ORIGINAL RESEARCH

Ecology and Evolution
Open Access

WILEY

Roadsides provide refuge for orchids: characteristic of the surrounding landscape

Réka Fekete[1] 🄳 | Judit Bódis[2] | Bence Fülöp[2,3] | Kristóf Süveges[1] | Renáta Urgyán[1,4] | Tamás Malkócs[1] | Orsolya Vincze[4,5] 🄳 | Luís Silva[6,7] | Attila Molnár V.[1] 🄳

[1]Department of Botany, University of Debrecen, Debrecen, Hungary

[2]Department of Plant Sciences and Biotechnology, Georgikon Campus, Szent István University, Keszthely, Hungary

[3]Balaton-felvidéki National Park Directorate, Csopak, Hungary

[4]Wetland Ecology Research Group, Department of Tisza Research, Centre for Ecological Research-DRI, Debrecen, Hungary

[5]Evolutionary Ecology Group, Hungarian Department of Biology and Ecology, Babeş-Bolyai University, Cluj Napoca, Romania

[6]Faculty of Sciences and Technology, University of Azores, Ponta Delgada, Portugal

[7]InBIO, Research Network in Biodiversity and Evolutionary Biology, CIBIO-Açores, University of the Azores, Ponta Delgada, Portugal

Correspondence
Réka Fekete, Department of Botany, University of Debrecen, Egyetem tér 1, H-4032 Debrecen, Hungary.
Email: feketereka722@gmail.com

Abstract

Seminatural habitats are declining throughout the world; thus, the role of small anthropogenic habitats in the preservation of plants is becoming increasingly appreciated. Here, we surveyed the orchid flora of roadside verges in five Central European countries (Austria, Hungary, Romania, Slovakia, and Slovenia) and tested how the surrounding landscape matrix affects the overall number of species and individuals, and also different functional groups of orchids. We found more than 2,000 individuals of 27 orchid species during our surveys. According to our results, the increasing coverage of agricultural and urban areas negatively affects both the number of orchid species and individuals on roadsides. Our study further suggests that differences in the surrounding habitats affect which species are found on roadsides, since the increasing coverage of grasslands or forested areas around orchid occurrences had a significant positive effect on the number of grassland or forest-dwelling species and individuals, respectively. Most variance in orchid numerosity and diversity was explained by the cover of the suitable habitat types of the respective taxa in the surrounding landscape of the sampling points. This highlights the importance of roadsides acting as refugia for numerous species and valuable plant communities as well as in supporting biodiversity in general.

KEYWORDS
anthropogenic habitats, ecological corridor, landscape matrix, linear landscape elements, Orchidaceae, roadside

1 | INTRODUCTION

Seminatural habitats are dominated by native flora, characterized by a typical diversity and species composition, but they bear human-induced alterations. Despite disturbance, they generally host a large number of threatened plant species and have long been considered as hotspots for biodiversity (Benton et al., 2003; Henle et al., 2008). During the last century, intensification of human activities has led to a dramatic reduction of seminatural habitats, contributing to the severe decline of biodiversity worldwide (Butchart et al., 2010; Hooftman & Bullock, 2012; Malcolm & Markham, 2000). Seminatural habitats are subject to several threats, such as habitat degradation, destruction and fragmentation (Nascimbene et al., 2016; Tikka et al., 2000; Tilman et al., 2001), intensification of agricultural land use, and abandonment of traditional agricultural practices (Bignal & McCracken, 1996). For instance, seminatural grasslands are often converted into arable lands in response to a higher demand for food production (Hodgson et al., 2005) and afforested for timber production (Mason, 2007), or they are frequently lost to urbanization (Feranec et al., 2010). These alterations to natural and seminatural habitats urge the shift of focus of conservation-oriented research toward anthropogenic habitats that have a potential to provide refuge for native flora elements. Several anthropogenic habitats were shown to provide such refuges, including cemeteries, poplar plantations, orchards, and roadsides (Bódis et al., 2018; Djordjević & Tsiftsis, 2020; Fekete et al., 2017; Löki et al., 2015; Süveges et al., 2019).

Road constructions are among the most widespread modifications to natural landscapes, which have intensified in both frequency and structural complexity during the last century (Ascensão et al., 2018; Bennett, 1991; Noss & Cooperrider, 1994). Roads impose numerous negative effects on natural ecosystems, including light and sound pollution, introduction of novel mortality risk factors (e.g., collision with vehicles), imposing barriers to dispersal, inducing alterations to the behavior of animals, and their physical and chemical environment, but they also contribute to the spread of exotic species (Trombulak & Frissell, 2000). Despite these negative effects, the beneficial role of roadsides as linear landscape elements is increasingly appreciated. For instance, roadsides appear to serve as refuges in the landscape and aid the maintenance of plant species richness, and have been considered as important areas due to their function in supporting native vegetation in Brazil (Allem, 1997), Pakistan (Ahmad et al., 2009; Akbar et al., 2003), Saudi Arabia (Batanouny, 1979), Australia (Bennett, 1991; Hussey, 1999; Schabel & Eldridge, 2001), South Africa (Dawson, 1991), and several regions across Europe, including Belgium (Deckers et al., 2005; Godefroid, 1999), Finland (Jantunen et al., 2006), Norway (Hovd & Skogen, 2005), Sweden (Cousins, 2006), the Balkans, the Eastern Mediterranean region (Djordjević & Tsiftsis, 2020; Fekete et al., 2017, 2019), and the United Kingdom (Atherden, Rotherham, & Handley, 2018; Harrington, 1994; Perring, 1969; Way, 1970).

Given that appropriate management practices are adopted, road verges might allow the persistence of valuable grassland communities, as well as the maintenance of rare species, conveying a significant conservation value to these man-made habitats (Auestad et al., 2011; Hovd & Skogen, 2005). In some regions, roadside habitats have even been regarded as "Roadside Nature Reserves" and they receive special management due to their recognized conservation priority (Dawson, 1991; Parr & Way, 1988; Spooner, 2005). In the United Kingdom, for instance, almost half of the native plant species can be found on roadsides (Way, 1970). Moreover, even regularly mowed roadsides can serve as refuges for endangered grassland species, for instance, the highly cut-tolerant *Gentianella campestris* in Finland (Huhta & Rautio, 2007).

Roadsides not only provide refuge to native flora, but were shown to serve as ecological corridors for a wide range of taxa (Gustafsson & Hansson, 1997; Haddad et al., 2003). Nonetheless, at least in the case of plants, the ecological corridor role of roads is most widely demonstrated by the dispersal of alien and invasive species alongside them (Bacaro et al., 2015; Das & Duarah, 2013; Gulezian et al., 2012; Joly et al., 2011; Lin, 2007). Ecological or landscape corridors are strips of suitable habitats connecting isolated habitat patches and are considered to facilitate gene flow and the movement of species between these, thus increasing the number of native species in large-scale communities and reducing the negative effects of fragmentation (Cody et al., 1975; Damschen et al., 2006). Creating ecological corridors recently became a widespread ecological management practice; nonetheless, some studies question their effectiveness in aiding the movement of organisms between otherwise fragmented habitats (Beier & Noss, 1998; Hobbs, 1992; Merriam & Saunders, 1993; Simberloff et al., 1992). A survey by Tikka et al. (2001) suggests that roadsides play a direct role in the dispersal of grassland communities, clearly serving as ecological corridors. Nonetheless, Fritz and Merriam (1993) found no support of the role of fencerows serving as ecological corridors of forest floor herbs. A number of recent studies suggest a rather indirect impact of linear landscape elements on the spread of taxa, by facilitating pollination and seed dispersal between suitable habitats or by promoting plant–animal interactions (Haddad et al., 2003; Tewksbury et al., 2002; Van Rossum & Triest, 2012). According to previous studies, there could be a difference between grassland and woodland plant species in the use of ecological corridors. For instance, grassland species can easily spread to alternative open habitats, such as roadsides due to regular mowing of verges which keeps the vegetation low, but in the case of woodland species, the use of corridors is more difficult (Fritz & Merriam, 1993; Tikka et al., 2001). In the case of roadsides, the dispersal of small seeds can also be facilitated by the air turbulence of cars (Ross, 1986) or by the mud attached to the vehicles, which often contain large number of seeds, especially when the roadside vegetation is well developed (Clifford, 1959). Recent studies highlight the role of vehicles in the spread of alien species (Von Khan et al., 2018han et al., 2018; Nguyen, 2011; der Lippe & Kowarik, 2007).

Although roadsides are often isolated remnants of seminatural habitats, their species richness is largely dependent on the surrounding landscape (Cousins, 2006). For instance, Cousins and

Lindborg (2008) noted that in the most intensively managed landscapes, the species richness of roadsides and midfield islets declines with increasing distance to seminatural grasslands.

In order to investigate the role of roads as refugia in the context of the surrounding landscape, we performed a systematic study of the flora of roadsides, focusing in particular on orchids as model organisms. Orchids rely greatly on pollinators and mycorrhizal fungi (Waterman & Bidartondo, 2008); thus, they are good indicators of overall local biodiversity (Swarts & Dixon, 2009). Moreover, colonization by orchids has long been known in roadsides (Turrill, 1932) as well as in other anthropogenically strongly influenced habitats (Box , 1999; Bzdon, 2009; Deák et al., 2016; Esfeld et al., 2008; Grant & Koch, 2003; Jurkiewicz et al., 2001; Kelcey, 1984; Löki et al., 2015; Lundholm & Richardson, 2010; Molnár V. et al., 2017; Ratcliffe, 1974). For instance, in the Mediterranean region, orchids are frequently present on roadsides (Brandes, 1998a, 1998b; Fekete et al., 2019), *Himantoglossum* (lizard orchids) being one of the most characteristic genera utilizing these anthropogenic habitats (Bódis et al., 2018; Federici & Serpieri, 1868; Fekete et al., 2017; Good, 1936; Klaver, 2011; Zahariev, 2014).

The central aims of the current study were to (a) assess species and individual numbers using roadsides as habitats in Central European countries and (b) examine how the landscape matrix affects the species composition, diversity, and abundance of orchids generally and also different functional groups of orchids in the sampled habitats.

2 | MATERIALS AND METHODS

2.1 | Fieldwork

Field sampling was carried out in five Central European countries (Austria, Hungary, Romania, Slovakia, and Slovenia). Two types of sampling processes were adopted. First, we conducted thematic sampling by driving along asphalt roads and we stopped in every 5 km. Second, we conducted non-thematic sampling, meaning that we stopped at every road section, where orchids were spotted from the car while driving. Details of the sampling localities and sampling periods are given in Table 1. At every sampling point, we recorded geo-coordinates (WGS84 format) and altitude (m) using a Garmin eTrex Legend GPS Device. Where orchids were present, we additionally recorded the list of orchid species and the number of specimens belonging to each of these along a 50-m road section on one side of the road. The width of the surveyed area usually spanned from 0 to 10 m, being delimited by roadway on one side and ditches, walls, or taller vegetation on the other side. In some cases, identification of orchids to the species level was not possible, due to their vegetative phenological state. In the latter case, we counted the number of individuals, but these were only included in the overall count of orchid individuals. Taxa were identified following Delforge (2006), and the nomenclature used in this work follows this source.

TABLE 1 Number of the different sampling points and the date of the surveys carried out in the sampled countries

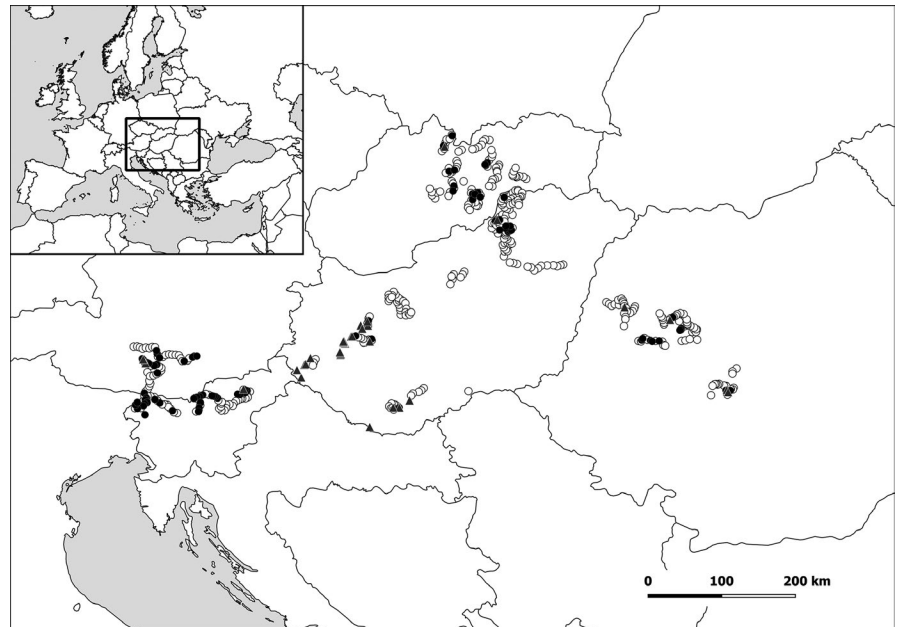| Country	Number of non-thematic sampling points	Number of thematic sampling points	Survey period
Austria	2	50	14–15 July 2018
Hungary	27	156	8 July 2015
			3–6 May 2017
			2–3 May 2018
			11–13 May 2018
Romania	4	92	17–20 June 2017
Slovakia	1	91	27–30 May 2017
Slovenia	1	76	11–13 July 2018

2.2 | Landscape variables

For each sampling point, we calculated land cover variables, based on the surrounding landscape matrix. For this, we used the 2018 CORINE Land Cover (CLC) dataset (available via the Copernicus Land Monitoring Service of the European Union). First, using default settings we have drawn buffer zones with 1 and 10 km radius around all sampling points in Quantum GIS (QGIS) version 3.4 (QGIS Development Team, 2019). Following this, we constructed zonal histograms using the Processing Toolbox of QGIS. Finally, we calculated cover percentages for the buffer zones in R (version 3.4.1, R Core Team, 2017). From the 44 landscape classes present in the original CLC database, 28 were present in the buffer zones of our sampling points. We estimated land cover for each of these categories, but we subsequently performed a categorization of these in order to reduce dimensionality in the analyses. We considered watercourses and water bodies as unsuitable places for orchids. We did not join the different forest types, since broad-leaved forest serves as habitats for some species which would not prefer shady coniferous forests; thus, different species have different forest type needs. We further considered vineyards, fruit trees, berry plantations, and land principally occupied by agriculture with significant areas of natural vegetation as "semi-agricultural areas," because when they are abandoned or extensively used, they could serve as orchid habitats. Details of the categorization are given in Table S1.

2.3 | Statistical analyses

Statistical analyses were carried out in the R statistical environment (version 3.4.1, R Core Team, 2017).

To avoid multicollinearity in the models, we performed VIF selection (Craney & Surles, 2002) using vif function in fmsb package (Nakazawa, 2017) which calculates the VIF values for all of our explanatory variables, then removes the variable with the highest value, and repeats this until all VIF values are below the threshold, which in our case was "2." Following this, the concerned variables were removed from the analyses. After testing the distribution of

FIGURE 1 Distribution of thematic and non-thematic sampling points in the surveyed countries. Gray triangles indicate non-thematic sampling points; black dots indicate thematic sampling points with orchid presence, while white dots indicate the thematic sampling points with orchid absence

TABLE 2 Summary of survey data regarding proportion of thematic sampling points with orchid presence, as well as the overall number of species and number of individuals found at these locations across the five surveyed countries

Country	Ratio of thematic sampling points with orchid presence	Number of species	Number of individuals
Austria	30%	10	940
Hungary	9%	14	343
Romania	12%	10	351
Slovakia	15%	10	288

the data, we built generalized linear mixed models (GLMM) with quasi-Poisson distribution due to significant overdispersion in the independent variables, using the *glmmPQL* function (*MASS* R package, Ripley et al., 2013). In all cases, we started by building full models containing all explanatory variables which were selected by VIF. This was followed by model simplification, when predictors were removed from the model using a stepwise backward procedure based on the largest p values. All predictors with $p < 0.1$ were retained in the minimal model. In all of the models, we used "country" and "sampling type (thematic or non-thematic)" as random factors. Altogether, eight models were built with the following dependent variables: total number of species, total number of individuals, number of grassland species, number of forest species, number of species with broad ecological tolerance, number of individuals of forest, grassland, and broad ecological tolerance species. RMSE (root-mean-square error) values were calculated using *RMSE* function in the *performance* package (Lüdecke et al., 2019), and pseudo R^2 values were calculated using the *r.squaredGLMM* function in the *MuMIn* package (Barton & Barton, 2019). Species were categorized into grassland, forest, and broad ecological tolerance categories using habitat descriptions of

Delforge (2006) (Table S2.). Explanatory variables were Urban areas; Agricultural areas; Semi-agricultural areas; Natural grasslands and pastures; Shrublands; Beaches, dunes, and sand plains; Sparsely vegetated areas; Wetlands; Broad-leaved forests; Mixed forests (composed principally of trees, including shrub and bush understorey, where neither broad-leaved nor coniferous species predominate); and Natural unsuitable places for vegetation within the 1-km-radius circle (the variable Coniferous forests was highly correlated with several land cover types and was thus eliminated from multivariate analyses by VIF). Another eight models were built with the same variables using 10-km-radius circle data (Table S3).

3 | RESULTS

3.1 | General results

Out of the 465 thematic sampling points, we found orchids at 83 locations, with records in all of the five surveyed countries (Figure 1.). The ratio of the sampling points where orchids were present was the highest in Slovenia and the lowest in Hungary (Table 2.). Altogether, we found 2,272 orchid individuals belonging to 27 species (among these, 324 individuals could not be identified at the species level belonging to the genera *Epipactis* and *Platanthera*).

The most abundant species with 801 individuals was *Dactylorhiza fuchsii*, which was present in four of the five countries. It was followed by *Gymnadenia conopsea* with 320 individuals found in three countries. *Neottia ovata* was the only species found in all five countries, at nine localities with 67 individuals (Table S2). The rarest were two locally distributed *Gymnadenia* taxa, *Gymnadenia × suavolens* and *Gymnadenia lithopolitanica*. Among the species, there were 14 grassland specialists, seven forest specialists, and seven species characterized with broad ecological tolerance (Table S2).

Using the non-thematic sampling protocol, at two sampling points in Austria, we found 23 individuals belonging to four species, including the rare and local *G. lithopolitanica*. In Hungary, 272 individuals were found belonging to 13 species at 33 non-thematic sampling points. In Romania, 53 individuals from four species were found at four sampling points. In Slovakia and Slovenia, one non-thematic locality was surveyed in both countries. In Slovakia, nine individuals were found from the species *Orchis mascula*, and in Slovenia, 61 individuals were found from two species (*D. fuchsii* and *Epipactis helleborine*) during non-thematic surveys.

3.2 | Landscape analyses

Multivariate models indicated a significant lower number of orchid species (Figure 2a,b) and individuals in sampling locations where the area of urban and agricultural land covers was higher within a 1 km radius (Table 3.). In the case of the total number of species, the cover of natural grasslands and pastures and broad-leaved forest also had a significant negative effect.

In the 1-km-radius circle, the cover of natural grasslands and pastures had a significant positive effect on the number of grassland species (Figure 3a) and number of grassland individuals. Shrublands also had a positive effect on both variables, but it showed marginal significance in the case of the number of individuals. Both in the case of number of forest orchid species (Figure 3b) and number of individuals belonging to these, the multivariate models indicated a significant positive effect on the land cover occupied by broad-leaved forest.

We found a significant negative effect of the cover of urban and agricultural areas, natural grasslands and pastures, and mixed forest both on the number of species and individuals with broad ecological tolerance.

4 | DISCUSSION

During our extensive field surveys, we found more than 2,000 orchid individuals of 27 different orchid species in roadsides. This alone suggests that roadsides provide an important habitat for orchids in Central Europe, similarly to other regions across Europe (Fekete et al., 2017, 2019). Furthermore, we found a number of rare orchid taxa on roadsides, including *G. × suaveolens* in Austria, *Orchis mascula* in Slovakia, a species that is near threatened according to the Red List of vascular plants of the Carpathian part of Slovakia (Turis et al., 2014). Additionally, we documented *Platanthera chlorantha* in roadsides of Hungary, a species listed as near threatened according to the Red List of the vascular flora of Hungary (Király, 2007). Overall, our surveys indicate that roadsides serve as suitable habitats for endangered taxa (according to IUCN Red List), such as *G. lithopolitanica* (Rankou, 2011). The highest number of orchid individuals present on roadsides belonged to *D. fuchsii*, a species that is characterized by a broad ecological tolerance.

Roadsides surveyed here hosted almost twice as many grassland specialist orchid species as forest specialists (i.e., 13 and 7, respectively), which might potentially be explained by road maintenance practices, namely the regular mowing of roadsides. Due to the latter, vegetation on roadsides is usually less closed, while mowing is known to have positive effects on grassland orchids in other habitat types (Curtis, 1946; Janečková et al., 2006; Sletvold et al., 2010; Smith & Cross, 2016). Forest specialist orchid species were also present on roadsides surveyed, being represented by more than 200 individuals. This suggests that despite being less adapted for regular mowing, they are able to cope and maintain populations in these anthropogenically influenced habitats. Roadsides are narrow grassland fragments and could act as ecotones (representing mainly transitions from grasslands to forest edges). Due to their weak competitive ability, orchids are frequently found in transitional, ecotone habitats, such as mesoxeric scrubland patches and forest edges (Bray & Wilson, 1992; Djordjević et al., 2016; Duchoň, 2012; Rai et al., 2010; Slaviero et al., 2016). Furthermore, they often colonize newly created habitat patches (such as roadsides), where the abundance of dominant plant species and the cover of trees and shrubs are low (Arditti & Ghani, 2000). Based on Grime's theory, orchids are considered as stress tolerators or ruderal species, (Dressler, 1981; Hágsater & Dumont, 1996) competing for resources and space, thus orchids around roadsides might compete for favorable light conditions, that
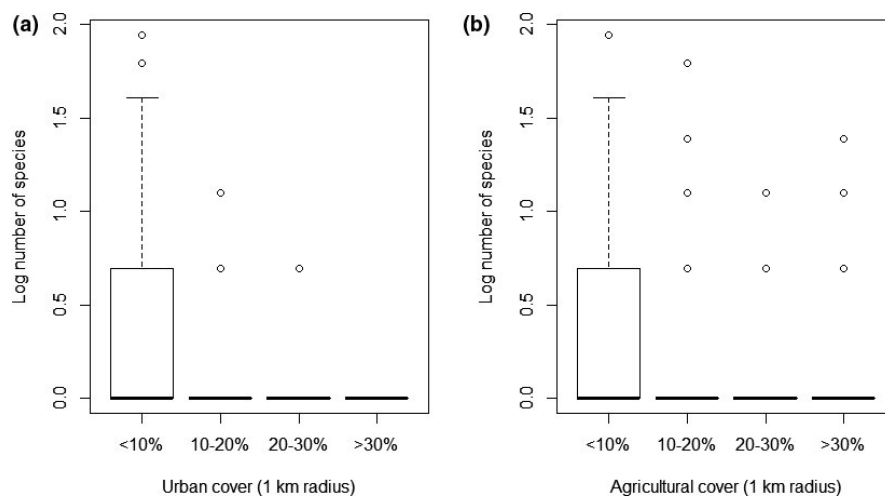
FIGURE 2 (a) Box plots showing the cover of urban areas within 1-km-radius circle and the logarithmized number of species in different coverage categories. (b) Box plots showing the cover of agricultural areas within 1-km-radius circle and the logarithmized number of species in different coverage categories

TABLE 3 The eight minimal models (GLMMPQL) explaining variance in the number of species (left) and number of individuals (right) in overall, in grassland specialist and forest specialist and broad ecological tolerance orchids, respectively, in function of land cover within a 1 km radius

	Total number of orchid species				Total number of orchid individuals			
	β	SE	t	p	β	SE	t	p
Intercept	−1.00	0.33	−3.07	0.002	2.60	1.85	1.41	0.160
Urban areas	−0.80	0.23	−3.45	0.001	−1.58	0.51	−3.09	0.002
Agricultural areas	−0.66	0.15	−4.44	0.001	−0.65	0.26	−2.49	0.013
Natural grasslands and pastures	−0.27	0.10	−2.67	0.008				
Broad-leaved forests	−0.24	0.12	−1.98	0.048				
Shrubland					0.17	0.09	1.99	0.047
Semi-agricultural areas	−0.19	0.11	−1.69	0.091				
DF = 488 RMSE = 2.374, R^2c = 0.602					DF = 490 RMSE = 3.825, R^2c = 0.999			

	Number of grassland-specialist orchid species				Number of grassland-specialist orchid individuals			
	β	SE	t	p	β	SE	t	p
Intercept	−2.55	0.53	−4.81	0.001	−1.27	0.69	−1.85	0.065
Urban areas					−1.56	0.83	−1.89	0.060
Natural grasslands and pastures	0.40	0.15	2.60	0.010	0.73	0.15	4.89	0.001
Shrublands	0.18	0.11	1.66	0.097	0.51	0.12	4.16	0.001
Sparsely vegetated areas	0.14	0.07	1.94	0.053				
Mixed forests	0.42	0.17	2.46	0.014				
DF = 489 RMSE = 7.321, R^2c = 0.999					DF = 490 RMSE = 15.890 R^2c = 0.999			

	Number of forest-specialist orchid species				Number of forest-specialist orchid individuals			
	β	SE	t	p	β	SE	t	p
Intercept	−1.05	2.69	−0.39	0.696	−1.01	0.45	−2.25	0.025
Urban areas	−0.80	0.47	−1.71	0.088				
Broad-leaved forests	0.70	0.20	3.48	0.001	0.84	0.20	4.20	0.001
DF = 491 RMSE = 6.264, R^2c = 0.418					DF = 492, RMSE = 3.437, R^2c = 0.987			

	Number of orchid species with broad ecological tolerance				Number of orchid individuals with broad ecological tolerance			
	β	SE	t	p	β	SE	t	p
Intercept	−2.03	0.38	−5.31	0.001	12.00	12.39	0.97	0.333
Urban areas	−0.94	0.30	−3.15	0.002	−2.18	0.90	−2.44	0.015
Agricultural areas	−0.83	0.20	−4.20	0.001	−0.70	0.30	−2.31	0.021
Natural grasslands and pastures	−0.55	0.14	−3.99	0.001	−0.76	0.18	−4.34	0.001
Broad-leaved forests	−0.58	0.16	−3.73	0.001				
Mixed forests	−0.24	0.11	−2.17	0.031	−0.68	0.25	−2.77	0.006
DF = 488 RMSE = 3.027, R^2c = 0.081					DF = 489 RMSE = 19.601, R^2c = 0.999			

are available at roadside verges, due to regular mowing (Djordjević & Tsiftsis, 2020).

Our multivariate models indicated a significant negative impact of agricultural and urban land covers on orchid diversity and abundance in general. Greater proportion of land cover occupied by urban and agricultural areas in the landscape matrix resulted in a lower number of orchid species and individuals present on roadsides. These land cover variables also had significant negative

effects on the number of species with broad ecological tolerance and the number of individuals belonging to these species. Earlier study has already indicated that the surrounding landscape matrix has a high impact on species composition of habitats along roads (Tikka et al., 2000). Moreover, a decline in species richness on linear landscape fragments with increasing distance from seminatural habitats was also reported (Cousins & Lindborg, 2008). A study discussing drainage ditches showed that the proximity of natural grasslands

(a)

(b)
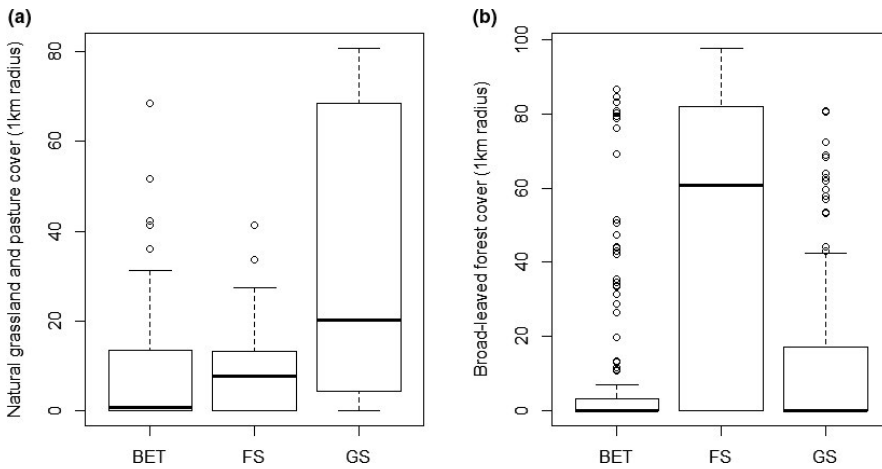
FIGURE 3 (a) Coverage of natural grassland and pasture within 1 km radius in the three orchid groups: species with broad ecological tolerance (BET), forest species (FS), and grassland species (GS). (b) Coverage of broad-leaved forest within 1 km radius in the three groups: species with broad ecological tolerance (BET), forest species (FS), and grassland species (GS)

increased the value of grassland vegetation of the ditches subsequently filled for restoration purposes, suggesting that their vegetation is highly dependent on the landscape matrix (Valkó et al., 2017).

We found that grassland specialists are mostly present on verges, where there are suitable grassland habitats adjacent to the roadside, while forest specialist is more common on roadsides where there are forests in the surrounding landscape. It is important to note that these linear landscape elements are often highly influenced by agricultural activities (e.g., use of fertilizers and herbicides) on adjacent fields (van Dorp, 1996); thus, species of nutrient-poor ecosystems (such as orchids) are particularly unlikely to migrate along these elements (van Dorp et al., 1997; Thiele et al., 2018). When the landscape matrix environment is unsuitable for the dispersal of plants along ecological corridors, or dispersal is ineffective due to a high percentage of low-quality patches, it is unclear whether they could truly function as a corridor. Under such circumstances, roadside patches might rather serve as refugia (van Dorp, 1996; van Dorp et al., 1997). Although according to Forman (1991) plants may in theory migrate along ecological corridors, there has been little empirical support for this; thus, it is more likely that the dispersal of native and rare plants occurring along the linear landscape elements is saltatory. However, the spread of less sensitive, successful alien and invasive species along roads is a well-known phenomenon (Benedetti & Morelli, 2017; Dar et al., 2018; Vakhlamova et al., 2016). This is an especially likely scenario in the case of orchids since their microscopic seeds are effectively dispersed by the wind, even over long distances (Arditti & Ghani, 2000), thus facilitating the effective colonization of new habitat patches. This is in correspondence with another study, suggesting that corridor use is common mostly in case of plant species that lack the ability of long-distance dispersal (Thiele et al., 2018). Nonetheless, the conservation importance of roadsides is not to be underrated due to these facts, since these corridors most likely still function as linear reserves for plants (Forman, 1991). Consequently, the conservation value of these narrow fragments of seminatural habitats is becoming increasingly appreciated worldwide (Bernes et al., 2017; Hopper, 1990; Melman & Verkaar, 1991; Niu et al., 2019; Ryttäri & Kettunen, 1997; Saunders & Hobbs, 1991), and in some countries, they have been identified as Sites of Special Scientific Interest (Parr & Way, 1988).

Overall, it is becoming clear that plants are able to disperse to roadsides from the surrounding landscape, but the possibility exists that colonizations might occur the other way around as well, which could facilitate the natural restoration of degraded grasslands adjacent to roads. Moreover, roadsides with properly managed native vegetation could contribute to pollinator conservation, which is particularly important today, as we are facing a global pollination crisis (Hopwood, 2008; Hopwood et al., 2015; Wojcik & Buchmann, 2012). Many orchids are specialist species; therefore, their conservation is important because their disappearance leads to functional homogenization in ecosystems, promoting biodiversity loss (Clavel et al., 2011). Thus, orchids might serve as general indicators of the ecological state of roadside vegetation. Moreover, considering tendencies of decline in seminatural habitats worldwide, it is possible that roadsides will serve as important refugia that could aid the maintenance of floristic diversity.

5 | IMPLICATIONS FOR MANAGEMENT

Here, we emphasize that floristic surveys of roadsides and adjacent areas are key for planning appropriate road management. We believe that management planning should be conducted in accordance with local and regional conservation efforts, because roadside vegetation and its importance changes along the roads, depending on the habitats they pass through. Appropriate planning, building, and management of roads should focus on creating and maintaining roadsides in states that are suitable for natural vegetation. Generally speaking, during planning, it is desirable to avoid creating steep or concrete retaining walls; gentle slopes should be established instead, in order to form a gradual transition to the natural landform. Terracing with rock outcrops can support this by facilitating the establishment of vegetation and by creating microclimatic niches, while they stabilize the structure of road cuttings (Iuell et al., 2003). Whenever possible and when more time is available for the stabilization of verges, during road building or broadening, the use of subsoil—instead of topsoil—would be favorable for the reduction of soil fertility, since high fertility

negatively affects the floristic composition of natural grasslands (Gough & Marrs, 1990). Local origin of the soil used during construction is also very important, as soils from a different source can contain seeds of alien species (Greenberg et al., 1997). To facilitate floristic and pollinator diversity after construction, it is also favorable to revegetate roadsides using specific seed mixtures appropriate for adjacent vegetation. Pollinators are key factors in the maintenance of native vegetation on roadsides; thus, it is very important to reduce their collision with cars, by keeping the meadows a few meters away from the road's edge and keeping long continuous flower meadows, reducing their will to cross the road for flowering patches (Hopwood et al., 2010; Keilsohn et al., 2018). As a part of roadside management, regular mowing is a cost-efficient element of their maintenance, and it is obligatory in most of the countries for safety reasons. According to a previous study from the Mediterranean, the regularly mowed 0–2-m part of the roadside is the most suitable for orchid individuals (Fekete et al., 2019). However, there could be a difference in regularity of roadside mowing due to climatic differences between the Mediterranean and the European roadside verges. In the Mediterranean region, the growth of the vegetation could be slower, while the best practice for creating and maintaining species-rich meadows along European roads should be mowing twice per year (this being better compared to once a year), and the hay should be removed after each cutting (Jakobsson et al., 2018). The use of herbicides and paving of roadsides is strongly unadvised. We further urge local authorities to conduct appropriate field surveys and impact assessments before broadening roads.

ACKNOWLEDGMENTS

CONFLICT OF INTEREST

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

AUTHOR CONTRIBUTIONS

Réka Fekete: Conceptualization (equal); data curation (equal); formal analysis (equal); writing – original draft (lead). **Judit Bódis:** Investigation (equal); writing – review and editing (supporting). **Bence Fülöp:** Investigation (equal). **Kristóf Süveges:** Investigation (equal). **Renáta Urgyán:** Investigation (equal). **Tamás Malkócs:** Formal analysis (equal); writing – review & editing (supporting). **Orsolya Vincze:** Formal analysis (lead); methodology (equal); writing – review & editing (equal). **Luís Silva:** Conceptualization (equal); formal analysis (lead). **Attila Molnár V.:** Conceptualization (equal); supervision (equal).

DATA AVAILABILITY STATEMENT

All sample data used in the analyses are available from Dryad at https://doi.org/10.5061/dryad.tdz08kpxv.

ORCID

Réka Fekete https://orcid.org/0000-0002-9255-0012
Orsolya Vincze https://orcid.org/0000-0001-5789-2124
Attila Molnár V. https://orcid.org/0000-0001-7096-9579

REFERENCES

Ahmad, S. S., Fazal, S., Valeem, E. E., Khan, Z. I., Sarwar, G., & Iqbal, Z. (2009). Evaluation of ecological aspects of roadside vegetation around Havalian city using multivariate techniques. *Pakistan Journal of Botany*, *411*, 53–60.

Akbar, F., Ahmad, Z., Shad, M., & Ansari, T. M. (2003). An ecological study of roadside vegetation and soils in Sahiwal district. *Online Journal of Biological Sciences*, *37*, 627–634.

Allem, A. (1997). Roadside habitats: A missing link in the conservation agenda. *The Environmentalist*, *171*, 7–10.

Arditti, J., & Ghani, A. K. A. (2000). Numerical and physical properties of orchid seeds and their biological implications. *New Phytologist*, *145*, 367–421.

Ascensão, F., Fahrig, L., Clevenger, A. P., Corlett, R. T., Jaeger, J. A., Laurance, W. F., & Pereir, H. M. (2018). Environmental challenges for the Belt and Road Initiative. *Nature Sustainability*, *1*, 206–209. https://doi.org/10.1038/s41893-018-0059-3

Atherden, M., Rotherham, I. D., & Handley, C. (2018). Roadside assistance: Management and conservation of North Yorkshire's wayside flowers. In *Back from the Edge: The Fall & Rise of Yorkshire's Wildlife* (p. 73–82). Sheffield: Wildtrack Publishing.

Auestad, I., Rydgren, K., & Austad, I. (2011). Road verges: Potential refuges for declining grassland species despite remnant vegetation dynamics. *Annales Botanici Fennici*, *48*(4), 289–303. https://doi.org/10.5735/085.048.0401

Bacaro, G., Maccherini, S., Chiarucci, A., Jentsch, A., Rocchini, D., Torri, D., Gioria, M., Tordoni, E., Martellos, S., Altobelli, A., Otto, R., Escudero, C. G., Fernández-Lugo, S., Fernández-Palacios, J. M., & Arévalo, J. R. (2015). Distributional patterns of endemic, native and alien species along a roadside elevation gradient in Tenerife, Canary Islands. *Community Ecology*, *16*(2), 223–234. https://doi.org/10.1556/168.2015.16.2.10

Barton, K. (2019). *Package 'MuMIn'. Model selection andmodel averaging based on information criteria. R package version 1.7.11*. R package version, 16. http://cran.r-project.org/web/packages/MuMIn/MuMIn.pdf

Batanouny, K. H. (1979). Vegetation along the Jeddah-Mecca road: Pattern and process as affected by human impact. *Journal of Arid Environments*, *2*(1), 21–30. https://doi.org/10.1016/S0140-1963(18)31701-4

Beier, P., & Noss, R. F. (1998). Do habitat corridors provide connectivity? *Conservation Biology*, *12*(6), 1241–1252. https://doi.org/10.1111/j.1523-1739.1998.98036.x

Benedetti, Y., & Morelli, F. (2017). Spatial mismatch analysis among hotspots of alien plant species, road and railway networks in Germany

and Austria. *PLoS One*, *12*(8), e0183691. https://doi.org/10.1371/journal.pone.0183691

Bennett, A. F. (1991). Roads, roadsides and wildlife a conservation: A review. In D. A. Saunders, & R. J. Hobbs (Eds.), *Nature conservation 2: The role of corridors* (pp. 99–118). Minnesota:Univ of Minnesota Pr.

Benton, T. G., Vickery, J. A., & Wilson, J. D. (2003). Farmland biodiversity: Is habitat heterogeneity the key? *Trends in Ecology and Evolution*, *18*(4), 182–188. https://doi.org/10.1016/S0169-5347(03)00011-9

Bernes, C., Bullock, J. M., Jakobsson, S., Verheyen, K., & Lindborg, R. (2017). How does roadside vegetation management affect the diversity of vascular plants and invertebrates? A systematic review protocol. *Environmental Evidence*, *6*(1), 16. https://doi.org/10.1186/s13750-017-0094-y

Bignal, E. M., & McCracken, D. I. (1996). Low-intensity farming systems in the conservation of the countryside. *Journal of Applied Ecology*, *33*(3), 413–424. https://doi.org/10.2307/2404973

Bódis, J., Biró, É., Nagy, T., Takács, A., Molnár, V. A., & Lukács, B. A. (2018). Habitat preferences of the rare lizard-orchid *Himantoglossum adriaticum* H. Baumann = Habitatpräferenzen der seltenen Adria-Riemenzunge *Himantoglossum adriaticum* H. *Baumann. Tuexenia*, *38*, 329–345.

Box, J. (1999). Nature conservation and post-industrial landscapes. *Industrial Archaeology Review*, *21*(2), 137–146. https://doi.org/10.1179/iar.1999.21.2.137

Brandes, D. (1998a). Vegetation der Straßenränder Korfus. – Vegetationsökologie von Habitatinseln und linearen Strukturen. *Braunschweiger Geobotanische Arbeiten*, *5*, 247–262.

Brandes, D. (1998b). Flora und Vegetation der Straßenränder von Mallorca. – Vegetationsökologie von Habitatinseln und linearen Strukturen. *Braunschweiger Geobotanische Arbeiten*, *5*, 275–293.

Bray, T. E., & Wilson, B. L. (1992). Status of *Platanthera praeclara* Sheviak and Bowles (western prairie fringed orchid) in the Platte River Valley in Nebraska from Hamilton to Garden counties. *Transactions of the Nebraskan Academy of Sciences*, *19*, 57–62.

Butchart, S. H. M., Walpole, M., Collen, B., van Strien, A., Scharlemann, J. P. W., Almond, R. E. A., Baillie, J. E. M., Bomhard, B., Brown, C., Bruno, J., Carpenter, K. E., Carr, G. M., Chanson, J., Chenery, A. M., Csirke, J., Davidson, N. C., Dentener, F., Foster, M., Galli, A., … Watson, R. (2010). Global biodiversity: Indicators of recent declines. *Science*, *328*(5982), 1164–1168. https://doi.org/10.1126/science.1187512

Bzdon, G. (2009). Floristic diversity of gravel-pits of the Siedlce Plateau-an analysis of the flora. *Biologia*, *64*(1), 35–66. https://doi.org/10.2478/v10067-010-0004-y

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: Toward a global functional homogenization? *Frontiers in Ecology and Environment*, *9*(4), 222–228. https://doi.org/10.1890/080216

Clifford, H. T. (1959). Seed dispersal by motor vehicles. *Journal of Ecology*, *47*(2), 311–315. https://doi.org/10.2307/2257368

Cody, M. L., MacArthur, R. H., & Diamond, J. M. (1975). *Ecology and evolution of communities*. Harvard University Press. https://doi.org/10.1038/260204c0

Cousins, S. A. (2006). Plant species richness in midfield islets and road verges–the effect of landscape fragmentation. *Biological Conservation*, *127*(4), 500–509. https://doi.org/10.1016/j.biocon.2005.09.009

Cousins, S. A., & Lindborg, R. (2008). Remnant grassland habitats as source communities for plant diversification in agricultural landscapes. *Biological Conservation*, *141*(1), 233–240. https://doi.org/10.1016/j.biocon.2007.09.016

Craney, T. A., & Surles, J. G. (2002). Model-dependent variance inflation factor cutoff values. *Quality Engineering*, *14*(3), 391–403. https://doi.org/10.1081/QEN-120001878

Curtis, J. T. (1946). Use of mowing in management of white ladyslipper. *Journal of Wildlife Management*, *10*(4), 303–308. https://doi.org/10.2307/3796237

Damschen, E. I., Haddad, N. M., Orrock, J. L., Tewksbury, J. J., & Levey, D. J. (2006). Corridors increase plant species richness at large scales. *Science*, *313*(5791), 1284–1286. https://doi.org/10.1126/science.1130098

Dar, P. A., Reshi, Z. A., & Shah, A. B. (2018). Altitudinal distribution of native and alien plant species along roadsides in Kashmir Himalaya, India. *Tropical Ecology*, *59*, 45–55.

Das, K., & Duarah, P. (2013). Invasive alien plant species in the roadside areas of Jorhat, Assam: Their harmful effects and beneficial uses. *International Journal of Engineering Research and Applications*, *35*, 353–358.

Dawson, B. L. (1991). South African road reserves: Valuable conservation areas. In D. A. Saunders, & R. J. Hobbs (Eds.), *Nature conservation 2: The role of corridors* (pp. 119–130). Surrey Beatty.

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. *Biodiversity and Conservation*, *25*, 2473–2490. https://doi.org/10.1007/s10531-016-1081-2

Deckers, B., Becker, P. D., Honnay, O., Hermy, M., & Muys, B. (2005). Sunken roads as habitats for forest plant species in a dynamic agricultural landscape: Effects of age and isolation. *Journal of Biogeography*, *32*(1), 99–109. https://doi.org/10.1111/j.1365-2699.2004.01101.x

Delforge, P. (2006). *Orchids of Europe, North Africa and the Middle East*. AandC Black Publishers Ltd.

Djordjević, V., & Tsiftsis, S.(2020). The role of ecological factors in distribution and abundance of terrestrial orchids. In J.-M. Merillon, & H. Kodja (Eds.), *Orchids phytochemistry, biology and horticulture. Fundamentals and applications* (pp. 1–71). Springer International Publishing. https://doi.org/10.1007/978-3-030-11257-8_4-1

Djordjević, V., Tsiftsis, S., Lakušić, D., Jovanović, S., & Stevanović, V. (2016). Factors affecting the distribution and abundance of orchids in grasslands and herbaceous wetlands. *Systematics and Biodiversity*, *14*(4), 355–370. https://doi.org/10.1080/14772000.2016.1151468

Dressler, R. L. (1981). *The orchids: Natural history and classification*. Harvard University Press.

Duchoň, M. (2012). Nové lokality druhu *Himantoglossum adriaticum* (Orchidaceae) v horskej skupine Drieňova v južnej časti Strážovských vrchov. *Bulletin Slovenskej Botanickej Spoločnosti*, *34*(2), 151–157.

Esfeld, K., Hensen, I., Wesche, K., Jakob, S. S., Tischew, S., & Blattner, F. R. (2008). Molecular data indicate multiple independent colonizations of former lignite mining areas in Eastern Germany by *Epipactis palustris* (Orchidaceae). *Biodiversity and Conservation*, *17*(10), 24–41. https://doi.org/10.1007/s10531-008-9391-7

Federici, A., & Serpieri, A. (1868). Saggio di una Flora dell'agro urbinate ed epoca della fioritura di molte piante. *Bullettino meteorologico di Urbino*, *1*, (5), 32–38.

Fekete, R., Löki, V., Urgyán, R., Süveges, K., Lovas-Kiss, Á., Vincze, O., & Molnár V., A. (2019). Roadsides and cemeteries: Comparative analysis of anthropogenic orchid habitats in the Eastern Mediterranean. *Ecology and Evolution*, *9*(11), 6655–6664. https://doi.org/10.1002/ece3.5245

Fekete, R., Nagy, T., Bódis, J., Biró, É., Löki, V., Süveges, K., Takács, A., Tökölyi, J., & Molnár V., A. (2017). Roadsides as habitats for endangered lizard-orchids (*Himantoglossum* spp.): Ecological traps or refuges? *Science of the Total Environment*, *607*, 1001–1008. https://doi.org/10.1016/j.scitotenv.2017.07.037

Feranec, J., Jaffrain, G., Soukup, T., & Hazeu, G. (2010). Determining changes and flows in European landscapes 1990–2000 using CORINE land cover data. *Applied Geography*, *30*, 19–35. https://doi.org/10.1016/j.apgeog.2009.07.003

Forman, R. T. T. (1991). Landscape corridors: From theoretical foundations top public policy. In D. A. Saunders, & R. J. Hobbs (Eds.), *The role of corridors, Surrey Beatty, Chipping Norton* (pp. 71–84). Land mosaics.

Fritz, R., & Merriam, G. (1993). Fencerow habitats for plants moving between farmland forests. *Biological Conservation*, 64(2), 141–148. https://doi.org/10.1016/0006-3207(93)90650-P

Godefroid, S. (1999). Study of the roadside vegetation in the Walloon region (South Belgium) and in particular in the Upper Ardennes: Phytosociology, ecology, pedology. *Acta Botanica Gallica*, 146(3), 291–292. https://doi.org/10.1080/12538078.1999.10515399

Good, R. (1936). On the Distribution of the Lizard Orchid (*Himantoglossum hircinum* Koch). *New Phytologist*, 35, 142–170.

Gough, M. W., & Marrs, R. H. (1990). A comparison of soil fertility between semi-natural and agricultural plant communities: Implications for the creations of species-rich grassland on abandoned agricultural land. *Biological Conservation*, 51(2), 83–96. https://doi.org/10.1016/0006-3207(90)90104-W

Grant, C. D., & Koch, J. (2003). Orchid species succession in rehabilitated bauxite mines in Western Australia. *Australian Journal of Botany*, 51(4), 453–457. https://doi.org/10.1071/BT02127

Greenberg, C. H., Crownover, S. H., & Gordon, D. R. (1997). Roadside soils: A corridor for invasion of xeric shrub by nonindigenous plants. *Natural Areas Journal*, 17(2), 99–109.

Gulezian, P. Z., Ison, J. L., & Granberg, K. J. (2012). Establishment of an invasive plant species (*Conium maculatum*) in contaminated roadside soil in Cook County, Illinois. *American Midland Naturalist*, 168(2), 375–395. https://doi.org/10.1674/0003-0031-168.2.375

Gustafsson, L., & Hansson, L. (1997). Corridors as a conservation tool. *Ecological Bulletins*, 46, 182–190.

Haddad, N. M., Bowne, D. R., Cunningham, A., Danielson, B. J., Levey, D. J., Sargent, S., & Spira, T. (2003). Corridor use by diverse taxa. *Ecology*, 843, 609–615. https://doi.org/10.1890/0012-9658(2003)084%5B0609:CUBDT%5D2.0.CO;2

Hágsater, E., & Dumont, V. (Eds.) (1996). *Orchids: Status, survey and conservation action plan*. IUCN.

Harrington, J. A. (1994). Roadside landscapes prairie species take hold in midwest rights-of-way. *Ecological Restoration*, 12, 8–15. https://doi.org/10.3368/er.12.1.8

Henle, K., Alard, D., Clitherow, J., Cobb, P., Firbank, L., Kull, T., McCracken, D., Moritz, R. F. A., Niemelä, J., Rebane, M., Wascher, D., Watt, A., & Young, J. (2008). Identifying and managing the conflicts between agriculture and biodiversity conservation in Europe–A review. *Agriculture Ecosystems and Environment*, 124(1-2), 60–71. https://doi.org/10.1016/j.agee.2007.09.005

Hobbs, R. J. (1992). The role of corridors in conservation: Solution or bandwagon? *Trends in Ecology and Evolution*, 7(11), 389–392. https://doi.org/10.1016/0169-5347(92)90010-9

Hodgson, J. G., Grime, J. P., Wilson, P. J., Thompson, K., & Band, S. R. (2005). The impacts of agricultural change (1963–2003) on the grassland flora of Central England: Processes and prospects. *Basic and Applied Ecology*, 6(2), 107–118. https://doi.org/10.1016/j.baae.2005.01.009

Hooftman, D. A. P., & Bullock, J. M. (2012). Mapping to inform conservation: A case study of changes in semi-natural habitats and their connectivity over 70 years. *Biological Conservation*, 145(1), 30–38. https://doi.org/10.1016/j.biocon.2011.09.015

Hopper, S. D. (1990). *Western Australia's endangered flora and other plants under consideration for declaration*. Dept. of Conservation and Land Management, WA Wildlife Research Centre.

Hopwood, J. L. (2008). The contribution of roadside grassland restorations to native bee conservation. *Biological Conservation*, 141(10), 2632–2640. https://doi.org/10.1016/j.biocon.2008.07.026

Hopwood, J., Black, S., & Fleury, S. (2015). *Roadside best management practices that benefit pollinators: Handbook for supporting pollinators through roadside maintenance and landscape design* (No. FHWA-HEP-16-059). U.S. Department of Transportation, Federal Highway Administration.

Hopwood, J., Winkler, L., Deal, B., & Chivvis, M. (2010). *Use of roadside prairie plantings by native bees*. Living Roadway Trust Fund [online].

Retrieved from http://www.iowalivingroadway.com/ResearchProjects/90-00-LRTF-011.pdf

Hovd, H., & Skogen, A. (2005). Plant species in arable field margins and road verges of central Norway. *Agriculture Ecosystems and Environment*, 110(3-4), 257–265. https://doi.org/10.1016/j.agee.2005.04.013

Huhta, A. P., & Rautio, P. (2007). A case with blue gentian blues: Roadside-cutters creating neo grasslands as refugia for endangered *Gentianella campestris*. *Nordic Journal of Botany*, 25(5–6), 372–379. https://doi.org/10.1111/j.0107-055X.2008.00131.x

Hussey, B. M. J. (1999). The flora roads survey – Volunteer recording of roadside vegetation in Western Australia. In D. A. Saunders (Ed.), *Nature conservation 4: The role of networks* (pp. 41–48). Surrey Beatty and Sons Propriety.

Iuell, B., Bekker, H., Cuperus, R., Dufek, J., Fry, G., Hicks, C., Hlaváč, V., Keller, V., Rosell, C., Sangwine, T., Tørsløv, N., & Wandall, B. M. (2003). Earthworks: cuttings and embankments. *Wildlife and traffic: A European handbook for identifying conflicts and designing solutions*. (9–11). Luxembourg: Office for Official Publications of the European Communities.

Jakobsson, S., Bernes, C., Bullock, J. M., Verheyen, K., & Lindborg, R. (2018). How does roadside vegetation management affect the diversity of vascular plants and invertebrates? A systematic review. *Environmental Evidence*, 7(). 1–14. https://doi.org/10.1186/s13750-018-0129-z

Janečková, P., Wotavová, K., Schödelbauerová, I., Jersáková, J., & Kindlmann, P. (2006). Relative effects of management and environmental conditions on performance and survival of populations of a terrestrial orchid, *Dactylorhiza majalis*. *Biological Conservation*, 129(1), 40–49. https://doi.org/10.1016/j.biocon.2005.09.045

Jantunen, J., Saarinen, K., Valtonen, A., & Saarnio, S. (2006). Grassland vegetation along roads differing in size and traffic density. *Annales Botanici Fennici*, 43, 107–117.

Joly, M., Bertrand, P., Gbangou, R. Y., White, M. C., Dubé, J., & Lavoie, C. (2011). Paving the way for invasive species: Road type and the spread of common ragweed (*Ambrosia artemisiifolia*). *Environmental Management*, 48(3), 514–522. https://doi.org/10.1007/s00267-011-9711-7

Jurkiewicz, A., Turnau, K., Mesjasz-Przybyłowicz, J., Przybyłowicz, W., & Godzik, B. (2001). Heavy metal localisation in mycorrhizas of *Epipactis atrorubens* (Hoffm.) Besser (Orchidaceae) from zinc mine tailings. *Protoplasma*, 218(3–4), 117–124.

Keilsohn, W., Narango, D. L., & Tallamy, D. W. (2018). Roadside habitat impacts insect traffic mortality. *Journal of Insect Conservation*, 22(2), 183–188. https://doi.org/10.1007/s10841-018-0051-2

Kelcey, J. G. (1984). Industrial development and the conservation of vascular plants, with special reference to Britain. *Environmental Conservation*, 11(3), 235–245. https://doi.org/10.1017/S0376892900014259

Khan, I., Navie, S., George, D., O'Donnell, C., & Adkins, S. W. (2018). Alien and native plant seed dispersal by vehicles. *Austral Ecology*, 43, 76–88. https://doi.org/10.1111/aec.12545

Király, G. (2007). *Red list of the vascular flora of Hungary*. Private Edition.

Klaver, J. M. I. (2011). *Himantoglossum adriaticum* H. Baumann in Central-East Italy (Pesaro-Urbino, Marche) and FFH-Directive 92/43/EEC. *Journal of European Orchids*, 43(3), 590–602.

Lin, S. (2007). *The distribution and role of an invasive plant species*, Lantana camara, *in disturbed roadside habitats in Moorea, French Polynesia*. [online]. Retrieved from http://www.escholarship.org

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

Lüdecke, D., Makowski, D., & Waggoner, P. (2019). *Performance: Assessment of regression models performance*. R package version 0.4, 2. https://CRAN.R-project.org/package=performance

Lundholm, J. T., & Richardson, P. J. (2010). Habitat analogues for reconciliation ecology in urban and industrial environments. *Journal of Applied Ecology*, 47(5), 966–975.

Malcolm, J. R., & Markham, A. (2000). *Global warming and terrestrial biodiversity decline*. WWF.

Mason, W. L. (2007). Changes in the management of British forests between 1945 and 2000 and possible future trends. *Ibis*, 149, 41–52. https://doi.org/10.1111/j.1474-919X.2007.00696.x

Melman, P. J. M., & Verkaar, H. J. (1991). Layout and management of herbaceous vegetation in road verges. In H. D. van Bohemen D. A. G. Buizer & A Littel (Eds.). *Nature engineering and civil engineering works* (pp. 62–78). Wageningen: Centre for Agricultural Publishing and Documentation (Pudoc).

Merriam, G., & Saunders, D. A. (1993). Corridors in restoration of fragmented landscapes. In D. A. Saunders, R. J. Hobbs, & P. R. Ehrlich (Eds.), *Nature conservation 3: Reconstruction of fragmented ecosystems* (pp. 71–87). Surrey Beatty and Sons.

Molnár, V. A., Nagy, T., Löki, V., Süveges, K., Takács, A., Bódis, J., & Tökölyi, J. (2017). Graveyards as refuges for Turkish orchids against salep harvesting. *Ecology and Evolution*, 7, 11257–11264. https://doi.org/10.1002/ece3.3562

Nakazawa, M. (2017). *fmsb: Functions for medical statistics book with some demographic data, 2014*. R package. https://CRAN.R-project.org/package=fmsb.R

Nascimbene, J., Zottini, M., Ivan, D., Casagrande, V., & Marini, L. (2016). Do vineyards in contrasting landscapes contribute to conserve plant species of dry calcareous grasslands?. *Science of the Total Environment*, 545, 244–249. https://doi.org/10.1016/j.scitotenv.2015.12.051

Nguyen, T. L. T. (2011). *The invasive potential of parthenium weed (Parthenium hysterophorus L.) in Australia*. PhD Thesis, University of Queensland, Brisbane.

Niu, L., Ye, H., Pang, L., & Fan, J. (2019). Ecological environment restoration of roadside vegetation in expressway of Alpine regions. *Ekoloji*, 28, 2629–2641.

Noss, R. F., & Cooperrider, A. (1994). *Saving nature's legacy: Protecting and restoring biodiversity*. Island Press.

Parr, T. W., & Way, J. M. (1988). Management of roadside vegetation: The long-term effects of cutting. *Journal of Applied Ecology*, 25, 1073–1087. https://doi.org/10.2307/2403767

Perring, F. H. (1969). The botanical importance of roadsides. In J. M. Way (Ed.), *Road verges: Their function and management* (pp. 8–14). Monks Wood Experimental Station.

QGIS Development Team (2019). *QGIS Geographic Information System. Open Source Geospatial Foundation Project*. QGIS Development Team. Retrieved from http://qgis.osgeo.org

R Core Team (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from https://www.R-project.org/

Rai, I. D., Adhikari, B. S., & Rawat, G. S. (2010). A unique patch of timberline ecotone with three species of Lady's slipper orchids in Garhwal Himalaya. *India. Journal of Threatened Taxa*, 2(3), 766–769. https://doi.org/10.11609/JoTT.o2121.766-9

Rankou, H. (2011). *Gymnadenia lithopolitanica. The IUCN Red List of Threatened Species* 2011:e.T175943A7150321. Retrieved from https://dx.doi.org/10.2305/IUCN.UK.2011-2.RLTS.T175943A7150321.en

Ratcliffe, D. A. (1974). Ecological effects of mineral exploitation in the United Kingdom and their significance to nature conservation. In *Proceedings of the Royal Society of London A: Mathematical, Physical and Engineering Sciences* (Vol. 339, No. 1618, pp. 355–372). The Royal Society.

Ripley, B., Venables, B., Bates, D. M., Hornik, K., Gebhardt, A., Firth, D., & Ripley, M. B. (2013). *Package 'mass'*. Cran R, 538. CRAN:http://cran.rproject.org/web/packages/MASS/MASS.pdf

Ross, S. M. (1986). Vegetation change on highway verges in southeast Scotland. *Journal of Biogeography*, 13(2), 109–117. https://doi.org/10.2307/2844986

Ryttäri, T., & Kettunen, T. (1997). *Uhanalaiset kasvimme.[Our endangered plant species]*. Suomen ympäristökeskus, Tammer-Paino Oy.

Saunders, D. A., & Hobbs, R. J. (1991). The role of corridors in conservation: What do we know and where do we go?. In: D. A. Saunders, & R. J. Hobbs (Eds.), *Nature conservation 2: The role of corridors. Proceedings of a workshop/conference (WA: September, 1989)* (pp. 421–427). Surrey Beatty & Sons.

Schabel, J., & Eldridge, D. J. (2001). *A comparison of roadside and paddock vegetation in the box woodlands of eastern Australia*. School of Geography, University of NSW.

Simberloff, D., Farr, J. A., Cox, J., & Mehlman, D. W. (1992). Movement corridors: Conservation bargains or poor investments? *Conservation Biology*, 6(4), 493–504. https://doi.org/10.1046/j.1523-1739.1992.06040493.x

Slaviero, A., Del Vecchio, S., Pierce, S., Fantinato, E., & Buffa, G. (2016). Plant community attributes affect dry grassland orchid establishment. *Plant Ecology*, 217(12), 1533–1543. https://doi.org/10.1007/s11258-016-0666-x

Sletvold, N., Øien, D. I., & Moen, A. (2010). Long-term influence of mowing on population dynamics in the rare orchid *Dactylorhiza lapponica*: The importance of recruitment and seed production. *Biological Conservation*, 143(3), 747–755. https://doi.org/10.1016/j.biocon.2009.12.017

Smith, P. H., & Cross, S. (2016). Effect of mowing regime on abundance of green-winged orchid *Anacamptis morio* on coastal grassland in Merseyside, England. *Conservation Evidence*, 13, 79–81.

Spooner, P. G. (2005). On squatters, settlers and early surveyors: Historical development of road reserves in southern New South Wales. *Australian Geography*, 36, 55–73. https://doi.org/10.1080/00049180500050870

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(3), 401–409. https://doi.org/10.3372/wi.49.49310

Swarts, N. D., & Dixon, K. W. (2009). Terrestrial orchid conservation in the age of extinction. *Annales of Botany*, 104(3), 543–556. https://doi.org/10.1093/aob/mcp025

Tewksbury, J. J., Levey, D. J., Haddad, N. M., Sargent, S., Orrock, J. L., Weldon, A., Danielson, B. J., Brinkerhoff, J., Damschen, E. I., & Townsend, P. (2002). Corridors affect plants, animals, and their interactions in fragmented landscapes. *Proceedings of the National Academy of Sciences*, 99(20), 12923–12926. https://doi.org/10.1073/pnas.202242699

Thiele, J., Schirmel, J., & Buchholz, S. (2018). Effectiveness of corridors varies among phytosociological plant groups and dispersal syndromes. *PLoS One*, 13, e0199980. https://doi.org/10.1371/journal.pone.0199980

Tikka, P. M., Högmander, H., & Koski, P. S. (2001). Road and railway verges serve as dispersal corridors for grassland plants. *Landscape Ecology*, 16(7), 659–666.

Tikka, P. M., Koski, P. S., Kivelä, R. A., & Kuitunen, M. T. (2000). Can grassland plant communities be preserved on road and railway verges? *Applied Vegetation Science*, 3(1), 25–32. https://doi.org/10.2307/1478915

Tilman, D., Fargione, J., Wolff, B., D'Antonio, C., Dobson, A., Howarth, R., Schindler, D., Schlesinger, W. H., Simberloff, D., & Swackhamer, D. (2001). Forecasting agriculturally driven global environmental change. *Science*, 292(5515), 281–284. https://doi.org/10.1126/science.1057544

Trombulak, S. C., & Frissell, C. A. (2000). Review of ecological effects of roads on terrestrial and aquatic communities. *Conservation Biology*, 14(1), 18–30. https://doi.org/10.1046/j.1523-1739.2000.99084.x

Turis, P., Kliment, J., Feráková, V., Dítě, D., Eliáš, P., Hrivnák, R., Košťál, J., Šuvada, R., Mráz, P., & Bernátová, D. (2014). Red List of vascular plants of the Carpathian part of Slovakia. *Thaiszia Journal of Botany*, 24(1), 35–87.

Turrill, W. B. (1932). On the Flora of the Nearer East: XI. A contribution to the flora of Albania. *Bulletin of Miscellaneous Information*, *1932*(4), 193–198.

Vakhlamova, T., Rusterholz, H. P., Kanibolotskaya, Y., & Baur, B. (2016). Effects of road type and urbanization on the diversity and abundance of alien species in roadsides in Western Siberia. *Plant Ecology*, *217*(3), 241–252. https://doi.org/10.1007/s11258-016-0565-1

Valkó, O., Deák, B., Török, P., Kelemen, A., Miglécz, T., & Tóthmérész, B. (2017). Filling up the gaps—Passive restoration does work on linear landscape elements. *Ecological Engineering*, *102*, 501–508. https://doi.org/10.1016/j.ecoleng.2017.02.024

van Dorp, D. (1996). *Seed dispersal in agricultural habitats and the restoration of species-rich meadows*. PhD-Thesis, Wageningen Agricultural University.

van Dorp, D., Schippers, P., & van Groenendael, J. M. (1997). Migration rates of grassland plants along corridors in fragmented landscapes assessed with a cellular automation model. *Landscape Ecology*, *12*(1), 39–50. https://doi.org/10.1007/BF02698206

Van Rossum, F., & Triest, L. (2012). Stepping-stone populations in linear landscape elements increase pollen dispersal between urban forest fragments. *Plant Ecology and Evolution*, *145*(3), 332–340. https://doi.org/10.5091/plecevo.2012.737

Von der Lippe, M., & Kowarik, I. (2007). Long-distance dispersal of plants by vehicles as a driver of plant invasions. *Conservation Biology*, *21*(4), 986–996. https://doi.org/10.1111/j.1523-1739.2007.00722.x

Waterman, R. J., & Bidartondo, M. I. (2008). Deception above, deception below: Linking pollination and mycorrhizal biology of orchids. *Journal of Experimental Botany*, *59*(5), 1085–1096. https://doi.org/10.1093/jxb/erm366

Way, J. M. (1970). Roads and the conservation of wildlife. *Journal of the Institution of Engineers*, *17*(7), 5–11.

Wojcik, V. A., & Buchmann, S. (2012). Pollinator conservation and management on electrical transmission and roadside rights-of-way: A review. *Journal of Pollination Ecology*, *7*, 16–26.

Zahariev, D. (2014). Favorable impact of road infrastructure on the distribution and abundance of populations of *Himantoglossum caprinum* (M. Bieb.) Spreng. in Shumensko plato Protected area (BG0000382) and Rishki prohod Protected area (BG0000149) from the European ecological network Natura 2000. *Acta Scientifica Naturalis*, *1*, 166–174.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.