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RESEARCH ARTICLE

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Road verges provide alternative habitats for some, but not all, meadow plants

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Abstract

Questions: Agricultural intensification has led to the decline of biodiverse meadows and other semi-natural grasslands. Road verges offer potential alternative habitats for meadow species, but they may not be suitable for all meadow species due to different soil properties, frequent disturbances, pollution or suboptimal management. Are their communities of vascular plants and bryophytes similar or dissimilar to those in mown or grazed meadows? What kind of species are associated with road verges, mown meadows or grazed meadows? How do the habitat types differ in their soil conditions and disturbance intensity?

Location: The study was conducted at 36 sites in central Finland.

Methods: We compared the vascular plant and bryophyte flora and the habitat characteristics of road verges, mown meadows and grazed meadows.

Results: The community composition of both vascular plants and bryophytes differed among the habitat types. Many species occurred in all three habitat types, but several meadow specialists were absent or less frequent in the road verges. In contrast, road verges hosted more forest species and ruderal species, especially bryophytes. Road verges differed from meadows in their soil conditions.

Conclusions: We conclude that although road verges may host some species typical to meadows, their value as alternative habitats could be increased by improved soil preparation and vegetation management. Meanwhile, the continued decline of quality habitats for meadow species underscores the need to maintain, increase and improve meadow management.

KEYWORDS

bryophyte, disturbance, grazing, meadow, mowing, novel ecosystem, semi-natural grassland, traditional rural biotope, vascular plant

1 | INTRODUCTION

Agricultural intensification has led to the decline of biodiverse semi-natural grasslands throughout northern Europe (Vainio et al., 2001; Eriksson et al., 2002; Hamre et al., 2007). Most of the European species-rich semi-natural grasslands have been mowed as part of traditional agricultural animal husbandry (Pykälä, 2000) and can thus be referred to as meadows. In Finland, the area of meadows with conservation values declined to less than 1% from the late 19th century by the 1990s (Vainio et al., 2001). At present, all types of traditional meadows are classified as endangered or critically endangered habitats (Lampinen & Lahti, 2018), and together with other cultural habitats (such as parks, gardens and arable land) they provide primary habitat for 24% of all threatened species in Finland (Hyvärinen et al., 2019). In addition, the quality of remaining meadow habitats has often declined due to suboptimal or neglected management (Lehtomaa et al., 2018).

Most traditionally mown hay meadows are nowadays managed by grazing (Vainio et al., 2001), which results in changes in plant communities (Norderhaug et al., 2000; Raatikainen et al., 2018). This is due to the differences in the ecological disturbances caused by mowing and grazing, which are further influenced by habitat characteristics (Tälle et al., 2016). Mowing was traditionally done once in late summer and affected meadows relatively uniformly and with similar intensity. Mowing decreases the number of competitive tall plants and enhances the survival of stress-tolerant, low-growing species (Parr & Way, 1988; Blakesley & Buckley, 2016). Grazing causes repeated but uneven and selective removal of vegetation, providing advantage to unpalatable and/or low-growing plants. Grazing, as well as soil disturbance due to trampling, and the addition of dung and urine, all result in increased patchiness of the sward (Blakesley & Buckley, 2016; Oldén & Halme, 2016).

Other human-modified, managed habitats may provide alternative habitats for meadow specialist species. The most extensive frequently mown habitats are road verges. In Finland, mown road verges are estimated to cover an area 50 times that of meadows (Jantunen et al., 2006). Road verges could provide alternative and refuge habitats and form dispersal corridors for grassland species (Cousins & Eriksson, 2001; Huhta & Rautio, 2007; Auestad et al., 2011; Lindborg, 2014). However, previous studies in the Nordic countries have found that vascular plant communities on road verges differ from those in semi-natural grasslands. Road verges host more weed, cultivated and forest species but less light-demanding grassland species, although many grassland specialist species do occur on road verges (Norderhaug et al., 2000; Tikka et al., 2000; Jantunen et al., 2006; Auestad et al., 2011). Contrary to vascular plants, very little is known about bryophytes (mosses and liverworts) on road verges. Zechmeister et al. (2003) showed that bryophytes are less species-rich on road verges than in pastures or meadows. Experiments have further shown that bryophyte biomass and richness is increased by low vascular plant biomass and litter mass, therefore benefiting from mowing or grazing (Bergamini, 2001; Aude & Ejrnæs, 2005; Peintinger & Bergamini, 2006). Bryophytes are also sensitive to pollutants, which may impact their community composition on road verges (Bignal et al., 2008). Especially nitrogen dioxide can increase bryophyte growth, membrane leakage and chlorophyll concentration (Bignal et al., 2008).

Road verges differ from meadows and other grasslands in several ways. Road verges are relatively young habitats that are periodically disturbed by road or ditch maintenance such as digging or tilling the soil (Jantunen et al., 2006). In Finland, the soil used for verge construction is usually coarse sand, which is sometimes covered with fertile soil. The soil is often sown with grass seeds, although in recent decades the aim has been to use local soil material and to allow natural revegetation (Tielaitos, 1996; Jantunen et al., 2004). Road verge management also differs from the late-summer mowing that is typical to meadows in northern Europe, which may not allow successful flowering and seed set for all plant species (Persson, 1995; Jantunen et al., 2007). Usually the mowing residues are left on the verges, which can affect vegetation by suffocating smaller plants (e.g., bryophytes) and increasing nutrient accumulation (Parr & Way, 1988; Persson, 1995; Auestad et al., 2011). Chemical conditions can be harsh on the verges. For example, heavy metals, organic molecules and nitrogen compounds may accumulate in road verges (Trombulak & Frissell, 2000; Viard, 2004). Similarly, sodium from de-icing salt accumulates in the soil and plants and can damage plants directly (Bryson & Barker, 2002), decreasing species diversity (Tikka et al., 2000). Finally, road verges may function as dispersal corridors and habitats for alien species, some of which are invasive and hamper the growth of native flora (Trombulak & Frissell, 2000; Jantunen et al., 2004; Zeng, 2010).

In this paper, we report a comparison of road verges of paved main roads to meadows that are currently either mown and grazed, located in central Finland where meadows have decreased drastically (Raatikainen et al., 2018). We compare the communities of both vascular plants and bryophytes in the three habitat types and test for the effects of habitat characteristics (soil conditions and disturbance intensity). We hypothesize that, because of the unequal disturbance regimes associated with the current management, mown and grazed meadows host distinct plant species communities; yet, their similar history as hay meadows should be reflected in shared soil conditions and species. We also hypothesize that road verges differ from the two meadow types, due to their soil conditions, mowing regimes and younger age.

2 | METHODS

2.1 | Study sites

The study included 12 mown meadows, 12 grazed meadows and 12 road verges. The sites are located in the southern and middle boreal vegetation zones in central Finland (Figure 1). The region is forest-dominated, and meadows and traditionally managed pastures cover only 0.04% of the total land area (Komonen & Elo, 2017). The meadows in the area were historically used for mowing winter fodder with

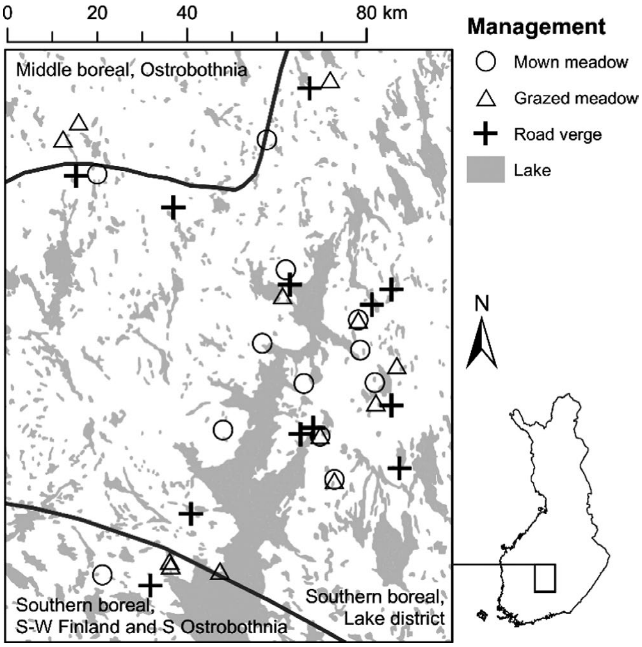

FIGURE 1 Map of the locations of the study sites in Central Finland. Black lines indicate borders of the vegetation zones named in the map

possible aftermath grazing in the autumn, and in many sites also time periods when they were grazed all summer. Nowadays many of the meadows are managed by extensive grazing, so we decided to study both those that are still mown and those that are nowadays grazed. Due to the scarcity of meadows, we studied all mown and grazed meadows that fulfilled the following criteria: (a) area of meadow >0.1 ha; (b) mesic or dry meadow or a combination of these; (c) managed by mowing or grazing for over 10 years and still under management in the year 2014; (d) not having been fertilized; and (e) classified as locally, regionally or nationally valuable in the Finnish inventory of traditional rural biotopes during the 1990s (Vainio et al., 2001). The meadows were surrounded by forests and/or agricultural grasslands and fields. In the grazed sites, the grazing animals were sheep, cattle or horses, which together with the variation in the number of grazers, induced variation in vegetation among pastures. Mown meadows and grazed meadows were paired spatially with each other (minimum and maximum distances between the pairs were 50 m and 64 km, respectively). However, because the median distance between the pairs was 10 km, the pairing was not considered in the statistical analyses.

Road verges were chosen such that their geographic distribution would be similar to that of the meadows. To do this, we chose the closest road to each pair of meadows that fulfilled these criteria: (a) asphalt-covered public roads where the verge is at least 3 m wide; (b) built >20 years ago to allow the vegetation time to develop; and (c) no visible maintenance actions such as digging or tilling the soil. After selecting the road, we drove from the predetermined starting point (the point closest to both meadows) and selected the first suitable point for the sampling site: to reduce variance among the verge sites, the verge had to be on the south or southeast side of the road and bordered by forest or hedge on this side (not by field, buildings or water). To select the road verges comparable with the mown and grazed meadows, we avoided very moist (peatlands or marshes) or dry (sandy heathlands) verges. In Finland, road verges are mown once or twice each summer, and the timing is usually determined by road safety and practical aspects; the first mowing is usually done in June and the second from July to September. Such yearly mowing typically covers the area between the road edge and the ditch, whereas tree seedlings on the other side of the ditch are cut every 2–3 years (Jantunen et al., 2004). Sampling site selection was done in mid-May (some weeks after the snow melts in the area) so there was practically no green vegetation influencing the selection. Information about the study sites and example photos are provided in Appendix S1.

2.2 | Sampling design

At each site, we placed five study plots of 2 m × 2 m (4 m^2) on a transect that was 44 meters long. The first plot was placed at two meters from the beginning of the transect, and the other plots were placed at 10-meter intervals. In the meadows, the transect started from the edge of the meadow at a randomized point and ran toward the center of the meadow. Some of the meadows were too small or narrow to fit a single 44-meter transect, and in these cases the transect was halved and the two transects were set perpendicular to each other so that they crossed in the middle (see also Raatikainen et al., 2018). In the road verges, the transect ran along the road and the plot edge was about 1 m from the edge of the asphalt so that the plot was not placed on bare gravel but at a distance where there was vegetation. The plots were marked so that their location was permanent throughout the study season.

2.3 | Data collection

The occurrence and cover of all vascular plants on the plots were surveyed between late June and early July 2014. We used a predefined classification of meadow specialist plants (appendix 1 in Pykälä, 2001), which includes those vascular plant species that were characteristic to dry and mesic meadows in Finland in the late 1800s. However, we excluded those species that Pykälä stated as having been at least equally common in other habitat types. This was done to include only those species that were most dependent on the traditional meadows. The nomenclature of vascular plants follows Lampinen and Lahti (2018).

Bryophytes were surveyed between late July and late August in 2014. Only those bryophyte species that grew on soil were included to reduce the effect of substrate availability on the data. Specimens were collected for microscopic identification, when necessary. The nomenclature of mosses follows Hodgetts (2015) and that of liverworts follows Söderström et al. (2016). There is no a priori classification for meadow bryophytes in Finland. Out of the observed bryophyte species, *Abietinella abietina* (recorded from one grazed meadow) is the only one having a clear association with traditional rural biotopes, and *Brachythecium albicans* (recorded from almost all sites) is common in traditional rural biotopes as well as in other human-modified habitats (Takala et al., 2012).

2.4 | Habitat characteristics

We estimated the intensities of trampling and cutting on each plot during both the vascular plant and bryophyte surveys, and the means of these values (from both visits and all five plots) were used in the following analyses. Trampling intensity was estimated as the proportion of soil surface that was clearly broken due to grazers, humans or machinery. Cutting intensity was estimated as the proportion of vascular plant shoots that exceeded a height of 5 cm and had been cut by grazing or mowing.

The average height of all vascular plant shoots in each plot was also estimated during the vascular plant and bryophyte surveys, and the average of these values was used to describe the mean height of vascular plants. In addition, during the vascular plant survey, the percentage cover of each species was recorded in each plot, and their sum was used to describe the total cover of all vascular plants. This sum can exceed 100% because vegetation forms layers.

Soil samples were collected during five subsequent days in May 2014. A sample was taken from two opposite corners of each plot and the resulting 10 samples were mixed together. A soil corer of 3 cm diameter was used and soil was collected to the depth of 5 cm, but excluding undecayed litter. The mixed soil sample was sieved through a 4-mm mesh sieve and preserved in a freezer until measurements were done. The dominant grain size was classified as (a) fine or medium silt (0.002–0.02 mm); (b) coarse silt (0.02–0.06 mm); (c) fine sand (0.06–0.2 mm); (d) medium sand (0.2–0.6 mm); or (e) coarse sand (0.6–2.0 mm; classification system SFS-EN ISO 14688–1 2007, see Ronkainen, 2012). Soil pH was measured from a suspension of 6 ml of soil and 30 ml of 0.01 M $CaCl_2$ after one hour of shaking. The median of three pH measurements was used in the analyses. To measure soil moisture content, a subsample was placed in a crucible, weighed, dried in an oven (at 105°C for 12 h), and weighed again. For the calculation of soil organic matter content, the subsample was then burned in the oven (at 475°C for 4 h) and weighed again.

2.5 | Principal components analysis

There were several strong correlations between the following habitat characteristics: soil grain size, soil pH, soil moisture content, soil organic matter content, vascular plant cover, vascular plant height, cutting intensity and trampling intensity (Appendix S1). Therefore, it was not possible to analyze their separate effects on the plant communities. We used Principal Components Analysis (PCA, function rda in R package *vegan*, Oksanen et al., 2018) to form two uncorrelated principal components. Prior to PCA, the values of each habitat characteristic were standardized to zero mean and unit variance so that their effect sizes are similar on the PCA result.

2.6 | Statistical analyses

We used non-metric multidimensional scaling (NMDS, function metaMDS in R package *vegan*, Oksanen et al., 2018) to visualize the effects of habitat type (mown meadow, grazed meadow, road verge), soil conditions (principal component 1, see *Results*) and disturbance intensity (principal component 2, see *Results*) on the community compositions of vascular plants and bryophytes. The Bray–Curtis dissimilarity index was used to calculate the pairwise distances of sites from community data where the frequency of a species on the five plots of a site was used as an estimate of its abundance on the site. The NMDS was run separately for vascular plants (including all observed species) and for bryophytes, and two-dimensional ordinations were chosen to visualize the results. To analyze for the effect of habitat type, soil conditions (principal component 1) and disturbance intensity (principal component 2) on the community compositions, we used Permutational Multivariate Analysis of Variance (PerMANOVA, function adonis2 in package *vegan*). PerMANOVA is a non-parametric multivariate test that uses permutations of the community dissimilarity matrix to analyze the significance of experimental variables. Similar to the NMDS ordinations, the analysis was run separately for vascular plants and for bryophytes, and we used Bray–Curtis dissimilarity. The analyses were done separately for the pairwise combinations of the three habitat types (mown meadows, grazed meadows and road verges). First, only the effect of habitat type was tested. Second, the effects of soil conditions and disturbance intensity were analyzed. Third, habitat type was analyzed together with soil conditions and disturbance intensity. This was done to see if habitat type and either soil conditions or disturbance intensity reduce the effect of each other in the model (i.e., if they explain the same differences in community composition) or if they complement each other in the model (i.e., if they explain independent differences in community composition).

We tested the association of individual species with one or two of the habitat types (mown meadow, grazed meadow, road verge) with multi-level pattern analysis (function multipatt in package *indicspecies*, De Cáceres & Legendre, 2009). This is an indicator species analysis that is extended so that it looks for the habitat type or combination of two habitat types that a species is associated with. The analysis calculates the indicator value of the species for the habitat type or habitat type combination based on the frequency of the species on the sites (how many sites it was observed in) and the abundance of the species on the sites, which in our data was the frequency of the species on the five plots of each site. Further, the analysis uses a permutation test to assess the probability of finding such an association (De Cáceres et al., 2010). We classified species with $p < 0.05$ as significantly associated with the habitat type or combination of habitat types for which the species had the highest indicator value. In addition, we classified species with $0.05 < p < 0.5$ as showing some association with the habitat type or combination, meaning that there is less than 50% risk that the species is truly randomly distributed. Species with $p > 0.5$ were classified as indifferent to the habitat types if they were observed in all of the three habitat types. The remaining species were too infrequent to be classified at all.

We compared the species richness of plants on the road verges vs mown or grazed meadows with generalized linear models (GLM with Poisson ditribution, function *glm* in R, R Core Team, 2020). Analyses were done separately for meadow specialists, other vascular plant species and bryophyte species.

3 | RESULTS

3.1 | Habitat characteristics

The first principal component was affected by soil conditions so that high values correspond to high moisture, high organic matter, small grain size and low pH (Figure 2; Appendix S1). The second principal component was affected by disturbance intensity so that high values correspond to high cutting intensity, low vascular plant cover and low vascular plant height (Figure 2; Appendix S1). Trampling intensity was correlated with both principal components, because a higher amount of disturbance increases the proportion of broken soil, but the soil also breaks more easily when it has a small grain size

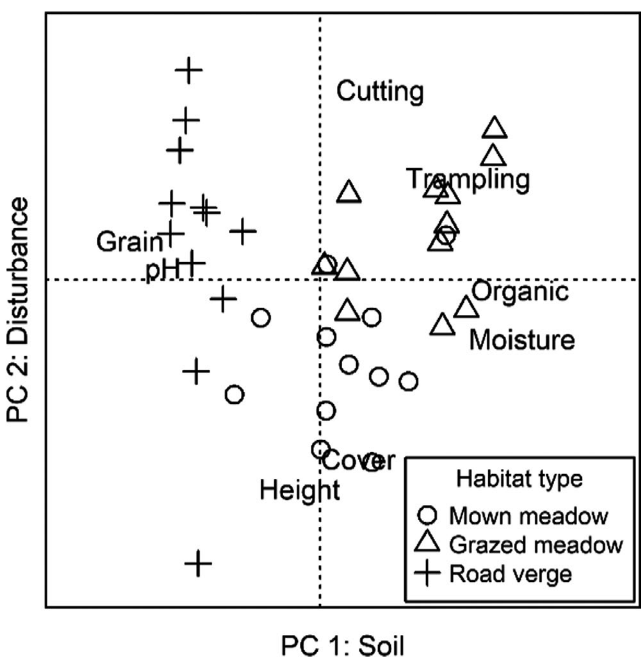

FIGURE 2 Results of the Principal Components Analysis on the habitat characteristics of mown meadows, grazed meadows and road verges. Principal component 1 corresponds to soil conditions (grain size, pH, organic matter content and moisture content) and principal component 2 corresponds to disturbance intensity (cutting intensity, trampling intensity, height and cover of vascular plants)

and high moisture and organic matter contents. The first principal component (soil conditions) explained 43% of the variance in the recorded habitat characteristics in the study sites, while the second (disturbance intensity) explained 33% of the variance.

Road verges had low values for soil conditions (principal component 1). Compared to mown and grazed meadows, they had larger grain size, higher soil pH, lower soil moisture and lower soil organic matter content (Figure 2 and boxplots in Appendix S1). Mown and grazed meadow sites were more similar to each other, but on average grazed meadows had higher disturbance intensity (principal component 2): higher cutting and trampling intensities and lower vascular plant cover and height (Figure 2 and Appendix S1). Road verges varied in the values they had for disturbance intensity, but most of them had high cutting intensity, as well as low cover and low height of vascular plants, similar to grazed meadows (Figure 2 and Appendix S1).

3.2 | Community composition

Both vascular plant and bryophyte communities differed between the three habitat types (Figure 3a, b; Table 1; $R^2 = 0.10–0.23$ for "habitat type" in the different models; detailed results in Appendix S1). The differences between road verges and the meadow types were larger than the difference between the two meadow types (Figure 3a, b). When mown and grazed meadows were included in the PerMANOVA analysis, soil conditions did not affect the community composition of either vascular plants or bryophytes, but disturbance intensity affected them significantly (Table 1; $R^2 = 0.07–0.09$ for "disturbance"). When the habitat type was included in the analyses together with the habitat characteristics, the habitat type and disturbance intensity reduced each other's effects so that the habitat type did not have any significant marginal effects left (Table 1).

When road verges were included in the PerMANOVA analysis with either mown or grazed meadows, both soil conditions ($R^2 = 0.11–0.19$ for "soil") and disturbance intensity ($R^2 = 0.08–0.11$ for "disturbance") affected the communities of both species groups (Table 1). When the habitat type was included in the model together with the habitat characteristics, disturbance intensity still had an effect ($R^2 = 0.09–0.11$ for "disturbance"), but soil conditions did not have any marginal effect beyond the effect of the habitat type (Table 1). In these models, the significance of habitat type decreased as well, but there was still a significant marginal effect on vascular plant communities when comparing mown meadows and road verges (Table 1; $R^2 = 0.06$ for "habitat type"), and a nearly significant effect on bryophyte communities when comparing grazed meadows and road verges (Table 1; $R^2 = 0.06$ for "habitat type").

3.3 | Individual species

A total of 171 vascular plant species were observed, including 35 predefined (Pykälä, 2001) meadow specialists (Appendix S1). The total

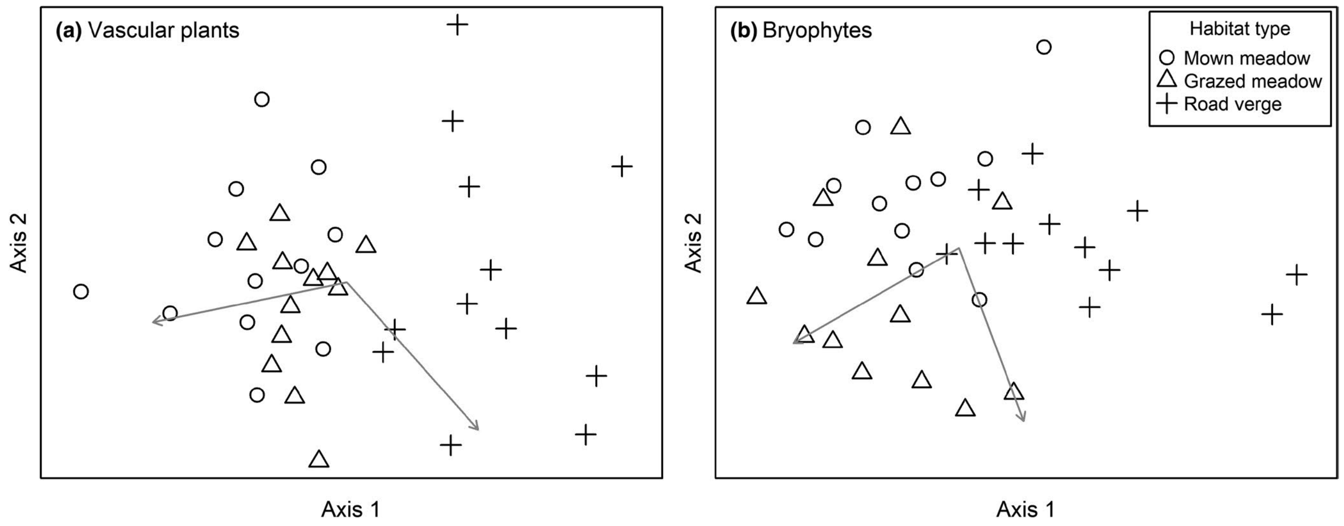

FIGURE 3 The non-metric multidimensional scaling (NMDS) ordination of (a) vascular plants and (b) bryophytes on mown meadows, grazed meadows and road verges. The gray arrows correspond to the direction and strength of the effects of soil conditions and disturbance intensity which are integrated measures derived from PCA axes

TABLE 1 Summary on the pairwise community comparisons among mown meadows, grazed meadows and road verges

Habitat types included	Vascular plants	Bryophytes
Mown meadow & grazed meadow	Type ***	Type ***
	Soil + Disturbance***	Soil + Disturbance*
	Type + Soil + Disturbance *	Type + Soil + Disturbance
Mown meadow & road verge	Type ***	Type ***
	Soil** + Disturbance**	Soil** + Disturbance*
	Type* + Soil + Disturbance**	Type + Soil + Disturbance**
Grazed meadow & road verge	Type***	Type***
	Soil*** + Disturbance**	Soil*** + Disturbance**
	Type + Soil + Disturbance**	Type + Soil + Disturbance**

Note: The effects of habitat type (Type), soil conditions (Soil) and disturbance intensity (Disturbance) on the community compositions of vascular plants and bryophytes were analyzed with PerMANOVA. Each row corresponds to the results of one analysis. Asterisks denote the significance of the variables that were included in the model. Detailed results from each analysis are provided in Appendix S1. Significance: ***, <0.001; **, 0.001–0.01; *, 0.01–0.05; 0.05–0.1.

number of observed bryophyte species was 67 (Appendix S1). In the multi-level pattern analysis, the species that were frequent enough to be classified as either indifferent or as showing some association with one or two habitat types included 28 meadow specialists, 83 other vascular plant species and 42 bryophyte species. Out of these, almost half were indifferent to the three habitat types (i.e., their frequency and abundance did not differ between the three types): 50% of meadow specialists, 34% of other vascular plants and 45% of bryophytes (Figure 4a–c). On the other hand, there were several species that were associated with only one or two of the habitat types.

Among meadow specialists, 25% were associated with both types of meadows but not with road verges (Figure 4a). Among other vascular plants, 18% were associated with the two kinds of meadows, and an equal number were associated only with road verges (Figure 4b). Among bryophytes the most common association was with road verges (24%; Figure 4c). The detailed results of all species are shown in Appendix S1.

3.4 | Species richness

Mown meadow sites hosted a higher number of pre-defined (Pykälä, 2001) meadow specialists than road verges (Figure 5a, GLM: Estimate = 0.29, *SE* = 0.11, z = 2.6, p = 0.010). Grazed meadows had slightly more meadow specialists than road verges (Figure 5a), but this difference was not significant (GLM: Estimate = 0.18, *SE* = 0.11, z = 1.6, p = 0.111). The richness of other vascular plants did not differ between the three habitat types (Figure 5b). Bryophytes had higher species richness on road verges than in mown meadows or in grazed meadows (Figure 5c, GLM for both comparisons: Estimate = 0.29, *SE* = 0.09, z = 3.1, p = 0.002).

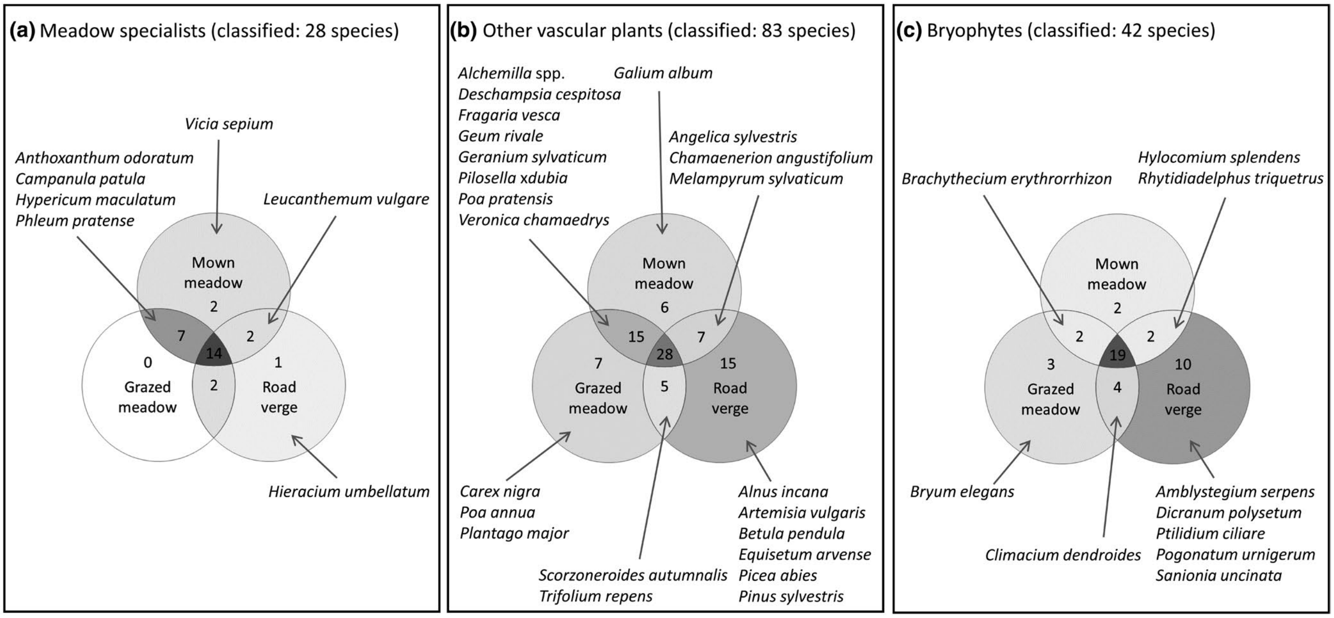

FIGURE 4 The association of individual species of (a) meadow specialists, (b) other vascular plants, and (c) bryophytes to the three habitat types. The numbers show the number of species with an association to the particular habitat type, the combination of two habitat types, or no difference between the types (indifferent species, in the middle). The darkness of the area corresponds to the numbers by representing a darker shade with a larger proportion of species with that association (for illustrative purposes). Only the named species had significant ($p < 0.05$) associations in the multi-level pattern analysis

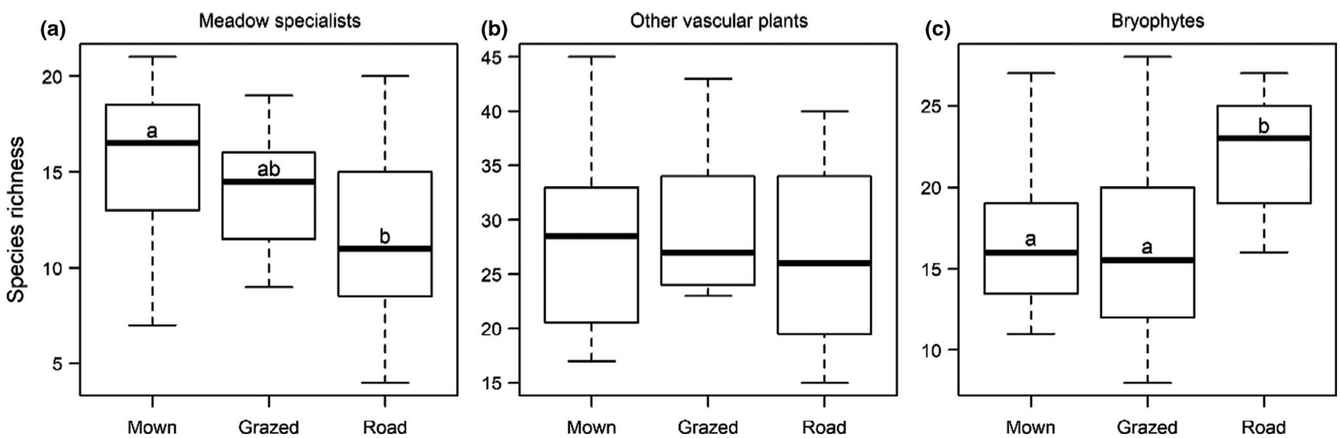

FIGURE 5 The species richness of (a) meadow specialists, (b) other vascular plants, and (c) bryophytes on mown meadows, grazed meadows and road verges. The boxplots show median values, 25% quartiles and minimum and maximum values. In (a) and (c) significant differences are denoted by different letters (a and b) in the boxplots

4 | DISCUSSION

4.1 | Road verges hosted different plant communities than meadows, reflecting different soil conditions

The community composition of both vascular plants and bryophytes differed between road verges and meadows, which was largely caused by different soil conditions. Compared to the meadows, the soils in road verges had larger grain size, lower soil moisture and organic matter content, and higher pH. The larger grain size results from the sand and gravel that are used in the construction of roads and verges, and low moisture and organic matter contents follow from that (Aaltonen, 1949). The higher pH is likely to result from the de-icing salt sodium chloride (NaCl), which increases soil pH, but also damages plants directly and accumulates in the soil (Bryson & Barker, 2002). Together these soil properties explained most of the differences in plant community composition between road verges and meadows, thus indicating that road verges cannot provide habitat for all meadow species.

As expected, disturbance intensity varied markedly between road verges. Most, though not all, road verges had high cutting intensity, which resulted in low cover and low height of vascular plants. Low cover and low height of vascular plants were also typical in grazed meadows. Some road verges and most of the mown meadows had lower disturbance intensity. These patterns of disturbance intensity did not cause differences in plant community composition between road verges and the studied meadow types, but they did cause differences between the differently managed meadows. It is well known that the distinct disturbances caused by grazing and mowing result in differences in vascular plant communities (Blakesley & Buckley, 2016). On the other hand, the grazed and mown meadows did not differ from each other in their soil conditions, which we also expected due to their shared land-use history.

We did not measure several environmental factors that may further increase the differences between road verges and meadows. Since road verges are narrow linear habitats, they are particularly prone to edge effects, which affect the quality of the habitat (Coffin, 2007). In our study, there were trees or bushes on the southern side of the studied verges, which limits light availability. It would be interesting to compare these road verges to those that are sun-exposed the whole day. The deep slope on a road verge may also restrict plant species richness as Tikka et al. (2000) found that both total species richness and the number of grassland species decreased with increasing inclination angle on verges. On the other hand, the environmental variation from the dry, frequently mown road edge to the moist ditch bottom increases plant species diversity (Auestad et al., 2011; Jantunen et al., 2004). The vehicles emit pollutants, such as heavy metals and nitrogen compounds, which are likely to accumulate in the soil and induce selection against species that are unable to inhabit the chemically altered verges (Trombulak & Frissell, 2000; Viard, 2004). Wind and direct damage from vehicles may also damage plants as well as animals, including insects and vertebrates (Jantunen et al., 2004; Coffin, 2007). In addition, roads and ditches are repaired at intervals of about 20 to 30 years, which disrupts vegetation (Jantunen et al., 2004). Although species may survive in the seed bank or in nearby areas, the community composition may not have enough time to develop similarly to that of meadows that have been managed for decades or centuries without heavy soil disturbance (Jantunen et al., 2006).

4.2 | Many species were shared between road verges and meadows, but not all

Nearly half of both vascular plant and bryophyte species were equally or nearly equally frequent on the three habitat types, demonstrating that both road verges and meadows are suitable habitats for these species. Notably, half of the meadow specialists found in this study were indifferent to the three habitat types, for example *Achillea millefolium*, *Centaurea phrygia*, *Pimpinella saxifraga*, *Rhinanthus minor*, *Stellaria graminea* and *Vicia cracca*. For those meadow species that grow successfully on road verges, these alternative habitats increase the total habitat available in the landscape, and should be regarded as refugia or stepping stones (Huhta & Rautio, 2007; Auestad et al., 2011; Lindborg, 2014). Previous studies have shown that road verges are valuable alternative habitats for several individual vascular plant species, although the species occur in different combinations on road verges than in semi-natural grasslands (Norderhaug et al., 2000; Tikka et al., 2000; Jantunen et al., 2006). Our results support this conclusion for vascular plants, and show that the same is also true for bryophytes, which were more species-rich on the road verges than in the other habitat types.

On the other hand, several species were significantly more frequent on mown and/or grazed meadows, including many meadow specialists such as *Anthoxanthum odoratum*, *Campanula patula* and *Hypericum maculatum*. The species richness of meadow specialists was also higher in meadows than on road verges, although the difference was significant only between mown meadows and road verges. These results show that in their current state, the majority of road verges of main roads do not provide additional habitat for all meadow species. Due to the scarcity of suitable alternative habitats, the management of meadows has to be continued, expanded and improved, which supports the earlier findings by, e.g., Norderhaug et al. (2000) and Raatikainen et al. (2018).

The management of road verges should be improved to better accommodate for the requirements of meadow species. Mowing only once in late summer would improve flowering and reproduction for many species, and removing the mowing residue should be done to reduce the suffocation of small plants and nutrient build-up (Persson, 1995; Jantunen et al., 2007; Auestad et al., 2011). Furthermore, new road verges can be vegetated using seeds of meadow plants, which would directly benefit rare species and prevent priority effects of unwanted species. Such management practices are already used in Finland on verges that are specifically managed as valuable meadows or as habitats of threatened species (Liikennevirasto, 2014). Such sites are scarce and our study did not include them, but further studies should compare valuable verges with valuable meadows. In addition, small gravel roads often have verges where the plant communities are more like those of hay meadows due to less intensive disturbances and higher dispersal of species from surrounding areas (Norderhaug et al., 2000; Tikka et al., 2000). This suggests that main road verges or sections of them could easily be improved by balancing biodiversity management with safety, visual beauty and economic savings (see also Lampinen, 2020).

Road verges also hosted species that were less common on the meadows, including several species of bryophytes and vascular plants that are not meadow specialists. The majority of these are tree seedlings (e.g., *Alnus incana*, *Betula pendula*, *Picea abies* and *Pinus sylvestris*) or generalist forest bryophytes (e.g., *Amblystegium serpens*, *Dicranum polysetum*, *Ptilidium ciliare* and *Sanionia uncinata*). Forest species grew typically further away from the road edge, near the ditch to where mowing equipment often does not fully reach. Increasing the width of the mown zone could decrease the cover of forest species and thus improve the growing conditions for less competitive grassland species. Also, some ruderal species were associated to road verges, including *Artemisia vulgaris* and *Equisetum arvense*. Several ruderal bryophytes were recorded only from road verges, although infrequently: *Bryum argenteum*, *Pogonatum urnigerum*, *Racomitrium* *canescens* and *Tortula truncata*. They benefit from coarse soil that is frequently disturbed by vehicles, mowing and verge construction. Invasive alien species often benefit from these conditions as well, decreasing the habitat quality or availability for native species through competition. Among semi-natural habitats, the highest level of invasion by alien species has been observed in fields and on road verges under frequent disturbance (Jauni & Hyvönen, 2010). In our data invasive aliens were not common, but *Lupinus polyphyllus* occurred on two road verges and one mown meadow.

Bryophytes had higher species richness on road verges than in mown meadows or grazed meadows, and ten species were associated to road verges only. These were mostly forest species or ruderal species (Ulvinen et al., 2002). The higher species richness on road verges may result from more variable habitat conditions and disturbance regimes. There was variation between the roads in their light conditions, slope and soil properties. The conditions also varied within one road verge, with dry and frequently disturbed habitats near the road supporting ruderal species and moist, often shadowy conditions closer to the ditch supporting forest species. The coarse soil, frequent mowing and irregular soil disturbance result in low cover and height of vascular plants. In agricultural habitats, bryophytes tend to be more species-rich in those habitats where vascular plant biomass is low (Zechmeister et al., 2003; Aude & Ejrnæs, 2005). However, in contrast to our study, Zechmeister et al. (2003) documented lower bryophyte species richness on roadsides than in meadows or pastures. Also, the bryophyte species found in our study are all common species and no threatened species were observed from the road verges. Therefore, the conservation value of road verges seems to be low for bryophytes despite the higher species richness.

5 | CONCLUSIONS

Road verges of main roads hosted diverse communities of both vascular plants and bryophytes, but for both species groups the community composition differed from that of mown or grazed meadows. Although nearly half of the species occurred with similar frequency in the three habitat types, we found that several meadow specialists were absent from road verges, indicating that road verges are not suitable habitats for all meadow species. Meanwhile, several species of other vascular plants and bryophytes were associated to road verges. However, these species are not of conservation concern.

If the aim is to improve the function of road verges as habitats for meadow species, we recommend paying attention to both soil conditions (finer soil, no addition of fertile topsoil, avoiding frequent soil disturbance and minimizing the use of de-icing salt) and management (mowing once in late summer, removing mowing residue and mowing as widely as possible).

6 | DATA AVAILABILITY STATEMENT

The data sets used in this paper are available as Supporting Information (Appendices S2, S3 and S4).

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AUTHOR CONTRIBUTIONS

PH, AK and KJR conceived of the research idea; AO and TP collected data; AO performed statistical analyses; AO, with contributions from all other authors, wrote the paper; all authors discussed the results and commented on the manuscript.

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SUPPORTING INFORMATION

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

Appendix S1. Supporting information on study sites, data and analyses

Appendix S2. Data: species richness and habitat characteristics

Appendix S3. Data: vascular plant species and their frequencies on the sites

Appendix S4. Data: bryophyte species and their frequencies on the sites

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