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Urban scavenging: vertebrates display greater sensitivity to land-cover and garden vegetation cover than invertebrates

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Abstract

Scavenging removes carrion or littered food waste from the environment, promoting nutrient cycling, and reducing waste management costs. These ecosystem services are important in urban environments, where high human population densities result in increased littered food waste. It is unclear how the magnitude of scavenging across urban-rural gradients is influenced by agent, land-cover type, and patch size. We investigated scavenging provision by vertebrates and invertebrates across a gradient of urbanisation, based on impervious surface cover, in woodlands and gardens in Liverpool, UK. The percentage dry weight loss of bait after 48 h, deployed within vertebrate exclusion cages or exposed to vertebrates and invertebrates, was used to quantify scavenging provision. General linear mixed effects models were used to assess the relative contributions of vertebrates and invertebrates across an urban-rural gradient, variation in scavenging between woodlands and gardens, and the effects of semi-natural vegetation cover on scavenging in gardens. We consider patch size as a preliminary assessment of how fragmentation influences scavenging. Vertebrates contributed substantially more to scavenging than invertebrates across the urbanisation gradient. Vertebrate scavenging was greater in woodlands than gardens, while invertebrate scavenging remained consistent. Scavenging increased with patch size in gardens, but not woodlands. Vertebrate scavenging increased with patch size and garden semi-natural vegetation cover. Urban woodlands and gardens make important contributions to scavenging-mediated ecosystem services. There is a need to increase the cover of semi-natural vegetation in gardens to increase their contributions, and protect and expand woodlands, especially in areas with a high demand for scavenging-mediated ecosystem services.

Keywords Resource removal · Woodland · Ecosystem services · Urbanisation gradient · Baiting

Introduction

Scavenging, the consumption of carrion or littered anthropogenic food waste, is a vital ecosystem process. Scavenging provides numerous ecosystem services including nutrient cycling (Beasley et al. 2015), regulating disease risk by reducing pathogen spread (Le Sage et al. 2019), enhancing aesthetic value of greenspaces (Colvin et al. 1996; Ellaway et al. 2005) and reducing contamination of freshwater (Santori et al. 2020). Provision of these services significantly reduces waste management costs: for example, the USA government spent $11.5 billion on litter removal in 2008, up to 26% of which comprised food waste (KAB, 2009). Youngsteadt et al. (2015) estimated that arthropods alone can remove 600–975 kg of littered food waste annually from New York streets. This process is underpinned by a broad range of taxonomic groups, including vertebrates (especially mammals and birds; Contesse et al. 2004; Huijbers et al. 2015; Inger et al. 2016a, b) and a wide range of invertebrates, especially insects (Penick et al. 2015; Youngsteadt et al. 2015; Griffiths et al. 2018).

Provision of scavenging is particularly important in urban environments as high human population densities increase the amount of anthropogenic food waste (Verstegen et al., 2023). Towns and cities also support the majority of the world's people (United Nations, 2019), especially in

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developed regions such as the UK (83% of the population is urbanised; DEFRA, 2020), and thus there is the greatest demand for ecosystem services in urban environments. However, urban ecosystems are associated with reduced native species richness and a shift in community composition towards generalist species that are able to adapt to numerous urban selection pressures (McKinney 2008). This alteration in biotic assemblages often alters functional diversity, with potential adverse effects on ecosystem service provision (Sanford, 2009).

Despite its importance, and particular relevance in urban environments, the provision of scavenging is underrepresented in the existing urban ecology literature, with studies typically investigating scavenging provision in either urban or rural environments (Griffiths et al. 2018; Inger et al. 2016a; Youngsteadt et al. 2015), resulting in a lack of data representing provision along urbanisation gradients. The majority of studies focus on vertebrate scavengers (Contesse et al. 2004; Huijbers et al. 2015; Inger et al., 2016a; Morales-Reyes et al. 2017; Sebastián-González et al. 2019; Turner et al. 2020), even though invertebrates are also important contributors to urban scavenging provision (Penick et al., 2015; Youngsteadt et al. 2015). Of the studies that do investigate invertebrate scavenging, the majority focus on ants (Hymenoptera: Formicidae) in rural or untransformed tropical regions (Bestelmeyer and Wiens 2003; Gray et al. 2015; Griffiths et al. 2018). Therefore, the contribution of broader invertebrate communities on scavenging in urban and temperate regions is insufficiently understood. Moreover, few studies have focused on identifying the factors, such as habitat type and patch size, which determine the magnitude of scavenging in urban environments, instead focusing on the identity and relative contributions of vertebrate scavenger species (Inger et al. 2016a; Morales-Reyes et al. 2017; Turner et al. 2020).

Patch size is an indicator of the magnitude of habitat fragmentation (Didham et al. 2012), which is associated with urbanisation and typically has negative effects on biodiversity and ecosystem function (Fahrig 2003; McKinney 2008). Furthermore, it is unclear to what extent small patches of habitat are able to maintain levels of ecosystem function. Urban landscapes are mosaics of many different habitat types, which have been found to vary considerably in ecosystem function (Eldridge et al. 2021) and species distribution (Li et al. 2019). Urban woodlands, for example, can maintain ecosystem functions similar to those of more natural communities, despite being highly modified (Roy et al. 1999; Croci et al. 2008). Domestic gardens comprise approximately 25% of urban landscapes in the UK and many other developed regions in the global north (Loram et al. 2007), and can provide valuable wildlife habitat (Davies et al. 2009), although there is much variation in how wildlife-friendly gardens are (Larson et al. 2022).

The overall objective of this study was to assess how scavenging provision varies along an urbanisation gradient and the ecological factors associated with service provision. Specifically, we first tested how the contribution of invertebrate and vertebrate species to scavenging varies along the urbanisation gradient. We anticipated greater declines in invertebrate contributions in more urbanised locations as urbanisation is typically associated with invertebrate population declines (Sánchez-Bayo and Wyckhuys, 2019), whilst vertebrate scavengers typically maintain population densities and service provision in urban areas (Inger et al. 2016a). Second, we assess how the magnitude of scavenging activity varies across two major urban land-cover types. Specifically, we contrast domestic gardens with semi-natural woodland which is the most mature and natural vegetation type present in most urbanised landscapes. We also assess how habitat features (e.g. trees and wildflowers) of domestic gardens influence the magnitude of scavenging that occurs within them. When addressing these aims, we consider habitat patch size, enabling us to conduct a preliminary assessment of how urban-induced fragmentation of greenspace influences scavenging.

Materials & methods

Site selection

The study was conducted from June to August 2022 in the Liverpool region, UK. Liverpool (53.41°N, -2.99°W) is a major city in North West England with an average population density of c. 4,347 people/km^2, and a total population of c. 486,100 (ONS 2021).

We calculated the percentage impervious surface of each 1 km x 1 km grid cell using European Environment Agency data (2018) across the Liverpool City region and its surrounding countryside, excluding grid cells that had both ≥ 25% mean impervious surface cover and were outside of the City region, to avoid urban locations in neighbouring towns. Focal grid cells were selected using random stratification across the urbanisation gradient, aiming to select four cells within each urbanisation category, i.e. 0–10% impervious surface, 11–20% impervious surface etc. Only one grid cell was available in the 91–100% impervious surface category giving a total of 37 grid cells (Fig. 1; Table S1). Within each grid cell we selected the closest woodland to the cell's centre as a sampling site. Garden sites were recruited by distributing 'access request' leaflets to houses within approximately 400 m of each woodland and selecting the garden of the first resident to accept the request. Woodland sites were

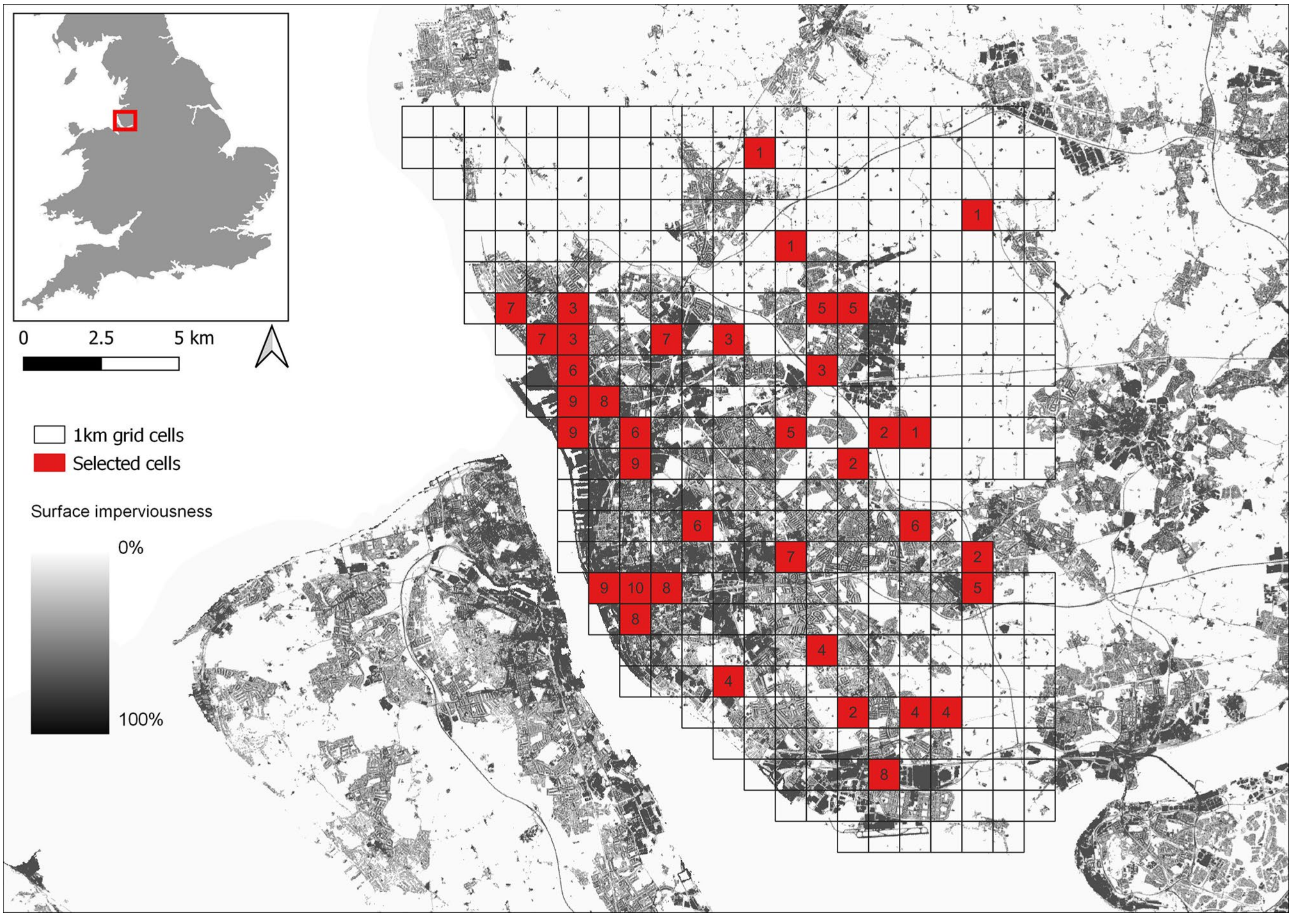

Fig. 1 Map of the Liverpool area, with the sampling region being defined by the gridded area (each grid cell is 1 km x 1 km). Sampling sites were located within cells that were selected via random stratified sampling. Numbers shown within selected cells indicate urbanisation categories based on mean surface imperviousness within that cell, such that Category 1 = 0–10% impervious surface, Category 2 = 11–20%, etc

dominated by deciduous trees such as oak (*Quercus robur/patraea*) and sycamore (*Acer pseudoplatanus*) and had a mean size of 128235 m^2 [median = 21491 m^2; range = 661–1318902 m^2). Gardens typically featured a combination of grey (i.e. impervious surfaces) and greenspace, mean greenspace size of 106 m^2 [median = 60 m^2; range = 13–789 m^2).

Quantifying scavenging

Four different bait types were used to measure scavenging rates: frankfurter sausages (Wikinger Hotdogs, Wikinger Fleischwaren, Böklund, Germany), potato crisps (Seabrook Sea Salted Potato Crisps, Seabrook Crisps, Bradford, UK), dried mealworms and sunflower seeds. The first two bait types were selected to represent anthropogenic food waste, and the second two bait types represent natural food sources. Together, these four bait types consist of a variety of proteins, carbohydrates and fats that may be attractive to a broad range of scavengers. Ten bait stations were set up at each site, each comprising four petri dishes containing 5 g of bait, with each petri dish containing a different bait type. Bait stations were spaced a minimum of 2 m apart, more where possible. At each site, five of the bait stations were left exposed (allowing vertebrate and invertebrate access), with a plastic rain cover (Fig. S1a). Another five bait stations were placed within vertebrate exclusion cages, composed of 6 mm wire mesh and a rain cover, fixed into the ground using steel wire (Fig. S1b). Petri dishes within the vertebrate exclusion cages were accessible to the majority of invertebrates, with the exception of soil-dwelling organisms. Cages were large enough that the petri dishes within them could not be accessed by vertebrates from the outside when placed in the centre. Baits at sites within the same grid cell (i.e. paired woodland and garden sites) were deployed within a maximum of two days of each other, and were typically deployed on the same day, to reduce the probability of baits in different land-covers being exposed to very different weather conditions.

Baits were left on site and collected after 48 h, then dried and re-weighed. The percentage dry weight lost was calculated using reference samples that had been dried without being placed in the field. The mean percentage dry weight loss of each caged bait type from each site was used as the measure of invertebrate scavenging. To calculate vertebrate scavenging, mean percentage dry weight loss of each caged bait type from each site was subtracted from the mean percentage dry weight loss of each exposed bait type from each site, following Griffiths et al. (2018). This method differentiates between vertebrate and invertebrate scavengers based on body size (i.e. vertebrates are too large to access the caged bait).

Patch size and garden features

Patch size was measured using high resolution imagery from Google Earth by drawing a polygon around the perimeter of a woodland site or the vegetated area of a garden site and recording area size (m^2). A patch was defined as an area of woodland or vegetated garden that was not interrupted by an impervious surface of 7 m or more in width, which is the typical impervious surface width of small roads in the study region (based on measurements using aerial imagery from Google Earth). Patch size was logarithmically transformed to base ten prior to data analysis to account for skewness in its frequency distribution. We calculated the percentage cover of each garden's trees, hedges, shrubs, wildflowers, ornamental flowers and mown grassland to the nearest 5%, relative to total vegetated area, based on in situ observations. We then calculated the percentage cover of semi-natural vegetation (trees, hedges, shrubs and wildflowers) because mown amenity grassland has limited biodiversity value (Norton et al. 2019), and ornamental flowers are often considered to provide reduced biodiversity benefits relative to native vegetation (Garbuzov et al. 2017; Tallamy et al. 2021; but see Seitz et al. 2020 for an alternative view). Our metric of semi-natural vegetation cover is, however, strongly correlated with an alternative measure that includes ornamental flowers ($r = 0.707$, $P = 2.2 \times 10^{-16}$), indicating that the use of this alternative measure in our analyses would have no meaningful effect on corresponding model outputs. Semi-natural vegetation cover was logarithmically transformed to base ten prior to data analysis to account for skewness in its frequency distribution.

Data analysis

Data were analysed in R (R Core Team 2021) using general linear mixed effects models (lme4; Bates et al. 2015) with a Gaussian error distribution and a full model approach (following Whittingham et al. 2006), and diagnostic plots were checked to confirm model assumptions were met. Correlation coefficients between all predictor variables were less than the threshold (0.7) at which collinearity hinders interpretation of linear models (Dormann et al. 2013).

In the models described below, patch size of garden sites was measured as the total area of vegetated greenspace in each garden. However, patch size for garden sites was also measured as the total area of greenspace that each garden was connected to (i.e. ignoring the boundaries of the property), but this alternative metric is not used in the models reported in the main manuscript as it resulted in models with higher Akaike information criterion (AIC) values (Table S2). We constructed a single full model, with percentage dry weight loss of bait (per bait type) as a function of percentage impervious surface cover, scavenger taxon (i.e. vertebrate or invertebrate), bait type (i.e. frankfurters, mealworms, crisps or sunflower seeds), habitat type (i.e. woodland or garden), and patch size, with grid cell ID as a random intercept. We then added each of four interaction terms in turn, enabling a more complete assessment of our core research questions. To assess changes in the contribution of vertebrates and invertebrates to scavenging along the urban-rural gradient, we added the interaction between scavenger taxon and impervious surface cover. To assess how the scavenging contribution of vertebrates and invertebrates varies between woodlands and gardens, we added the interaction between scavenger taxon and habitat type. To determine if the effects of patch size on scavenging varied between woodlands and gardens, we added the interaction between patch size and habitat type. To assess how the scavenging contribution of vertebrates and invertebrates varies by patch size, we added the interaction between scavenger taxon and patch size. Each of these four interactions terms were statistically significant and thus we present the results of each of these four full models.

Then, focusing only on data from gardens, we assessed how the percentage cover of semi-natural vegetation influenced scavenging provision. We constructed a single full model of percentage dry weight loss of bait in gardens as a function of percentage impervious surface cover, scavenger taxon, bait type, patch size, and percentage semi-natural vegetation cover within the garden. To assess if the effects of semi-natural vegetation cover varied between vertebrate and invertebrate scavengers we also added the interaction between scavenger taxon and percentage semi-natural vegetation cover.

We checked each model for spatial autocorrelation by calculating Moran's I values using the residuals from each model using the "Moran.I" function in the "ape" R package (Paradis & Schliep 2019). There was no evidence for spatial autocorrelation (see supplementary material for further information).

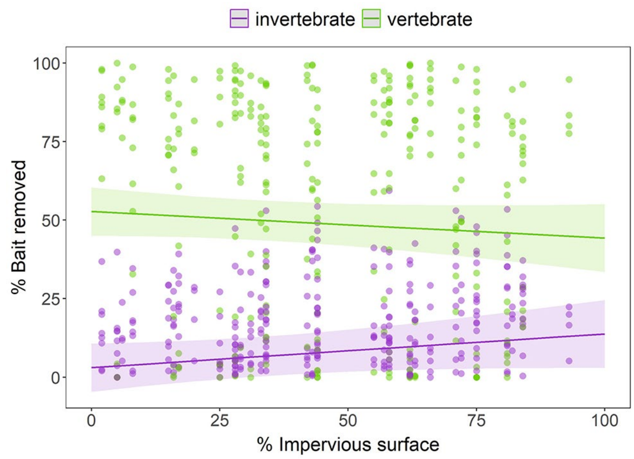

Fig. 2 The relationship between bait removal by vertebrates and invertebrates, and % impervious surface cover. Points show observed % dry weight loss of bait (each point representing one bait type), lines with shading show predicted values from Model 1 (Table 1) and associated 95% confidence intervals, respectively. Vertebrates consumed significantly more bait than invertebrates, and urbanisation is associated with a decline in vertebrate scavenging. % bait removed by vertebrates was calculated by subtracting the % dry weight loss of caged baits from that of open baits

Results

Vertebrates consistently contributed more to scavenging than invertebrates across the urbanisation gradient (Fig. 2; Table 1). The minimum mean % bait (averaged across all bait types) removed from a woodland site by vertebrates was 61%, whereas the maximum removed by invertebrates from a woodland site was 32%. The amount of bait removed was greater in woodlands than gardens, due to reduced scavenging by vertebrates in gardens compared with woodlands, while the magnitude of scavenging by invertebrates was not influenced by land-cover type (Fig. 3; Table 1). The mean % bait removed from vertebrates in gardens ranged from 1 to 91% while that of invertebrates ranged from 9 to 37%. Scavenging provision increased with patch size across the observed variation in garden size (12.81m^2 – 789.22m^2; Fig. 4a; Table 1), but not across the observed variation in woodland size (660m^2 – $1318{,}902\text{m}^2$; Fig. 4b; Table 1). Vertebrate scavenging increased across the complete range of patch sizes, whilst invertebrate scavenging decreased with patch size (Fig. 4c; Table 1).

We found a strong positive effect of semi-natural vegetation cover on scavenging provision by vertebrates in gardens, while scavenging provision by invertebrates was

Table 1 Linear mixed effects model outputs showing parameter estimates ± standard error, and *p*-values. The single full model, with percentage dry weight loss of bait was modelled as a function of percentage impervious surface cover, scavenger taxon (vertebrate or invertebrate), bait type (frankfurters, mealworms, crisps or sunflower seeds), land-cover type (woodland or garden), and $\log_{10}$(patch size), with grid cell ID as a random intercept. Four different interaction terms were then added in turn: Model 1) interaction between impervious surface cover and scavenger taxon; Model 2) interaction between scavenger taxon and land-cover type; Model 3) interaction between land-cover type and $\log_{10}$(patch size); and Model 4) interaction between scavenger taxon and $\log_{10}$(patch size)

	Model outputs			
Predictor	Model 1 Impervious surface : Taxa	Model 2 Taxa : Land-cover	Model 3 Land-cover : Log_{10}(patch size)	Model 4 Taxa : Log_{10}(patch size)
Intercept	-4.366 ± 5.520, $P=0.430$	12.061 ± 4.795, $P=0.013$	-17.379 ± 7.208, $P=0.017$	24.464 ± 5.077, $P=2.800\times10^{-6}$
% Impervious surface	0.107 ± 0.067, $P=0.111$	0.016 ± 0.052, $P=0.757$	-0.038 ± 0.052, $P=0.474$	0.016 ± 0.052, $P=0.763$
Taxa (vertebrate)	49.706 ± 4.053, $P=2\times10^{-16}$	16.011 ± 2.319, $P=1.44\times10^{-11}$	40.963 ± 1.917, $P=2\times10^{-16}$	-8.718 ± 3.864, $P=0.024$
Bait (frankfurter)	5.001 ± 2.711, $P=0.066$	5.001 ± 2.287, $P=0.029$	5.001 ± 2.712, $P=0.066$	5.001 ± 2.323, $P=0.032$
Bait (crisp)	-1.047 ± 2.711, $P=0.699$	-1.047 ± 2.287, $P=0.647$	-1.047 ± 2.712, $P=0.700$	-1.047 ± 2.323, $P=0.652$
Bait (seed)	0.624 ± 2.675, $P=0.818$	0.624 ± 2.287, $P=0.785$	0.624 ± 2.712, $P=0.818$	0.624 ± 2.323, $P=0.788$
Land-cover (woodland)	17.153 ± 4.692, $P=3\times10^{-4}$	-7.644 ± 4.444, $P=0.086$	49.808 ± 10.507, $P=4.11\times10^{-6}$	16.679 ± 4.188, $P=8.360\times10^{-5}$
Log_{10} (patch size)	1.033 ± 0.720, $P=0.153$	0.104 ± 0.638, $P=0.084$	5.737 ± 1.554, $P=3\times10^{-4}$	-2.372 ± 0.690, $P=0.001$
% Impervious surface : Taxa (vertebrate)	-0.192 ± 0.078, $P=0.015$	*NA*	*NA*	*NA*
Taxa (vertebrate) : Land-cover (woodland)	*NA*	48.554 ± 3.235, $P=2\times10^{-16}$	*NA*	*NA*
Land-cover (woodland) : Log_{10}(patch size)	*NA*	*NA*	-6.005 ± 1.756, $P=0.001$	*NA*
Taxa (vertebrate) : Log_{10}(patch size)	*NA*	*NA*	*NA*	6.939 ± 0.489, $P=2\times10^{-16}$

Table 2 Linear model output showing parameter estimates ± standard error, and *p*-values. Percentage dry weight loss of bait was modelled as a function of percentage impervious surface cover, scavenger taxon (vertebrate or invertebrate), bait type (frankfurters, mealworms, crisps or sunflower seeds), $\log_{10}$(patch size), $\log_{10}$(1 + % semi-natural vegetation cover) and the interaction term between taxa and $\log_{10}$(1 + % semi-natural vegetation cover)

Predictor	Model output Parameter estimate
Intercept	1.795 ± 7.886, $P = 0.820$
% Impervious surface	0.040 ± 0.073, $P = 0.584$
Taxa (vertebrate)	2.627 ± 4.337, $P = 0.545$
Bait (frankfurter)	10.320 ± 2.109, $P = 1.780 \times 10^{-16}$
Bait (crisp)	-3.231 ± 4.131, $P = 0.454$
Bait (seed)	1.006 ± 4.313, $P = 0.816$
Log_{10} (patch size)	3.538 ± 1.737, $P = 0.043$
Log_{10} (1 + % semi-natural vegetation cover)	-1.550 ± 1.638, $P = 0.345$
Taxa (vertebrate) : Log_{10} (1 + %Semi-natural vegetation cover)	10.320 ± 2.109, $P = 1.780 \times 10^{-16}$

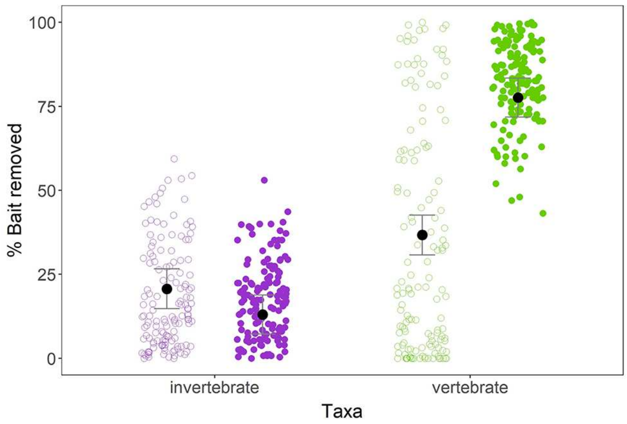

Fig. 3 Bait removal by vertebrates and invertebrates in relation to land-cover type. Coloured points show observed % dry weight loss of bait. Open points = gardens, closed points = woodland. Purple points = invertebrates, green points = vertebrates. Black points with error bars show predicted values by Model 2 (Table 1) and 95% confidence intervals. Vertebrate scavengers removed significantly more bait in woodlands than gardens, while invertebrates removed similar amounts of bait in both habitats

similar across the range of semi-natural vegetation cover levels (Fig. 5; Table 2).

Discussion

Summary of results

We show that both invertebrate and vertebrate scavenging guilds play a role in removing resources, including littered food waste, from greenspaces across a range of urbanisation intensities, but that their relative importance and contribution to this ecosystem process is affected by a number of factors. Invertebrate contributions to scavenging provision were consistent regardless of impervious surface cover, land-cover type, and garden semi-natural vegetation cover, but decreased in response to increasing patch size. Scavenging provision by vertebrates was consistently greater than that of invertebrates in woodlands, regardless of impervious surface cover. Vertebrate scavenging increased with both patch size and garden semi-natural vegetation cover. Scavenging provision as a whole increased with garden patch size, but not with woodland patch size.

Scavenging provision across the urban-rural gradient

Contrary to our predictions, invertebrate scavenging did not decline with impervious surface cover and was consistent across the urban-rural gradient. Urbanisation is typically associated with a decline in native species richness and ecosystem function (McKinney 2008; Sanford, 2009), although in some cases those species that remain in urban areas are highly adapted to them, and thus occur at high densities enabling them to carry out ecosystem processes effectively (Inger et al. 2016b). Indeed, some important invertebrate scavengers are likely to be resilient to urbanisation, such as ants (Dijon et al. 2023), which concurs with our frequent observations of *Lasius niger* and *Myrmica* species at invertebrate baiting stations. Increased incidences of littered food waste in urban areas may also provide additional scavenging opportunities for generalist invertebrate species, thus allowing them to persist in relatively high densities and maintain scavenging provision.

Invertebrates removed 8–32% of the bait in woodlands (equates to 4.5–18.2 g dry weight of littered food waste in 48 h), and 9–37% in gardens (equates to 5.1–21.0 g). Whilst these values are somewhat lower than those reported in another study (New York – 59% of bait; Youngstead et al. 2015) they equate to removal of substantial amounts per annum of c. 15.3–61.4 kg and c. 16.3–67.1 kg respectively across all 37 woodlands and 35 gardens, respectively. These values are calculated based on the median value, summed across a six-month period of assumed similar activity. This demonstrates that substantial quantities of food waste could potentially accumulate in Liverpool's greenspaces, or be consumed by vertebrates, without the action of scavenging invertebrates. If invertebrate scavenging were to decline in urban environments, there would be more available food resources for potential disease-vector species such as brown rats (*Rattus norvegicus*) and feral pigeons (*Columbia livia domestica*) (Haag-Wackernagel and Moch 2004; Himsworth et al. 2013), hence any decline in invertebrate scavenging services could increase human disease risk given

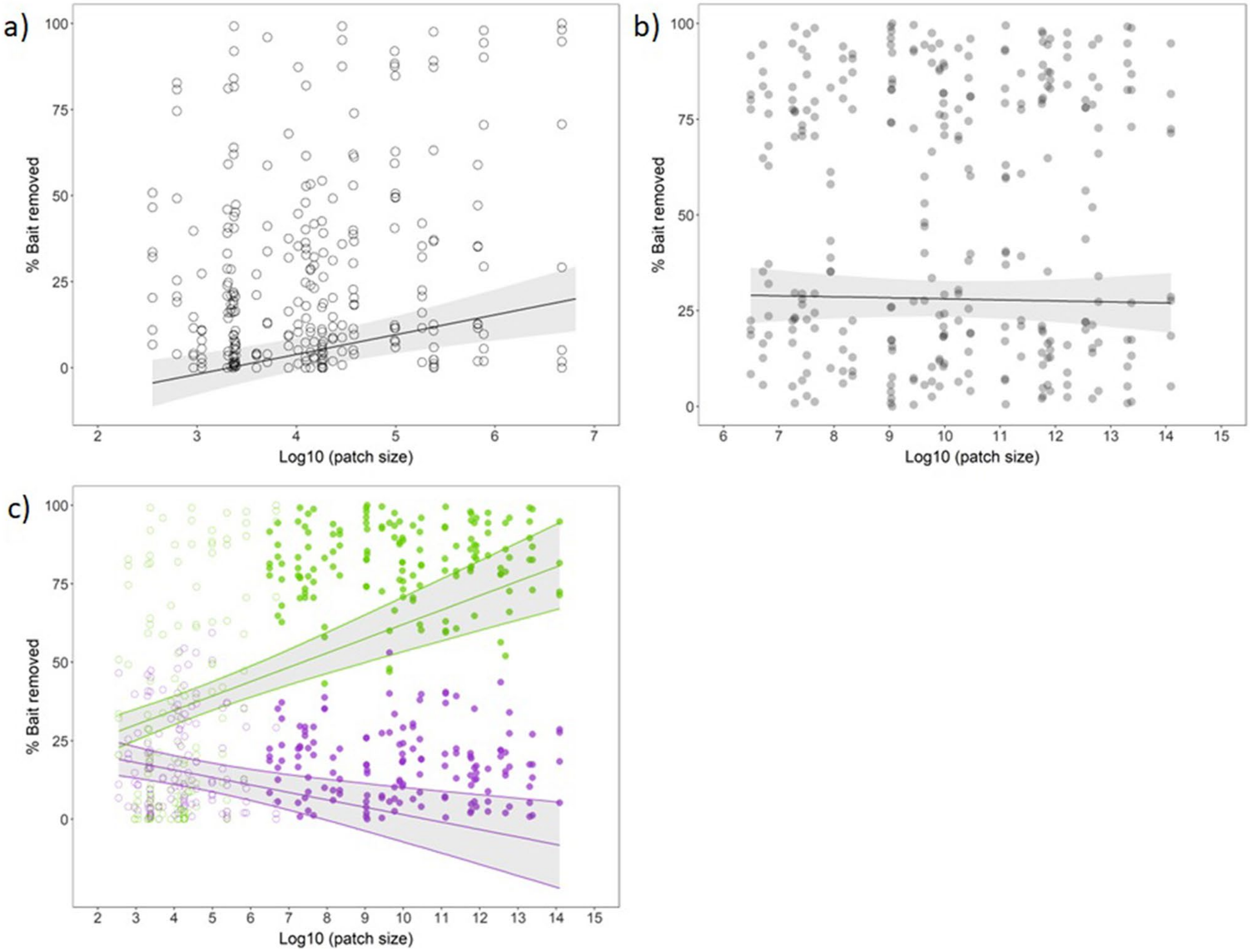

Fig. 4 The relationship between patch size and bait removal in (**a**) gardens; (**b**) woodlands; (**c**) gardens and woodlands. Points show observed % dry weight loss of bait by both vertebrates and invertebrates, lines show predicted values from (**a** & **b**) Model 3 (Table 1) and (**c**) Model 4 (Table 1). Shading shows 95% confidence intervals. In (**c**) green points show vertebrate consumption while purple points show invertebrate consumption. Significantly more bait was removed from larger gardens than smaller gardens, while the magnitude of bait removal was not associated with woodland size. When considering all sites regardless of land-cover type, vertebrate scavenging increased with patch size, while invertebrate scavenging decreased

that the primary invertebrate scavengers are not transmitters of zoonotic disease to people.

We found that scavenging provision by vertebrates declines with increasing impervious surface cover, but that the effect of this is marginal. Previous research has suggested that a small number of resilient scavenging vertebrate species, notably Corvidae and red foxes (*Vulpes vulpes*) are capable of maintaining their population densities, and therefore scavenging provision, in UK urban areas (Inger et al. 2016a, b), although Eurasian magpies (*Pica pica*) have been found to have lower population densities in highly urbanised areas (Tratalos et al. 2007). Fox population densities tend to increase with urbanisation (Scott et al. 2014) and are potentially the most abundant wild carnivore in the UK urban areas (Soulsbury et al. 2010). Greater population densities of brown rats are also associated with greater urban intensity (Feng and Himsworth 2014). Our findings support existing evidence that vertebrates are able to maintain scavenging service provision in urban environments despite the declines in species richness that are typically associated with urbanisation (Inger et al. 2016b).

Scavenging provision in woodlands and gardens

Our second aim was to test how the magnitude of scavenging activity varied between woodlands and gardens. While there is evidence that vertebrate scavengers can maintain population densities and activity in urban landscapes (Inger et al. 2016b), it may be that their foraging activity is moderated by land-cover type. Common urban vertebrate scavengers such as foxes and corvids have large foraging ranges, much greater than the distances between the paired

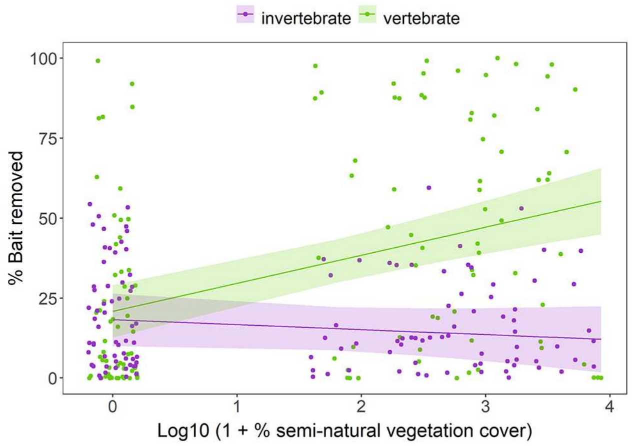

Fig. 5 The relationship between semi-natural vegetation cover in gardens, and bait removal by vertebrates and invertebrates. Points show observed % dry weight loss of bait, lines with shading show linear model predicted values (Table 2) and 95% confidence intervals, respectively. Points have been jittered slightly along the x-axis to help with visualisation. More bait was removed by vertebrates in gardens with more semi-natural vegetation cover

woodland and garden sites in this study (Meek and Saunders 2000; Marzluff and Neatherlin 2006). Many woodland sites showed evidence of fox activity (removal and scattering of rain covers from exposed baits, scent marking), and 100% of exposed baits were removed at these sites. In contrast, no gardens showed evidence of fox activity, even those in close proximity to woodlands where foxes were present. This suggests that scavenging provision by foxes may be less common in gardens, despite other studies demonstrating that foxes are highly active in private gardens and may even prefer this land-cover type to others (Newman et al. 2003; Walter et al. 2018). Scott et al. (2023) found that the exploitation of anthropogenic food provision in domestic gardens by vertebrates can result in agonistic interactions between foxes and domestic cats, with cats typically “winning” these interactions. In residential areas, domestic cats exist in high densities compared with wild predators, and predate on birds and small mammals (Sims et al. 2008). This may inhibit scavenging provision by wild vertebrates in gardens. We do not know to what extent domestic animals contributed to vertebrate scavenging in this study. Residences with dogs were not accepted when recruiting garden sites, but it is possible that dogs may have contributed to scavenging in woodlands. Reduced scavenging provision by vertebrates in gardens suggests that the relative importance of invertebrate communities in carrying out this process is greater in this land-cover type than in woodlands. Vertebrates may also be more affected by human disturbance and consequently spend less time foraging in gardens due to there being more human activity. Our results indicate that woodlands may be important habitats for sustaining vertebrate scavenger populations, despite the small size of some of the woodlands used in this study (14 woodland sites were smaller than 1 hectare).

Scavenging provision and patch size

While scavenging provision in woodlands did not change in relation to patch size, there was little overlap between garden and woodland patch size, with almost all woodland sites being larger than garden sites. It is therefore worth noting that this lack of overlap may be the cause of the different responses to patch size seen in these two habitats, so we cannot predict how scavenging may differ in very small woodland patches of a similar size to the vegetated areas of gardens. Additionally, it is possible that some of the variation in scavenging provision between land-cover types may be explained by their difference in size, rather than difference in land cover, or vice-versa. Woodland fragments generally become smaller and more fragmented with increasing urbanisation (Medley et al. 1995), and we demonstrate that, at least across the range of woodland sizes considered in this study, small urban woodland fragments are valuable in facilitating scavenging provision and act similarly in this regard to larger woodlands. Across both land-cover types, vertebrate scavenging increased with patch size, while invertebrate scavenging decreased. Many vertebrate scavengers have large foraging ranges (Marzluff and Neatherlin 2006; Meek and Saunders 2000), and foxes specifically have been found to increase their foraging ranges in response to greater habitat fragmentation and smaller habitat patches (Tolhurst et al. 2020). It may be that patch size is a particularly important variable influencing the magnitude of scavenging provision by vertebrates, irrespective of land-cover type. The inverse response seen in invertebrate scavengers may be due to increased competition with vertebrate scavengers, as competition with vertebrates has been found to be a limiting factor in invertebrates’ ability to colonise carrion (Sawyer et al. 2022).

Scavenging provision and semi-natural vegetation cover in gardens

Our finding that vertebrate scavenging increases with the proportion of semi-natural vegetation cover in gardens provides evidence that, while vertebrate scavenging provision is typically reduced in gardens, their contribution can be influenced by gardening practices. Smaller gardens exhibited less scavenging than larger gardens, but this effect may be mitigated by providing more semi-natural vegetation such as wildflowers and hedges, although residents with smaller gardens are likely to be the most constrained in their capacity to provide additional vegetation features due to limited space. Our results indicate that domestic gardens can facilitate important ecosystem processes, which can be improved further by managing them effectively. However, it is difficult to predict from our results how much semi-natural vegetation cover, or in what composition, would be required to achieve similar vertebrate scavenging provision between a garden and a woodland of the same size. Gardens are a prevalent form of habitat in UK cities, comprising up to 47% of total urban greenspace (Loram et al. 2007), and thus provide an opportunity to deliver important ecosystem services in urban landscapes if managed effectively. Gaston et al. (2007) found that wildlife gardening/management in some form is generally popular in UK private gardens, but that food provision is the most common activity, influencing bird distribution and abundance. This could potentially influence the capacity for birds and other vertebrates utilising gardens to contribute to scavenging if their foraging needs are supplemented by intentional food provision. The structural complexity of vegetation is understood to be important for predicting vertebrate (Daniels and Kirkpatrick 2006; Van Heezik et al. 2008) and invertebrate abundance in gardens (Smith et al. 2006), suggesting that a variety of semi-natural vegetation may be beneficial in promoting ecosystem processes. A key constraint in the creation of complex vegetation structures and native vegetation cover is the association between socio-economic status and garden management practices, where some residents will lack the money and time to dedicate to “wildlife gardening” (Kinzig et al. 2005), and social norms result in gardens being managed similarly to those in close proximity (Zmyslony and Gagnon 1998). Promoting scavenging provision, and other ecosystem processes, may require incentives and resources for residents to manage their gardens to include more semi-natural vegetation.

Conclusions and management implications

Our findings suggest that the provision, conservation, and expansion of woodlands are important actions in ensuring the effective provision of scavenging by vertebrates. This may be of particular importance in urban environments, where the amount of littered food waste, and therefore the need for scavenging, are greater. Urban woodlands provide many public benefits, including improving air quality (Beckett et al. 1998) and mitigating the effects of the urban heat island (Fung and Jim 2019), and here we provide evidence for yet another benefit of these habitats. We demonstrate that the management of domestic gardens to provide more semi-natural vegetation is also beneficial for facilitating vertebrate scavenging, which is reduced in gardens relative to woodlands.

Scavenging-mediated ecosystem services are valuable in urban areas, where human populations are dense and food littering is frequent. Consequently, it is important that efforts are made to facilitate scavenging provision in urban environments. Our study highlights the value of woodland patches in facilitating scavenging provision, and we recommend that local authorities protect and expand urban woodlands and wooded areas of public parks. Our evidence suggests that even woodlands as small as 661m^2, which are likely to be more isolated, support scavenging provision comparable to much larger, less isolated patches. We also recommend that members of the public are encouraged and provided adequate incentives and resources to provide semi-natural vegetation features, such as trees, hedges and wildflowers, in their gardens where possible.

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Declarations

Competing interests The authors declare no competing interests.

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