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Life after death: Hidden diversity of orchids across European cemeteries

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ABSTRACT

Habitats sensitive to anthropogenic pressures are growing in conservation importance in the protection and perpetuation of rare animal and plant species. Although natural habitats sensitive to disturbance in urban areas have mostly declined in availability, patches offer conservation opportunities for wildlife that are fundamental to maintaining biodiversity. Human burial sites can contribute to this: they are more numerous and greater in extent in more urbanized areas, but their significance in the maintenance and promotion of biodiversity has not been considered across Europe and other continents. Because of their high sensitivity to even minor disturbance to natural habitats, orchid diversity is a key bioindicator of terrestrial ecosystem function. We evaluated orchid diversity in cemeteries of 13 European countries. Comprehensive field surveys of orchid flora in 2079 locations revealed that they occurred in every country visited and in high variability in both the number of taxa (n = 65) and individual plant counts (n = 44680). We propose that cemeteries are of major importance as refugia in conserving orchids in most of the visited European countries; however, one of the most urgent issues is to identify the many anthropogenic factors determining biodiversity of cemeteries, and to eliminate some newly emerged management practices in cemeteries that undermine biodiversity, including the orchid flora. Human burial grounds are therefore not just important in preserving the history of humankind; they are key in protecting biodiversity in this modern era of unprecedented

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anthropogenic changes to our terrestrial environments, especially as a result of rapid and unrelenting urbanization.

1. Introduction

Habitats, and the species they support, have seen unprecedented changes in recent decades because of the burgeoning impacts of human population growth and its accompanying anthropogenic pressures from processes such as urbanization (Adams, 1994; McKinney, 2008). Some synanthropic habitats (i.e. those near to human settlements that accrue benefits from us and the environmental modifications that we impose) can host rich biodiversity even close to urban areas (Gallo et al., 2017) where otherwise anthropogenic pressures can be high and homogenizing (McKinney, 2006). Such habitat types include mines (Batty, 2005; Shefferson et al., 2008), roadside verges (Cousins, 2006; Fekete et al., 2017, 2019, 2020, 2023a), plantations (Adamowski and Conti, 1991; Fekete et al., 2023b; Molnár et al., 2022; Süveges et al., 2019, 2022), and urban parks (Cornelis and Hermy, 2004). Burial sites such as sacred groves (Rebancos and Buot, 2007) and kurgans (Deák et al., 2016) are also such habitat types.

For European citizens until the 18th Century, deceased humans could only be buried in churchyards due to historical and religious strictures (Rugg, 2000). As a result, churchyards became overcrowded (Anthony, 2015), and the demand intensified for the establishment of cemeteries. Although cemeteries were mostly established in the past few hundred years in Europe (Rugg, 2000), the oldest cemeteries were formed when natural habitats with a more diverse flora were widespread (Van Calster et al., 2008). The extent and location of cemeteries were determined by practical considerations such as what was practicable defensively against flash floods or spread of human diseases (Mytum, 1989). Ethnographers have suggested that the first cemeteries contained extensive grasslands and were often established at higher altitudes, symbolizing that the deceased had been elevated closer to God in death (Storm, 2014). These beliefs contributed significantly to the conservation of natural vegetation on European burial grounds, partly due to the lack of radical habitat modification in these protected areas resulting from enforcement of strong historical laws and nature ethics (Verschuuren et al., 2010). Furthermore, cemeteries are bounded by barriers such as fences and walls that have prevented grazing by livestock and free-living species such as deers (Cervidae) over many centuries (Lunt and Spooner, 2005).

While burial grounds such as cemeteries and churchyards preserve emotional and spiritual heritages of human societies, they also sometimes contain remnant animal and plant populations in urban areas (Barrett and Barrett, 2001; Löki et al., 2019a; Nordh and Evensen, 2018). Throughout the world, they are ecological refugia for non-vascular (bryophyte) plants (Fudali, 2001), aging trees (Antkowiak and Heine, 2005), medicinal plants (Dafni et al., 2006; Hadi et al., 2014; Rahman et al., 2008), and a wide variety of vascular plants (Czarna, 2016; Czarna and Nowinska, 2010; Czarna and Piskorz, 2005; Phillippe et al., 2010; Ruch et al., 2014; Trzaskowska and Karczmarz, 2013), including protected and rare species (Löki et al., 2020; Molnár et al., 2017b, 2018). Although important preliminary investigations of the conservation importance of burial grounds have already taken place in the early 2000s (e.g., Barrett and Barrett, 2001; Bhagwat and Rutte, 2006; Bhagwat, 2009), more thematic research focusing on the wildlife of cemeteries has mainly occurred in the last decade (e.g., Hewitt, 2013; Holden and McDonald-Madden, 2017; Gallo et al., 2017; Nordh and Evensen, 2018). However, these studies have been rather limited geographically and taxonomically, under-representing the conservation potential of cemeteries in sustaining a rich biodiversity (Löki et al., 2019a).

While some cemeteries can be considered as small natural 'islands' surrounded by heavily human-modified habitat, their potential for preserving rare organisms is significant (Hewitt, 2013; Holden and McDonald-Madden, 2017; Löki et al., 2019a). To date, vegetation of cemeteries in Europe has been intensively studied in Poland where the diversity of bryophytes (Fudali, 2001), vascular plants (Czarna, 2016; Czarna and Piskorz, 2005; Sigiel and Jagodzinski, 2011; Trzaskowska and Karczmarz, 2013), and woody vegetation (Antkowiak and Heine, 2005) were studied in cemeteries across different religious denominations. In Moscow, Russia, 59 cemeteries contained 426 vascular plant species (Kelcey and Müller, 2011), whilst the largest Jewish cemetery in Berlin, Germany contained 608 different species, 363 of which were plants, 72 lichens, 26 bryophytes, and 147 animals (Buchholz et al., 2016). More recent studies have shown that European cemeteries contain important habitats for at least 73 protected vascular plant species (Löki et al., 2019a), while Löki et al. (2020) found that Hungarian cemeteries harbored hundreds of thousands individuals of 92 protected plant species.

Orchids in Europe are a highly diverse and ecologically specialized group, with hundreds of species distributed across a variety of habitats (Kreutz, 2024). Their distribution patterns are influenced by factors such as climate, soil type, and the presence of specific mycorrhizal fungi, with species richness generally higher in southern Europe and declining toward the north (Pillon and Chase, 2007). European orchids face numerous threats, including habitat loss due to agriculture and urbanization, local environments altered by climate change, and the disruption of their complex pollination and symbiotic systems (Swarts and Dixon, 2009). Over the past 30 years, populations of several European terrestrial orchids have steadily declined because of climate change, habitat loss, and fragmentation, leading to widespread conservation efforts focused on their protection and preservation (Sletvold et al., 2013). Conservation efforts, therefore, are critical to be prioritized (Lussu et al., 2024) to protect these fragile species, many of which are now considered endangered (Kull et al., 2016).

Among endangered plant species, many species of orchid are unable to thrive in disturbed habitats (Duncan et al., 2011), and thus, they are effective bioindicators of terrestrial ecosystem function because of their sensitivity to changes in the network of organisms (plants, fungi, insects, birds etc.) and high dependence on many insect pollinators (Newman, 2009). In contrast, some orchid genera native to the Mediterranean region were adapted to intermediate levels of disturbance, such as grazing and fire, which help to maintain open habitats (Caballero et al., 2009). However, vegetation succession in the absence of such disturbances may lead to shrub and forest encroachment, ultimately affecting orchid diversity and composition (Vogt-Schilb et al., 2016).

During the last 30–40 years, orchids have been found in sacred burial sites across the world (Hewitt, 2013; Molnár et al., 2021; Plumwood, 2007). For example, orchids have been intensively studied in Turkish cemeteries since the 1980s (Kreutz and Çolak, 2009) and the known orchid diversity of European cemeteries is ever growing (Kreutz and Peter, 2007; Kreutz, 2010; Kreutz and Krüger, 2014; Löki et al., 2015). Orchids are also plants of major cultural interest: the tubers (called '*salep*' in most countries and '*salepi*' in Greece) of orchids have been harvested for hundreds of years for culinary purposes (Kasparek and Grimm, 1999). Although human disturbance intensifies with human population size and in some cases can push both terrestrial and epiphytic orchids to the brink of extinction in our towns and cities (Duncan et al., 2011), cemeteries can sometimes shelter orchids from *salep* harvesting (Molnár et al., 2017c).

The pan-European occurrence of orchids is poorly documented (Löki et al., 2019a), including only records of the broad-leaved helleborine (*Epipactis helleborine*) in Berlin (Kowarik et al., 2016), and a total of only 12 orchid species numbering 7378 individual plants in 80 rural cemeteries of Hungary (Löki et al., 2020).

The orchid flora and the role of different abiotic and biotic factors, such as climatic conditions, religious habits, and landscape management impacts, affecting conservation potential are poorly understood on a broader geographic scale. We predict that countries in Europe will offer high potential for effective conservation actions in these sacred burial places as highlighted through their orchid diversity. Orchids are core organisms in various communities and important components of food webs. Areas rich in orchids will also likely contain many insects, birds, mammals etc., i.e., having increased biodiversity, as orchid diversity can be considered a proxy of ecosystem health (Koju et al., 2023; Löki et al., 2019b; Newman, 2009). Therefore, we aimed to: (1) quantify the orchid flora of cemeteries in Europe; (2) reveal the most important factors impacting orchid diversity, especially (3) evaluating the structural quality of cemeteries in conserving orchid diversity. To do so, we undertook a continent-wide census of orchid diversity using data collected from 13 countries at more than 2000 locations, applying multiple regression approaches for testing three predictions regarding the major characteristics of cemeteries and surrounding landscape that influence orchid diversity. First, we predicted that orchid diversity, i.e., the number of taxa and individual plants, would be higher in cemeteries in more natural conditions, where artificial elements, such as concreted graves or asphalt roads, are less frequent. Secondly, we predicted higher orchid diversity in cemeteries located closer to settlements containing smaller human populations and/or further away from the settlement boundaries. Finally, we predicted that higher proportions of open habitats, such as grasslands, in the proximity of cemeteries would result in greater orchid diversity through higher opportunities for propagation and dispersal.

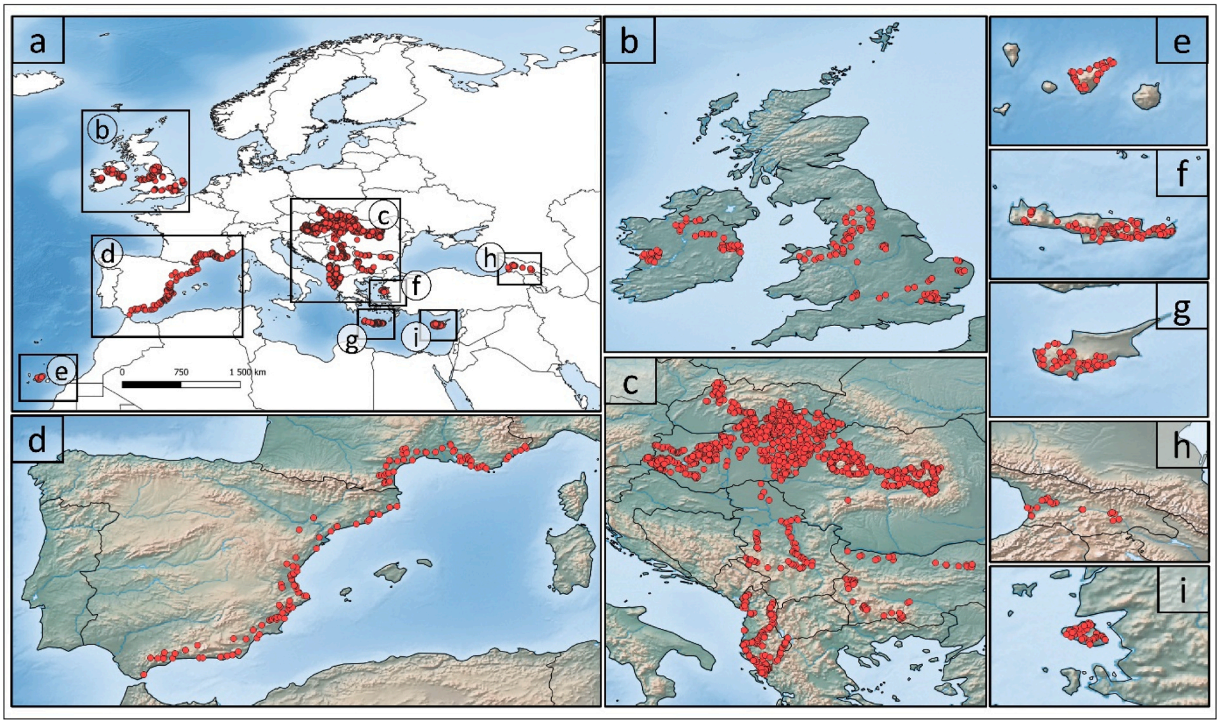

Fig. 1. European locations of cemeteries evaluated for orchid diversity between 2015 and 2019 (inclusive). (a) Overview of the studied countries and cemeteries in Europe. (b) British Isles including the UK and Ireland. (c) Central and Southern Europe including Slovakia, Hungary, Romania, Serbia, Albania, and Bulgaria. (d) South-western Europe including France and Spain. (e) Tenerife (Spain). (f) Crete (Greece). (g) Cyprus. (h) Georgia. (i) Lesvos (Greece).

2. Materials and methods

2.1. Field surveys and basic orchid diversity measures

In total, 2079 locations were visited in 13 countries between 2015 and 2019 (inclusive), including the islands of Crete, Lesvos, and Tenerife (Fig. 1). During the surveys, all orchid taxa and individual plants were identified and counted, respectively. Geocoordinates were also recorded of the visited cemeteries using a Garmin eTrex Legend GPS handheld device in WGS84 projection. All orchid taxa were identified based upon Delforge (2006), and their scientific names followed The World Flora Online (https://www.worldfloraonline.org/).

To determine basic diversity measures, we calculated Shannon's diversity index (H; Shannon, 1948) using Eq. (1):

$$H = -\sum_{i=1}^{n} p_i \log p_i \tag{1}$$

where H is the entropy of a set of probabilities $p_1, \ldots, p_n$ (p_i is the proportion of taxon i), as defined in Eq. (2):

$$p_i = \frac{n}{N} \tag{2}$$

where n is the number of individuals of taxon i, and N is the total number of individuals in the observed assemblage. Using Eq. (1), we also calculated the evenness (E) of the community (after Pielou, 1966) using Eq. (3):

$$E = \frac{H}{\log S} \tag{3}$$

where S is the number of taxa. H is greater when there are more taxa in a community (at a maximum when every individual belongs to a unique taxon) and 0 if only one taxon occurs. E is between 0 and 1, where 1 indicates equally abundant taxa in the community.

Finally, we computed Simpson's (1949) unbiased estimator of diversity (D) using Eq. (4):

$$D = 1 - \frac{\sum n(n-1)}{N(N-1)} \tag{4}$$

In this case, D is between 0 and 1, where 0 corresponds to low diversity, and 1 indicates high diversity of the sampled assemblage. From the perspective of biodiversity conservation, an assemblage is healthier when all indices are closer to their maximum possible values.

2.2. Physical characteristics of cemeteries

We measured the physical characteristics of the visited cemeteries using the distance and area tools available in Google Earth Pro v7.3.4.8248 (Google 2022). Based on the satellite images of the censused cemeteries, we calculated the distance (in meters) between its location and the nearest settlement applying the following rules:

1. If the location was within the boundaries of a settlement, the distance was recorded as 0.
2. Otherwise, we measured the minimum distance, i.e., the distance between the location and the nearest building of a settlement.

In addition to the total area (in hectares) of a cemetery determined by using satellite images, we also calculated the area of the cemetery covered in forest, grassland, graves, and miscellaneous areas that could not be classified as the previous three types (e.g., areas covered with concrete, service buildings, etc.). Furthermore, we collected information on the altitude above sea level (in meters) of each location and the human population size of the nearest settlement. We used online sources, such as the latest available human demographic censuses in each settlement/country visited, and to complete the database, we searched City Population (https://www.citypopulation.de/) and City-facts (https://www.city-facts.com/).

2.3. Surrounding landscape features

We obtained data to calculate land cover variables from the CORINE Land Cover (CLC) database (https://land.copernicus.eu/en/products/corine-land-cover/) at each location. We calculated the percentage cover of all CLC classes at 1, 5, 10 and 25 km concentric buffers around each location and derived 12 main landscape categories by summing the values of CLC classes grouped together (Supporting Information and see also Fekete et al., 2020).

2.4. Statistical analyses

To investigate the effect of our explanatory variables on the diversity of orchids, we used the generalized linear mixed model (GLMM) approach ('glmmTMB' package, Brooks et al., 2017). To reduce the number of predictors, we performed a separate principal component analysis (PCA) at each of the four concentric landscape buffers (1, 5, 10 and 25 km) on a covariance matrix of the 12 landscape variables and retained only the first three principal components (PCs) from each PCA.

We included PCs belonging to each buffer zone in separate models, whilst also adding the characteristics of the cemeteries. We calculated variance inflation factors (VIFs) for the predictors to avoid collinearity among them (‘usdm’ package, Naimi et al., 2014), and retained in each model only those with a VIF < 2 (after Zuur et al., 2010). We included latitude and its quadratic form as covariates, and ‘Country’ as a random factor in each model.

Since all three diversity measures were highly correlated (H ~ E: Spearman’s $\rho = 0.76$, $p < 0.001$; H ~ D: $\rho = 0.99$, $p < 0.001$; E ~ D: $\rho = 0.90$, $p < 0.001$), we used Shannon’s diversity index (H) as a response variable to maximize the number of records ($n = 270$) included in the models. All predictors describing the characteristics of the cemeteries were centered (subtracting the mean) and scaled (divided by the standard deviation) before entering the model (Harrison et al., 2018). We also derived additional sets of models including either the number of taxa or the number of individual plants as the response variable to model the chance of occurrence of any orchid in the sampled cemeteries (see Supporting Information).

Then, we performed a backward stepwise selection procedure to find the best-fitting minimal model. We eliminated the predictor with the highest p value in each iteration until we reached a model with the lowest Akaike’s Information Criterion (AIC) value. Data preparation and analysis were performed in R v4.2.1 (R Core Team, 2022)

3. Results

3.1. Orchid diversity in European cemeteries

Of a total of 2079 cemeteries surveyed, 316 (15.2 %) contained orchids. In total 65 different orchid taxa (Table 1) were found in cemeteries in the 13 countries visited. The highest orchid diversity was found in Albania, Greece (Crete and Lesvos) and Romania, whilst no orchids were found on Tenerife and only one taxon was found in continental Spain. Between one and 10 orchid taxa were found in single cemetery surveys (Table 2). The highest numbers of taxa were found in cemeteries in Çerenec i Sipërm (Albania), Drashovicë (Albania), and Borod (Romania). The most widely distributed species of orchid were the Pyramidal Orchid (*Anacamptis pyramidalis*) and the Green-winged Orchid (*Anacamptis morio*) that were found in eight and six countries, respectively. Of 44680 individual orchid plants surveyed, the Green-winged Orchid was the most common, contributing 24885 records (55.7 % of all plants).

Shannon’s diversity index (H) of orchid assemblages ranged widely (mean ± 1 SD: 0.92 ± 0.66), when records were pooled by country (Table 2, Fig. 2), as well as the evenness (E) (0.52 ± 0.27), and Simpson’s index (D) (0.55 ± 0.29). The top 10 cemeteries with the highest diversity indices were in Albania (1st to 5th), Romania, Serbia, UK, Hungary, and Cyprus. In terms of evenness, the top 10 locations were found in the same countries, except UK, but this time Hungary hosted most of the cemeteries with the highest values.

3.2. Orchid diversity, the characteristics of cemeteries and their surrounding landscape patterns

Based on PCA of landscape variables within 1, 5, 10, and 25 km concentric buffer zones around each cemetery, the first three principal components (PCs 1–3) captured 72–77 % of the total variance (Table S1 in the online Supporting Information). Therefore, we used these PC scores in subsequent analyses.

According to the best-fitting minimal GLMMs (Table 3; see the corresponding PCA results in Table S2), orchid diversity was significantly lower in cemeteries located at higher latitudes or surrounded by a higher proportion of agricultural areas, but for the latter, the relationship was only marginal ($0.05 < \alpha < 0.10$) or even less significant. In addition, latitude showed a ‘hump-shaped’ rather than a linear relationship (Fig. S1) suggesting an optimal latitudinal belt for the diversity of orchids within the studied region. Moreover, orchid diversity was predicted to be higher when the landscape around the cemeteries within a 25 km radius is covered by mainly urban, semi-agricultural areas or natural grasslands. Cemeteries at varying distances from settlements and with varying grassland coverage within their boundaries were statistically similar in orchid diversity (Table 3).

We provide the results of alternative model sets without latitudinal components (Table S2), and using the number of orchid taxa (Table S3) and the number of individual orchid plants (Table S4) as response variables in the online Supporting Information.

4. Discussion

Here, we evaluated orchid diversity in cemeteries of 13 European countries. Orchids occurred in cemeteries of every country we censused, but there was significant variability in both the number of taxa ($n = 65$) and individual orchid plant counts ($n = 44680$) between cemeteries and countries. Based on our findings, we believe that European cemeteries play a much greater role in the conservation of orchids than former studies (e.g., Löki et al., 2019a, 2020) suggested. Although these relatively under-investigated habitat patches are heavily human-influenced, they appear to provide highly valuable habitat patches that support floristic diversity in otherwise nature-poor, heavily urbanized sites.

4.1. The potential role of cemeteries in the conservation of orchid biodiversity

Certain cemeteries and other burial sites may prove invaluable in biodiversity conservation, especially in habitats that have been heavily transformed by human activities such as in urban centers. Although only a relatively small percentage of cemeteries (15.2 %) hosted orchid taxa in our sampled locations, this highlights a considerable untapped potential for enhancing their role in biodiversity

Table 1
The distribution of different orchid taxa by numbers of countries, cemeteries and individual plants found in pan-European surveys conducted between 2015 and 2019 (inclusive). Country codes: **Al** – Albania; **Bg** – Bulgaria; **Cy** – Cyprus; **Fr** – France; **Ge** – Georgia; **Gr** – Greece (Cr – Crete, Lv – Lesvos); **Hu** – Hungary; **Ir** – Ireland; **Ro** – Romania; **Sl** – Slovakia; **Sp** – Spain; **Sr** – Serbia; **UK** – United Kingdom.

Orchid taxon with authority	Countries of occurrence	Number of		
		countries	cemeteries	individual plants
Anacamptis pyramidalis (L.) Rich.	Al, Cy, Ge, Gr (Cr), Ir, Hu, Ro, UK	8	25	921
Anacamptis morio (L.) R.M.Bateman, Pridgeon & M.W.Chase	Al, Bg, Hu, Ro, Sl, Sr	6	133	24885
Ophrys apifera Huds.	Al, Ge, Ro, Sl, UK	5	14	375
Neotinea tridentata (Scop.) R.M.Bateman, Pridgeon & M.W.Chase	Al, Hu, Ro, Sr	4	33	1284
Neottia ovata Bluff & Fingerh.	Al, Ir, Ro, UK	4	6	452
Orchis purpurea Huds.	Al, Bg, Hu, Ro	4	18	381
Spiranthes spiralis (L.) Chevall.	Gr (Lv), Hu, Ro, Sr	4	41	1032
Dactylorhiza fuchsii (Druce) Soó	Ir, Ro, UK	3	11	964
Dactylorhiza sambucina (L.) Soó	Al, Ro, Sl	3	6	37
Gymnadenia conopsea (L.) R.Br.	Ro, Sr, UK	3	9	164
Neotinea ustulata (L.) R.M.Bateman, Pridgeon & M.W.Chase	Bg, Ro, Sr	3	5	189
Ophrys sphegodes Mill.	Al, Hu, Ro	3	4	182
Cephalanthera longifolia (L.) Fritsch	Al, Hu	2	2	5
Epipactis helleborine (L.) Crantz	Al, Hu	2	6	20
Neotinea maculata (Desf.) Stearn	Al, Cy	2	4	48
Ophrys cinereophila Paulus & Gack	Cy, Gr (Cr)	2	2	2
Ophrys fuciflora (F.W. Schmidt) Mönch	Hu, Sk	2	2	59
Ophrys mammosa Desf.	Al, Cy	2	9	76
Anacamptis collina (Banks & Sol. ex Russell) R.M.Bateman, Pridgeon & M.W.Chase	Cy, Gr (Cr)	2	4	205
Anacamptis fragrans (Pollini) R.M.Bateman	Al, Gr (Cr)	2	14	2237
Orchis italica Poir.	Cy, Gr (Cr)	2	3	22
Orchis militaris (L.)	Hu, Ro	2	4	10
Platanthera bifolia (L.) Rich.	Ro, Sr	2	8	44
Serapias sp.	Gr (Cr), Sp	2	2	3
Serapias bergonii E.G.Camus subsp. *politisii* (Renz) Kreutz	Cy, Gr (Lv)	2	1	3
Ophrys sp.	Sl	1	8	1
Cephalanthera damasonium (Druce)	Hu	1	2	101
Cephalanthera rubra (L.) Rich.	Al	1	1	50
Dactylorhiza viridis (L.) R.M.Bateman, Pridgeon & M.W.Chase	Ro	1	1	15
Dactylorhiza majalis (Rchb.) P.F.Hunt & Summerh.	Ro	1	1	5
Dactylorhiza x grandis (Druce)	UK	1	1	3
Epipactis microphylla (Sieber). ex Nyman	Al	1	6	77
Epipactis palustris (L.) Crantz	Ro	1	2	81
Gymnadenia odoratissima (L.) Rich.	Ro	1	1	250
Himantoglossum jankae Somlyay, Kreutz & Óvári	Al	1	6	108
Himantoglossum robertianum (Loisel.) P.Delforge	Cy	1	6	20
Limodorum abortivum (L.) Sw.	Al	1	5	16
Neottia nidus-avis (L.) Rich.	Hu	1	1	2
Ophrys umbilicata (Desf.)	Al	1	1	8
Ophrys bombyliflora Spreng.	Al	1	3	32
Ophrys epirotica (Renz) Devillers-Tersch., & Devillers	Al	1	1	20
Ophrys episcopalis (Poir.)	Gr (Cr)	1	1	1
Ophrys ferrum-equinum (Desf.)	Al	1	3	35
Ophrys flavomarginata (Renz) H.Baumann & Künkele	Cy	1	1	150
Ophrys gortynia (H. Baumann & Künkele) Paulus	Gr (Cr)	1	2	3
Ophrys lutea Cav. subsp. *minor* (Guss.) O.Danesch & E.Danesch ex Gölz & H.R.Reinhard	Gr (Cr)	1	3	41
Ophrys oestrifera (M. Bieb.)	Al	1	12	369
Ophrys lutea (Cav.)	Al	1	11	455
Ophrys speculum Link	Al	1	1	2
Anacamptis coriophora (L.) R.M.Bateman, Pridgeon & M.W.Chase	Ro	1	22	750
Anacamptis laxiflora (Lam.) R.M.Bateman, Pridgeon & M.W.Chase	Al	1	5	2011
Orchis mascula (L.) subsp. *mascula*	UK	1	4	23
Orchis mascula (L.) subsp. *signifera*	Ro	1	1	3
Anacamptis papilionacea (L.) R. M. Bateman, Pridgeon & M. W. Chase	Gr (Cr)	1	2	22
Orchis quadripunctata (Cirillo) ex Ten.	Gr (Cr)	1	1	20
Anacamptis sancta (L.) R. M. Bateman, Pridgeon & M. W. Chase	Gr (Lv)	1	3	30
Orchis sp.	Fr	1	1	1
Anacamptis morio (L.) R. M. Bateman, Pridgeon & M. W. Chase subsp. *syriaca* (Boiss. ex H. Baumann & Künkele) H. Kretzschmar, Eccarius & H. Dietr.	Cy	1	1	2
Platanthera chlorantha (Custer) Rchb.	Al	1	5	77
Serapias bergonii subsp. *bergonii* E. G. Camus	Gr (Cr)	1	2	215

(*continued on next page*)

Table 1 (*continued*)

Orchid taxon with authority	Countries of occurrence	Number of		
		countries	cemeteries	individual plants
Serapias cordigera (L.)	Gr (Cr)	1	1	2
Serapias feldwegiana H. Baumann & Künkele	Ge	1	1	1
Serapias orientalis (Greuter) H.Baumann & Künkele	Gr (Cr)	1	2	5
Serapias parviflora (Parl.)	Al	1	44	5873
Serapias vomeracea (Burm.f.) Briq.	Al	1	12	166

conservation. First, heritage preservation and biodiversity conservation can proceed hand in hand, as their proximity to urban areas means that they are accessible for humans to maintain biodiversity conservation in a culturally shaped urban landscape (Kowarik et al., 2016). Secondly, because of their continued importance in honoring the dead in modern human societies (Sayer, 2010) and protection from religious establishments that oversee them (Velivasaki, 2010), they endure and presumably will continue to persist even in the face of sometimes radical land-use change brought about by human demographic pressures (Smith, 2018). Thirdly, although cemeteries are sometimes closed or relocated due to settlement planning policy (Kay, 1998), the area of habitat devoted to functioning cemeteries is less likely to decrease. As well as habitat type heterogeneity, area of available habitat is one of the best predictors of variability in species richness in the case of orchids (Löki et al., 2019b). With appropriate management methods, a mosaic habitat structure, mostly with dynamic transformation of small habitat patches in cemeteries, can be maintained.

Although the main factor determining the diversity of orchid species is the size of favorable contiguous habitat (Schödelbauerová et al., 2009), we suggest that cemeteries can still accommodate significant diversity, despite their degree of disconnectedness. This was well studied in Turkey where three-quarters of the total orchid flora of the country was found in cemeteries (Löki et al., 2019b). Although it is now known that Muslim cemeteries may harbor higher orchid diversity (Molnár et al., 2017a), we still lack basic information about the colonization, recolonization, and remnant status of orchid populations found in cemeteries. Viable orchid populations in cemeteries may also be the result of the relatively easy dispersal of their propagules by the wind (Barthlott et al., 2014). However, there are limited data on fruit-set rates, population dynamics and the susceptibility to ecological traps for orchid populations in anthropogenically influenced habitats (Fekete et al., 2017), including cemeteries. The effects of direct human disturbance are also under-studied; they can vary spatiotemporally across Europe due to differences between countries in culture, religion, tradition, but also in ethnobotany (Molnár et al., 2017c).

Habitat fragmentation is strongly associated with the extinction of animal and plant species and causes a significant loss in biodiversity (Harrison and Bruna, 1999), while homogenization and destruction of the remaining habitats are major causes of biodiversity loss in Europe, and worldwide (Jongman, 2002). Using the data collected in 13 countries at more than 2000 unique locations, we found that the overall orchid diversity was significantly higher in cemeteries located at lower latitudes and where the percentage of landscape covered by urban, semi-agricultural areas or natural grasslands within a 25 km radius was higher, but agricultural areas within a 10 km radius was lower. This may be related to the stepping stone function of cemeteries that works better when the availability of agricultural land of the surrounding areas is lower, and orchid seeds, which are easily dispersed by wind (Barthlott et al., 2014), are more likely to fall either on the cemetery site or on natural or semi-natural habitat around the cemetery. Thus, they can easily colonize the reserve areas of the cemetery over time, which has been supported by previous studies (Baum et al., 2004; Murphy and Lovett-Doust, 2004).

4.2. *The significance of cemeteries in future conservation of plant biodiversity*

Geographically far reaching investigations, including the effective management of disjunct habitat patches, or even networks, might hold the key to biodiversity conservation at local or even global scales (Debinski and Holt, 2000), while also special attention should be paid to the areas around the valuable fragmented habitats. Despite significant differences between the number of orchid taxa and individual plants recorded in cemeteries, they were found in all 13 European countries in our study. This under-researched diversity of the members of a plant family, which is responding to the transformation of urban habitats very quickly (Duncan, 2011), indicates that the role of cemeteries as habitats for orchids can be of much significance and worthy of protection than previously thought. As the landscape of cemeteries is mostly under radical transformation due to changes in social structure, economic interests, and in the aesthetic values held by modern people, implications should be carefully considered for conserving the biodiversity of cemeteries.

4.3. *Our recommendations for the conservation of cemeteries are listed below*

1) The safeguarding of traditional burials is crucial because the use of headstones and traditional gravestones not only conserves the cultural heritage of cemeteries but also represents a long-term and sustainable service of cemeteries compared to the high energy demands of modern burial methods such as cremation (Lee et al., 2022). Besides traditional burial methods, other alternatives such as eco-burials (Davies and Rumble, 2012) and conservation burials (Holden and McDonald-Madden, 2017) are coming to the fore.

Table 2
Summary of orchid diversity in the cemeteries of 13 European countries. Orchid diversity measures: H – Shannon's diversity index, E – Evenness, D – Simpson's diversity index. N/A is not applicable. The number of orchid species in the country were determined based on C. A. J. Kreutz's book on the orchids of Europe, North Africa and the Middle East (Kreutz, 2024).

Country	Number of:				Mean number (± SD) of orchid taxa in:		Total number of orchid plants	Orchid diversity measures		
	cemeteries surveyed	cemeteries with orchids (% of total)	orchid species known in country	orchid species (% of entire orchid flora)	all cemeteries	cemeteries with orchids		H	E	D
Albania	166	88 (53.01)	83	30 (36.14)	1.28 (± 1.81)	2.42 (± 1.85)	24,953	1.45	0.43	0.65
Bulgaria	51	3 (5.88)	82	3 (3.66)	0.08 (± 0.34)	1.33 (± 0.58)	108	0.40	0.36	0.22
Cyprus	90	18 (20.00)	52	12 (23.08)	0.39 (± 0.70)	1.38 (± 0.62)	538	1.90	0.76	0.82
France	50	1 (2.00)	134	1 (0.75)	0.02 (± 0.14)	N/A	1	0	N/A	N/A
Georgia	21	2 (9.52)	53	3 (5.66)	0.14 (± 0.48)	1.50 (± 0.71)	3	1.10	1.00	1.00
Greece (Crete and Lesvos)	125	15 (12.00)	193	18 (9.33)	0.22 (± 0.71)	1.87 (± 1.06)	878	1.40	0.48	0.61
Hungary	955	80 (8.38)	71	12 (16.90)	0.11 (± 0.39)	1.30 (± 0.54)	7377	1.08	0.43	0.48
Ireland	60	7 (11.67)	30	3 (10.00)	0.12 (± 0.32)	1.00 (± 0.00)	321	0.07	0.07	0.02
Romania	262	71 (27.10)	77	20 (25.97)	0.50 (± 1.07)	1.85 (± 1.32)	7589	1.49	0.50	0.58
Serbia	73	12 (16.44)	58	8 (13.79)	0.39 (± 0.93)	1.71 (± 1.27)	1694	0.42	0.20	0.19
Slovakia	71	5 (7.04)	77	5 (6.49)	0.07 (± 0.26)	1.00 (± 0.00)	22	1.23	0.76	0.68
Spain (continental and Tenerife)	100	1 (1.00)	101	1 (0.99)	0.01 (± 0.1)	N/A	1	0	N/A	N/A
United Kingdom	90	9 (10.00)	45	7 (15.56)	0.20 (± 0.61)	1.46 (± 0.97)	1181	1.45	0.75	0.73

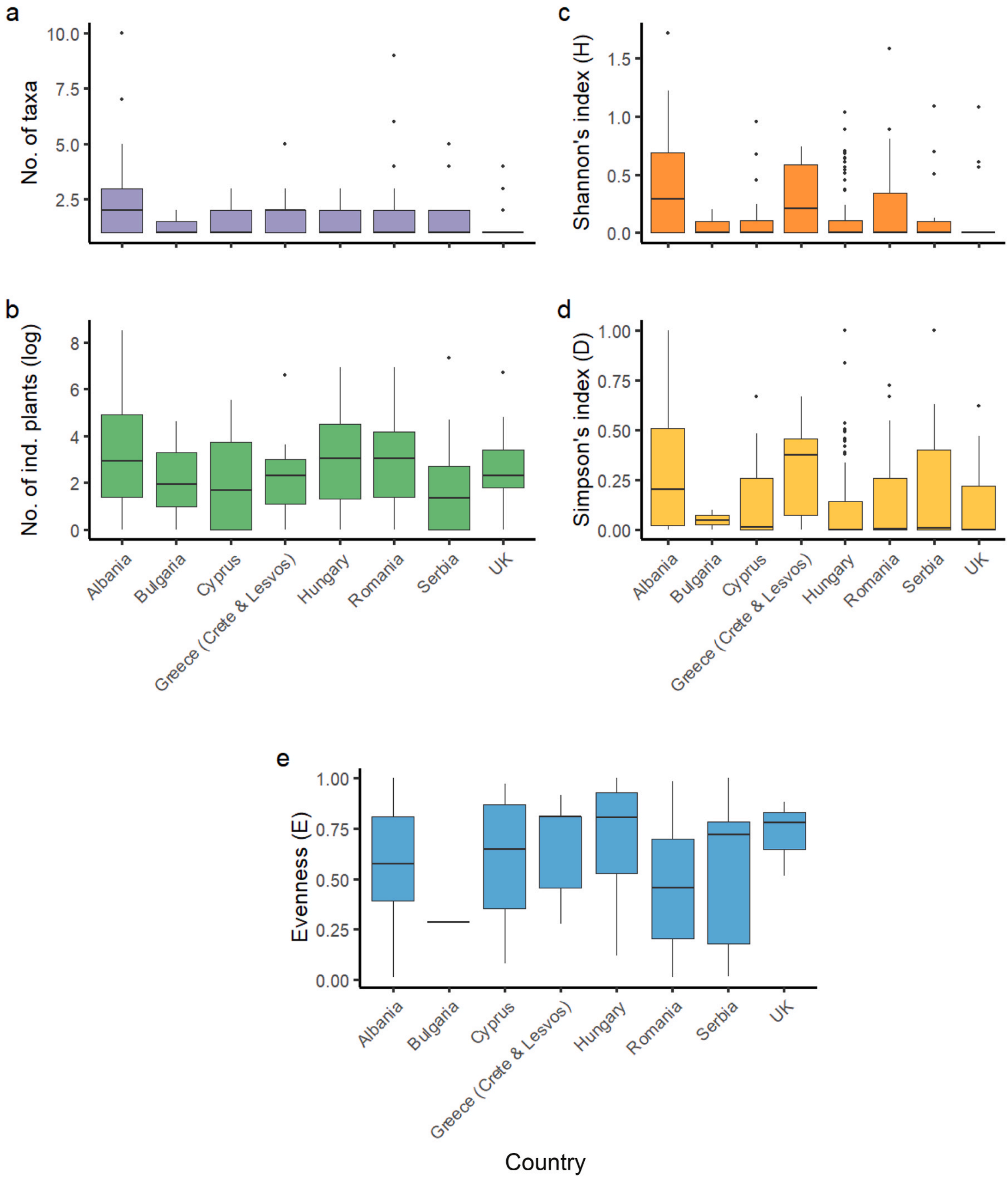

Fig. 2. The number of (a) orchid taxa and (b) individual plants (log-transformed), and the diversity as measured by (c) Shannon's index (H), (d) Simpson's index (D), and (e) Evenness (E), obtained from surveys of cemeteries carried out between 2015 and 2019 (inclusive) across Europe. Countries with extremely small numbers of taxa and individual plants (France, Georgia, Ireland, Slovakia, Spain) are not shown.

As observed in many visited cemeteries across Europe, the ability of orchids to grow on traditionally maintained graves is also important in their conservation.

2) The establishment of modern graves should be avoided on the most diverse natural patches of cemeteries that are predominantly located on the edges of cemeteries. Instead, where possible, new areas for burials should be designated close to areas where plant propagule sources of natural habitat patches could also help to recolonize the extended areas of cemeteries.
3) To increase the quality and proportion of natural grassland patches in cemeteries, manual trimming should replace mechanical mowers and reduction in sward height should take place only two-three times a year, depending on the local traditions. The most

Fig. 3. Some characteristic orchid species of European cemeteries. A: *Dactylorhiza fuchsii* (Shanaglish, Ireland); B: *Orchis mascula* subsp. *mascula* (Aldborough, United Kingdom); C: *Dactylorhiza sambucina* (Radola, Slovakia); D: *Orchis purpurea* (Zádorfalva, Hungary); E: *Spiranthes spiralis* (Rutosi, Serbia); F: *Gymnadenia odoratissima* (Borod, Romania); G: *Epipactis microphylla* (Zgosht, Albania); H: *Anacamptis papilionacea* (Damania in Crete, Greece); I: *Himantoglossum robertianum* (Pentakomo, Cyprus). Photographs were taken by Viktor Löki (A-C, E-F, H-I) and Attila Molnár V. (D, G).

obviously inappropriate management of potentially 'orchid-friendly' sites was observed in cemeteries of the British Isles in our study where 88 % of the surveyed locations were at least partially mowed to ground level in Ireland, and this increased to 92 % in the UK. Lawns slowly became the symbol of household affluence across the world. Therefore, their potential transformation and

Table 3
Summary of the best-fitting minimal GLMMs with Shannon's diversity index (H) as a response variable and its main predictors (within boundary characteristics and 1, 5, 10, and 25 km buffer zones), associated estimated regression coefficients (β) and standard errors (SE), test statistics (Z) and the corresponding significance value (p). The Akaike's Information Criterion (AIC) of each model and the difference compared to its corresponding full model (ΔAIC) is also shown, $p \leq 0.05$ is marked with an asterisk.

Predictor	β	SE	Z	p
1 km buffer zone				
Latitude	−0.44	0.15	−2.91	0.004 *
Latitude (quadratic form)	−0.18	0.10	−1.80	0.073
Altitude	−0.17	0.12	−1.42	0.156
Distance	0.12	0.11	1.14	0.256
AIC = 430.05, ΔAIC = 11.03				
5 km buffer zone				
Latitude	−0.41	0.14	−2.90	0.004 *
Latitude (quadratic form)	−0.19	0.10	−1.99	0.047 *
Altitude	−0.23	0.13	−1.79	0.074
Distance	0.13	0.11	1.21	0.226
PC1 within 5 km	−0.51	0.39	−1.29	0.196
AIC = 430.46, ΔAIC = 9.33				
10 km buffer zone				
Latitude	−0.45	0.14	−3.15	0.002 *
Latitude (quadratic form)	−0.19	0.10	−1.95	0.054
Altitude	−0.24	0.12	−1.92	0.055
Distance	0.16	0.11	1.51	0.132
Grass area in the cemetery	0.14	0.10	1.32	0.187
PC1 within 10 km	−1.28	0.67	−1.91	0.056
AIC = 429.68, ΔAIC = 8.90				
25 km buffer zone				
Latitude	−0.54	0.15	−3.55	< 0.001 *
Latitude (quadratic form)	−0.23	0.10	−2.24	0.025 *
PC3 within 25 km	2.57	1.22	2.10	0.036 *
AIC = 427.16, ΔAIC = 11.85				

associated changes in their maintenance require a transdisciplinary approach in the future (Ignatieva et al., 2015). This conservation potential of cemeteries depends largely on the presence and future persistence of open, natural or semi-natural habitats within their boundaries, since cemeteries may serve as refugia for orchids only where suitable habitat conditions (such as grassland or open forest patches) are maintained and not entirely replaced by graveyard infrastructure.

4) The application of pesticides and insecticides within cemeteries should be avoided as their use creates a less diverse habitat mostly suitable for ruderal weeds, and profoundly disrupts community structure in which orchids and most plants which do not tolerate disturbance are unable to sustain viable populations (Relyea, 2013; Schmidt and Steinbach, 1983).
5) Native plant species should be preferred over ornamental ones in decoration of headstones and grave surrounds. We recommend that the cultivated flora of the ecoregion should be used, thereby promoting the collection of propagules from the wild.
6) According to our field observations during this study, in the Mediterranean, overgrazing and the accelerated use of marble and concrete in cemeteries pose the greatest threats to native flora such as orchids. Although fences are built around most cemeteries, they still should be established and maintained to prevent livestock from entering them. Nevertheless, sustainable grazing by mostly cattle (*Bos taurus*) or sheep (*Ovis aries*) can be applied and can be crucial in certain regions in Central and Western Europe, especially in the British Isles, where this kind of grazing has a long tradition.
7) In certain countries such as Albania, Bulgaria, Georgia, Greece, and Serbia, *salep* harvesting should be avoided, or controlled in a culturally sensitive manner in cemeteries to protect populations of mostly salient orchid species. However, despite newly emerged regulations and implications for conservation (e.g., Charitonidou et al., 2019; Düzenlemeler, 2013), the cultural background of the process must of course be respected, especially as *salep* harvesters can also help in the discovery of rare populations of orchids in cemeteries due to their traditional ecological knowledge (TEK) of the local vegetation (Molnár et al., 2017d).
8) Cemeteries are clearly key in maintaining cultural and natural heritage and, therefore, (re-)familiarizing people with, and educating them about, these values are eminently important. Signifying the importance of these invaluable cemeteries nationally and regionally, such as through placing information boards at locations, is fundamental for communicating their cultural and natural values to visitors and local people alike (Affifi and Christie, 2019; Tsiouri, 2023).
9) To conserve cemeteries with the highest biodiversity, local communities of residents and parishioners need to work alongside local authorities such as councils and churches to maintain such sites for religious and biodiversity purposes. While cemeteries must serve the burial requirements of the local community, conserving biodiversity can occur in concert. Those who wish to advocate conservation of nature clearly need to be a part of the communal debate (Cooper, 1995), and thankfully so-called 'cemetery wars' are rare (Plumwood, 2007).

4.4. Suggestions for further research

Despite some recent studies of the conservation value of European cemeteries (e.g., Kowarik et al., 2016; Löki et al., 2020), there are still many gaps in our knowledge. We believe that some key directions should be followed in future research. For example, we need to quantify the level of both bio- and cultural diversity within cemeteries at the landscape scale, identifying the relationship between the biodiversity within cemeteries and the surrounding matrix, and investigating as a matter of urgency the impacts of cemetery management on biodiversity contained therein (Barrett and Barrett, 2001). Twenty-four years have elapsed since this publication but its sentiments and specifications for their implementation are just as relevant today. Due to accelerating anthropogenic pressures on the natural world, the need for such studies grows ever more acute (Uslu et al., 2009). Further research within cemeteries will inevitably provide valuable data on the life history and ecology of orchid species.

While we found some key factors driving orchid diversity in European cemeteries, inevitably a few more may have been overlooked. Orchids have specific soil and mycorrhizal requirements (Chauhan and Attri, 2024; McCormick and Jacquemyn, 2014). Unfortunately, detailed and consistent data on the geological substrate were not available at the scale of our study, since we also did not sample the soil in the visited cemeteries. Therefore, it could not be incorporated into the current analyses. However, future studies in the topic may focus on this potentially important aspect (Phillips et al., 2020).

Although human disturbance has a major negative impact on the orchid flora of cemeteries (Löki et al., 2019b), we believe that they can act as arenas for conservation of other vascular plants (e.g. old trees or rare scrubs) or animal species (e.g. birds or reptiles), especially because of the orchids' dependence on natural vegetation. Currently in Europe, we found that cemeteries in France and Spain offer little potential for conserving natural habitat patches (Kelcey and Müller, 2011). Likely, cemeteries in countries such as Belgium, Italy, Portugal, and The Netherlands that share similar burial traditions and management methods to France and Spain, also may provide low conservation potential for biodiversity but are countries we did not visit. Expansion of orchid surveys in such countries is a priority.

The situation is even more complex in the secondarily conserved natural habitats close to radically and rapidly transforming urban areas. Although in modern times economic interests are not aligned with nature conservation, we also can act to conserve the orchid flora of cemeteries by returning to the traditional and more sustainable methods in maintaining the graves of our deceased loved ones, including the surrounding environment. Furthermore, a similar effect on maintaining diversity may be provided by choosing sustainable and ecofriendly alternatives to burial. Wooden crosses will disappear without a trace from cemeteries within two generations, but a natural cemetery rich in orchids will endure for far longer.

Ethics Statement

Not applicable: This manuscript does not include human or animal research.

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Declaration of Competing Interest

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

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecco.2025.e03613.

Data availability

Data will be made available on request.

References

Adamowski, W., Conti, F., 1991. Mass occurrence of orchids in poplar plantations near Czeremcha village as an example of apophytism. Phytocoenosis 3, 259–267.
Adams, L.W., 1994. Urban Wildlife Habitats: A Landscape Perspective. University of Minnesota Press, Minneapolis, MN, USA. Vol. 3.
Affifi, R., Christie, B., 2019. Facing loss: pedagogy of death. Environ. Educ. Res. 25, 1143–1157. https://doi.org/10.1080/13504622.2018.1446511.
Anthony, S., 2015. Hiding the body: ordering space and allowing manipulation of body parts within modern cemeteries. In: Tarlow, S. (Ed.), The Archeology of Death in Post-Medieval Europe. De Gruyter, Berlin, Germany, pp. 170–188. https://doi.org/10.1515/9783110439731-009.
Antkowiak, W., Heine, A., 2005. Dendroflora and current state of historic cemeteries of the Kolo District in Central Poland. Rocz. Akad. Rol. w Pozn. 9, 3–12.
Barrett, G.W., Barrett, T.L., 2001. Cemeteries as repositories of natural and cultural diversity. Conserv. Biol. 15, 1820–1824. https://doi.org/10.1046/j.1523-1739.2001.00410.x.
Barthlott, W., Große-Veldmann, B., Korotkova, N., 2014. Orchid seed diversity. Englera 32, 1–245.
Batty, L.C., 2005. The potential importance of mine sites for biodiversity. Mine Water Environ. 24, 101–103. https://doi.org/10.1007/s10230-005-0076-0.
Baum, K.A., Haynes, K.J., Dillemuth, F.P., Cronin, J.T., 2004. The matrix enhances the effectiveness of corridors and stepping stones. Ecology 85, 2671–2676. https://doi.org/10.1890/04-0500.
Bhagwat, S.A., 2009. Ecosystem services and sacred natural sites: reconciling material and non-material values in nature conservation. Environ. Values 18, 417–427. https://doi.org/10.3197/096327109X12532653285731.
Bhagwat, S.A., Rutte, C., 2006. Sacred groves: potential for biodiversity management. Front. Ecol. Environ. 4, 519–524. https://doi.org/10.1890/1540-9295(2006)4[519:SGPFBM]2.0.CO;2.
Brooks, M.E., Kristensen, K., van Benthem, K.J., Magnusson, A., Berg, C.W., Nielsen, A., Skaug, H.J., Maechler, M., Bolker, B.M., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. R. J. 9, 378–400. https://doi.org/10.32614/RJ-2017-066.
Buchholz, S., Blick, T., Hannig, K., Kowarik, I., Lemke, A., Otte, V., Scharon, J., Schönhofer, A., Teige, T., von der Lippe, M., Seitz, B., 2016. Biological richness of a large urban cemetery in Berlin. Results of a multi-taxon approach. Biodivers. Data J. (4), e7057. https://doi.org/10.3897/BDJ.4.e7057.
Caballero, R., Fernandez-Gonzalez, F., Badia, R.P., Molle, G., Roggero, P.P., Bagella, S., D'Ottavio, P., Papanastasis, V.P., Fotiadis, G., Sidiropoulou, A., Ispikoudis, I., 2009. Grazing systems and biodiversity in Mediterranean areas: Spain, Italy and Greece. Pastos 39, 9–154.
Charitonidou, M., Stara, K., Kougioumoutzis, K., Halley, J., 2019. Implications of salep collection for the conservation of the Elder-flowered Orchid (*Dactylorhiza sambucina)* in Epirus, Greece. J. Biol. Res. Thessalon. 26, 18. https://doi.org/10.1186/s40709-019-0110-1.
Chauhan, P., Attri, L., 2024. Mycorrhizal associations in orchids: a review. Asian J. Biol. Life Sci. 13, 278–286. https://doi.org/10.5530/ajbls.2024.13.36.
Cooper, N.S., 1995. Wildlife conservation in churchyards: a case-study in ethical judgements. Biodivers. Conserv. 4, 916–928. https://doi.org/10.1007/BF00056198.
Cornelis, J., Hermy, M., 2004. Biodiversity relationships in urban and suburban parks in Flanders. Landsc. Urban Plan. 69, 385–401. https://doi.org/10.1016/j.landurbplan.2003.10.038.
Cousins, S.A., 2006. Plant species richness in midfield islets and road verges – the effect of landscape fragmentation. Biol. Conserv. 127, 500–509. https://doi.org/10.1016/j.biocon.2005.09.009.
Czarna, A., 2016. Vascular plant flora in the Cytadela cemeteries in Poznań (Poland). Acta Agrobot. 69, 1–17. https://doi.org/10.5586/aa.1695.
Czarna, A., Nowinska, R., 2010. Vascular plants of certain old Jewish cemeteries in Western Carpathians. Botanika – Steciana 14, 45–52.
Czarna, A., Piskorz, R., 2005. Vascular flora of cemeteries in the town of Zakopane in the Tatra Mountains. Botanika – Steciana 9, 47–58.
Dafni, A., Lev, E., Beckmann, S., Eichberger, C., 2006. Ritual plants of Muslim graveyards in northern Israel. J. Ethnobiol. Ethnomed. 2, 38. https://doi.org/10.1186/1746-4269-2-38.
Davies, D., Rumble, H., 2012. Natural Burial: Traditional-secular Spiritualities And Funeral Innovation. Continuum International Publishing Group, London, UK.
Deák, B., Tóthmérész, B., Valkó, O., Sudnik-Wójcikowska, B., Moysiyenko, I.I., Bragina, T.M., Apostolova, I., Dembicz, I., Bykov, N.I., Török, P., 2016. Cultural monuments and nature conservation: a review of the role of kurgans in the conservation and restoration of steppe vegetation. Biodivers. Conserv. 25, 1–18. https://doi.org/10.1007/s10531-016-1081-2.
Debinski, D.M., Holt, R.D., 2000. A survey and overview of habitat fragmentation experiments. Conserv. Biol. 14, 342–355. https://doi.org/10.1046/j.1523-1739.2000.98081.x.
Delforge, P., 2006. Orchids of Europe, North Africa and the Middle East. Timber Press Inc, Oregon, USA.
Duncan, R.P., Clemants, S.E., Corlett, R.T., Hahs, A.K., McCarthy, M.A., McDonnell, M.J., Schwartz, W.M., Thompson, K., Vesk, A.P., Williams, N.S., 2011. Plant traits and extinction in urban areas: a meta-analysis of 11 cities. Glob. Ecol. Biogeogr. 20, 509–519. https://doi.org/10.1111/j.1466-8238.2010.00633.x.
Düzenlemeler, Đ.Đ.Y., 2013. Regulations relating to the salep and its trade in Turkish official gazette archives from 1920 to the present. J. Hist. Cult. Art. Res. 2, 172–180. https://doi.org/10.7596/taksad.v2i1.187.
Fekete, R., Nagy, T., Bódis, J., Biró, É ., Löki, V., Süveges, K., Takács, A., Tökölyi, J., Molnár, V.A., 2017. Roadside verges as habitats for endangered lizard-orchids (*Himantoglossum* spp.): Ecological traps or refuges. Sci. Total Environ. 607, 1001–1008. https://doi.org/10.1016/j.scitotenv.2017.07.037.
Fekete, R., Löki, V., Urgyán, R., Süveges, K., Lovas-Kiss, Á., Vincze, O., Molnár, V.A., 2019. Roadside verges and cemeteries: comparative analysis of anthropogenic orchid habitats in the Eastern Mediterranean. Ecol. Evol. 9, 6655–6664. https://doi.org/10.1002/ece3.5245.
Fekete, R., Bódis, J., Fülöp, B., Süveges, K., Urgyán, R., Malkócs, T., Vincze, O., Silva, L., Molnár, V.A., 2020. Roadsides provide refuge for orchids: Characteristic of the surrounding landscape. Ecol. Evol. 10, 13236–13247. https://doi.org/10.1002/ece3.6920.
Fekete, R., Vincze, O., Nagy, J., Löki, V., Süveges, K., Bódis, J., Malkócs, T., Lovas-Kiss, Á., Molnár, V.A., 2023a. North-facing roadside slopes: anthropogenic climate microrefugia for orchids. Glob. Ecol. Conserv. 47, e02642. https://doi.org/10.1016/j.gecco.2023.e02642.
Fekete, R., Vincze, O., Süveges, K., Bak, H., Malkócs, T., Löki, V., Urgyán, R., Molnár, V.A., 2023b. The role of olive groves in the conservation of Mediterranean orchids. Glob. Ecol. Conserv. 44, e02490. https://doi.org/10.1016/j.gecco.2023.e02490.
Fudali, E., 2001. The ecological structure of the bryoflora of Wroclaw's parks and cemeteries in relation to their localization and origin. Acta Soc. Bot. Pol. 70, 229–235. https://doi.org/10.5586/asbp.2001.030.
Gallo, T., Fidino, M., Lehrer, E.W., Magle, S.B., 2017. Mammal diversity and metacommunity dynamics in urban green spaces: Implications for urban wildlife conservation. Ecol. Appl. 27, 2330–2341. https://doi.org/10.1002/eap.1611.
Hadi, F., Ibrar, M., Zaidi, N., 2014. Role of Dag Behsud graveyard in conservation of indigenous medicinal flora of district Nowshera, Pakistan. Sch. J. Agric. Sci. 4, 87–89.
Harrison, S., Bruna, E., 1999. Habitat fragmentation and large-scale conservation: What do we know for sure. Ecography 22, 225–232. https://doi.org/10.1111/j.1600-0587.1999.tb00496.x.
Harrison, X.A., Donaldson, L., Correa-Cano, M.E., Evans, J., Fisher, D.N., Goodwin, C.E., Robinson, B.S., Hodgson, D.J., Inger, R., 2018. A brief introduction to mixed effects modelling and multi-model inference in ecology. PeerJ 6, e4794. https://doi.org/10.7717/peerj.4794.
Hewitt, A., 2013. Revisiting Tony Price's (1979) account of the native vegetation of Duck River and Rookwood Cemetery, western Sydney. Cunninghamia 13, 25–124. https://doi.org/10.7751/cunninghamia.2013.13.002.
Holden, M.H., McDonald-Madden, E., 2017. Conservation from the grave: Human burials to fund the conservation of threatened species. Conserv. Lett. 11, 1–4. https://doi.org/10.1111/conl.12421.
Ignatieva, M., Ahrné, K., Wissman, J., Eriksson, T., Tidåker, P., Hedblom, M., Kätterer, T., Marstorp, H., Berg, P., Eriksson, T., Bengtsson, J., 2015. Lawn as a cultural and ecological phenomenon: A conceptual framework for transdisciplinary research. Urban For. Urban Green. 14, 383–387. https://doi.org/10.1016/j.ufug.2015.04.003.
Jongman, R.H.G., 2002. Homogenisation and fragmentation of the European landscape: Ecological consequences and solutions. Landsc. Urban Plan. 58, 211–221. https://doi.org/10.1016/S0169-2046(01)00222-5.
Kasparek, M., Grimm, U., 1999. European trade in Turkish salep with special reference to Germany. Econ. Bot. 53, 396–406. https://doi.org/10.1007/BF02866718.

Kay, D.H., 1998. Cemetery relocation: Emerging urban land development issue. J. Urban Plan. Dev. 124, 1–10. https://doi.org/10.1061/(ASCE)0733-9488(1998)124:1(1).
Kelcey, J.G., Müller, N. (Eds.), 2011. Plants and Habitats of European Cities. Springer Science & Business Media, London, UK.
Koju, L., Shrestha, N., Raskoti, B.B., Ale, R., Ghimire, N.P., Shrestha, S., 2023. Spatial patterns, underlying drivers and conservation priorities of orchids in the central Himalaya. Biol. Conserv. 283, 110121. https://doi.org/10.1016/j.biocon.2023.110121.
Kowarik, I., Buchholz, S., von der Lippe, M., Seitz, B., 2016. Biodiversity functions of urban cemeteries: Evidence from one of the largest Jewish cemeteries in Europe. Urban For. Urban Green. 19, 68–78. https://doi.org/10.1016/j.ufug.2016.06.023.
Kreutz, C.A.J., 2010. Beitrag zur Kenntnis europäischer, mediterraner und vorderasiatischer Orchideen. Ber. Arb. Heim. Orchid. 27, 171–236.
Kreutz, C.A.J., 2024. Orchids of Europe, North Africa and the Middle East. Kreutz Publishers, The Neatherlands.
Kreutz, C.A.J., Çolak, A.H., 2009. Türkiye Orkideleri. İstanbul: Rota Yayınları.
Kreutz, C.A.J., Krüger, B., 2014. Über *Ophrys isaura* und *Ophrys kreutzii* in der Türkei. J. Eur. äischer Orchid. 46, 53–66.
Kreutz, C.A.J., Peter, R., 2007. *Ophrys konyana* Kreutz & Ruedi Peter, eine neue *Ophrys*-Art aus Südwesttürkei (Konya). J. Eur. äischer Orchid. 39, 71–77.
Kull, T., Selgis, U., Pecina, M.V., Metsare, M., Ilves, A., Tali, K., Sepp, K., Kull, K., Shefferson, R.P., 2016. Factors influencing IUCN threat levels to orchids across Europe on the basis of national red lists. Ecol. Evol. 6, 6245–6265. https://doi.org/10.1002/ece3.2363.
Lee, K.H., Huang, C.C., Chuang, S., Huang, C.T., Tsai, W.H., Hsieh, C.L., 2022. Energy saving and carbon neutrality in the funeral industry. Energies 15, 1457. https://doi.org/10.3390/en15041457.
Löki, V., Tökölyi, J., Süveges, K., Lovas-Kiss, Á., Hürkan, K., Sramkó, G., Molnár, V.A., 2015. The orchid flora of Turkish graveyards: a comprehensive field survey. Willdenowia 45, 231–243. https://doi.org/10.3372/wi.45.45209.
Löki, V., Molnár, V.A., Süveges, K., Heimeier, H., Takács, A., Nagy, T., Fekete, R., Lovas-Kiss, Á., Kreutz, C.A.J., Sramkó, G., Tökölyi, J., 2019b. Predictors of conservation value of Turkish cemeteries: A case study using orchids. Landsc. Urban Plan. 186, 36–44. https://doi.org/10.1016/j.landurbplan.2019.02.016.
Löki, V., Deák, B., Lukács, B.A., Molnár, V.A., 2019a. Biodiversity potential of burial places a review on the flora and fauna of cemeteries and churchyards. Glob. Ecol. Conserv. 18, e00614. https://doi.org/10.1016/j.gecco.2019.e00614.
Löki, V., Schmotzer, A., Takács, A., Süveges, K., Lovas-Kiss, Á., Lukács, B.A., Tökölyi, J., Molnár, V.A., 2020. The protected flora of long-established cemeteries in Hungary: Using historical maps in biodiversity conservation. Ecol. Evol. 10, 7497–7508. https://doi.org/10.1002/ece3.6476.
Lunt, I.D., Spooner, P.G., 2005. Using historical ecology to understand patterns of biodiversity in fragmented agricultural landscapes. J. Biogeogr. 32, 1859–1873. https://doi.org/10.1111/j.1365-2699.2005.01296.x.
Lussu, M., Ancillotto, L., Labadessa, R., Di Musciano, M., Zannini, P., Testolin, R., Santi, F., Dolci, D., Conti, M., Marignani, M., Martellos, S., Peruzzi, L., Chiarucci, A., 2024. Prioritizing conservation of terrestrial orchids: A gap analysis for Italy. Biol. Conserv. 289, 110385. https://doi.org/10.1016/j.biocon.2023.110385.
McCormick, M.K., Jacquemyn, H., 2014. What constrains the distribution of orchid populations? N. Phytol. 202, 392–400. https://doi.org/10.1111/nph.12639.
McKinney, M.L., 2006. Urbanization as a major cause of biotic homogenization. Biol. Conserv. 127, 247–260. https://doi.org/10.1016/j.biocon.2005.09.005.
McKinney, M.L., 2008. Effects of urbanization on species richness: A review of plants and animals. Urban Ecosyst. 11, 161–176. https://doi.org/10.1007/s11252-007-0045-4.
Molnár, V.A., Takács, A., Mizsei, E., Löki, V., Barina, Z., Sramkó, G., Tökölyi, J., 2017a. Religious differences affect orchid diversity of Albanian graveyards. Pak. J. Bot. 49, 289–303.
Molnár, V.A., Löki, V., Máté, A., Molnár, A., Takács, A., Nagy, T., Lovas-Kiss, Á., Sramkó, G., Tökölyi, J., 2017b. The occurrence of *Spiraea crenata* and other rare steppe plants in Pannonian graveyards. Biologia 72, 500–509. https://doi.org/10.1515/biolog-2017-0060.
Molnár, V.A., Süveges, K., Molnár, Z., Löki, V., 2017c. Using local people's traditional ecological knowledge in discovery of rare plants: A case study from Turkey. Acta Soc. Bot. Pol. 86, 1–10. https://doi.org/10.5586/asbp.3541.
Molnár, V.A., Nagy, T., Löki, V., Süveges, K., Takács, A., Bódis, J., Tökölyi, J., 2017d. Graveyards as refuges for Turkish orchids against salep harvesting. Ecol. Evol. 7, 11257–11264. https://doi.org/10.1002/ece3.3562.
Molnár, V.A., Mészáros, A., Csathó, A.I., Balogh, G., Takács, A., Löki, V., Lovas-Kiss, Á., Tökölyi, J., Somlyay, L., Bauer, N., 2018. Distribution and seed production of the rare, dry grassland specialist *Sternbergia colchiciflora* (Amaryllidaceae) in Pannonian cemeteries. Tuexenia 38, 371–384.
Molnár, V.A., Süveges, K., Fekete, R., Archaux, F., Chevalier, R., Takács, A., 2022. Orchids of poplar plantations – a review. Nyárfaültetvények orchideái – irodalmi áttekintés. Kitaibelia 27, 102–117. https://doi.org/10.17542/kit.27.012.
Molnár, V.A., Löki, V., Verbeeck, M., Süveges, K., 2021. Orchids of Azerbaijani cemeteries. Plants 10, 2779. https://doi.org/10.3390/plants10122779.
Murphy, H.T., Lovett-Doust, J., 2004. Context and connectivity in plant metapopulations and landscape mosaics: does the matrix matter? Oikos 105, 3–14. https://doi.org/10.1111/j.0030-1299.2004.12754.x.
Mytum, H., 1989. Public health and private sentiment: the development of cemetery architecture and funerary monuments from the eighteenth century onwards. World Archaeol. 21, 283–297. https://doi.org/10.1080/00438243.1989.9980107.
Naimi, B., Hamm, N.A., Groen, T.A., Skidmore, A.K., Toxopeus, A.G., 2014. Where is positional uncertainty a problem for species distribution modelling? Ecography 37, 191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x.
Newman, B. (2009). Orchids as indicators of ecosystem health in urban bushland fragments. Unpublished doctoral dissertation, Murdoch University, Perth, Australia.
Nordh, H., Evensen, K.H., 2018. Qualities and functions ascribed to urban cemeteries across the capital cities of Scandinavia. Urban For. Urban Green. 33, 80–91. https://doi.org/10.1016/j.ufug.2018.01.026.
Phillippe, L.R., Marcum, P.B., Busemeyer, D.T., Ebinger, J.E., 2010. Vascular flora of Short Pioneer Cemetery Prairie Nature Preserve, Grundy County, Illinois: Composition and change since 1977. Erigenia 5, 5–11.
Phillips, R.D., Reiter, N., Peakall, R., 2020. Orchid conservation: From theory to practice. Ann. Bot. 126, 345–362. https://doi.org/10.1093/aob/mcaa093.
Pielou, E.C., 1966. The measurement of diversity in different types of biological collections. J. Theor. Biol. 13, 131–144. https://doi.org/10.1016/0022-5193(66)90013-0.
Pillon, Y., Chase, M.W., 2007. Taxonomic exaggeration and its effects on orchid conservation. Conserv. Biol. 21, 263–265. https://doi.org/10.1111/j.1523-1739.2006.00573.x.
Plumwood, V., 2007. The cemetery wars: cemeteries, biodiversity and the sacred. Local-Glob.: Identit., Secur., Community 3, 54–71.
R Core Team, 2022. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.R-project.org/.
Rahman, A.H.M.M., Anisuzzaman, M., Haider, S.A., Ahmed, F., Islam, A., Naderuzzaman, A.T.M., 2008. Study of medicinal plants in the graveyards of Rajshahi city. Res. J. Agric. Biol. Sci. 4, 70–74.
Rebancos, C.M., Buot Jr., I.E., 2007. Sacred groves and plant biodiversity conservation. J. Nat. Stud. 6, 31–36.
Relyea, D., 2013. Guidelines to Enhance the Ecological value of cemeteries in Southern Ontario. Doctoral dissertation. University of Guelph, Ontario, Canada.
Ruch, D.G., Torke, B.G., Badger, K.S., Rothrock, P.E., 2014. The vascular flora in three prairie cemeteries in Henry County, Indiana. Proc. Indiana Acad. Sci. 119, 35–51.
Rugg, J., 2000. Defining the place of burial: what makes a cemetery a cemetery? Mortality 5, 259–275. https://doi.org/10.1080/713686011.
Sayer, D., 2010. Who's afraid of the dead? Archaeology, modernity and the death taboo. World Archaeol. 42, 481–491. https://doi.org/10.1080/00438243.2010.498665.
Schmidt, K.H., Steinbach, J., 1983. Low breeding-success of great tits (*Parus major*) in urban parks and cemeteries. J. Für Ornithol. 124, 81–83. https://doi.org/10.1007/BF01650664.
Schödelbauerová, I., Roberts, D.L., Kindlmann, P., 2009. Size of protected areas is the main determinant of species diversity in orchids. Biol. Conserv. 142, 2329–2334. https://doi.org/10.1016/j.biocon.2009.05.015.
Shannon, C.E., 1948. A mathematical theory of communication. Bell Syst. Tech. J. 27, 379–423. https://doi.org/10.1002/j.1538-7305.1948.tb01338.x.
Shefferson, R.P., Kull, T., Tali, K., 2008. Mycorrhizal interactions of orchids colonizing Estonian mine tailings hills. Am. J. Bot. 95, 156–164. https://doi.org/10.3732/ajb.95.2.156.

Sigiel, D.A., Jagodzinski, A.M., 2011. Materials to the vascular flora of the neglected evangelical cemeteries of the western part of the Drawsko Landscape Park (Poland). Botanika – Steciana 15, 57–64.

Simpson, E.H., 1949. Measurement of diversity. Nature 163, 688. https://doi.org/10.1038/163688a0.

Sletvold, N., Dahlgren, J.P., Øien, D.I., Moen, A., Ehrlén, J., 2013. Climate warming alters effects of management on population viability of threatened species: Results from a 30-year experimental study on a rare orchid. Glob. Change Biol. 19, 2729–2738. https://doi.org/10.1111/gcb.12167.

Smith, C.M.A., 2018. Grave concerns: Capturing religious diversity in cemetery planning. Master's thesis, York University, Toronto, Ontario, Canada.

Storm, W., 2014. The Creation of Heaven in the Middle Ages. Marquette University, Milwaukee, WI, USA.

Süveges, K., Löki, V., Lovas-Kiss, Á., Ljubka, T., Fekete, R., Takács, A., Vincze, O., Lukács, B.A., Molnár, V.A., 2019. From European priority species to characteristic apophyte: *Epipactis tallosii* (Orchidaceae). Willdenowia 49, 401–409. https://doi.org/10.3372/wi.49.49310.

Süveges, K., Vincze, O., Löki, V., Lovas-Kiss, Á., Takács, A., Fekete, R., Tüdősné Budai, J., Molnár, V.A., 2022. Native and alien poplar plantations are important habitats for terrestrial orchids. Preslia 94, 429–445. https://doi.org/10.23855/preslia.2022.429.

Swarts, N.D., Dixon, K.W., 2009. Terrestrial orchid conservation in the age of extinction. Ann. Bot. 104, 543–556. https://doi.org/10.1093/aob/mcp025.

Trzaskowska, E., Karczmarz, K., 2013. Spontaneous vascular flora of selected cemeteries in Lublin and the surrounding area. Acta Agrobot. 66, 107–122. https://doi.org/10.5586/aa.2013.028.

Tsiouri, A., 2023. Postwar remnants in the periurban forest of Thessaloniki, Greece: A two paths proposal for tourism and environmental education. Acad. Res. Community Publ. 7, 11–19. https://doi.org/10.21625/archive.v7i2.968.

Uslu, A., Bariş, E., Erdoğan, E., 2009. Ecological concerns over cemeteries. Afr. J. Agric. Res. 4, 1505–1511.

Van Calster, H., Vandenberghe, R., Ruysen, M., Verheyen, K., Hermy, M., Decocq, G., 2008. Unexpectedly high 20th century floristic losses in a rural landscape in northern France. J. Ecol. 96, 927–936. https://doi.org/10.1111/j.1365-2745.2008.01412.x.

Velivasaki, E., 2010. Accommodating Religious Pluralities: The Case of Greece. In: Horváth, I., Székely, T., Tonk, M. (Eds.), *Minority politics within the Europe of regions*. Scientia Kiadó, Cluj-Napoca, Romania, pp. 455–472.

Verschuuren, B., Wild, R., McNeely, J., Oviedo, G. (Eds.), 2010. Sacred Natural Sites: Conserving Nature and Culture. Earthscan, London, UK and Washington, DC, USA.

Vogt-Schilb, H., Pradel, R., Geniez, P., Hugot, L., Delage, A., Richard, F., Schatz, B., 2016. Responses of orchids to habitat change in Corsica over 27 years. Ann. Bot. 118, 115–123. https://doi.org/10.1093/aob/mcw070.

Zuur, A.F., Ieno, E.N., Elphick, C.S., 2010. A protocol for data exploration to avoid common statistical problems. Methods Ecol. Evol. 1, 3–14. https://doi.org/10.1111/j.2041-210X.2009.00001.x.