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Research article

Challenging assumptions about burial ground biodiversity using flying beetles as indicators in urban areas

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Abstract

Biodiversity is fundamental to the provision of ecosystem services that benefit urban communities, yet one type of green space is largely overlooked in ecological research and local governance: urban burial grounds. Their longevity, profound importance to society, and ubiquitous nature, provide unique opportunities for urban biodiversity. However, there has been little scientific exploration of their potentials. To quantify biodiversity in urban burial grounds, a low impact methodology for the capture of flying beetles was developed and deployed at 20 sites in southern England. To the authors' knowledge this work represents the largest sampling of burial grounds in a single study. We used Generalized linear Mixed Models to examine the influence of weather, local demographic variables, urban landscape and burial ground vegetation management on the abundance of flying beetles. We found significant variability in beetle assemblages over time and between burial grounds. Burial ground age was not significantly associated with flying beetle abundance, challenging long-standing assumptions about older burial grounds being more valuable for biodiversity. Increasing area of domestic gardens and hedgerows in the surrounding urban landscape was positively associated with beetle abundance, whereas the most significant negative association was with burial ground size. Additionally, management of burial grounds significantly influenced beetle abundance: more stringent regimes typically resulted in lower abundance, but sites with horticultural landscaping or biodiversity-focused regimes exhibited higher abundances.

Key words: biodiversity, Coleoptera, burial ground, indicator, management, urban

Introduction

Urban green spaces, a form of green infrastructure, are widely acknowledged as key components of the urban environment with regard to supporting urban biodiversity, providing they are well-planned and managed (MacGregor-Fors et al. 2016; Aronson et al. 2017; Lepczyk et al. 2017; Threlfall et al. 2017). This, in turn, is what underpins the delivery of ecosystem services for urban communities, with evidence showing direct and indirect links between biodiversity and human physical and mental wellbeing (as reviewed in Harrison et al. 2014; Ziter 2016; Kondo et al. 2018). Within the body of research exploring urban green spaces, the biodiversity therein, and their benefits to people, definitions of what types of places constitute urban green space differ between studies (Taylor and Hochuli 2017), and many focus on just one or two types with public parks and gardens being prevalent. There is however, one type of urban green space that is often excluded from definitions in research, policy and land management contexts, despite being globally ubiquitous out of necessity—burial grounds. Here we explore the impacts of urban landscape, human population density and site-scale management decisions on the biodiversity of urban burial grounds, using beetles as indicator taxa.

In ecological research terrestrial invertebrates are commonly used as biodiversity indicator taxa (Gerlach, Samways, and Pryke 2013), with their diversity used to estimate the wider diversity of other taxa within a habitat to monitor how this changes over time (McGeogh 1998). The ubiquitous insect order Coleoptera (beetles) has long been used in population, conservation and landscape ecology studies (Hirao et al. 2008; Kyrö et al. 2018), with carabids (ground beetles) in particular gaining status as model organisms and indicators of wider biodiversity patterns (Johan Kotze et al. 2011; Koivula 2011). Beetles meet important criteria for maximising indicator species usefulness (Noss 1990), such as well-understood biology, life history and taxonomy, being easily captured or observed in the field, and occurring in a wide range of habitat types (Pearson and Cassola 1992; Bohac 1999; Brin, Brustel and Jactel 2009; Koivula 2011). Recognised issues with using indicator taxa include: (i) a lack of understanding of how well they represent other taxa and (ii) the rare reporting of statistically strong correlations (Rainio and Niemelä 2003; Gao, Nielsen and Hedblom 2015). However, beetles have successfully been used as biodiversity indicators in urban areas, using ground-dwelling families (Do, Lineman and Joo 2014; Kyrö et al. 2018), and in forests, using flying species (Ohsawa 2010), and beetles are often used as proxies in the context of ecosystem service provision (Noriega et al. 2018). In addition, several ground beetle species have been identified as indicators of habitat age in urban cemeteries (Kowarik et al. 2016). Therefore, evidence suggests that examining Coleoptera as a biodiversity indicator could produce valuable results in the context of burial grounds as urban green spaces.

Due to their unique positioning in society as places of profound cultural and historical importance, it is not possible to examine burial grounds as green spaces purely through an ecological lens. To build a comprehensive understanding of urban burial grounds as green spaces, their value for biodiversity and therefore more widely for ecosystem service generation, it is necessary to integrate historical, social changes with land management and ecological understanding. With greater urbanisation pressures in modern towns and cities, and subsequently an increased focus on ecosystem services for human health and wellbeing (Haase et al. 2014; Costanza et al. 2017; Hegetschweiler et al. 2017), it can be argued that ecological recognition of and protection for urban burial grounds is ever more necessary.

An unresolved issue regarding burial grounds in the UK is uncertainty regarding their number and coverage. Estimates put the overall number of burial grounds (classified as Christian churchyards, official sites of burial for all other religions and cultures, and cemeteries) between 12 000 and over 25 000 (Home Office 2004; CABE 2007). The most comprehensive survey covering England and Wales reported 9747 sites and a total of approximately 20 000 acres (80.94 km^2) His Majesty's Court Service (HMCS 2007); the true current acreage is unknown but likely to be significantly higher. Recent statistics for the UK as a whole specifically noted 'cemeteries' and 'religious grounds' as publicly accessible green spaces, forming an estimated 8.9% (18 878 acres or 76.40 km^2) and 6.7% (14 211 acres or 57.51 km^2) of the UK's total urban green space respectively (Office for National Statistics 2019). Whilst parks, gardens and playing fields dominate publicly accessible green spaces, 15.6% (133.91 km^2) is a meaningful contribution from burial grounds that merits research and policy attention. However, there is currently very little coordination between managers, owners and other stakeholders of burial grounds in the UK.

From an ecological management perspective, a piecemeal legislative situation and lack of legally binding site management practices pose serious issues when considering burial grounds as green spaces. The lack of legislative ecological protection for urban burial grounds stems from a profound lack of relevant research into them (Jackson and Ormsby 2017). Although there is a general assumption that many graveyards are unique, often ancient, and minimally managed habitats that can sustain a wealth of biodiversity, there has been little scientific exploration of this. A recent review of global research on burial ground biodiversity (Löki et al. 2019) found a total absence of studies looking at the direct effect of management practices on burial ground biodiversity, and reported just six articles published from the UK before March 2018, none of which addressed burial grounds in urban areas specifically. One of these was a report on an ecological survey undertaken in a single churchyard (Baker 2004) focusing on flora, and there was only a single mycological exploration (Fortey 2000). Another study reported results of a grasshopper strip experiment in a rural churchyard (Gardiner, Gardiner and Cooper 2011), the single UK animal-based study found by the review. The trend found by Löki et al. (2019) was for thematic surveys and descriptive studies of single locations, which dominate the limited ecological literature on burial grounds. Although these types of study can be of restricted scope and impact, they do provide baseline data, and even these are very much missing from the UK.

Beyond thematic biodiversity descriptions, there is some evidence of urban cemeteries being examined as green spaces in the UK. A study from Scotland found that cemeteries play an important role as green spaces for 'perceived restorativeness' of visitors (Lai et al. 2020). Another recent study examined the potential for natural burial spaces within traditional cemeteries to enhance urban ecosystem service provision (Clayden et al. 2018), which highlights the ecological importance of municipal cemeteries in the urban landscape, but is largely descriptive of site layouts and is limited by a focus on only three sites across the UK.

Overall, ecological research in urban burial grounds in the UK is limited to a small number of isolated studies that do not constitute an overview of their contributions to biodiversity or their value as urban green spaces.

Aims and objectives

Here we examined the factors influencing biodiversity within 20 urban burial grounds in different urban areas in the south of England, using flying beetles as an indicator. The majority of ecological studies in burial grounds focus on one to five sites, so this represents a large-scale ecological investigation of these spaces. By quantifying measures of biodiversity, namely abundance and family-level diversity of the indicator and capturing a range of urban landscape and environmental variables, we set out to examine the role that urban burial grounds play as ecological units in urban landscapes and the factors that influence their value for biodiversity. To begin to address the global absence of research into the impacts of burial ground management on urban biodiversity, we further investigated whether different types of landscape management practices influenced flying beetle biodiversity.

We investigated the following research questions: (i) What is the family-level biodiversity of flying beetles in urban burial grounds, in terms of abundance and richness? (ii) Is their biodiversity affected by the age or size of urban burial grounds, or by human population pressure in the wider urban area? (iii) Does the composition of the landscape surrounding urban burial grounds influence their biodiversity? (iv) Does the grounds management of urban burial grounds influence their biodiversity?

Methods

Study sites

Permissions were gained to conduct sampling in 20 burial grounds in towns within the English counties of Berkshire, Hampshire, Surrey and Buckinghamshire (Table 1, Fig. 1 and Supplementary Table S0a). Population size was used as a proxy for defining 'urban', and towns with burial grounds were chosen that had a minimum population of 20 000 people; considered 'large towns' according to a popular settlement hierarchy used in UK planning policy (Doxiades 1968). Each site was allocated to one of four management categories based on information provided by site managers (Table 2).

Flying beetle sampling development

Pitfall trapping has long been a widely accepted, convenient technique for sampling ground-dwelling arthropods (Greenslade 1964; Johan Kotze et al. 2011; Montgomery et al. 2021). However, for this project the profound social and sacred importance attached to the actual ground in graveyards meant that a less invasive methodology needed to be employed. This was at the behest of site managers, due to concerns about public perceptions.

Light traps have also been used successfully to capture beetles (Hébert et al. 2000; Hirao et al. 2008) and are much less invasive, however safety considerations of working in urban areas and site managers' concerns over public perceptions precluded this method from being used here. Therefore, whilst beetles are the focus of this study's sampling effort based on their demonstrable value in previous ecological research, neither carabids specifically nor light traps were deemed suitable. Hence, an alternative minimally invasive survey method was developed for the capture of flying beetles, to be used as a proxy measure of biodiversity.

Sampling protocol

The final apparatus used was a white, UK standard single size (180 cm×260 cm) bedsheet affixed to two tent poles (or alternatively, affixed to the poles at the top end and pegged into the ground at the bottom) held upright by guy ropes pegged into the ground with small diameter metal pegs (see Supplementary Fig. S1). It was important to ensure the sheet was as taut as possible to prevent movement or snapping in a breeze so as not to divert or dislodge insects, and this was achieved by using adjustable height poles and tethering them to the ground with guy ropes in a tripod fashion for stability a suitable distance apart.

In addition, another identical white sheet was placed flat on the ground as a further sampling area, as it was unknown whether flying beetles would preferentially land on the ground or sampling would be more successful when intercepting them in the air. The design of this sheet trap meant that upon its removal, only four small peg holes would be left in the ground (which due to grass cover would be unnoticeable) and the surrounding grass flattened by footsteps, which would recover.

Sampling took place between the 19 April and 7 September 2018. Four samples were conducted within each site; a randomised list of sites was created for each replicate using the 'rand ()' function in Excel 2016. Samples were conducted in this randomised order, during daylight hours on days when climatic conditions were considered suitable for beetles to take wing i.e. when warm enough (min. 18°C) (Caprio and Grafius 1990; Cox, Wakefield and Jacob 2007; Gaylord et al. 2008) with low wind speed (max. 7 mph) (Blau and Stinner 1983; Vanwoerkom, Turpin and Barrett 1983). Placement of the sheet trap within the site for each replicate was decided upon arrival, as it was necessary to ensure that it was set up away from any visitors present and not encroaching on graves.

Each sample was conducted for a 2-hr period, whereby a pooter was used to capture beetles landing on both the upright

Table 1: Details of the 20 sample sites used for flying beetle sampling in 2018

Site	Name	Abbreviated name	Town	Pop. by 2017 census	Population density (people/km^2)	Size (m^2)	Age (years)
1	Henley Road Cemetery	Hen.Rd	Reading	229 274	4483	195 640	91
2	Caversham Cemetery	Cav	Reading	229 274	4483	15 587	133
3	Reading Old Cemetery	Old	Reading	229 274	4483	46 782	175
4	Larges Lane Cemetery	Lar.Lane	Bracknell	83 491	4057	11 147	128
5	Worting Road Cemetery	Wor.Rd	Basingstoke	114 329	3917	52 617	104
6	Shaw Cemetery	Shaw	Newbury	41 883	3574	49 188	105
7	Newtown Road Cemetery	Newt.Rd	Newbury	41 883	3574	18 413	168
8	All Saints Churchyard	All.Sts	Maidenhead	67 441	3862	3152	162
9	Braywick Cemetery	Bray	Maidenhead	67 441	3862	32 041	65
10	Slough Cemetery and Crematorium	Slo.Crem	Slough	164 046	5410	139 929	86
11	High Wycombe Cemetery	Wyc.Cem	High Wycombe	124 073	3794	99 216	163
12	Wokingham Free Church Burial Ground	Wok.FBG	Wokingham	46 745	3233	4463	97
13	St Michael's Churchyard	St.Mic	Camberley	39 541	2949	21 430	167
14	Fleet Cemetery	Flt.Cem	Fleet	41 233	3440	20 746	104
15	Windsor Cemetery	Winds.Cem	Windsor	32 207	4409	45 843	164
16	London Road Cemetery	That.Cem	Thatcham	26 217	4530	27 056	129
17	Stoke Old Cemetery	Stk.Old	Guildford	85 208	4104	28 304	135
18	Mount Cemetery	Mount	Guildford	85 208	4104	34 688	162
19	Eashing Cemetery	Eash	Godalming	23 410	3331	61 256	118
20	Nightingale Cemetery	Ngale	Godalming	23 410	3331	17 576	161

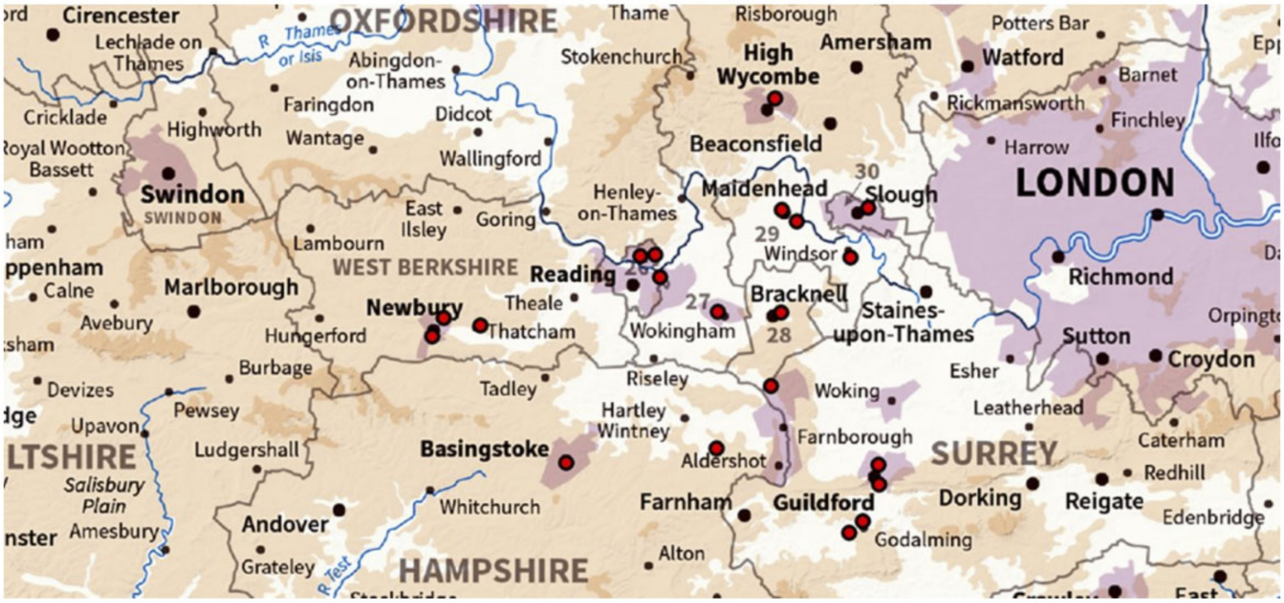

Figure 1: Map showing locations of study sites (red circles) within the wider geographical context of the South of England

Table 2: Description of study site management categories and the sites allocated to each category

Management category	Description	Sites allocated
Clear	Usage: in use	6. Shaw
	Horticultural design elements: few/none	9. Braywick
	Trees and hedges: sparse, heavily pruned	12. Wokingham Free
	Lawn: ubiquitous, close-cropped	14. Fleet
	Mowing/strimming: non-discriminatory, 2–4 per month	15. Windsor
	Free growing areas: none	19. Eashing
	Biodiversity management: none	20. Nightingale
Scape	Usage: in use	1. Henley Road
	Horticultural design elements: present, well-kept (e.g. planted flower/shrub arrangements)	5. Worting Road
	Trees and hedges: present, well-kept	10. Slough
	Lawn: present	11. High Wycombe
	Mowing/strimming: 1–3 per month	16. London Road
	Free growing areas: none to very few	
	Biodiversity management: none	
Wild	Usage: full or in use	4. Larges Lane
	Horticultural design elements: few	7. Newtown Road
	Trees and hedges: present, no or minimal pruning	8. All Saints
	Lawn: present	17. Stoke Old
	Mowing/strimming: minimal to none	18. Mount
	Free growing areas: set-aside for grassland/wildflowers	
	Biodiversity management: present, part or whole	
Min	Usage: full except family plots, no to few interments	2. Caversham
	Horticultural design elements: few/none	3. Reading Old
	Trees and hedges: present, safety management only	13. St Michael’s
	Lawn: not present (patches of grassland)	
	Mowing/strimming: once per year (late summer)	
	Free growing areas: present (safety management only)	
	Biodiversity management: present but unintentional (safety management only)	

and ground sheets (both sides of the upright sheet were used). An anemometer was used to record ambient temperature at the start and finish of each sample, initial wind speed and relative humidity. An approximation by eye was made by the sampler of the percentage cloud cover at the start of each sample. Collected Coleoptera samples were kept in the collection tubes and frozen at −20°C for a minimum of 24 hr. They were then identified to the family level and preserved in 70% (v/v) ethanol at the Health and Life Sciences Building, University of Reading, Berkshire, UK.

Land category data

Data were obtained on the positioning of each burial ground in relation to other land use types within their urban landscapes. As these data were to be used in investigations of beetle abundance and diversity, a suitable area around the sample sites needed to be established. Other studies sampling Coleoptera in urban areas to understand community dynamics obtained landscape data for a maximum buffer area of 400 m around each sample site (Braaker et al. 2014; Kyrö et al. 2018), and based on this a maximum radial buffer of 400 m was used here.

Ordnance Survey map, topography and satellite image data for each site and its immediate surrounding area were obtained from the EDINA Digimap Ordnance Survey Service. These files were loaded into and manipulated using ArcGIS version 10.5.1 to create maps with the site at the centre and radial buffers around it at intervals of 50, 100, 200 and 400 m (Fig. 2). Where polygons had not been assigned a land type, the satellite image was used to determine their nature and then a land type was manually assigned. Land types were assigned to five categories (Table 3), and the total area in m^2 for each category was calculated for each buffer interval.

Statistical analysis

Indicator species analyses (IA) was performed for the multivariate beetle family dataset using Monte Carlo significance testing with 999 randomisations (Dufrêne and Legendre 1997) in PC-Ord 5.0 (Wild Blueberry Media LLC, Corvallis, OR, USA) to examine whether specific beetle families were significant indicators of Site, Replicate, or Management type. All other statistical analyses were conducted in R version 4.0.3 (R Core Team 2020) using R Studio Version 1.3.959.

Predictor variables were first screened for multicollinearity using pairwise correlation matrices. Landscape variables (Table 3) within the 50, 100, 200 and 400 m buffer zones (Fig. 2) were strongly and positively correlated with each other ($0.95 \leq r \leq 0.60$), with the sole exception of hedges (Hdg) inside the 400-m buffer ($r < 0.20$). Hence, in further analyses only one buffer level (200 m) was used for each land category. A significant positive correlation was found between total town population and both (i) population density ($r = 0.63$) and (ii) the area of buildings and impervious surfaces ($r = 0.54$; see BSMS in Table 3). Lastly, a moderate but significant negative correlation was found between average temperature and relative humidity recorded at the time of sampling ($r = -0.45$). All variables were scaled and centred to allow for meaningful comparison.

To address our research questions regarding whether total beetle abundance was affected by (i) environmental conditions at the time of sampling, (ii) urban landscape and population factors, or (iii) site management, we used additive and interactive generalised linear mixed models (GLMMs). Based on the collection of count data, a Poisson error structure was initially used to model the response, but the residuals of all such models were found to be overdispersed. To account for this, we instead used GLMMs with a negative binomial error structure. All models used sampling replicate as a random effect and we confirmed the lack of multicollinearity using tests of variance-inflation factors (VIF). Relative humidity showed consistently high VIF values and was therefore removed prior to further analyses.

Due to the large number of potential explanatory variables, we explored all combinations of predictor variables using the dredge function in MuMIn package (Bartoń 2020). We then applied a multi-model averaging approach to the set of potentially informative candidate models [all models with ΔAICc < 7, as suggested by Burnham et al. (2011)] to assess which of the multiple predictors (weather, human population, landscape) were most strongly related to beetle abundance. The GLMMs were constructed with R package 'lme4' (Bates et al. 2015) using a negative binomial error structure (log link). Multi-model averaging was conducted using R package 'MuMIn' (Bartoń 2020). Model validation, including tests of singularity, VIFs, and model fit was assessed using R package 'performance' (Lüdecke et al.

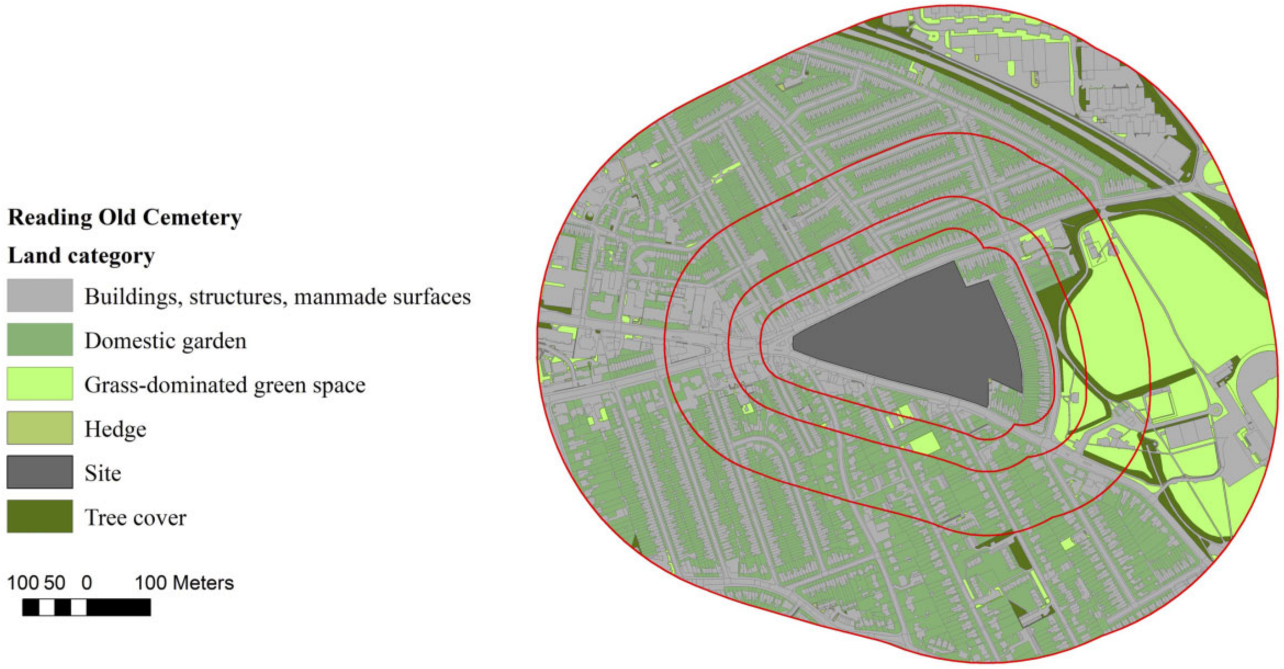

Figure 2: Map of Reading Old Cemetery (Site 3) and surrounding 50, 100, 200 and 400 metre radial buffers, created using the OS MasterMap^{TM} Topography Layer in EDINA Digimap Ordnance Survey Service

Table 3: Land categories assigned to the OS MasterMap^{TM} Topography Layer polygons within radial buffers around each study site

Code	Land category	ArcGIS Topography land types assigned
BSMS	Buildings, structures and manmade surfaces	Building, structure, path, road or track, car park, rail
GDGS	Grass-dominated green space	Amenity grassland, allotment, green roundabout, agric grass, golf course, nature reserve, parkland, park, graveyard (other than site)
Hdg	Hedge	Hedge
Gdn	Domestic garden	Garden
TC	Tree cover	Broad tree cover, conifer tree cover, scattered tree cover, mixed tree cover

Table 4: Indicator analysis for all beetle families between temporal replicates (1) and for families with significantly higher abundance/incidence between management categories within temporal replicates (2).

Beetle family	Group	Observed indicator value	Monte-Carlo Mean	Monte-Carlo SD	*P* value[a]
1. Replicate					
Apionidae	1	32.6	12.1	4.55	**0.003**
Cryptophagidae	1	15.8	9.4	4.53	0.099
Staphylinidae	1	21.8	13.4	5.09	0.074
Nitidulidae	3	57.3	22.8	6.65	**0.001**
Chrysomelidae	4	62.9	25.5	5.94	**0.001**
Coccinellidae	4	23.4	16.8	5.28	0.113
Endomychidae	1	15.0	6.1	3.68	0.055
Curculionidae	1	16.4	19.2	5.51	0.644
Carabidae	1	12.4	7.4	4.13	0.134
Elateridae	1	4.3	6.3	3.84	0.614
Oedemeridae	2	11.4	8.1	3.89	0.176
Scraptiidae	1	6.2	6.1	3.66	0.563
Erotylidae	1	5.0	5.8	0.67	1
Dasytidae	1	5.0	5.8	0.67	1
Ptinidae	2	6.7	5.8	0.67	0.236
Melyridae	2	6.7	5.8	0.66	0.194
Dermestidae	3	12.5	5.3	3.52	0.105
Cerambycidae	3	6.2	5.8	0.67	0.485
Tetratomidae	2	6.7	5.8	0.67	0.218
Byturidae	2	6.7	5.8	0.67	0.217
Ptilidae	4	5.6	5.8	0.68	0.685
Latridiidae	4	16.7	6.2	3.61	**0.031**
Corylophidae	4	5.6	5.8	0.67	0.721
Melandryidae	4	11.1	5.5	3.2	0.148
2. Management (replicate)					
Apionidae	Scape (R3)	50.0	25.1	15.10	0.051
Chrysomelidae	Clear (R4)	56.3	41.1	8.32	**0.042**

[a]Proportion of 999 randomized trials with indicator value equal to or exceeding the observed indicator value. P=(1 + number of randomized runs ≥ observed)/(1 + number of randomized runs).

Values in bold indicate statistical significance (P = < 0.05).

2021). Importance values were calculated for each predictor and the significance of predictor variables was assessed using the 95% confidence intervals of their coefficients. These analyses were conducted on total abundance across all beetle families, and for individual families with sufficient abundance ($n \geq 50$).

Results

Overall abundance, diversity and temporal change

The sheet trap surveys captured a total of 884 individuals within 24 Coleopteran families, with Nitidulidae (sap beetles), Chrysomelidae (leaf beetles) and Curculionidae (true weevils) making up 48.2%, 25.9% and 7.8% of the total capture, respectively.

Across all sites the total observed beetle community changed significantly over time during the sampling period (19 April to 7 September 2018) (Supplementary Fig. S2 and Supplementary Table S5a). Jaccard coefficients were calculated as a measure of taxonomic family similarity between samples, and show that replicates 1, 2 and 3 are very similar in terms of community composition, sharing between 44% and 56% of families. Replicate 4 was relatively distinct from all previous replicates, sharing between 35% and 37.5% of families (Supplementary Table S6a). Both Shannon and Simpson diversity indices showed that Replicate 1 had the highest beetle family diversity, followed by Replicates 2, 4 and 3 respectively (Supplementary Table S5a).

Indicator analyses show that certain families were significantly associated with a particular temporal replicate, based on abundance and incidence (Table 4). Apionidae (seed weevils) were significantly associated with Replicate 1 ($P = 0.003$), Nitidulidae with Replicate 3 ($P = 0.001$) and both Chrysomelidae and Latridiidae (minute brown scavenger beetles) with

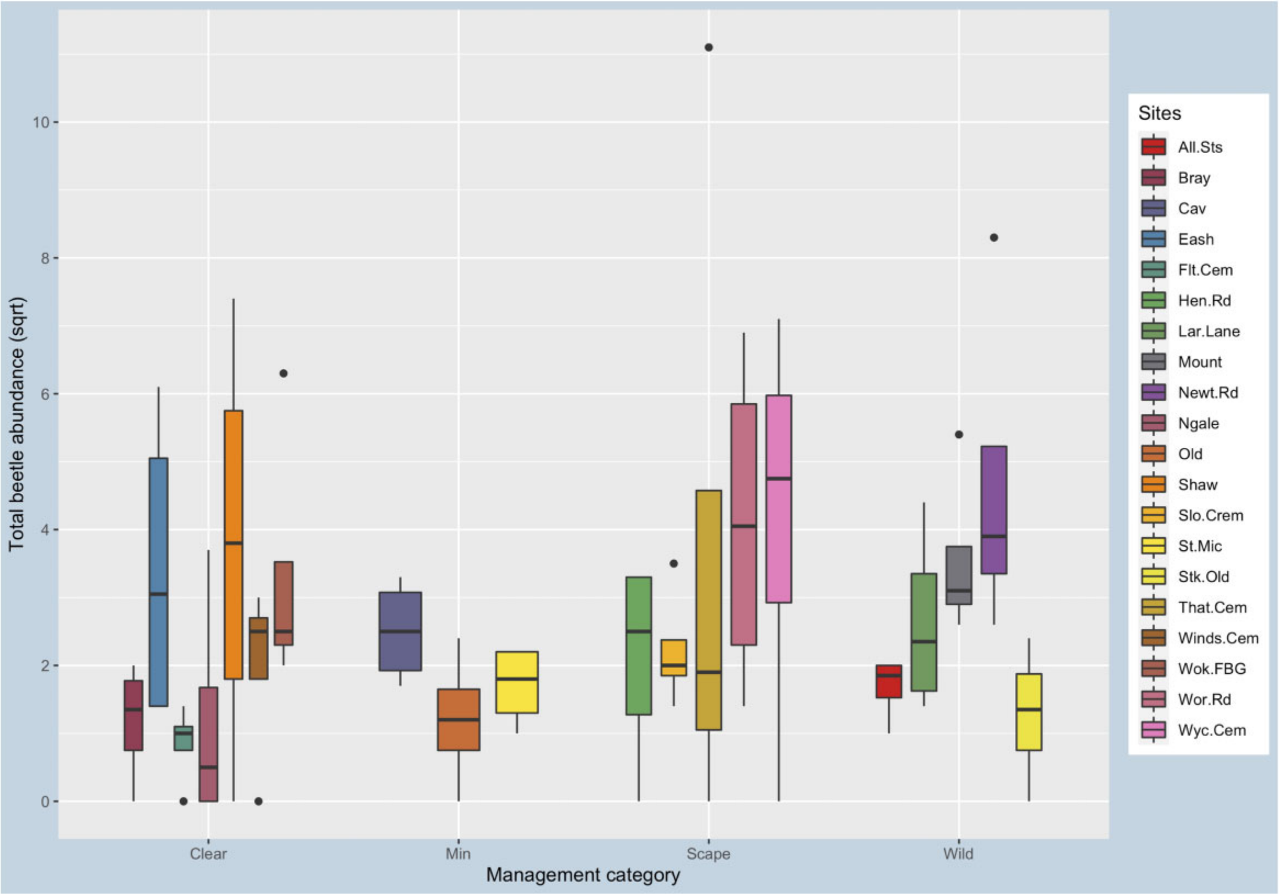

Figure 3: Boxplot of total beetle abundance (square root transformed) grouped by management category for each sample site

Replicate 4 (P = 0.001 and 0.031, respectively). In addition to these changes in family composition over time, total beetle abundance showed distinct inter-site variation (Fig. 3).

Influence of size, age and local human population factors

Site size was, *a priori*, predicted to positively influence biodiversity. Using multi-model inferencing, from the set of all plausible models (see Supplementary Table S1a), we found that site size had a significant negative influence on total beetle abundance in the AICc 'best' model (Supplementary Table S1b). Site size was the fifth most important factor in the multi-model inferencing analysis, with a negative effect on abundance, but this was not found to be statistically significant (RI = 0.39, P = 0.286; Table 5). Burial ground age was also predicted to have a positive influence on biodiversity. However, age did not appear as a significant influencing factor based on relative importance values (Tables 5 and 6) and was not included in any of the 'best' models for total abundance or abundance of individual beetle families (see Supplementary Tables S1–S4). Increasing population pressure was predicted to have a negative influence on biodiversity. We found that population density was negatively associated with total beetle abundance and ranked fourth in terms of relative importance (Table 5). However, in both the AICc 'best' model including management (Supplementary Table S1b) and the multi-model inferencing (Table 5), this association did not constitute a significant effect. Similarly, total town population was included in the AICc 'best' model (Supplementary Table S1c) and was negatively associated with beetle abundance, but this effect was not statistically significant (Supplementary Table S1c). Using multi-model inferencing town population was ranked sixth in terms of relative importance.

Influence of the surrounding urban landscape

The total abundance of flying beetles was positively influenced by the area of grass-dominated green space (P = 0.049) and domestic gardens (P = 0.045) within 200 m in the AICc 'best' model including management (Supplementary Table S1b). Relative importance values from the multi-model inferencing supported the cover of domestic gardens (RI = 0.72) and hedges (RI = 0.65) as the two most important, and only statistically significant, surrounding landscape factors influencing total abundance, with grass-dominated green space showing a weakly positive association and tree cover weakly negative (Table 5).

The abundance of the Nitidulidae family was also positively influenced by the area of domestic gardens (P = 0.001) and hedges (P = 0.006) in the AICc 'best' model including management (Supplementary Table S2b), which were also ranked as the most important of the explanatory variables modelled (RI = 0.98 and 0.93, respectively) using multi-model inferencing (Table 6).

Influence of site management

Burial grounds under 'Clear' management (the strictest regime) exhibited lower total beetle abundances than those with less intensive management. However, analysis of estimated marginal

Table 5: Model-averaged coefficients for factors influencing total abundance based on multi-model inference ordered by relative importance value (RI)[a]

Factor	Coef	Adj. SE	95% CI	Z value	P value	RI
Domestic garden	**0.022**	**0.0102**	**(0.0021, 0.0426)**	**2.162**	**0.031**	**0.72**
Hedge	**0.017**	**0.0085**	**(0.0002, 0.0338)**	**1.984**	**0.047**	**0.65**
Average temperature	0.012	0.0073	(−0.0027, 0.0265)	1.600	0.110	0.50
Population density	−0.014	0.0134	(−0.0402, 0.0127)	1.018	0.309	0.40
Site size	−0.018	0.0164	(−0.0500, 0.0148)	1.067	0.286	0.39
Town population	−0.010	0.0148	(−0.0391, 0.0192)	0.668	0.504	0.36
Tree cover	−0.011	0.0094	(−0.0301, 0.0075)	1.179	0.239	0.36
Grass-dominated green space	0.011	0.0130	(−0.0144, 0.0371)	0.864	0.388	0.33
Management category	NA	NA	NA	NA	NA	0.32
Min	−0.003	0.0134	(−0.0297, 0.0233)	0.235	0.815	NA
Scape	**0.032**	**0.0161**	**(0.0002, 0.0638)**	**1.975**	**0.048**	NA
Wild	0.008	0.0111	(−0.0141, 0.0300)	0.708	0.479	NA
Cloud cover	0.008	0.0083	(−0.0083, 0.0249)	0.979	0.328	0.31
Buildings, structures and man-made surfaces	−0.007	0.0104	(−0.0275, 0.0138)	0.646	0.518	0.30
Site age	0.000	0.0103	(−0.0201, 0.0209)	0.038	0.970	0.24
Wind speed	−0.001	0.0083	(−0.0172, 0.0156)	0.097	0.923	0.24

[a]Bold indicates significance based on 95% CI.

means using the AICc 'best' model (Supplementary Table S1b) showed no significant difference in total beetle abundance between pairwise combinations of 'Clear', 'Wild', and 'Min' management categories. The second most intensive management category, 'Scape', had a significantly higher total beetle abundance than 'Clear' ($P = 0.011$) and 'Min' ($P = 0.033$).

A priori it was hypothesised that burial grounds with the least intensive management would exhibit greater family-level diversity. However, as with total abundance, diversity did not exhibit the hypothesised trend. The results of diversity analyses are presented here with acknowledgement that groupings are unbalanced, as different numbers of sites were assigned to each management category. Categorisation was performed retrospectively after site visits and speaking to site managers, so the imbalance was not known in advance.

Both Shannon and Simpson diversity indices show that the 'Wild' management category had the highest beetle family diversity, followed by 'Clear', 'Min' and 'Scape' in that order, although the Simpson index values for 'Clear' and 'Min' are the same (Supplementary Table S5b). Pairwise Jaccard coefficients were calculated as a measure of taxonomic family similarity between management categories and produced a varied picture (Supplementary Table S6b). The 'Clear' category showed the highest levels of similarity overall, to 'Scape' and 'Wild' with 59% and 55% family similarity respectively. The 'Wild' category showed the most dissimilarity to other categories; 'Scape' and 'Min' at 47% and 43% respectively. When the most and least intensive management categories were compared, 'Clear' and 'Min', 45% family similarity was observed.

Some beetle families were only found in one of the four management types. Beetles from two families (Erotylidae, Cerambycidae) were only found at sites considered to be under 'Clear' management (15 families in total). Three families (Dasytidae, Byturidae, Ptilidae) were only found at sites under 'Min' management (14 families in total). No families were only found at sites with 'Scape' management (12 families in total, highest abundance). Four families (Ptinidae, Melyridae, Tetratomidae, Corylophidae) were only found at sites with 'Wild' management (16 families in total). Using indicator analyses Chrysomelidae were associated with management type 'Clear' during Replicate 4 ($P = 0.042$), and Apionidae were strongly associated with management type 'Scape' during Replicate 3 although this was not statistically significant ($P = 0.051$).

Summary of factors influencing the total abundance of flying beetles

Model averaging revealed that surrounding domestic gardens, hedges and the 'Scape' management category (see Table 2) all exhibited significant positive influences on the total abundance of flying beetles (Table 5). From the set of plausible models (see Supplementary Table S1a), the AICc 'best' model that included management indicated positive effects of grass-dominated green space, domestic garden, and 'Scape' management, and negative effects of population density and site size (see Supplementary Table S1b). The AICc 'best' model that did not include management indicated positive effects of domestic gardens and hedges, and a negative effect of town population (see Supplementary Table S1c).

When model fit was assessed, the global maximal model (model including all potential explanatory variables), which is the basis for model averaging, had marginal R^2=0.370 and conditional R^2=0.422 (Nakagawa R^2) with no singularity. For the total abundance of flying beetles there was strong support across all statistical modelling techniques for positive influences of the area of domestic gardens and other green spaces in the immediate urban surroundings of the burial grounds, positive influences of management focused on horticultural design, and weaker support for negative effects of burial ground size and total population or population density of the surrounding town.

Summary of factors influencing the abundance of specific beetle families

Each beetle family with abundance ≥50 was examined separately to assess the factors impacting these distinct groups. These were the Nitidulidae, Chrysomelidae and Curculionidae families.

Model averaging revealed that surrounding domestic gardens, hedges and the 'Wild' management category (see Table 2) all exhibited positive influences on the abundance of Nitidulidae based on model averaging results (Table 6). When

Table 6: Model-averaged coefficients for factors influencing Nitidulidae abundance based on multi-model inference ordered by relative importance value (RI)[a]

Factor	Coef	Adj. SE	95% CI	Z value	P value	RI
Domestic garden	**0.070**	**0.0210**	**(0.0285, 0.1108)**	**3.316**	**>0.001**	**0.98**
Hedge	**0.054**	**0.0186**	**(0.0171, 0.0899)**	**2.881**	**0.004**	**0.93**
Site size	−0.038	0.0245	(−0.0865, 0.0096)	1.570	0.116	0.46
Management category	NA	NA	NA	NA	NA	0.37
Min	0.016	0.0193	(−0.0217, 0.0541)	0.840	0.401	NA
Scape	−0.006	0.0292	(−0.0628, 0.0517)	0.190	0.850	NA
Wild	**0.041**	**0.0162**	**(0.0090, 0.0727)**	**2.515**	**0.012**	NA
Buildings, structures and man-made surfaces	−0.023	0.0178	(−0.0576, 0.0123)	1.269	0.204	0.36
Site age	0.018	0.0216	(−0.0243, 0.0603)	0.834	0.405	0.30
Tree cover	−0.017	0.0202	(−0.0568, 0.0225)	0.849	0.396	0.29
Average temperature	0.014	0.0177	(−0.0208, 0.0487)	0.788	0.431	0.28
Grass-dominated green space	0.006	0.0231	(−0.0392, 0.0515)	0.265	0.791	0.27
Population density	0.010	0.0205	(−0.0298, 0.0505)	0.506	0.613	0.25
Cloud cover	0.011	0.0177	(−0.0237, 0.0456)	0.621	0.535	0.25
Town population	−0.001	0.0227	(−0.0451, 0.0437)	0.031	0.975	0.23
Wind speed	−0.002	0.0158	(−0.0329, 0.0289)	0.126	0.900	0.22

[a] Bold indicates significance based on 95% CI.

model fit was assessed, the global maximal model had marginal R^2=0.341 and conditional R^2=0.776 (Nakagawa R^2) with no singularity. From the set of plausible models (see Supplementary Table S2a), the AICc 'best' model that included management indicated positive effects of domestic gardens, hedges, and 'Wild' management (see Supplementary Table S2b). The AICc 'best' model that did not include management (see Supplementary Table S2c) indicated positive effects of domestic gardens and hedges, and a negative effect of site size.

None of the measured weather, human population, or landscape factors significantly influenced the abundance of Chrysomelidae based on model averaging results (data not shown). The global model for Chrysomelidae abundance had marginal R^2=0.220 and conditional R^2=0.700 (using Nakagawa R^2). From the set of plausible models (see Supplementary Table S3), the AICc 'best' model for Chrysomelidae was the null model (intercept only, no predictor variables included).

None of the measured weather, human population, or landscape factors significantly influenced the abundance of Curculionidae based on model averaging results (data not shown). The global model for Curculionidae abundance indicated the random effect of temporal replicate did not improve model fit (both marginal and conditional Nakagawa R^2=0.425) suggesting, in agreement with indicator analysis, that there was little temporal change. From the set of plausible models (see Supplementary Table S4), the AICc 'best' model for Curculionidae was the null model (intercept only, no predictor variables included).

Discussion

Flying beetle communities recorded in the 20 urban burial grounds studied here changed over time in terms of family-level composition, richness, and abundance, and showed distinct inter-burial ground variation. Burial ground age (the number of years since the first recorded interment) did not exert a significant influence on total flying beetle abundance. Larger burial grounds yielded lower flying beetle abundances and we note that site size was positively correlated with the urban population, which was in turn positively correlated with the presence of man-made structures and surfaces in the surrounding urban landscape. The greater the amount of green space, public and private, surrounding the study burial grounds, the greater the abundance of flying beetles found within them.

The management regimes employed at the study burial grounds had significant effects on flying beetle abundance and diversity, however the expected trend of higher abundance and greater diversity with the least intensive management was not found. Rather, horticultural landscaping practices appear to promote greater flying beetle biodiversity than the most minimal management approaches. In addition, ground management practices to encourage biodiversity, and the most rigorous mowing and pruning regimes, resulted in greater flying beetle diversity than leaving a burial ground almost completely alone. Nine families were found only in one specific management type; two associated with the lightest touch management regimes are frequent flower visitors, with the remaining seven known to affiliate with deadwood, dead fungi and decaying organic matter (Duff and Schmidt 2012).

Research Question 1: overall abundance, diversity and indicator analyses

Our results indicate clear variation in the abundance and diversity of flying beetles at the family level. The flying beetle communities found within urban burial grounds were generally dominated by three families (Nitidulidae, Chrysomelidae, Curculionidae), however family-level similarity and community diversity between replicates exhibited meaningful differences. The highest level of family diversity was found earlier in the sampling period, whereas the last temporal sampling replicate showed the most distinctive community. Observed variations in abundance and diversity are reflective of the ecology of the beetle families. For example, chrysomelids were found both earlier and later in the year, with the late appearance identified as an indicator; many species within this family overwinter as adults and lay eggs in the spring, followed by a new generation of adults emerging in the autumn. Beetles of the family Nitidulidae were found in the greatest numbers in high summer when flower pollen availability is highest, and indicator analyses supported this association.

This establishes that not all urban burial grounds included in this study are equal in terms of the biodiversity they support, and that abundance and family diversity change over time. Whilst relevant research discourse generally identifies burial grounds, particularly in urban areas, as places of potentially high biodiversity value (Barrett and Barrett 2001; Löki et al. 2019), the current study illustrates that some may be of relatively low value for taxa of interest.

Nitidulidae, Chrysomelidae and Curculionidae

Most species within the family Nitidulidae are flower visitors that feed on pollen, and so greater floral resources are required to support larger populations (Frearson et al. 2005). Domestic garden and hedge coverage in the urban landscape surrounding the burial grounds were the two most important factors affecting Nitidulidae abundance and had a positive effect, as did burial grounds under the Wild management category. These factors could increase floral resources both within and surrounding the burial grounds, boosting Nitidulidae population sizes and potentially attracting beetles on the wing into the area, making them more likely to be sampled.

The family Chrysomelidae is large and diverse, with members feeding on leaves of a wide range of host plants. Some species could feasibly benefit from any of the management types, so it could be expected that no one variable predicts their abundance. The family Curculionidae is similarly diverse with specific host plant associations; however, they typically feed on different parts of the plant to chrysomelids, namely the stems and roots. Based on their resource requirements, we predicted that the same factors that were important for Nitidulidae would be so for these other abundant beetle families, as an increase in green space coverage and wildlife-focused management practices such as pruning and mowing reductions may increase vegetative biomass in addition to floral resources. However, our study found that none of the measured variables explained the abundances of these two taxonomic families.

Research Question 2: burial ground size, age and local human population factors

Burial grounds are often positioned as the last remnants of natural habitats in urban areas, with the longevity of their land use within these dynamic, transformed landscapes viewed as fundamental to their value for biodiversity (Barrett and Barrett 2001; Buchholz et al. 2016; Löki et al. 2019). Studies have found that older urban burial grounds harbour considerable biological richness, however these mainly focus on vascular plants, sometimes lichens, mosses, bats and birds, with invertebrates either excluded or reduced to ground-dwelling groups such as ground beetles or spiders (Buchholz et al. 2016; Kowarik et al. 2016; Löki et al. 2020). Our findings based on a novel taxonomic group challenge these assumptions, as burial ground age was not found to have a significant effect on flying beetle biodiversity.

A key aspect of older burial grounds may be the presence of older vegetation and greater tree cover, and in those burial grounds that are minimally managed due to being closed to new interments, a greater quantity of deadwood. Therefore, in newer burial grounds older vegetation cover and deadwood habitats may be largely replaced by younger shrubs and trees as part of modern horticultural installations and flower displays; the most abundant flying beetle families we found are associated with pollen, leaves and developing stems, hence newer vegetative resources and floral resource availability may be more important for these taxa, meaning the age of a burial ground would not have the expected impact. Burial ground size did appear to exert a significant influence on beetle abundance, but not in the predicted direction. It was hypothesised that larger sites, by virtue of having greater surface area (and hence more green space), would support higher levels of biodiversity. Previous studies produce a mixed but limited picture of the importance of urban burial ground size; it was not found to be significant for Turkish orchid taxa (Löki et al. 2015) or birds in Chile despite expectations that it would be important (Villaseñor and Escobar 2019), however a positive correlation was found between size and vascular plant species richness in Poland, although it was the least important explanatory variable (Nowińska, Czarna and Kozłowska 2020). Studies examining urban green spaces more generally have found patch area to be one of the most important positive influences on biodiversity of multiple taxonomic groups (Beninde, Veith and Hochkirch 2015; Callaghan et al. 2018); however these findings are discussed in the context of green spaces and their various attributes such as tree cover and distance to water, rather than the investigation of specific green space land use types.

The current study provides some evidence of a negative effect of larger burial grounds on total flying beetle abundance, potentially because they are associated with urban areas of higher population size and density, which also have negative impacts on beetle abundance. Larger burial grounds are required in more populous urban communities to support the higher number of deaths, and urban areas with greater human pressure by necessity have more man-made infrastructure; a more impermeable, hostile landscape surrounding larger burial grounds has a negative impact on the abundance of flying beetles. Similar results regarding the surrounding landscape have been found for native birds (Villaseñor and Escobar 2019), although the limited number of sites was thought to obscure any influence of burial ground size. Previous studies that sampled invertebrates were either conducted in a single burial ground (Orstan and Kosemen 2009; Gardiner, Gardiner and Cooper 2011; Atay, Jansson and Gürkan 2012; Tan 2012; Buchholz et al. 2016; Kowarik et al. 2016), so that size could not be examined as an explanatory variable, or otherwise did not include it as a variable of interest (Hartley et al. 2007; Matteson, Grace and Minor 2013; Tan et al. 2013). Future research building on the relationships observed here between urban populations and burial ground biodiversity could be beneficial, for example the exploration of links between ecological and social values or pressures within a human-ecological functional model (*sensu* Tan 2017).

Research Question 3: the surrounding urban landscape

Analyses show statistically strong and consistent effects of different land use types in the immediate surroundings on flying beetle abundances (total and Nitidulidae) in burial grounds. Variables associated with green infrastructure in the urban landscape surrounding the study burial grounds were prominent in both the modelling and relative importance analyses. This strongly suggests that increased coverage of green infrastructure in an urban landscape can have significant, positive impacts on the biodiversity within urban burial grounds. Specifically, increasing area of domestic gardens and hedges were associated with total abundance of flying beetles and the abundance of Nitidulidae, and there was some evidence for the importance of grass-dominated green space for total abundance of flying beetles.

The influence of wider land use in urban areas on biodiversity within a green space is a topic of research interest at different scales. For example, within 1 km of cemeteries (Villaseñor and Escobar 2019) found an important positive impact of surrounding vegetation cover on native bird diversity but did not break this down into specific green infrastructure types. An investigation of vegetation cover influence on flower-visiting insects within urban green spaces found that smaller spatial scales (30 m) were more explanatory than larger ones (200–500 m) (Matteson, Grace and Minor 2013). By contrast, from the perspective of beetle dispersal distances, our study found that green infrastructure within a 200 m buffer had significant effects on flying beetles. There is evidence that local-scale, rather than landscape-scale, habitat area and connectivity are more important for supporting higher levels of biodiversity (Philpott et al. 2014; Beninde, Veith and Hochkirch 2015; Callaghan et al. 2018), although explicit definitions of 'landscape-scale' and delineations of the extent of an urban landscape often either differ or are not provided. The buffer intervals used in our study were found to be strongly colinear, meaning that they were all as explanatory as each other. Therefore, green infrastructure coverage within up to a 400 m radius of urban burial grounds could be considered important for the biodiversity of flying beetles within them.

The significant positive effect of domestic gardens and hedges on flying beetle abundances indicates that management and retention of garden space by individual households can play a significant role in the maintenance of urban biodiversity, which could be especially important in large, densely populated towns and cities. Our results are supported by prior work on the biodiversity value of urban gardens, which consistently finds them to be an important type of green space for enhancing and retaining biodiversity of multiple taxonomic groups (Davies et al. 2009; Goddard, Dougill and Benton 2010; Cameron et al. 2012; Belaire, Whelan and Minor 2014).

The increased presence of Nitidulidae beetles specifically, whose ecology shows a strong affinity with flowering plants, may indicate that the enhancement and elongation of the flowering period within gardens is especially important for the maintenance of, at least, flying beetle abundances.

Research Question 4: site management

Our analysis shows that caretakers of burial grounds in urban areas directly influence biodiversity through management practices. More specifically, our results show that a hands-off approach (the 'Min' category) yields higher richness and uniqueness of beetle families, more so than purposeful ecologically sensitive initiatives such as cultivating areas of wildflower meadow and a 'light touch' pruning regime (the 'Wild' category). In terms of the size of flying beetle communities, our results suggest that the second most intensive management type, 'Scape', generated higher overall abundances, but of fewer families. *A priori* it was expected that more intense management would negatively affect biodiversity, however a small degree of management and horticultural installations as characterised by the 'Scape' category were found here to generate higher beetle abundance than no management at all (the 'Min' category). Flying carabid beetles have been found to fly more in graveyards than other grassland habitats, possibly allowing for more effective dispersal due to increased topsoil disturbance from digging and trampling (Hartley et al. 2007). This could contribute to in-use, actively managed graveyards such as those in the 'Scape' category supporting higher abundances of generalist flying beetles such as the family Nitidulidae.

Any of these approaches result in higher beetle abundance than the most intensive management (the 'Clear' category). This is not necessarily to say that urban burial grounds under these stringent management regimes are not valuable for flying beetles; the family Chrysomelidae was identified as an indicator during late-Summer sampling in the Clear management type.

The burial grounds allocated to the management category 'Wild' were associated with higher flying beetle diversity in addition to greater Nitidulidae abundance. Four beetle families known to be deadwood affiliates were found only in burial grounds within this category. Along with the greater abundance of flower visitors, this suggests that active management for deadwood retention is more important than the presence of incidental deadwood due to tree age in older burial grounds, as supported by our results showing that burial ground age was not an important influence.

A previous study investigating the effect of management intensity on the biodiversity of urban cemeteries used a single management technique, the uprooting of tree saplings, to represent management effort (Kowarik et al. 2016) and found that although spiders responded negatively to increasing management pressure, there was no significant effect on ground beetles. Our study incorporates entire management regimes, not just a single practice, and the impacts on the biodiversity of flying beetles demonstrated here suggests that flying and ground-dwelling invertebrate communities may respond differently to management practices in urban burial grounds. Research conducted on the biodiversity of arthropods in other green space types found little impact of management intensity on highly mobile taxa, but a negative impact on those with low mobility (Sattler et al. 2010), although again only a single practice was used to represent site management. Further work is needed to better understand the effects of grounds management regimes on different functional invertebrate groups in urban burial grounds.

Sampling method

This study presents a beetle capture methodology suitable for deployment in environments where high mobility and preservation of the ground are key considerations. The use of this low-invasive sampling method has translated into positive working relationships for future projects, providing opportunities for further sensitive investigation of biodiversity in burial grounds.

Conclusions

Our study of flying beetles challenges assumptions about biodiversity in urban burial grounds. Larger, older sites were not found to contain a higher abundance of flying beetle families and had a negative influence on beetle abundance that may have been related to larger urban populations. We found that an increase in the green space surrounding an urban burial ground, particularly gardens and hedges, had the most significant positive impact on abundance of flying beetles within the burial grounds.

Perhaps most importantly, our study provides the first insights into the effects of site management on urban burial ground biodiversity, showing that expensive and high intensity maintenance practices appear to be detrimental. A positive outcome of this work is that burial grounds managed as horticultural public garden landscapes can support high abundances of wild taxa similar to those that are managed, at least in part, as wildlife refuges or not actively managed at all; an arguably rare situation in which public perception and demand correlate with benefits to nature. However, ecologically sensitive management practices in urban burial grounds are shown here for the first time to promote higher level of diversity and provide opportunities for specialist species to persist in ever-changing urban landscapes.

Supplementary data

Supplementary data are available at *JUECOL* online.

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Conflict of interest statement. None declared.

Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

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