plant phenology depends on regional temperature. *Nature Ecology & Evolution* , *3* (12), pp.1661-1667. https://doi.org/10.1038/s41559-019-1004-1 Lopez-Villalta, J.S., 2010. Ecological trends in endemic Mediterranean butterflies. Bulletin of Insectology, 63(2), pp.161-170. ISSN 1721-8861.

Londt, J.G., 1999. Butterfly predation by robber flies (Diptera: Asilidae). Lepidopterists' Society of Africa, p.24.

McKinney, M.L., 2008. Effects of urbanisation on species richness: a review of plants and animals. Urban ecosystems, 11(2), pp.161-176. https://doi.org/10.1007/s11252-007-0045-4

Nason, L.D., Eason, P.K., Carreiro, M.M., Cherry, A. and Lawson, J., 2021. Caterpillar survival in the city: attack rates on model lepidopteran larvae along an urban-rural gradient show no increase in predation with increasing urban intensity. Urban Ecosystems, pp.1-12. https://doi.org/10.1007/s11252-020-01091-2

Nason, R., 2020. Birds of Greece. 1st ed. Bloomsbury Publishing.

Numa, C., van Swaay, C. and Wynhoff, I., 2016. The status and distribution of Mediterranean butterflies. IUCN. DOI:10.2305/IUCN.CH.2016.MRA.6.en

Ockinger, E., Dannestam, A. and Smith, H.G., 2009. The importance of fragmentation and habitat quality of urban grasslands for butterfly diversity. Landscape and Urban Planning, 93(1), pp.31-37. https://doi.org/10.1016/j.landurbplan.2009.05.021

Oksanen, J. Blanchet, G. Friendly, M. Kindt, R. Lengendre, P. McGlinn, D. Minchin, P.R. O'Hara, R.B. Simpson, G.L. Solymos, P. Henry, M. Stevens, H. Szoeca, E. and Wagner, H. (2019). vegan: Community Ecology Package. R package version 2.5-6. https://CRAN.R-project.org/package=vegan

Paladini, A., Takiya, D.M., Urban, J.M. and Cryan, J.R., 2018. New World spittlebugs (Hemiptera: Cercopidae: Ischnorhininae): Dated molecular phylogeny, classification, and evolution of aposematic coloration. Molecular phylogenetics and evolution, 120, pp.321-334. https://doi.org/10.1016/j.ympev.2017.12.020

Peng, Y. and Liu, X., 2007. Research progress in effects of urbanization on plant biodiversity. Biodiversity Science, 15(5), p.558. doi: 10.1360/biodiv.070058

Pignataro, T., Bressan, P., Santos, A.L. and Cornelissen, T., 2020. Urban gradients alter the diversity, specific composition and guild distribution in tropical butterfly communities. Urban Ecosystems, 23(4), pp.723-730. https://doi.org/10.1007/s11252-020-00975-7

Pinheiro, C.E. and Cintra, R., 2017. Butterfly predators in the neotropics: which birds are involved? The Journal of the Lepidopterists' Society, 71(2), pp.109-114. https://doi.org/10.18473/lepi.71i2.a5

QGIS Development Team (2021). QGIS Geographic Information System. Open-Source Geospatial Foundation Project. http://qgis.osgeo.org

R Core Team (2021). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

Rega-Brodsky, C.C., Aronson, M.F., Piana, M.R., Carpenter, E.S., Hahs, A.K., Herrera-Montes, A., Knapp, S., Kotze, D.J., Lepczyk, C.A., Moretti, M. and Salisbury, A.B., 2022. Urban biodiversity: State of the science and future directions. Urban Ecosystems, 25(4), pp.1083- 1096. https://doi.org/10.1007/s11252-022-01207-w .

Rodrigues, A.G., Borges-Martins, M. and Zilio, F., 2018. Bird diversity in an urban ecosystem: the role of local habitats in understanding the effects of urbanization. Iheringia. Serie Zoologia, 108. https://doi.org/10.1590/1678-4766e2018017

Skorka, P., Settele, J. and Woyciechowski, M., 2007. Effects of management cessation on grassland butterflies in southern Poland. Agriculture, ecosystems & environment, 121(4), pp.319-324. https://doi.org/10.1016/j.agee.2006.11.001

Seress, G. and Liker, A., 2015. Habitat urbanisation and its effects on birds. Acta Zoologica Academiae Scientiarum Hungaricae, 61(4), pp.373-408. https://dx.doi.org/10.17109/AZH.61.4.373.2015

Seven, S., 2017. Comparative Analysis of Habitat Preferences of the Diurnal Lepidoptera of Tuz Lake, Turkey. Acta Zoologica Bulgarica, 69(1), pp.49-54.

Sevilleja, C.G., van Swaay, C.A.M., Bourn, N., Collins, S., Settele, J., Warren, M.S., Wynhoff, I. and Roy, D.B. (2019). Butterfly Transect Counts: Manual to monitor butterflies. Report VS2019.016, Butterfly Conservation Europe & De Vlinderstichting/Dutch Butterfly Conservation, Wageningen.

Silva, B.F., Pena, J.C., Viana-Junior, A.B., Vergne, M. and Pizo, M.A., 2021. Noise and tree species richness modulate the bird community inhabiting small public urban green spaces of a Neotropical city. Urban Ecosystems, 24, pp.71-81. https://doi.org/10.1007/s11252-020-01021-2

Stefanescu, C., Herrando, S. and Paramo, F., 2004. Butterfly species richness in the north- west Mediterranean Basin: the role of natural and human-induced factors. Journal of biogeography, 31(6), pp.905-915. https://doi.org/10.1111/j.1365-2699.2004.01088.x

Theodorou, P., 2022. The effects of urbanisation on ecological interactions. Current Opinion in Insect Science, p.100922. https://doi.org/10.1016/j.cois.2022.100922

Toledo, M.C.B., Donatelli, R.J. and Batista, G.T., 2012. Relation between green spaces and bird community structure in an urban area in Southeast Brazil. Urban Ecosystems, 15, pp.111-131. https://doi.org/10.1007/s11252-011-0195-2.

Townsend, C.R., 2008. Ecological applications toward a sustainable world (No. 639.9 T6).

Tzortzakaki, O., Kati, V., Kassara, C., Tietze, D.T. and Giokas, S., 2018. Seasonal patterns of urban bird diversity in a Mediterranean coastal city: the positive role of open green spaces. Urban ecosystems, 21(1), pp.27-39. https://doi.org/10.1007/s11252-017-0695-9

Tzortzakaki, O., Kati, V., Panitsa, M., Tzanatos, E. and Giokas, S., 2019. Butterfly diversity along the urbanisation gradient in a densely built Mediterranean city: land cover is more decisive than resources in structuring communities. Landscape and Urban Planning, 183, pp.79-87. https://doi.org/10.1016/j.landurbplan.2018.11.007

Van Swaay, C. and Warren, M., 1999. Red data book of European butterflies (Rhopalocera) (Vol. 99). Council of Europe.

Vincze, E., Seress, G., Lagisz, M., Nakagawa, S., Dingemanse, N.J. and Sprau, P., 2017. Does urbanization affect predation of bird nests? A meta-analysis. Frontiers in Ecology and Evolution, 5, p.29. https://doi.org/10.3389/fevo.2017.00029

Warren, M.S., Maes, D., van Swaay, C.A., Goffart, P., Van Dyck, H., Bourn, N.A., Wynhoff, I., Hoare, D. and Ellis, S., 2021. The decline of butterflies in Europe: Problems, significance, and possible solutions. *Proceedings of the National Academy of Sciences* , *118* (2), p.e2002551117. https://doi.org/10.1073/pnas.2002551117

Weeks, J.R., 2010. Defining urban areas. Remote sensing of urban and suburban areas, pp.33-45. https://doi.org/10.1007/978-1-4020-4385-7_3

White, J.G., Antos, M.J., Fitzsimons, J.A. and Palmer, G.C., 2005. Non-uniform bird assemblages in urban environments: the influence of streetscape vegetation. Landscape and urban planning, 71(2-4), pp.123-135. https://doi.org/10.1016/j.landurbplan.2004.02.006

Wickham, H., Averick, M., Bryan, J., Chang, W., McGowan, L.D., Francois, R., Grolemund, G., Hayes, A.,Henry, L.,Hester, J., Kuhn, M., Pedersen, T.L., Miller, E., Bache, S.M., Muller, K., Ooms, J., Robinson, D., Seidel, D.P., Spinu, V., Takahashi, K., Vaughan, D., Wilke, C., Woo, K., Yutani, H., 2019. Welcome to the tidyverse. Journal of Open Source Software, 4(43), 1686

Wilke, C.O., 2019. cowplot: Streamlined Plot Theme and Plot Annotations for 'ggplot2'. R package version 1.0.0. https://CRAN.R-project.org/package=cowplot

Yeager, J. and Barnett, J., 2021. Variable utility in the enigmatic presence of ultraviolet reflectance in conspicuous aposematic signals. Authorea Preprints. DOI: 10.22541/au.162499980.03470126/v1

Zografou, K., Sfenthourakis, S., Pullin, A. and Kati, V., 2009. On the surrogate value of red-listed butterflies for butterflies and grasshoppers: a case study in Grammos site of Natura 2000, Greece. Journal of Insect Conservation, 13(5), pp.505-514. https://doi.org/10.1007/s10841-008-9198-6

Figure Legends

Fig. 1. Study location. Map of Lipsi Island, Greece. Yellow dots indicate the nine urban sites and red dots indicate the nine rural sites (created in QGIS, satellite imagery from ESRI, 2011).

Fig. 2. Effects of urbanisation on butterflies. (A) Abundance, (B) species richness, and (C) Shannon diversity of butterflies at nine urban and nine rural sites. The black boxplots illustrate the median (bold black line), interquartile range (box margins), 1.5 × interquartile range (whiskers), and outliers (black data points), whilst the mean ± SE are represented by the green diamond and whiskers.

Fig. 3. Effects of urbanisation on birds. (A) Abundance, (B) species richness, and (C) Shannon diversity of birds at nine urban and nine rural sites. The black boxplots illustrate the median (bold black line), interquartile range (box margins), 1.5 × interquartile range (whiskers), and outliers (black data points), whilst the mean ± SE are represented by the green diamond and whiskers.

Fig. 4. Effects of urbanisation on vegetation. Percentage cover of (A) bare ground, (B) shrubs, (C) trees, and (D) plants, (E) plant species richness, and (F) Shannon diversity of plants at nine urban and nine rural sites. The black boxplots illustrate the median (bold black line), interquartile range (box margins), 1.5 × interquartile range (whiskers), and outliers (black data points), whilst the mean ± SE are represented by the green diamond and whiskers.

Fig. 5. Effects of urbanisation on community composition. Non-metric multidimensional scaling of (A) butterfly, (B) bird, and (C) vegetation community composition. The black circles represent the sites, the red crosses indicate the species, and ellipses indicate the standard deviation of urban (blue) and rural (red) sites. The stress indicates the reliability of the points in two dimensions (lower values of stress equate to higher confidence).

Fig. 1. Study location. Map of Lipsi Island, Greece. The red square indicates the location of Lipsi Island in the Aegean Sea. Yellow dots indicate the nine urban sites and red dots indicate the nine rural sites (created in QGIS, satellite imagery from ESRI, 2011).

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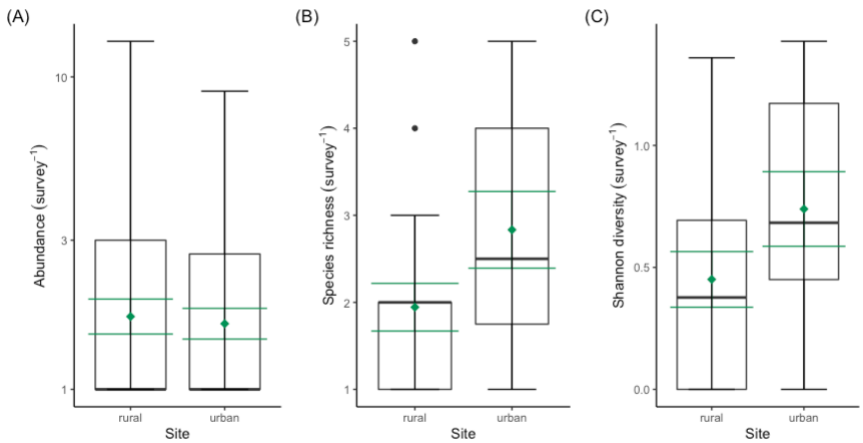
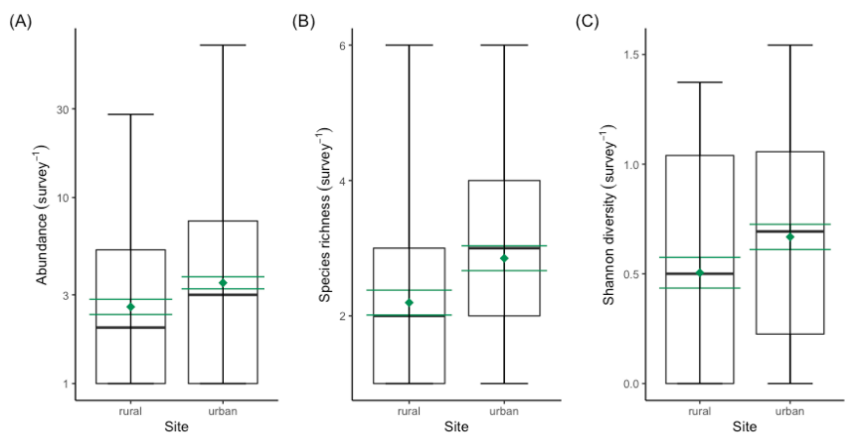


Fig. 3. Effects of urbanisation on birds. (A) Abundance, (B) species richness, and (C) Shannon diversity of birds at nine urban and nine rural sites. The black boxplots illustrate the median (bold black line), interquartile range (box margins), 1.5 × interquartile range (whiskers), and outliers (black data points), whilst the mean ± SE are represented by the green diamond and whiskers.



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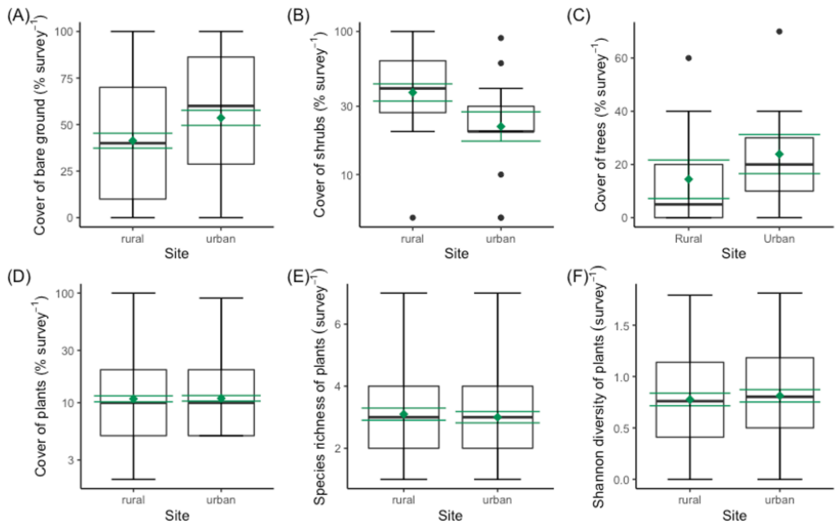

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