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Urban tree cover improves breeding bird abundance across all public cemeteries in one of Europe's largest cities

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Abstract

Urbanisation can lead to the destruction and fragmentation of natural landscapes, significantly reducing biodiversity and disrupting ecological functions and services. Green spaces within cities, including cemeteries, act as refuges for urban biodiversity and provide vital habitats for various taxonomic groups, such as birds. Understanding how local and landscape factors influence biodiversity in urban cemeteries is essential to inform effective conservation efforts. This study assessed breeding bird abundance, richness, and diversity across all of Munich's public cemeteries during May and June 2022. The influence of local variables (cemetery size and tree cover) and landscape variables (tree cover and road cover within a 1 km radius) was analysed using GIS. Surprisingly, none of these explanatory variables had a strong effect on species richness, species diversity, or taxonomic diversity. This may indicate the need to examine other spatial scales or use different measures of urbanisation. However, bird abundance within fixed-radius point counts in the largest and most densely wooded cemeteries was approximately two-thirds greater than in the smallest and least densely wooded cemeteries, indicating that both area and tree cover are critical for supporting bird populations. These findings highlight trees as key habitat features in urban cemeteries, suggesting that tree conservation and health should be top priorities for urban green space management. This further supports the need to conserve urban trees for the multiple benefits they provide to human residents. Further research into the functional diversity of urban cemetery birds and the influence of cemetery tree age on these avian communities is warranted.

Keywords: Avian ecology, avifauna, tree cover, urban ecology, urban green spaces, urbanisation.

1. Introduction

In highly urbanised landscapes, such as cities, semi-natural habitat patches that have been left relatively undisturbed are of great conservation importance (Löki *et al*., 2019; Ramírez-Albores *et al*., 2024). Commonly referred to as urban green spaces, these patches are open or semi-open green areas, containing vegetation and other resources that provide suitable habitat for urban flora and fauna (Curzel *et al*., 2021). These spaces are also of great importance to humans in terms of their social value as public areas that contribute significantly to mental well-being of urban residents (Botzat *et al*., 2016). The importance of this ecosystem service became even more apparent during the COVID-19 pandemic (Ugolini *et al*., 2020). Examples include wooded streets (Curzel *et al*., 2021), parks (Godoy *et al*., 2024), allotments (Korányi *et al*., 2021), urban forests (de Groot *et al*., 2021), sacred sites such as shrines and temples (Matsumoto *et al*., 2024), and cemeteries (Villaseñor and Escobar, 2019). Cemeteries can be defined as "burial grounds, especially a large, landscaped park or ground laid out expressly for the deposition or interment of the dead, not being a churchyard attached to a place of worship" (Rugg, 2000, p. 260). Previous research has shown that cemeteries can represent key refuges for biodiversity in heavily urbanised areas (Barrett and Barrett, 2001; Čanády and Mošanský, 2017; Tryjanowski *et al*., 2017; Villaseñor and Escobar, 2019). The long-term existence and undisturbed status of many urban cemeteries allow them to support relatively high biodiversity compared to surrounding urban land use types and therefore to act as biodiversity refuges in heavily urbanised landscapes (Löki *et al*., 2019).

Recently, urban ecology research has attempted to categorise bird species based on their ability to exploit urban habitats and tolerate urban disturbances, broadly dividing species into one of three categories: urban avoiders, urban adaptors, and urban exploiters (Geschke *et al*., 2018; Korányi *et al*., 2021). For example, urban exploiters have generally been shown to have broader dietary niches than urban avoiders, allowing them to better utilise food resources provided by cities (Palacio, 2020). Urban avoiders, in contrast, include many tree-foraging and insectivorous species, which are better adapted to woody habitats (Korányi *et al*., 2021). This contrasts with urban adaptors and exploiters, which are better adapted to make use of human-based resources, including an improved ability to breed successfully on artificial structures such as buildings (MacGregor-Fors and Schondube, 2011). This makes urban cemeteries, with their mixed habitat-matrix of semi-wooded grassland, heavily interspersed with human-made graveyard-related structures, unusual in their potential to host bird species from across these different urban-exploitation categories.

Species richness is a response variable frequently used to measure biodiversity in urban ecology research (Jiguet *et al*., 2005). For most taxa, the main factors affecting species richness are habitat size, heterogeneity of the area, degree of isolation from other similar habitat patches, and the productivity and age of the area (MacArthur and Wilson, 1967). Previous studies of bird communities in urban green spaces have mainly focused on determining how bird species richness is affected by certain explanatory variables, including patch-level attributes (local to each site) and landscape attributes. Commonly studied patch-level variables include green space type (de Groot *et al*., 2021; Korányi *et al*., 2021; Morelli *et al*., 2018), site size (Dale, 2018; Leveau, 2021; Oliver *et al*., 2011), vegetation (tree and shrub) coverage (Callaghan *et al*., 2018; Morelli *et al*., 2018; Villaseñor and Escobar, 2019), tree richness (Oropeza-Sánchez *et al*., 2024), and age of trees (Tryjanowski *et al*., 2017). Commonly studied landscape variables, on the other hand, include isolation (Dale, 2018), degree of urbanisation around the site (Korányi *et al*., 2021; Oliver *et al*., 2011; Villaseñor and Escobar, 2019), and vegetation coverage around the site (Callaghan *et al*., 2018; Villaseñor and Escobar, 2019).

However, species richness is not the only response variable that has been studied in urban ecology research on bird communities in urban green spaces. For example, abundance is another measure that has been used to investigate how local and landscape drivers affect bird communities in urban environments (Mayorga *et al*., 2020; Tryjanowski *et al*., 2017; Villaseñor and Escobar, 2019). Similarly, species diversity (Callaghan *et al*., 2018; Tryjanowski *et al*., 2017) and taxonomic diversity (Curzel *et al*., 2021; Morelli *et al*., 2018) are diversity indices that have commonly been used to investigate the influence of size-, local-, and landscape-level habitat factors on bird communities in urban green spaces.

The objective of this study was to broadly quantify the avian diversity of cemeteries within a major urban area and to investigate how this avian diversity relates to environmental characteristics at the patch level (local, within-site variables) and at the landscape level. Specifically, this study assessed how well the abundance, species richness, species diversity, and taxonomic diversity of breeding bird communities within Munich's urban cemeteries can be predicted by local variables (cemetery size and cemetery tree cover) and landscape variables (tree cover and road cover within 1 km of the cemetery). This study aimed to test the hypothesis that these diversity indices are significantly related to the local and landscape variables outlined above, as well as to combinations of, and interactions between, these local and landscape variables.

2. Materials and methods

2.1 Study area

This study was carried out in Munich, Bavaria, Germany (contextual information about the city provided in Supplementary Material 1). In total, the city contains approximately 30–40 public and private cemeteries, varying in size from less than 0.5 ha to approximately 50 ha, with the exception of the 160 ha Waldfriedhof forest cemetery (not included in this study for reasons discussed later). The cemeteries included in this study are typically made up of a matrix of lightly wooded areas and more open, lawned green spaces. They are dominated at ground level by a variety of stone structures (e.g. headstones, statues, and occasionally larger tombs) arranged in a regular pattern across large areas of the cemetery (example photographs provided in Supplementary Material 2).

2.2 Study design

In total, 23 urban cemeteries in the city of Munich were selected for bird surveys in this study (see Figure 1). These cemeteries were identified as being suitable for this study for several reasons. First, all cemeteries surveyed are classed as public cemeteries, meaning they are freely accessible to the public and open at 8:00 a.m. This allowed all surveys to be conducted at a favourable time (consistent with other urban bird studies), as the optimum time for bird surveys is during the 3–4-hour window after sunrise, when birds are most active and vocal, ensuring the highest

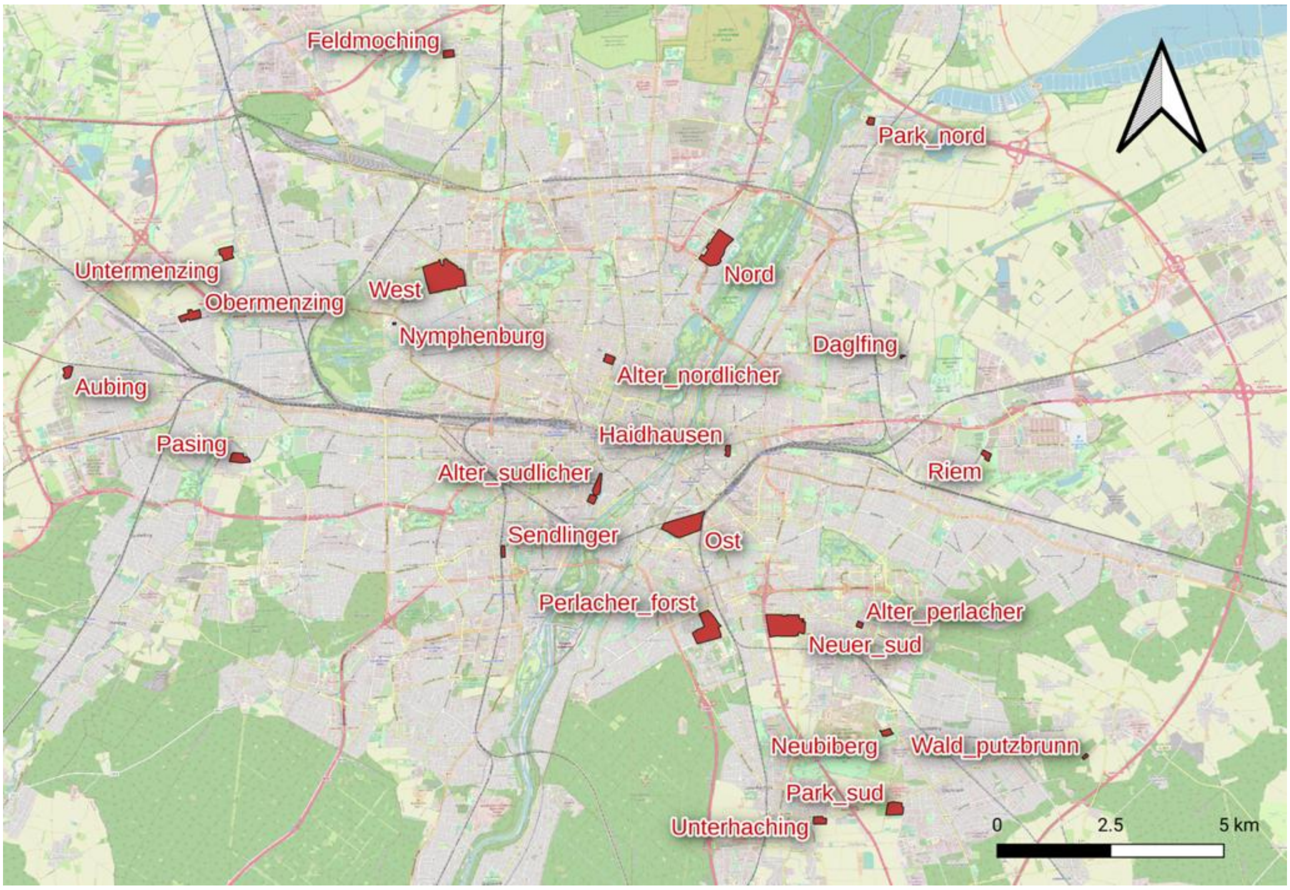

Figure 1. *A map showing all 23 Munich cemeteries selected for bird surveys for this study, with these cemeteries being shown in red. Other Munich cemeteries not selected for this study, of which there are very few, are not shown. The outer motorway ring road can be clearly seen, and all cemeteries surveyed are located within this ring road. Map created using QGIS (QGIS Development Team, 2022) and OpenStreetMap (OpenStreetMap contributors, 2022).*

detectability (Bibby *et al*., 2000). Second, all cemeteries surveyed are located within the outer motorway ring road, as beyond this the land use changes markedly and rapidly from an urban landscape (the focus of this study) to an agricultural one. Further study design choices and justifications can be found in Supplementary Material 3.

2.3 Extraction of local and landscape variables using GIS

The area of each cemetery was calculated using Quantum Geographic Information System (QGIS) and the road density within 1 km of each cemetery was calculated using QGIS and the Urban Atlas 2018 map provided by the Copernicus Land Monitoring Service (Copernicus Land Monitoring Service, 2022). Finally, tree cover within the 50 m point count radius, cemetery tree coverage and tree coverage within 1 km of each cemetery were calculated using QGIS and the Street Tree Layer (STL) 2018 map (see Figure 2) provided by the Copernicus Land Monitoring Service. To study the effect of local and landscape variables on the richness and diversity of cemetery birds, cemetery area, 50 m point count radius tree cover and cemetery tree cover were used as local variables and tree and road cover (within a 1 km buffer) were used as landscape variables (Figure 2b). Further justifications for this 1 km buffer can be found in Supplementary Material 4.

Bird species richness and diversity have been shown to be positively related to green space area (Mayorga *et al*., 2020; Pirzio Biroli *et al*., 2020), as well as vegetation (tree and shrub) coverage (Callaghan *et al*., 2018; Morelli *et al*., 2018; Villaseñor and Escobar, 2019), and therefore this study aimed to find out if these relationships also held true for urban cemeteries. As urbanisation has been frequently shown to reduce bird species richness (Batáry *et al*., 2018; Clergeau *et al*., 2006), this study used road cover as a landscape variable, since this provided a measure of the level of urbanisation surrounding each cemetery. However, some studies have not found such an effect (Korányi *et al*., 2021), so this study aimed to investigate whether the level of urbanisation surrounding cemeteries might affect bird species richness and diversity. Road cover was assumed to provide an accurate measure as the area of the roads was also taken into account (i.e. roads are treated as two-dimensional polygons rather than as simple one-dimensional linear structures) and therefore larger roads, which are likely to be busier, faster, and more noisy, potentially providing a greater disturbance to birds in more highly urbanised areas, were accounted for by using road cover as an explanatory variable.

2.4 Bird surveys and diversity indices

One observation point, located as close to the centre of each cemetery as possible, was assigned per cemetery. This

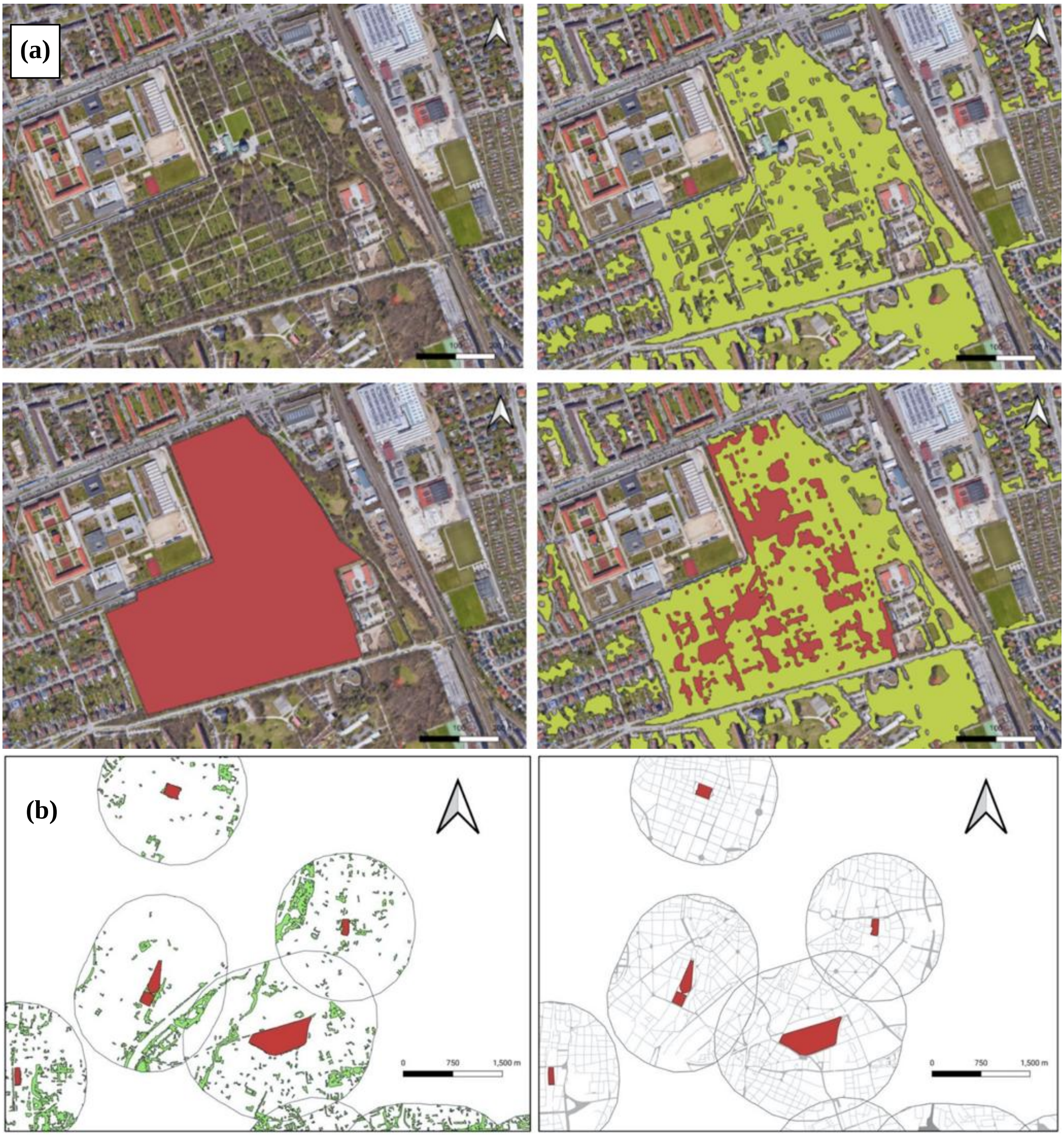

Figure 2. *Examples of how local and landscape variables were extracted using GIS, including:* ***(a)*** *Street Tree Layer (STL) 2018 map (Copernicus Land Monitoring Service, 2022) being used to calculate within-cemetery tree cover for a Munich urban cemetery (Friedhof am Perlacher Forst)—top left: satellite image of cemetery, top right: STL overlay, bottom left: cemetery polygon (also used to calculate area), bottom right: cemetery polygon with STL overlay (ready for analysis in QGIS). Maps created using QGIS (QGIS Development Team, 2022), and Google Maps (Google, 2022).* ***(b)*** *1 km buffers being used to measure the tree and road cover surrounding each cemetery—left: tree cover within 1 km, calculated using the Street Tree Layer 2018 map (Copernicus Land Monitoring Service, 2022), right: road cover within 1 km, calculated using the Urban Atlas 2018 map (Copernicus Land Monitoring Service, 2022). Maps created using QGIS (QGIS Development Team, 2022).*

was done to minimise edge effects of external disturbances, such as traffic, that could negatively affect bird detection. All cemeteries were surveyed twice during the survey period, which was the second half of May (the month of peak breeding activity) and the first half of June. All surveys were conducted between 08:00 and 10:00 on clear windless days (DeGraaf *et al*., 1991), which helped to ensure birds were not sheltering during surveys, maximising detectability. Two surveys were conducted per cemetery (with the data then being pooled across both surveys) as a precautionary measure to mitigate the impact of any fluctuations in factors such as the time at which the survey was conducted, the temperature, or any unexpected circumstances or disturbances such as funerals being held (which did occur once) or cemetery grounds-keeping and maintenance taking place (which occurred several times). Fixed-radius point counts were conducted by entering the observation point, waiting for one minute (Korányi *et al*., 2021), and then recording all birds heard or seen within a 50 m radius for 15 minutes (Jiguet, 2009). Further information and justifications for 50 m point counts are provided in Supplementary Material 5.

Several diversity indices were then calculated from the pooled data for each cemetery, including observed species richness (S_{obs}), Chao1 estimated species richness (S_{est}) for pooled data, Simpson's Index of diversity (1 - D), and taxonomic diversity (Δ). Total abundance of birds was also calculated for each cemetery. Further information and justifications for chosen diversity indices are provided in Supplementary Material 6.

2.5 Statistical analysis

First, all variables were checked for any pronounced skew by plotting the histograms and judging these by eye. Cemetery area (measured in hectares) showed strong positive skew with a large number of smaller cemeteries and a small number of much larger cemeteries (see Figure 1). Area was therefore natural log-transformed, which is a common transformation with positively skewed data (West, 2021) after which it showed a more symmetrical distribution. Multicollinearity across the five explanatory variables was then tested, as correlation between explanatory variables can make it difficult to interpret results of the statistical analyses used subsequently; for example, by decreasing the reliability of model parameter estimates (Alin, 2010). VIFs (Variance Inflation Factors) were calculated on the predictor set using the 'car' package in R (Fox and Weisberg, 2019). A VIF was calculated for each explanatory variable. Although less conservative thresholds may be used, VIF values of > 2.5 are generally considered to indicate "considerable collinearity" (Johnston *et al*., 2018). Since VIF for a predictor can change depending on which other variables are present in the predictor set, we took a stepwise approach, removing the predictor with the highest VIF that was > 2.5, where applicable, then recalculating VIFs of remaining variables, and repeating if necessary. When the variable with the highest VIF that exceeded this threshold (50 m tree cover; VIF = 4.65) was removed from the global model, all recalculated VIFs were below 2.5. This indicated that multicollinearity between the remaining four explanatory variables could now be assumed to be sufficiently low so as not to bias the interpretation of all subsequent models. Additionally, a correlation matrix for the remaining explanatory variables was produced, with Pearson correlation coefficients for all pairwise combinations of explanatory variables being ≤ 0.50.

Table 1. *Candidate set of a priori hypotheses and associated models for predicting the response variables: abundance, Chao1 species richness, Simpson's diversity, and taxonomic diversity (Δ), from four explanatory variables: cemetery size, cemetery tree cover, 1 km tree cover and 1 km road cover.*

Model	Explanatory variables	Hypotheses: Abundance/Chao1 species richness/Simpson's diversity/taxonomic diversity ( ) is predicted by…
1	(Null model)	…none of the variables measured
2	Area	…the size of the cemetery
3	Cemetery tree cover	…tree cover within the cemetery
4	1 km tree cover	…tree cover within 1 km of the cemetery
5	1 km road cover	…road cover within 1 km of the cemetery
6	Area + cemetery tree cover	…the size of the cemetery and tree cover within the cemetery
7	Area + 1 km tree cover	…the size of the cemetery and tree cover within 1 km of the cemetery
8	Area + 1 km road cover	…the size of the cemetery and road cover within 1 km of the cemetery
9	Cemetery tree cover + 1 km tree cover	…tree cover within the cemetery and tree cover within 1 km of the cemetery
10	Cemetery tree cover + 1 km road cover	…tree cover within the cemetery and road cover within 1 km of the cemetery
11	1 km tree cover + 1 km road cover	…tree and road cover within 1 km of the cemetery
12	Area * cemetery tree cover	…the interaction between the size of the cemetery and tree cover within the cemetery
13	Area * 1 km tree cover	…the interaction between the size of the cemetery and tree cover within 1 km of the cemetery
14	Area * 1 km road cover	…the interaction between the size of the cemetery and road cover within 1 km of the cemetery
15	Cemetery tree cover * 1 km tree cover	…the interaction between tree cover within the cemetery and tree cover within 1 km of the cemetery
16	Cemetery tree cover * 1 km road cover	…the interaction between tree cover within the cemetery and road cover within 1 km of the cemetery
17	1 km tree cover * 1 km road cover	…the interaction between tree and road cover within 1 km of the cemetery

Next, four candidate sets of generalised linear models were created. Apart from using a different response variable each time, these four candidate sets of models contained the same seventeen models (see Table 1 for an example candidate model set). Models were fitted with normal errors and identity-link functions. We tested the assumption of normality of residuals visually on quantile-quantile plots (White *et al*., 2019) and the residuals were approximately normally distributed. The four candidate model sets were then used to explore how well each of the four response variables (abundance, species richness, species diversity and taxonomic diversity) could be predicted from the four explanatory variables, as well as from pairwise combinations and first-order interactions between these explanatory variables. For the model comparison approach taken in this study, higher values for the ratio of sample size to number of parameters to be estimated (N:q) are typically preferred (Jackson, 2003). For this reason, models containing three- or four-way combinations and second- or third-order interactions between explanatory variables were not included in the candidate sets, as the number of parameter estimates required for such models would be too high relative to the sample size used in this study. Each candidate model set was created based on a priori hypotheses (see Table 1). A null (no terms) model was also included in each candidate model set. Using the 'MuMIn' package in R (Barton, 2018), all models in each candidate set were ranked according to their small-sample Akaike information criterion (AICc), with inferences then being taken from any models in the confidence set of AICc ≤ 2 (Anderson and Burnham, 2002;

Johnson and Omland, 2004). We also reported Akaike's weights which represent the relative likelihood of each model given the data (Johnson and Omland, 2004). As we were dealing with spatial data, we checked for spatial autocorrelation of model residuals using the 'ncf' package in R (Bjørnstad, 2022). We plotted spline correlograms with Moran's *I* to see if model residuals showed significant correlation with distance between cemeteries, with cemetery centres plotted as UTM coordinates (zone 32N covering Munich).

The R package 'sjPlot' (Lüdecke, 2021) was used to plot all models in the confidence set of AICc ≤ 2, as well as to plot marginal effects (i.e., the effects when covariates are kept constant). Finally, for models in the confidence set containing multiple explanatory variables, the 'tab model' function of the R package 'sjPlot' (Lüdecke, 2021) was used to calculate standardised beta estimates (β) to help compare effect sizes of the explanatory variables within these models. Using the 'MuMIn' package, we also calculated model-averaged parameter estimates and standard errors weighted by each model's Akaike's weight (*wi*), as well as relative variable importance, which is the sum of model weights over all models that include each explanatory variable (Barton, 2018).

Table 2. *A list of all the bird species observed during this study, along with their total abundance across all surveys, their abundance as a percentage of the total number of birds observed across all surveys, and the proportion of cemeteries in which they were observed. The species in this table have been ranked first by proportion of cemeteries in which observed, then by abundance. Species observed in >90% of cemeteries are shown in bold.*

Scientific name	Species name	Total number observed across all cemeteries	As a percentage of all birds observed	Proportion of cemeteries in which observed
Turdus merula	**Common blackbird**	**162**	**17.3**	**1.00**
Parus major	**Great tit**	**103**	**11.0**	**1.00**
Sylvia atricapilla	**Eurasian blackcap**	**94**	**10.1**	**1.00**
Corvus corone	**Carrion crow**	**77**	**8.2**	**0.96**
Cyanistes caeruleus	**Eurasian blue tit**	**81**	**8.7**	**0.91**
Phylloscopus collybita	**Common chiffchaff**	**51**	**5.5**	**0.91**
Fringilla coelebs	Common chaffinch	99	10.6	0.87
Dendrocopos major	Great spotted woodpecker	38	4.1	0.83
Erithacus rubecula	European robin	34	3.6	0.70
Columba palumbus	Common woodpigeon	32	3.4	0.61
Carduelis carduelis	European goldfinch	23	2.5	0.48
Chloris chloris	European greenfinch	18	1.9	0.48
Sitta europaea	Eurasian nuthatch	18	1.9	0.39
Troglodytes troglodytes	Eurasian wren	22	2.4	0.35
Certhia brachydactyla	Short-toed treecreeper	17	1.8	0.35
Turdus pilaris	Fieldfare	7	0.7	0.13
Garrulus glandarius	Eurasian jay	5	0.5	0.13
Picus viridis	European green woodpecker	4	0.4	0.13
Corvus frugilegus	Rook	10	1.1	0.09
Aegithalos caudatus	Long-tailed tit	8	0.9	0.09
Columba livia	Domestic pigeon	7	0.7	0.09
Muscicapa striata	Spotted flycatcher	4	0.4	0.09
Passer domesticus	House sparrow	4	0.4	0.09
Passer montanus	Eurasian tree sparrow	4	0.4	0.09
Periparus ater	Coal tit	3	0.3	0.09
Pica pica	Eurasian magpie	2	0.2	0.09
Pyrrhula pyrrhula	Eurasian bullfinch	2	0.2	0.09
Phoenicurus ochruros	Black redstart	2	0.2	0.04
Emberiza citrinella	Yellowhammer	1	0.1	0.04
Poecile montanus	Willow tit	1	0.1	0.04
Regulus regulus	Goldcrest	1	0.1	0.04
Turdus philomelos	Song thrush	1	0.1	0.04

Variable importance in this context can be interpreted as the probability that a variable will be in the best model (Giam and Olden, 2015).

3. Results

3.1 Results overview

In total, 935 birds from 32 species were observed during the 46 bird surveys (see Table 2). The four most abundant species were the Common blackbird (*Turdus merula*) (162), the Great tit (*Parus major*) (103), the Common chaffinch (*Fringilla coelebs*) (99), and the Eurasian blackcap (*Sylvia atricapilla*) (94), each of which represented over 10% of all individuals observed. The species found in the highest proportion of cemeteries were the Great tit, Eurasian blackcap, and Common blackbird, which were observed in all cemeteries surveyed (1.00), followed by the Carrion crow (*Corvus corone*) (0.96), Eurasian blue tit (*Cyanistes caeruleus*) (0.91) and Common chiffchaff (*Phylloscopus collybita*) (0.91).

The minimum and maximum values for all explanatory and response variables are shown in Table 3, along with the median and interquartile range (IQR) for each variable. The full results for each of these variables, for each cemetery surveyed, are available in Supplementary Material 7. In terms of the response variables, abundance and estimated species richness were relatively variable, varying by approximately a factor of two between the minimum and maximum values, whereas the values for Simpson's diversity and taxonomic diversity had a much smaller range by comparison.

Table 3. *Minimum, maximum, median, and interquartile range values for all variables analysed in this study.*

Explanatory variable	Minimum	Maximum	Median	IQR
Area (ha)	0.3	49.6	4.5	6.9
Cemetery tree cover (%)	0.0	91.2	65.9	22.1
1 km tree cover (%)	1.9	32.1	11.2	8.3
1 km road cover (%)	4.8	12.4	8.5	5.0
Response variable				
Total abundance	23	55	41.0	12.5
Estimated species richness (Chao1)	9.0	18.0	14.0	3.0
Simpson's index of diversity (1-D)	0.85	0.92	0.88	0.02
Taxonomic diversity (Δ)	2.61	3.07	2.83	0.17

Table 4. *Model comparison results for candidate models predicting bird abundance within fixed-radius point counts from four explanatory variables: cemetery size, cemetery tree cover, 1 km tree cover, and 1 km road cover. k, number of estimated parameters; ln(L), log-likelihood; AICc, small-sample Akaike's information criterion; ΔAICc, difference between AIC for the given model and the best model; w_i, Akaike's weights. The model in the confidence set (ΔAICc ≤ 2) is shown in bold.*

Model	Explanatory variables	*k*	ln(*L*)	AICc	ΔAICc	w_i
6	**Area + cemetery tree cover**	**4**	**-73.6**	**157.5**	**-**	**0.74**
12	Area * cemetery tree cover	5	-73.6	160.7	3.2	0.15
2	Area	3	-77.9	163.1	5.6	0.04
8	Area + 1 km road cover	4	-77.2	164.6	7.1	0.02
15	Cemetery tree cover * 1 km tree cover	5	-76.1	165.7	8.2	0.01
7	Area + 1 km tree cover	4	-77.8	165.8	8.4	0.01
3	Cemetery tree cover	3	-79.7	166.6	9.1	0.01
14	Area * 1 km road cover	5	-76.9	167.4	9.9	0.01
10	Cemetery tree cover + 1 km road cover	4	-78.9	168.0	10.5	0.00
5	1 km road cover	3	-80.5	168.2	10.8	0.00
9	Cemetery tree cover + 1 km tree cover	4	-79.1	168.4	11.0	0.00
13	Area * 1 km tree cover	5	-77.8	169.2	11.7	0.00
1	(Null model)	2	-83.0	170.6	13.1	0.00
16	Cemetery tree cover * 1 km road cover	5	-78.6	170.7	13.2	0.00
11	1 km tree cover + 1 km road cover	4	-80.5	171.2	13.7	0.00
4	1 km tree cover	3	-82.7	172.7	15.3	0.00
17	1 km tree cover * 1 km road cover	5	-80.4	174.4	16.9	0.00

3.2 Abundance

When comparing candidate models for predicting abundance from the four explanatory variables (as well as from pairwise combinations of, and first-order interactions between, these variables), only model 6 (abundance is predicted by cemetery size and cemetery tree cover) had a ΔAICc ≤ 2. This model had an Akaike's weight (w_i) of 0.74, with the next best model (model 12: abundance is predicted by the interaction between cemetery size and cemetery tree cover) having a ΔAICc of 3.2 and an Akaike's weight of 0.15 (see Table 4). Model 6 showed no significant spatial autocorrelation of residuals (correlogram in Supplementary Material 8).

For the two variables in the top model (cemetery size and cemetery tree cover), the marginal effects, along with their 95% confidence intervals, are plotted in Figure 3. The overall model predicting abundance from cemetery size and cemetery tree cover had a total explanatory power (conditional R^2) of 55.8% (see Table 5). The abundance of birds is significantly positively related to the logarithm of the area of the cemetery ($p < 0.001$, $\beta = 0.56$). The slope of this relationship is 3.78 (±1.02 SE). The abundance of birds is also significantly positively related to tree cover within the cemetery ($p = 0.003$, $\beta = 0.45$). The slope of this relationship is 0.20 (±0.07 SE). Although the standardised beta estimates (β) were similar for both explanatory variables, the β values show that the standardised effect size for cemetery area was slightly higher than for cemetery tree cover (see Table 5).

3.3 Chao1 species richness, Simpson's diversity, and taxonomic diversity

When comparing candidate models (see Table 1) for predicting the remaining three response variables from the four explanatory variables (as well as from pairwise combinations of, and first-order interactions between, these variables), the results were somewhat more equivocal than those regarding the abundance of birds. For Chao1 estimated species richness, five out of the seventeen models had a ΔAICc ≤ 2 and similar Akaike's weights (Supplementary Material 9). In fact, the null model was the best-supported. For predicting Simpson's diversity, only two models had a ΔAICc ≤ 2. Although the best-supported model was model 2 (species diversity is predicted by cemetery size), this was closely followed by model 1 (the null model), which had a ΔAICc of 0.4, and both models had very similar Akaike's weights (Supplementary Material 10). Similarly, for predicting taxonomic diversity, only two models had a ΔAICc ≤ 2. The best-supported model was model 5 (taxonomic diversity is predicted by road cover within 1 km of the cemetery), again closely followed by model 1 (the null model), which had a ΔAICc of 0.3. In both cases, the models had very similar Akaike's weights (Supplementary Material 11).

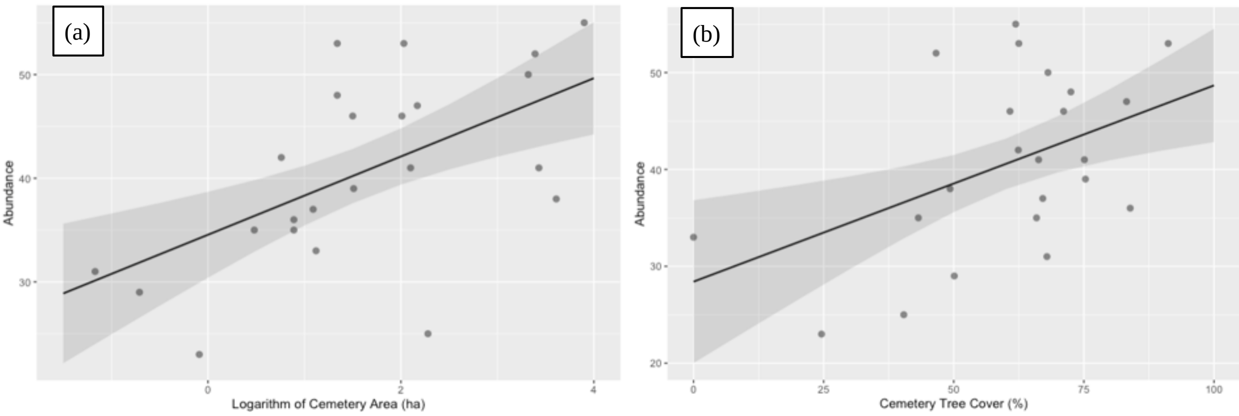

***Figure 3**. Predicted marginal effects, with 95% confidence regions, for the model shown in bold in Table 4, which includes the effects of: **(a)** the logarithm of cemetery area, and **(b)** cemetery tree cover, on the abundance of birds within fixed-radius point counts.*

***Table 5.** Slope estimates, 95% confidence intervals, standardised beta values, and significance (p) values, shown in bold, for the effect of cemetery area and cemetery tree cover on the abundance of birds (the model shown in bold in Table 4).*

Predictors	*Estimates*	*std. Beta*	*CI*	*standardised CI*	*p*
(Intercept)	22.31	0.00	13.59 – 31.03	-0.29 – 0.29	**<0.001**
Log cemetery area	3.78	0.56	1.79 – 5.76	0.26 – 0.85	**<0.001**
Cemetery tree cover	0.20	0.45	0.07 – 0.33	0.16 – 0.74	**0.003**

N = 23

R^2 0.558

3.4 Model averaging and variable importance

Model-averaged parameter estimates for each of the four model sets for the four bird response variables are in Table 6. For abundance, both area and cemetery tree cover had relative variable importance of > 0.90, with all others ≤ 0.15. For the three other response variables, there were no variables that showed as high relative importance, with area having the highest relative importance for estimated species richness, and Simpson's diversity, and road cover within 1 km for taxonomic diversity, but close to 0.5 in each case, interpreted as approximately 50% probability they would be in the best model.

Table 6*. Model-averaged parameter estimates, standard errors (SE), and relative variable importance values across the four response variables. The ':' symbol represents an interaction term between two variables. Parameters are ordered by variable importance, highest to lowest.*

Response variable	Parameter	Estimate	SE	Variable importance
Abundance	intercept	23.193	6.520	-
	ln(area)	3.601	2.417	0.97
	cemetary tree cover	0.204	0.098	0.91
	cemetary tree cover : ln(area)	0.022	0.091	0.15
	1 km road cover	0.967	0.948	0.04
	1 km tree cover	0.899	1.104	0.03
	cemetary tree cover : 1 km tree cover	-0.031	0.014	0.01
	1 km road cover : ln(area)	-0.356	0.572	0.01
	1 km tree cover : ln(area)	-0.002	0.146	0.00
	cemetary tree cover : 1 km road cover	-0.025	0.038	0.00
	1 km road cover : 1 km tree cover	-0.028	0.129	0.00
Chao1 species richness	intercept	14.183	2.107	-
	ln (area)	0.564	0.801	0.48
	cemetery tree cover	-0.034	0.041	0.36
	1 km road cover	-0.115	0.427	0.23
	1 km tree cover	-0.024	0.108	0.15
	cemetary tree cover : ln(area)	0.020	0.034	0.03
	1 km road cover : ln(area)	0.037	0.187	0.02
	cemetary tree cover : 1 km road cover	-0.014	0.012	0.01
	1 km tree cover : ln(area)	0.011	0.047	0.01
	cemetary tree cover : 1 km tree cover	-0.001	0.005	0.01
	1 km road cover : 1 km tree cover	0.011	0.039	0.00
Simpson's diversity	intercept	0.882	0.012	-
	ln(area)	0.003	0.006	0.55
	1 km road cover	0.000	0.003	0.21
	1 km tree cover	0.000	0.001	0.19
	cemetary tree cover	0.000	0.000	0.17
	cemetary tree cover : ln(area)	0.000	0.000	0.03
	1 km road cover : ln(area)	0.001	0.001	0.02
	1 km tree cover : ln(area)	0.000	0.000	0.01
	cemetary tree cover : 1 km road cover	0.000	0.000	0.01
	cemetary tree cover : 1 km tree cover	0.000	0.000	0.00
	1 km road cover : 1 km tree cover	0.000	0.000	0.00
Taxonomic diversity	intercept	2.761	0.101	-
	1 km road cover	0.015	0.012	0.48
	ln(area)	0.013	0.034	0.21
	cemetary tree cover	0.000	0.002	0.20
	1 km tree cover	0.000	0.006	0.18
	1 km road cover : 1 km tree cover	0.000	0.002	0.01
	1 km road cover : ln(area)	0.000	0.009	0.01
	cemetary tree cover : 1 km road cover	0.000	0.001	0.01
	cemetary tree cover : ln(area)	-0.001	0.002	0.01
	1 km tree cover : ln(area)	0.000	0.002	0.00
	cemetary tree cover : 1 km tree cover	0.000	0.000	0.00

4. Discussion

4.1 The effect of local and landscape variables on urban cemetery bird communities

In this study, the abundance of birds in urban cemeteries was found to increase with greater levels of within-cemetery tree cover. This is most likely because trees provide suitable habitat for a wide variety of species, including woodland insectivores and tree- and hollow-nesting birds (Ikin *et al*., 2015). Urban trees are well known for the wider ecosystem benefits they provide to urban residents, including their contribution to mental well-being, their pollution mitigation and air quality enhancement properties (Russo and Cirella, 2024), and their significant cooling effects (Li *et al*., 2024). This study provides further evidence that urban trees also support other forms of urban biodiversity, providing multiple benefits for both humans and wildlife in densely urbanised areas.

Bird abundance was also found to increase with cemetery size. This finding aligns with established ecological expectations and macroecological theories such as the theory of island biogeography (MacArthur and Wilson, 1967) and the occupancy-abundance relationship (Gaston, 1996). Interestingly, the abundance of birds in urban cemeteries could be best predicted when both cemetery area and cemetery tree cover were considered within the same model. This makes sense, as even a very large cemetery may not be able to support many species if it is predominantly composed of a simple grassland habitat. Likewise, a cemetery with extensive tree cover may still hold a lower abundance of birds if it has a small area.

Contrary to what was hypothesised, species richness, species diversity, and taxonomic diversity of birds were not found to be clearly related to the local variables of cemetery size or cemetery tree cover. In addition, the chosen landscape variables were not found to have a clear effect, with tree and road cover within 1 km of the cemetery having little predictive power for any of these measures of bird diversity. This was somewhat in contrast to what was expected, based on some previous findings (Villaseñor and Escobar, 2019). This may simply be because most cemeteries surveyed in this study were big enough and had sufficient tree coverage to support similarly broad ranges of species. It may also be true that the dispersal distances of most of the birds observed in this study are great enough, and the degree of isolation of cemeteries low enough, to ensure that the bird species inhabiting these cemeteries can easily move between them, resulting in fewer specialised species and therefore more similar levels of diversity between cemeteries. Indeed, Munich is a very green city with high densities of urban green spaces, frequently connected by wooded streets.

This appears to be the first study in which bird surveys have been conducted across all of Munich's public cemeteries. Therefore, as birds are an effective indicator or umbrella group for other types of urban fauna (Branton and Richardson, 2011), this study represents an important initial step in studying and monitoring the biodiversity of this particular urban green space type in southern Germany's largest city. This study only conducted bird surveys during May and June. Although this survey period was deliberately chosen to try to coincide as much as possible with the breeding season (leading to greater detectability of birds during surveys as birds are highly vocal and active), some research has found a seasonal effect on native birds in urban environments, with abundance and richness of birds being higher in the autumn compared to the summer (Villaseñor and Escobar, 2019). The average temperature and precipitation for Munich in May and June of 2022 was highly similar to the usual climate in Munich for those months. Different patterns of bird diversity might be observed outside the breeding season with a different community composition, with some breeding birds having left Munich and other wintering birds having arrived. As this was a single year study, it may not capture interannual variation in environmental conditions and resource availability that might influence the patterns of bird diversity in relation to cemetery characteristics. The weather was broadly representative of other recent bird breeding seasons in Munich, however. This study used road cover as a measure of the degree of urbanisation surrounding cemeteries. However, this may not be effective, as Munich's streets are generally lined with trees and may therefore be acting as green corridors for birds, rather than as urban barriers (Curzel *et al*., 2021). Other indicators may more accurately reflect the level of urbanisation surrounding urban green spaces, such as the percentage of impervious surfaces (Korányi *et al*., 2021).

The cemeteries surveyed here were found to have many features that enable them to act as biodiversity refuges in this very densely populated city. For example, the respectful way in which this green space type is used, with no cycling, jogging, or dogs allowed (based on personal observations of regulations), and the general quietness and calm behaviour of those using the cemeteries, means that disturbances to wildlife are kept to a minimum. The presence of a wide variety of vegetation types, including areas of open grassland, many shrubs, and generally a high level of tree coverage from a range of species, ages and sizes, provides opportunities for a wide range of bird species, from ground-feeders, such as European green woodpeckers (*Picus viridis*), to trunk-foragers, such as the short-toed treecreepers (*Certhia brachydactyla*) commonly heard (but less commonly seen) during this study.

A wide range of bird species were observed during this study, including species from 16 different families. Interestingly, 4 of the 32 species observed during surveys are currently classed as 'Near Threatened' by the German Red List Centre (Rote Liste Zentrum), including the Spotted flycatcher (*Muscicapa striata*), the House sparrow (*Passer domesticus*), the Eurasian tree sparrow (*Passer montanus*), and the Yellowhammer (*Emberiza citrinella*), with all other species observed classed as 'Not Threatened' (Grüneberg *et al*., 2016). At the very least, therefore, urban cemeteries in Munich appear to be providing suitable habitat for species that may be showing general trends of population decline across Germany, demonstrating the conservation value of urban cemeteries in heavily urbanised landscapes.

4.2 Future research

Increasingly, ecological research, particularly on birds, is looking at the composition of communities from a functional diversity perspective. Functional diversity is a biodiversity metric based on the functional traits of species and provides additional information to the traditional taxonomic diversity approach, making functional diversity another important measure of diversity that can be used to analyse bird communities (Curzel *et al*., 2021; Morelli *et al*., 2018; Petchey and Gaston, 2006). Examples of functional trait categories include body mass, foraging technique, diet, nest location, and migration status, amongst many others (Korányi *et al*., 2021). Functional homogenisation is known to occur alongside the biotic homogenisation caused by urbanisation, and the functional diversity of bird communities in urban habitats has been shown to decrease as the surrounding landscape becomes increasingly urbanised (Croci *et al*., 2008; Korányi *et al*., 2021). Future research on bird communities in Munich's urban cemeteries, as well as cemeteries in other urbanised areas, should include functional diversity as a response variable, to determine whether local and landscape variables are having a negative impact on this, even if similar effects are not observed in more standard biodiversity metrics such as species richness or diversity.

The weak predictive power of models for species richness, Simpson's diversity, and taxonomic diversity may imply that there are additional, unmeasured factors that we did not consider. During this study, it was clear that the cemeteries surveyed varied considerably in terms of their age and that the age (and often, therefore, the size) of the trees within them also varied widely as a result. Although some previous research has investigated the effects of fine-scale habitat characteristics, such as tree age, on birds in urban green spaces (Donnelly and Marzluff, 2006; Ferenc *et al*., 2014; Mörtberg and Wallentinus, 2000), a specific study investigating the effect of the age and size of cemetery trees on their bird communities would be valuable. This is because the rapid growth of cities means that many new cemeteries are also being created as areas at the urban fringe are developed. Indeed, this was the case with several of the cemeteries surveyed in Munich, which were clearly relatively new and therefore had a markedly different age composition of trees compared to some of the old, or *alter*, cemeteries in the city centre. These more ancient cemeteries clearly contain much older stands of trees and although they are still much visited and partially maintained by groundskeeping staff, they are not in 'active' use for new burials in the same way as the other, less ancient cemeteries are. The effect of such tree and cemetery age-related variables on the taxonomic and functional diversity of birds in urban cemeteries may therefore represent a valuable topic for future research.

4.3 Conclusion

This is the first time an extensive set of bird surveys has been completed across all of Munich's public urban cemeteries. This study aimed to determine if the abundance, richness, and diversity of breeding birds could be predicted by various local and landscape variables, including cemetery area, cemetery tree cover, tree cover within 1 km of the cemetery, and road cover within 1 km of the cemetery. Whilst abundance within a fixed-radius point count was found to be strongly related to cemetery area and cemetery tree cover, the absence of any relationship regarding various indices of diversity is an interesting result. Further research may be needed to explore whether relationships exist at different spatial scales or perhaps in different cities. This study does highlight how tree coverage can increase bird numbers in urban cemeteries, adding to the extensive list of benefits urban trees provide.

Declaration

The authors declare no competing interests.

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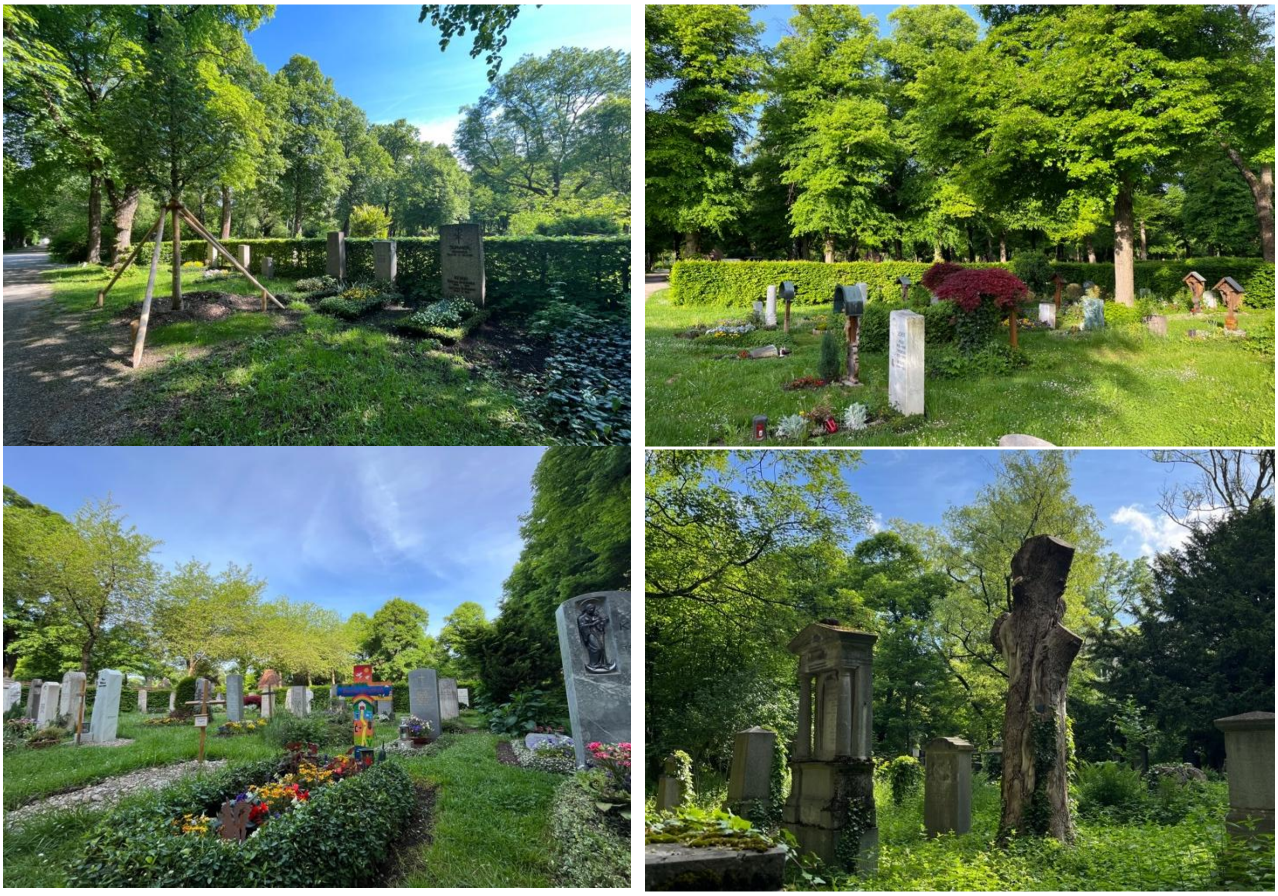
5. Supplementary material

5.1 Supplementary material 1. Contextual information about Munich.

Munich is a city with an area of 311 km^2 and a population of approximately 1.5 million residents (Landeshauptstadt München, 2022). The city is situated at 520 m above sea level in Bavaria, Germany (48°08′15″N 11°34′30″E). The land surrounding the city mainly consists of arable land, grassland, and forest. The climate is temperate with an annual average temperature of 9.7 C and an annual average rainfall of 944 mm (DWD, 2022). Munich is the most densely populated municipality in Germany. Despite this, the city contains one of the world's largest urban public parks: the *Englischer Garten* (the English Garden), which covers an area of 3.7 km^2, making it larger than Central Park in New York City (Dombart, 1972). In addition to its many parks, the city has numerous other green spaces, including allotments and cemeteries.

5.2 Supplementary Material 2. Examples of the typical matrix of vegetation (trees, shrubs, and grass) and human-made structures in Munich's urban cemeteries – top left: Perlacher Forst, top right and bottom left: Nordfriedhof, bottom right: Alter Südfriedhof.



5.3 Supplementary Material 3. Further study design choices and justifications.

All cemeteries surveyed are located within the outer motorway ring road. This ensured that all cemeteries were close enough that they could be reached by bicycle if possible, or, where necessary, by private vehicle or public transport, and that multiple cemeteries could be surveyed in one morning, maximising the overall sample size (number of cemeteries) that could be obtained for this study, the cemeteries selected are a variety of different sizes, ranging from 0.3 ha to 49.6 ha (see Table 3), representing, approximately, a 100-fold increase in size, which allowed the effect of cemetery area to be properly investigated and used as an explanatory variable in this study. As many suitable cemeteries as possible were surveyed within the data collection time period available for this study (i.e., the largest possible sample size was obtained), which helped to minimise any bias in terms of the locations of the cemeteries relative to the surveyor's residence by ensuring that a large geographical spread across the city was achieved (see Figure 1).

5.4 Supplementary Material 4. Justifications for the 1 km buffer surrounding each cemetery.

Although a somewhat arbitrary choice, the 1 km distance for the buffer surrounding each cemetery (see Figure 2b) was also chosen because similar research has previously used this distance over which to measure road and tree coverage (Farah Shafawati *et al*., 2016; Villaseñor and Escobar, 2019). In addition, although other research has suggested using buffers of 5 km or even greater (Callaghan *et al*., 2018), after viewing buffers of different sizes in QGIS, it was decided that a larger buffer size might result in too much overlap, potentially leading to a high degree of similarity in the measurements for tree and road cover between cemeteries (and therefore, potentially, less clear results). Conversely, although other research has used smaller buffers, such as 500 m (Korányi *et al*., 2021), it was decided that a buffer size smaller than 1 km might not be adequate to detect any effects, due to the large dispersal distances of the surveyed bird species.

5.5 Supplementary Material 5. Further information and justifications for 50 m point count.

Based on the findings of some preliminary surveys used to practice and assess survey techniques for this study, the chosen method, to be used for all bird surveys, was a 50 m fixed-radius point count (Bibby *et al*., 2000). This was preferred to the transect method as it involved less disturbance to birds (after the settling period), allowed the stationary surveyor to use binoculars effectively, and maximised the effectiveness of the smartphone app used to aid the identification of bird species (the effectiveness of which is greatly reduced by sounds made during a transect survey, such as footsteps on a gravel-covered cemetery path), all of which ensured higher levels of successful detection of bird species during surveys. A 50 m radius was used, as it was decided that accurate visual identification and abundance-scoring over a greater distance (e.g., 75 m or 100 m) could not be guaranteed, and that bird calls and songs, which provided the main method of identification during surveys, could also not be accurately detected or identified at distances greater than 50 m (as well as the fact that greater distances might begin to exaggerate any detection biases resulting from the different sizes and different call and song volumes of different species).

The one-minute settling-down period was used to give time for birds to resume normal behaviour (Chamberlain and Rolando, 2014) and was judged to be sufficiently long, as cemetery birds constantly experience human presence throughout the year anyway and are therefore well-habituated to human presence. To aid and verify bird identifications, the bird sound identification feature of the Merlin Bird ID smartphone application (developed by the Cornell Lab of Ornithology in partnership with Birds in the Hand, LLC) was used during all surveys. This ensured maximum accuracy of identification by aiding the surveyor when multiple bird calls could be heard at once and by allowing the surveyor to listen back to the audio recording after each survey, so that the surveyor could verify that species had been correctly identified from their songs and calls.

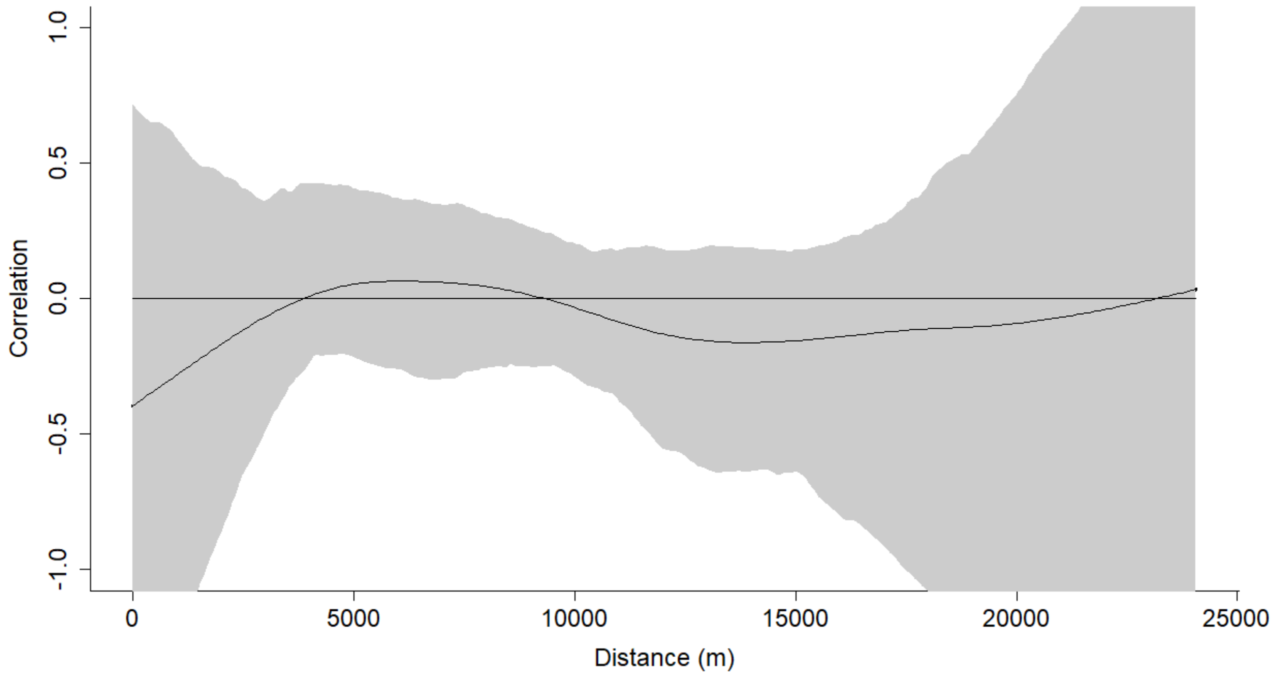
5.6 Supplementary Material 6. Further information and justifications for chosen diversity indices.

The Chao1 species richness estimator used estimates true species richness by also considering an estimate of the species missed by the sampling, based on the relative frequencies of rare species and less rare species in the data (Chao and Chiu, 2016). Alpha (α-) diversity relates to the local diversity of an individual site or habitat, and although species richness is an important element of this, α-diversity also includes a component of species evenness, which indicates how evenly the proportions of each species are distributed across a site (Magurran, 2004). Heterogeneity indices combine both of these elements of α-diversity. In this study, the heterogeneity index calculated for each cemetery was Simpson's Index of diversity (1 - D). A potential limitation of this diversity measure is that it treats species equally, only considering relative abundances. Diversity can also be quantified using taxonomic diversity, with the diversity of taxa representing diversity in evolutionary divergence among the taxa (Clarke and Warwick, 1998). Taxonomic diversity was therefore calculated for each site. First, a distance matrix containing pairwise taxonomic path lengths between all observed species was produced. This gave the number of taxonomic levels separating any two species. A measure of taxonomic diversity (Δ) was then calculated for each cemetery by taking the average taxonomic path length between any two individuals randomly selected from the pooled data for a site.

5.7 Supplementary Material 7. Summary statistics for each cemetery, ordered alphabetically.

Cemetery	Area (ha)	Cemetery tree cover (%)	1 km tree cover (%)	1 km road cover (%)	Total abundance	Observed species richness	Estimated species richness (Chao1)	Simpson's index of diversity (1-D)	Taxonomic diversity (Δ)
Alter Nordlicher	3.80	91.2	5.4	11.6	53	10	10.0	0.87	2.92
Alter Perlacher	1.62	65.9	21.1	12.4	35	10	11.5	0.85	2.91
Alter Südlicher	8.77	83.2	8.1	11.3	47	10	10.0	0.87	2.64
Aubing	4.52	75.3	7.9	6.6	39	11	11.0	0.88	2.79
Daglfing	0.49	50.1	9.4	5.1	29	13	14.7	0.89	2.86
Feldmoching	3.80	72.5	7.6	6.5	48	15	15.5	0.90	2.91
Haidhausen	2.43	83.9	9.1	12.0	36	12	12.6	0.88	3.01
Neubiberg	3.06	0.0	14.9	5.1	33	12	17.0	0.88	2.75
Neuer Süd	37.14	49.3	16.7	10.8	38	13	18.0	0.89	2.83
Nord	29.57	46.6	31.5	10.2	52	11	12.0	0.88	2.73
Nymphenburg	0.31	67.9	32.1	7.7	31	10	10.2	0.87	2.76
Obermenzing	8.13	75.1	11.2	8.5	41	12	18.0	0.89	2.75
Ost	30.86	66.3	9.4	11.8	41	14	14.8	0.90	2.95
Park Nord	2.43	43.2	9.5	4.8	35	9	9.0	0.86	2.75
Park Sud	9.81	40.4	11.8	7.1	25	11	12.5	0.88	3.07
Pasing	7.47	71.1	16.6	5.5	46	15	15.8	0.92	2.89
Perlacher Forst	27.60	68.1	19.6	11.4	50	14	14.2	0.89	2.97
Riem	2.97	67.1	10.0	7.7	37	13	13.9	0.87	2.75
Sendlinger	2.14	62.4	17.0	11.8	42	14	14.2	0.91	2.89
Unterhaching	4.49	60.8	6.3	6.5	46	12	14.0	0.87	2.61
Untermenzing	7.58	62.5	11.2	8.6	53	14	14.8	0.89	2.74
Wald Putzbrunn	0.91	24.6	1.9	5.7	23	12	13.7	0.89	2.78
West	49.58	61.9	19.7	11.6	55	14	14.2	0.91	2.96

5.8 Supplementary Material 8. Spline correlogram of model 6 for abundance analysis. Grey shaded areas represent 95% pointwise confidence intervals. The confidence intervals overlap zero across the whole distance range indicating no significant spatial autocorrelation.



5.9 Supplementary Material 9. Model selection, using Akaike's Information Criterion, for predicting species richness (Chao1 estimated species richness) from four explanatory variables: cemetery size, cemetery tree cover, 1 km tree cover, and 1 km road cover.

Model comparison results for candidate models. *k*, number of estimated parameters; *ln(L)*, log-likelihood; *AICc*, small-sample Akaike's information criterion; *ΔAICc*, difference between AIC for given model and best model; w_i, Akaike's weights. The models in the confidence set (ΔAICc ≤ 2) are shown in bold.

Model	Explanatory variables	*k*	ln(*L*)	AICc	ΔAICc	w_i
1	**(Null model)**	**2**	**-53.3**	**111.2**	**-**	**0.19**
2	**Area**	**3**	**-52.2**	**111.6**	**0.4**	**0.16**
6	**Area + cemetery tree cover**	**4**	**-50.9**	**112.0**	**0.8**	**0.13**
3	**Cemetery tree cover**	**3**	**-52.4**	**112.0**	**0.8**	**0.13**
8	**Area + 1 km road cover**	**4**	**-51.2**	**112.6**	**1.4**	**0.10**
5	1 km road cover	3	-53.2	113.6	2.4	0.06
4	1 km tree cover	3	-53.3	113.8	2.6	0.05
7	Area + 1 km tree cover	4	-52.0	114.3	3.1	0.04
9	Cemetery tree cover + 1 km tree cover	4	-52.3	114.8	3.7	0.03
12	Area * cemetery tree cover	5	-50.7	114.9	3.7	0.03
10	Cemetery tree cover + 1 km road cover	4	-52.4	115.0	3.8	0.03
14	Area * 1 km road cover	5	-51.1	115.8	4.6	0.02
16	Cemetery tree cover * 1 km road cover	5	-51.4	116.4	5.2	0.01
11	1 km tree cover + 1 km road cover	4	-53.1	116.5	5.3	0.01
13	Area * 1 km tree cover	5	-52.0	117.5	6.3	0.01
15	Cemetery tree cover * 1 km tree cover	5	-52.3	118.1	6.9	0.01
17	1 km tree cover * 1 km road cover	5	-53.1	119.7	8.5	0.00

5.10 Supplementary Material 10. Model selection, using Akaike's Information Criterion, for predicting species diversity (Simpson's index of diversity) from four explanatory variables: cemetery size, cemetery tree cover, 1 km tree cover, and 1 km road cover.

Model comparison results for candidate models. *k*, number of estimated parameters; *ln(L)*, log-likelihood; *AICc*, small-sample Akaike's information criterion; *ΔAICc*, difference between AIC for given model and best model; w_i, Akaike's weights. The models in the confidence set (ΔAICc ≤ 2) are shown in bold.

Model	Explanatory variables	*k*	ln(*L*)	AICc	ΔAICc	w_i
2	**Area**	**3**	**63.5**	**-119.7**	**-**	**0.27**
1	**(Null model)**	**2**	**61.9**	**-119.3**	**0.4**	**0.22**
8	Area + 1 km road cover	4	63.9	-117.5	2.2	0.09
7	Area + 1 km tree cover	4	63.5	-116.8	2.9	0.06
6	Area + cemetery tree cover	4	63.5	-116.8	2.9	0.06
4	1 km tree cover	3	61.9	-116.6	3.1	0.06
3	Cemetery tree cover	3	61.9	-116.6	3.1	0.06
5	1 km road cover	3	61.9	-116.6	3.1	0.06
12	Area * cemetery tree cover	5	64.5	-115.4	4.3	0.03
14	Area * 1 km road cover	5	64.2	-114.9	4.8	0.02
9	Cemetery tree cover + 1 km tree cover	4	61.9	-113.7	6.0	0.01
10	Cemetery tree cover + 1 km road cover	4	61.9	-113.7	6.0	0.01
11	1 km tree cover + 1 km road cover	4	61.9	-113.7	6.0	0.01
13	Area * 1 km tree cover	5	63.6	-113.6	6.1	0.01
16	Cemetery tree cover * 1 km road cover	5	63.2	-112.8	6.9	0.01
15	Cemetery tree cover * 1 km tree cover	5	62.1	-110.7	9.0	0.00
17	1 km tree cover * 1 km road cover	5	61.9	-110.4	9.3	0.00

5.11 Supplementary Material 11. Model selection, using Akaike's Information Criterion, for predicting taxonomic diversity (Δ) from four explanatory variables: cemetery size, cemetery tree cover, 1 km tree cover, and 1 km road cover.

Model comparison results for candidate models. *k*, number of estimated parameters; *ln(L)*, log-likelihood; *AICc*, small-sample Akaike's information criterion; *ΔAICc*, difference between AIC for given model, and best model; w_i, Akaike's weights. The models in the confidence set (ΔAICc ≤ 2) are shown in bold.

Model	Explanatory variables	*k*	ln(*L*)	AICc	ΔAICc	w_i
5	**1 km road cover**	**3**	**18.5**	**-29.8**	**-**	**0.26**
1	**(Null model)**	**2**	**17.0**	**-29.5**	**0.3**	**0.22**
2	Area	3	17.4	-27.6	2.2	0.09
3	Cemetery tree cover	3	17.3	-27.3	2.5	0.08
11	1 km tree cover + 1 km road cover	4	18.6	-26.9	2.9	0.06
8	Area + 1 km road cover	4	18.5	-26.9	2.9	0.06
10	Cemetery tree cover + 1 km road cover	4	18.5	-26.9	2.9	0.06
4	1 km tree cover	3	17.0	-26.8	3.0	0.06
6	Area + cemetery tree cover	4	17.6	-25.1	4.7	0.02
7	Area + 1 km tree cover	4	17.4	-24.6	5.2	0.02
9	Cemetery tree cover + 1 km tree cover	4	17.3	-24.4	5.4	0.02
17	1 km tree cover * 1 km road cover	5	18.6	-23.6	6.2	0.01
14	Area * 1 km road cover	5	18.5	-23.6	6.2	0.01
16	Cemetery tree cover * 1 km road cover	5	18.5	-23.6	6.2	0.01
12	Area * cemetery tree cover	5	17.7	-21.9	7.8	0.01
13	Area * 1 km tree cover	5	17.4	-21.3	8.5	0.00
15	Cemetery tree cover * 1 km tree cover	5	17.4	-21.3	8.5	0.00