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RESEARCH ARTICLE

Roadside diversity in relation to age and surrounding source habitat: evidence for long time lags in valuable green infrastructure

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Abstract

1. The severe and ongoing decline in semi-natural grassland habitat during the past two centuries means that it is important to consider how other, marginal grassland habitat elements can contribute to landscape-level biodiversity, and under what circumstances.

2. To examine how habitat age and the amount of core grassland habitat in the surrounding landscape affect diversity in green infrastructure, we carried out inventories of 36 rural road verges that were either historical (pre-1901) or modern (established post-1901 and before 1975), and were surrounded by relatively high (>15%) or low (<5%) levels of grassland habitat. We recorded the number of plant species, grassland specialists, grassland conservation species and the fraction of the landscape's species and specialists found in the road verge.

3. Road verge communities were characterised by high levels of grassland specialist species (35% of the 161 species recorded), with road verge sites supporting 15–20% of the specialist species found in the surrounding 25 km^2 landscape.

4. Richness of species and specialists were more closely related to road age than to the amount of surrounding habitat. Higher diversity in historical roads, despite the majority of modern roads being at least 60 years old, suggests a long time lag in the establishment of grassland communities in marginal grassland habitats. We identified no effect of historical surrounding land use on present day diversity in road verges.

5. Road verge richness was not affected by the amount of surrounding grassland. This could be due to the relatively low amounts of grassland remaining in all landscapes, together with dispersal limitation commonly found in grassland plant communities contributing to a potential time lag.

6. We identified road verges as potentially very important habitats for grassland communities. Because of the high levels of grassland specialists present, these and other marginal grasslands and grassland green infrastructure should be explicitly considered in landscape-scale conservation management. Practitioners looking to identify the most species-rich road verges should aim to find the oldest possible, while long time lags in community assembly suggests that seed sowing could be appropriate to enhance roadside diversity, even in decades-old road verges.

KEYWORDS
biodiversity, connectivity, dispersal, grassland, green infrastructure, landscape, road ecology, time lag

1 | INTRODUCTION

For the past 150 years, there has been a sharp and ongoing decline in the area of semi-natural grassland habitat across Europe, following the conversion or abandonment of ancient pastures and meadows (Auffret, Kimberley, Plue, & Waldén, 2018; Buitenwerf, Sandel, Normand, Mimet, & Svenning, 2018; Hooftman & Bullock, 2012). This loss, together with the high value of grassland habitat in terms of biodiversity and ecosystem services (Bengtsson et al., 2019; Billeter et al., 2008; Wilson, Peet, Dengler, & Pärtel, 2012), means that it is important to understand the role of alternative, marginal habitats in the landscape that are also able to support grassland communities. Such habitat elements – forming part of a landscape's green infrastructure – can make significant contributions to biodiversity, providing both valuable habitat area and landscape connectivity, which are vital for facilitating species- and community-level responses to ongoing environmental change (Auffret et al., 2017c; Filazzola, Shrestha, & MacIvor, 2019; Hodgson, Moilanen, Wintle, & Thomas, 2011). As such, green infrastructure is a key component of the European Union's long-term environmental strategy (European Commission, 2013).

Linear habitat elements represent one type of landscape feature providing valuable green infrastructure in fragmented landscapes (Damschen et al., 2019; Sullivan et al., 2017). For grassland species, linear elements can, for example, take the form of field margins (Jakobsson, Fukamachi, & Cousins, 2016; Smart, Bunce, Firbank, & Coward, 2002), along with 'rights-of-way infrastructure', including road verges, railway embankments and power-line corridors (Gardiner, Riley, Bommarco, & Öckinger, 2018). Such habitat elements are generally kept open by cutting and clearing vegetation for practical or safety reasons and can therefore provide habitat for grassland species. Roads, and road verges in particular have received a lot of attention, being found to provide habitat for multiple taxonomic groups in different regions of the world (Bellamy, Shore, Ardeshir, Treweek, & Sparks, 2000; Hopwood, 2008; Lindborg, Plue, Andersson, & Cousins, 2014; O'Farrell & Milton, 2006; Phillips, Gaston, Bullock, & Osborne, 2019; Spooner & Smallbone, 2009).

The majority of research into the biodiversity effects of roads has been conducted on plants (Bernes et al., 2017). In addition to providing functioning habitat patches for low-competitive grassland specialists species that depend on long-term, regular and low-intensity grassland management (Lindborg et al., 2014; Vanneste et al., in press), roads and road verges can also act as dispersal corridors for target species (Auffret & Cousins, 2013; Suárez-Esteban, Delibes, & Fedriani, 2013). On the other hand, previous work has also shown that road verges are often associated with the occurrence and spread of invasive alien species (Ansong & Pickering, 2013; Lázaro-Lobo & Ervin, 2019). Because of the pervasiveness of roads throughout rural landscapes, road verges have the potential to have a significant impact on landscape-level biodiversity, both positively and negatively, with national governmental agencies providing guidelines for appropriate road-verge management (Bromley, McCarthy, & Shellswell, 2019; Venner, 2006; Swedish Transport Administration, 2019). To promote biodiversity of grassland plant species, mowing more than once per year and removing the resulting material has been found to be most effective (Jakobsson, Bernes, Bullock, Verheyen, & Lindborg, 2018), while active restoration such as seed sowing can also be used to increase the number of target species present (Auestad, Rydgren, & Austad, 2016). However, due to the increased costs of these more intensive methods of management, it is not financially or practically feasible to implement them on all road verges in all landscapes. Therefore, it is important to understand how other factors can influence the role of road verges in providing valuable grassland habitat in rural areas, which can in turn help practitioners to make informed decisions about where available resources should be directed to maximise potential positive impacts on biodiversity.

An important consideration in grassland biodiversity is that of time. Species-rich semi-natural grassland communities are the result of a slow, gradual accumulation of plant species after long periods of low-intensity grazing and haycutting (Eriksson, 2013). Following the relatively rapid destruction and degradation of grassland habitat that has occurred with agricultural intensification, slow responses of plants to landscape change means that species richness of communities in remaining grasslands has regularly been shown to be better-predicted by previous habitat extent and configuration than by the modern landscape (e.g. Helm, Hanski, & Pärtel, 2006; Highland & Jones, 2014), a phenomenon that has also been observed in road verges (Koyanagi, Kusumoto, Yamamoto, Okubo, & Takeuchi, 2009). Such time lags can be a cause for optimism, in that timely and appropriate management can help to preserve remaining biodiversity despite previous loss of habitat (Kuussaari et al., 2009), while it also indicates that marginal habitats and other elements of green infrastructure provide an important functional role in maintaining grassland biodiversity at landscape scales.

Time lags also occur in the other direction. When grassland habitat is (re-)created or restored, it can take many years, decades or longer for target species and communities to establish at a new site (Isbell, Tilman, Reich, & Clark, 2019; Turley, Orrock, Ledvina, & Brudvig, 2017; Waldén & Lindborg, 2016). Studies on roadsides have shown that species richness reaches its maximum after 20 years in heavily degraded industrial landscapes (Zeng et al., 2011), while more shrubby and woody target vegetation is still developing after more than a century (Deckers, Becker, Honnay, Hermy, & Muys, 2005; Spooner & Lunt, 2004). Delays in recruitment in grassland plant species are usually attributed to dispersal limitation, whereby species must move to and establish in newly created or restored habitat patches (Aavik & Helm, 2018; Öster, Ask, Cousins, & Eriksson, 2009). Dispersal limitation is in turn related to the availability of source habitats from which grassland species can disperse to restored sites. As the majority of seeds from the majority of plant species disperse only very short distances (Bullock et al., 2017), the colonisation of target species is strongly dependent on the presence of source populations in nearby patches (Helsen, Hermy, & Honnay, 2013; Sperry et al., 2019).

It is clear that both time and the presence of source populations in the surrounding landscape are important determinants of grassland biodiversity. In this study, we explore how these factors are related to different measures of plant diversity in road verges in rural landscapes. Understanding what drives biodiversity in linear habitat elements will help in both elucidating their role in maintaining diversity in different landscapes, as well as providing valuable information for those wanting to identify potential landscapes or stretches of road-verge habitat for targeted conservation management. Due to the importance of age and surrounding source habitat in determining grassland diversity, we predict that older road verges and those with more grasslands in the surrounding landscape will support higher plant biodiversity. We aim to identify the relative and potentially interacting influence of road age and surrounding landscape and also examine the effect of the historical landscape on present-day diversity.

2 | MATERIALS AND METHODS

2.1 | Study area

This study was carried out in the province of Södermanland in southern Sweden (Figure 1). This lowland region (altitude generally below 100 m) is largely rural, with landscapes made up of a mosaic of arable fields, pastures, forest and small settlements. Annual precipitation is approximately 600–700 mm per year, with January and July temperatures averaging −4 to −5°C and +15 to +16°C, respectively (https://www.smhi.se/klimat). During the 20th century, there was an estimated 96% decline of semi-natural grassland in the region, when a large percentage of grazed grassland and forest on unproductive moraine soils was abandoned. Hay meadows that were situated on more nutrient-rich and productive clay soils were either abandoned or converted to cropland before being converted again to species-poor modern grassland (Cousins, Auffret, Lindgren, & Tränk, 2015).

2.2 | Site selection and field inventory

We identified 36 × 100 m stretches of road verge that were split equally across four categories according to the occurrence of surrounding source habitat and road age (Table 1). We used the Swedish government's GIS database of valuable grassland habitat (TUVA database: http://www.jordbruksverket.se/tuva) as our definition of source habitat. This is a comprehensive nationwide database of species-rich semi-natural grasslands that are overwhelmingly managed by livestock grazing (with very few examples of ancient meadows remaining). Grasslands are characterised by an open ground-flora including several grassland specialists, although trees are generally present in most grasslands. Road verges classed as having (relatively) low surrounding source habitat had <5% (1–4%) semi-natural grassland within a 500-m surrounding buffer of the road verge (a typical landscape size for studies of ecological time lags and linear habitat elements, e.g., Cousins & Vanhoenacker, 2011; Vanneste et al., in press). Verges with relatively high levels of source habitat had at least 15% semi-natural grassland in the buffer (usually 15–20%, but up to 31%). A broad classification of road age was determined by consulting historical maps of the area from 1901 and the 1950s, with historical roads defined as those present on the earlier maps, and modern roads absent from the earlier maps, but present in the 1950s. Due to difficulties finding road verges to fit all categories, one 'modern' road verge was slightly more recent, being absent from the 1950s maps, but present in a 1975 aerial photograph. We assume that no significant restructuring of the road verges occurred across time steps. In addition to the four categories of road verge, we made sure that as far as possible, road segments were surrounded on both sides by arable fields, but in some cases one side of the road was adjacent to forest or small dwellings. Verges were never directly adjacent to managed semi-natural grassland habitat, in order to exclude the direct spillover of grassland species or that the road verge would in effect be an extension of an existing grassland. Identification of road verges was carried out using ArcGIS v10 (ESRI, Redlands USA). The resulting 36 verges were on small, typical countryside roads, with all four categories of road including a mixture of paved and unpaved surfaces and a variety of speed limits (50–90 km hour^{-1}). All road verges were managed in the same manner as the vast majority of road verges in Sweden, with cutting once per year (June–July) and the cut material left on the verge.

Inventories took place in June 2014. On each road verge, 10 × 1 m^2 quadrat plots were placed at 10 m intervals in the grassy verge along one side of the road that was adjacent to an arable field. Road verges

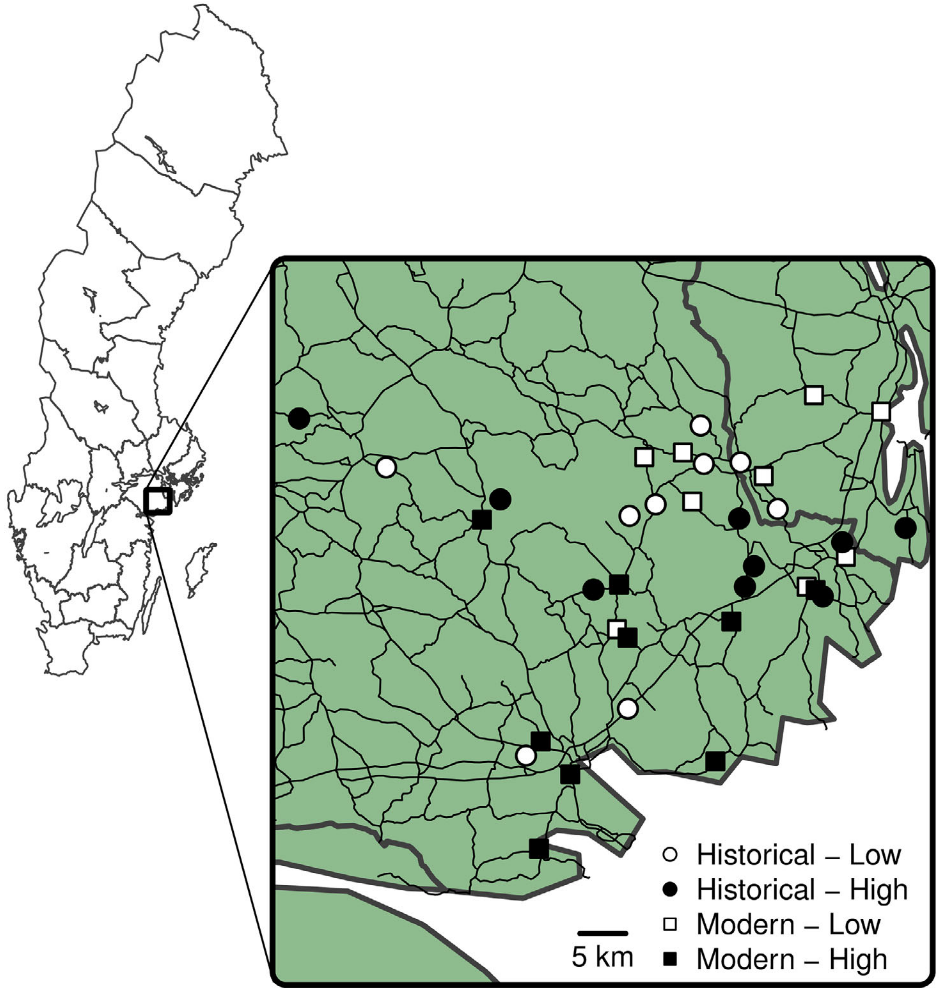

FIGURE 1 Map showing the location of 36 road verges (100 m long) within the study region and of the study region in Sweden. Symbols show categories of road verge according to whether they are historical (established pre-1901), modern (established post-1901), and if there is a high (> 15%) or low (< 5%) cover of semi-natural grassland habitat in a 500-m buffer around the road verge. Note that to prevent a messy figure, only major roads are shown. Road verge plots that appear to be separated from the road network are situated on minor roads

TABLE 1 Categories of 36 road verges surveyed for this study

	Historical roads	Modern roads
Low source habitat	Present on map from 1901 $<5\%$ semi-natural grassland in 500 m buffer $n = 9$	Absent on map from 1901, but present on map from 1950s $<5\%$ semi-natural grassland in 500 m buffer $n = 9$
High source habitat	Present on map from 1901 $>15\%$ semi-natural grassland in 500 m buffer $n = 9$	Absent on map from 1901, but present on map from 1950s (one exception) $>15\%$ semi-natural grassland in 500 m buffer $n = 9$

bordering arable fields were narrow (<5 m), generally consisting of a relatively flat area of vegetation close to the road, with a ditch directly at the border with the arable field. Plots were placed 1 m from the road edge, except for in especially narrow verges when this would mean that the plot was in a ditch, in which case the plot was placed closer to the road edge. The presence of all vascular plant species was recorded in each plot. Nomenclature follows the Swedish taxonomic database (https://www.dyntaxa.se/).

2.3 | Data analysis

Inventory data were analysed to assess the effect of road age and surrounding semi-natural grassland habitat on five different measures of plant diversity. At the road level, we assessed (1) total species richness across all plots; (2) number of Swedish grassland specialists listed in Krauss et al. (2010), (3) number of Swedish Environmental Protection Agency's Natura 2000 conservation species for grasslands (containing more exclusive species than grassland specialists; https://www.naturvardsverket.se/upload/stod-i-miljoarbetet/vagledning/natura-2000/naturtyper/typiskaarter.zip); (4) fraction of the landscape's species pool, the species pool being defined as all species present in the 5 × 5 km inventory grid square in which the geographic centroid of the road segment resides, according to data from the regional plant atlas (flora) covering the study area (Rydberg & Wanntorp, 2001; extracted from the Swedish Species Observation System https://www.artportalen.se/); and (5) fraction of the grassland specialist pool, that is the fraction of the grassland specialists that are also present in the landscape's species pool. To check for the presence of invasive alien species in the road verges, we also compared our inventory data with the list of alien species from a recent Swedish governmental report assessing their prominence and negative ecological effects (Strand, Aronsson, & Svensson, 2018)

For each measure of diversity, we created a generalised linear model (function glm in R; R Development Core Team, 2018), with the diversity measure as the response variable, and with road age (0 = modern road, 1 = historical road) and surrounding source habitat (0 = low, 1 = high) and their interaction as predictor variables. To account for the potential effect of spatial autocorrelation (nearby roads having similar levels of diversity), we also included the first axis of a principal coordinates of neighbour matrix (pcnm; Borcard & Legendre, 2002), as an additional predictor variable. This was calculated from a distance matrix of the *x* and *y* coordinates of the centroid of the road segment, using the R base function *dist* and the function *pcnm* from the vegan package (Oksanen et al., 2016). Models of species richness, grassland specialists and conservation species (count data) were built using Poisson error distributions, while those concerned with fractions of the species pool were built using Gaussian error distributions. In the cases where Poisson generalised linear models showed evidence of overdispersion, a quasi-Poisson correction was applied. Interaction effects were never significant ($p = < .05$) in any models and were therefore removed for model simplicity, with all final models only having the three fixed effects (road age, surrounding habitat and pcnm axis).

At the plot level, we assessed only (1) total species richness, (2) number of grassland specialists and (3) number of conservation species. Here, we also used generalised linear models with the diversity measure as the response variable, and with road age, surrounding source habitat and their interaction as predictor variables. The first axis of a pcnm for each road was again included, both to account for spatial autocorrelation between roads and to act as a unique identifier to account for autocorrelation between each road's plots. As with the models at the road level, interaction effects were never significant and were therefore removed from the final models.

2.3.1 | Effect of the historical landscape

Because of the lack of significant ($p = < .05$) effect of present-day surrounding source habitat on any measures of diversity at the road level (see Results, Table S1 in the Supporting Information), and because the historical landscape has sometimes been shown to strongly affect grassland and road-verge diversity (e.g. Helm et al., 2006; Koyanagi et al., 2009), we thought that it would be relevant to look into the potential influence of the historical landscape on our road verges. We used published digitisations of the 1950s maps (Auffret et al., 2017b), that classify land use into open (mainly grassland), forest, arable land and water. These digitisations were clipped to the 500-m buffer areas using R's *raster* package (Hijmans, 2016), and the proportion of open land within each buffer was calculated. This was added as an additional predictor variable in the generalised linear models explaining diversity measures at the road level, together with its two-way interactions with source habitat and road age. As with the previous models, interaction terms were removed due to non-significance. The historical proportion of open land did not have any effect on measures of plant diversity in the models (Table S2 in the Supporting Information). We therefore concentrate on the results from the original models for the remainder of the paper.

3 | RESULTS

We recorded a total of 161 plant species across the 360 plots placed in the 36 road verges. Of these species, 56 (35%) were grassland specialists and 20 (12%) were conservation species for grassland habitats. More than half of the Swedish grassland specialists named in Krauss et al. (2010) were present in our road verge plots. Only three invasive species (*Lolium multiflorum* Lam., three plots; *Matricaria discoidea* DC., one plot; and *Rosa villosa* L., one plot) were recorded in the study. We found that historical road verges (established pre-1901) were richer both in terms of the total number of species and number of grassland specialists, compared to modern verges (established post-1901; Figure 2a, Table 2). Modern road verges contained a mean ± standard deviation of 27.8 ± 8.6 species and 2.7 ± 1.3 grassland specialists, compared to 34.4 ± 8.2 species and 3.3 ± 1.9 specialists in the historical road verges. The 29 plant atlas inventory grid squares (5 × 5 km) in our study area contained a mean ± standard deviation of 545 ± 61 plant species, of which 90 ± 3 were grassland specialists and 73 ± 9 were conservation species for grasslands. Therefore, we found that 5% ± 2% and 6% ± 2% of the total species pool being represented in modern and historical road verges, respectively. For grassland specialists, 16% ± 6% (modern) and 20% ± 6% (historical) of the specialists present in the 25 million m^2 plant atlas grid square were found in our surveys covering 10 m^2 (0.00004%).

At the plot level, both historical road verges and those with relatively high amounts of surrounding semi-natural grasslands had higher species richness and more grassland specialists present, compared to modern roads and those with lower levels of semi-natural grassland in their surroundings (Figure 2b, Table 2). On average, a plot contained 11.1 ± 3.7 species, of which approximately half were grassland specialists (6.4 ± 2.8). Conservation species for grassland habitat were generally quite rare both at the road and plot level (3.1 ± 1.7 and 1.2 ± 0.8, respectively) and were not found to be influenced by road age or surrounding source habitat.

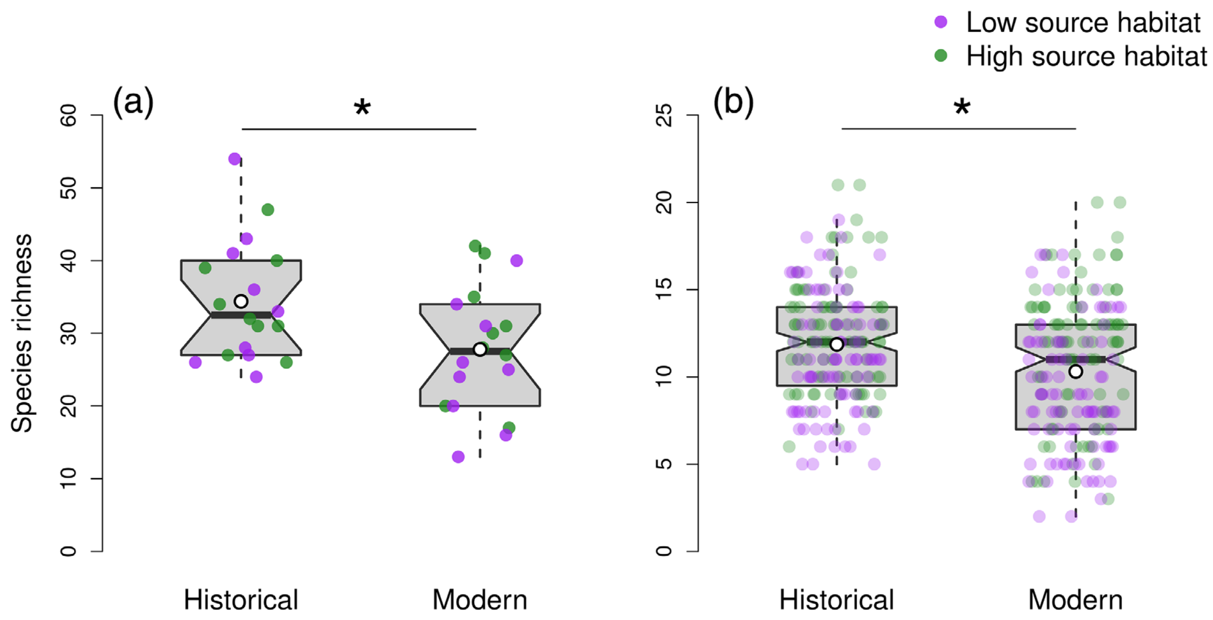

FIGURE 2 Species richness of 36 verges of historical (established pre-1901) and modern (established post-1901) roads at both the verge (a) and plot (b) level, with verge richness being the sum of unique species in each road's ten 1 m^2 plots. Boxplots show median and interquartile ranges, whiskers show range excluding outliers. Notches indicate approximate 95% confidence intervals of the medians, and asterisks show significant differences between historical and modern road verges. Coloured points indicate richness of each individual road/plot according to amount of surrounding semi-natural grassland source habitat (low < 5% and high > 15% in the 500-m surrounding the road verge), while white points show mean richness values. Transparency was plotted thanks to the scales package (Wickham, 2017)

TABLE 2 Simplified summary of results from generalised linear models relating different measures of diversity in road verges to road age and source habitat

	Age		Source habitat	
	Effect	Estimate	Effect	Estimate
Road				
Species richness	+	**0.24**		0.05
Grassland specialists	+	**0.28**		0.10
Conservation species		0.29		0.009
Fraction species pool	+	**0.02**		0.004
Fraction specialist pool	+	**0.05**		0.02
Plot				
Species richness	+	**0.16**	+	**0.15**
Grassland specialists	+	**0.15**	+	**0.17**
Conservation species		0.03		0.009

Parameter estimates show the average increase in number or fraction of species when changing from one category to another (i.e. modern to historical roads, low to high surrounding source habitat). Bold font and the sign of the effect (positive or negative) indicates that the predictor had a significant ($p = < .05$) effect in the model. Full model outputs, including estimates for pcnm indices, are given in Tables S1 and S3 in the Supporting Information.

4 | DISCUSSION

There is an increasing acceptance of the importance of relatively small and marginal habitat patches for landscape-level biodiversity and conservation (Gardiner et al., 2018; Wintle et al., 2019). In this study, we provide further evidence of the value of linear grassland elements. Our rural road verges were rich in grassland specialists, with some verges containing up to one-third of an entire landscape's specialists in only a tiny fraction (0.00004%) of the area. Exploring the effects of road age and surrounding source habitats, we found that despite almost all of the modern road verges existing for more than 60 years, they were still not as rich in species or specialists as road verges that had existed since before 1901. On the other hand, the amount of core semi-natural grassland habitat in the nearby surrounding landscape did not seem to influence the number of species or specialists at the road level, although a higher amount of surrounding grassland did contribute to a higher diversity at the plot level.

The higher plant biodiversity found in historical road verges could be evidence of a long time lag in the establishment of grassland communities at these sites. Although road verges are not likely to be able to host the full diversity of species found in managed semi-natural grassland habitat, it might be reasonable to expect that half a century or more in modern verges would suffice for communities to resemble those of historical road verges. However, spontaneous colonisation of target communities is generally slow and can take decades or more (Baasch, Kirmer, & Tischew, 2012; Isbell et al., 2019; Jírová, Klaudisová, & Prach, 2012), while other biologically valuable road-verge habitats have been found to continue developing after more than 100 years (Spooner & Smallbone, 2009). For grassland communities, results from seed-sowing experiments indicate that the slow build-up of communities is due to dispersal and establishment limitation (Öster et al., 2009; Turley et al., 2017). It has even been shown that dispersal may limit the occurrence of potentially suitable species in core semi-natural grassland patches (Riibak et al., 2015), indicating that immigration of grassland species can limit biodiversity even in very old grasslands. Our result of historical roads supporting higher fractions of both grassland specialists and the entire species pool from the surrounding landscape lends further evidence to the slow assembly process exhibited by grassland plants.

If the difference in species diversity between historical and modern road verges is related to dispersal limitation, then it might be seen as surprising that there was not a positive effect of having more core semi-natural grassland in the surrounding landscape that could be a source of propagules. Indeed, dispersal and colonisation are often linked to the availability of nearby habitat (Auffret, Aggemyr, Plue, & Cousins, 2017a; Minor, Tessel, Engelhardt, & Lookingbill, 2009), which in turn is – in combination with focal patch area – a key driver of species richness (Auffret et al., 2018; Weigelt & Kreft, 2013). It could be that in the modern agricultural landscape, where 15% cover of semi-natural grassland is relatively high, this amount of source habitat is still too low (or variation in habitat quality is too high) for habitat amount to exhibit a significant effect on the recruitment of grassland species on road verges and other marginal habitats. The majority of seeds of many species disperse only tens of metres or less (Bullock et al., 2017; Diacon-Bolli, Edwards, Bugmann, Scheidegger, & Wagner, 2013), and therefore the dispersal distances needed require rare long-distance dispersal events, compared to the spillover of target species that might be possible from adjacent habitats (Sperry et al., 2019). Recent studies showing the positive effect of surrounding source habitat for grassland recruitment are approximately 25–30 years in duration (Helsen et al., 2013; Waldén, Öckinger, Winsa, & Lindborg, 2017), and it is possible that this effect is no longer detectable due to the long time periods involved in our study. However, we found no statistical interaction between road verge age and surrounding source habitat, while a study of forest species in woodland roadsides found that older roadsides were actually more positively affected by nearby forest patches than more recent roadsides (Deckers et al., 2005).

The fact that both our modern and historical road verges were at least several decades old provides some interesting insights, but also leaves some questions unanswered. An important aspect to mention is that of the starting points of the different types of road verges. While the modern roads were generally established across arable fields, historical road verges that have existed for more than 100 years are likely to at some point have been part of a larger pasture or meadow, or at least a lower intensity agricultural landscape than the one that exists today. This means that for historical road verges communities probably represent remnant populations of grassland species. We saw no influence of the historical landscape composition on current richness, indicating that historical road verges might already be stable in terms of biodiversity and not experiencing a so-called extinction debt (Koyanagi et al., 2009; Krauss et al., 2010). On the other hand, modern road verges appear to still be in the colonisation and establishment phase and have the potential to develop and gain further species in the future (Isbell et al., 2019; Spooner & Smallbone, 2009). How many species could be gained is likely to depend on other factors such as road verge width, structure and road traffic intensity (Angold, 1997; Jimenez et al., 2013; Phillips et al., 2019), factors which can also covary with road age. Further study across a gradient of different road ages would give a greater indication of the rate build-up (or gradual loss) of species and specialists over time. Combined with a trait-based analysis, it could provide a more detailed understanding of which types of species, grassland specialists and conservation species are most likely to colonise to or are extirpated from road verges of different age, and how this relates to the availability of surrounding source habitat (e.g. Auffret et al., 2017a). This could then help to guide more site-specific conservation measures. Regardless of the community dynamics prevalent in the different categories of road verges, both historical and modern road verges supported relatively high percentages of the landscape's grassland specialist species, highlighting the value of marginal grassland habitats for landscape-scale biodiversity.

4.1 | Implications for conservation management

Our results show that road verges support diverse plant communities, including many grassland specialists, indicating their importance for landscape-scale biodiversity. We found that road age, and to a lesser extent the amount of surrounding grassland, can be useful predictors of the richness of road verge communities. The amount of grassland in the landscape was not related to the fractions of species- or specialist pool that were supported in the road verge as a whole, which suggests that road verges can be equally important for landscape-scale diversity in different types of landscape. Road verges and marginal grassland habitats as a whole should therefore be explicitly considered in conservation management plans, particularly in this time of ongoing grassland abandonment (Auffret et al., 2018; Buitenwerf et al., 2018). Nonetheless, the relatively low numbers of conservation species found in our plots means that it is imperative that remaining semi-natural grasslands are preserved. It is also important to remember that in many regions of the world, road verges entail a risk to native biodiversity due to the establishment and spread of invasive species (Lázaro-Lobo & Ervin, 2019).

Ideally, as much road verge habitat as possible should be managed for biodiversity, but if practitioners want to identify the most species-rich verges then we recommend the use of historical maps to find those stretches of roads that are older than 100 years. Although a discussion of appropriate management strategies is beyond the scope of this study, verge cutting at the appropriate time to benefit both plants and pollinators, plus hay removal is likely to have the most positive effect on biodiversity (Jakobsson et al., 2018; Phillips et al., 2019). Due to the apparent long time lags in community assembly, seed sowing can be an option to increase roadside diversity (Auestad et al., 2016), even for road verges that were established several decades ago. Where possible, local seed mixtures should be used to ensure that there are no negative genetic effects on existing populations (Aavik, Edwards, Holderegger, Graf, & Billeter, 2012), ensuring the long-term positive effect of grassland green infrastructure on landscape-scale biodiversity.

AUTHOR CONTRIBUTIONS

AGA and EL conceived and designed the study. EL collected data, AGA analysed data and wrote the paper.

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DATA AVAILABILITY

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.kwh70rz15 (Auffret & Lindgren, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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