RESEARCH ARTICLE

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The contribution of alternative habitats for conservation of plant species associated with threatened semi-natural grasslands

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Abstract

1. Conservation of species associated with semi-natural grasslands, a threatened habitat, is dependent on their ability to disperse between the few and fragmented patches remaining in the landscape. To maintain metapopulations dynamics and reduce the risk of regional extinction, it is essential to know whether other, more widespread, habitats can act as alternative habitat for the biodiversity associated with threatened habitats.

2. Here, we study how four widespread habitat types in boreal landscapes—forest, permanent grassland, abandoned grassland and road verge—can contribute to the conservation of plant species found in semi-natural grasslands which is a species-rich ecosystem important for plant and pollinator diversity that has experienced extensive reduction, fragmentation and isolation. We compare richness of all vascular plants, insect-pollinated plants and semi-natural grassland specialists among habitat types in two regions is Norway where semi-natural grasslands are few and fragmented.

3. Based on overlap in community composition and local species richness, road verges were the most promising alternative habitat for both insect-pollinated plants and semi-natural grasslands specialists. Several habitat specialist species were, however, only found in semi-natural grasslands and, for these species, no other habitat can be considered suitable as alternative habitat.

4. Our results highlight that a holistic management perspective is needed to maintain biodiversity associated with semi-natural grasslands. Thus, both the protection of remaining patches of the primary, threatened habitats as well as management of widespread, alternative habitats in the landscape should be prioritized.

KEYWORDS
community composition, fragmentation, functional traits, habitat specialist species, insect-pollinated plants, metapopulation, pollinators, road verge

1 | INTRODUCTION

Semi-natural grasslands are biodiversity hotspots for plants and pollinators but are a threatened habitat in Europe due to habitat loss, fragmentation and quality reduction (Emanuelsson, 2009; Finderup Nielsen et al., 2019; Veen et al., 2009). To help mitigate the effects of land-use change on species associated with threatened habitats such as semi-natural grasslands, alternative habitats must be identified in the landscape (examples in Waldén et al., 2017). Alternative habitats supplement declining primary habitats and can function as stepping stones between primary habitats (Ohwaki et al., 2018; Ram et al., 2020). They facilitate the distribution, resilience and persistence of species, and contribute towards metacommunity conservation (Chase et al., 2020). The size of alternative habitats must be sufficient to have a conservation value and to contribute to species persistence across wide spatial and temporal scales (Saura et al., 2014).

In Western Europe, agricultural intensification or abandonment has caused a rapid loss and fragmentation of semi-natural grasslands and other less intensive agricultural land. As a result, farmland and grassland species are declining due to habitat loss (Berg et al., 2015; Foley et al., 2005; Stoate et al., 2009). Semi-natural grasslands are hay meadows or pastures with a native flora without sown species (Bullock et al., 2011) and recognized as one of the most species-rich ecosystems in the world at small spatial grains, particular for plants and insects (Öckinger & Smith, 2007; Squires et al., 2018; Veen et al., 2009; Wilson et al., 2012). These grasslands have a high diversity of insect-pollinated plants that play an important role in the ecosystem by delivering resources (nectar and pollen) for pollinators throughout the season (Squires et al., 2018). Many of the plant species are semi-natural grassland habitat specialists that have their main distribution within semi-natural grasslands (Hamre et al., 2010; Lindborg et al., 2014). Due to the continuous loss and fragmentation of semi-natural grasslands and decreased habitat quality, there is a particular conservation and management interest for species associated with this habitat and an increasing need to identify alternative habitats or stepping stones for semi-natural grasslands species (Auestad et al., 2011; Eldegard et al., 2017; Ohwaki et al., 2018).

Semi-natural grasslands are characterized by a low-intensity disturbance regime and high light conditions and are dominated by a high abundance and richness of herbs and grasses adapted to these physical conditions (Bullock et al., 2011). In boreal landscapes, open habitats with similar characteristics to semi-natural grasslands may act as alternative habitat candidates. Such candidates may include other types of grasslands and edge habitats such as road verges (Auestad et al., 2011; Auffret & Lindgren, 2020; Eldegard et al., 2017; Ohwaki et al., 2018). In addition to amount of suitable alternative habitats, the capacity of species to exploit habitats depend on their functional traits (Saura et al., 2014). Long-lived and clonal plant species can persist for decades in a habitat after land-use change and represent an extinction depth (Eriksson, 1996; Johansen et al., 2016; Johansson et al., 2011). Even though forest and abandoned semi-natural grasslands encroached by trees and bushes are less suitable for light demanding grassland species, these habitats may be a candidate as alternative

habitat for long-lived plant species and contribute to metapopulation dynamics.

The presence of alternative habitats may be essential for conserving species associated with threatened habitats but the need for holistic perspectives on conservation of semi-natural grasslands has only recently been highlighted (Auffret & Lindgren, 2020; Berg et al., 2016; Oki et al., 2021; Wehn et al., 2018). To better understand the role of alternative habitats in semi-natural grassland conservation, our aim was to identify how multiple, widespread habitats in boreal landscapes can contribute to the conservation of semi-natural grassland ecosystems that are under pressure due to land-use change. We compare vascular plant communities in semi-natural grasslands with those in widespread grasslands (permanent grasslands, abandoned semi-natural grasslands) and edge habitat (road verges). We choose road verges, permanent grasslands and abandoned semi-natural grasslands because they have similar growing (high light conditions and low/medium disturbance) conditions to semi-natural grasslands and we, therefore, expect them to support semi-natural grasslands species. We also include forest because we expect the low-light forest habitat to support remnant clonal plant specialist (Johansen et al., 2017).

For two groups of vascular plants, that is semi-natural grassland specialists and insect-pollinated plants, we identify potential alternative habitats as habitats with high species richness and a large overlap in species composition and functional traits with semi-natural grasslands. We study the presence of insect-pollinated plants, as well as habitat specialist plants, to determine how alternative habitats can contribute to the essential role that semi-natural grasslands play in the conservation of both plants and pollinating insects (Squires et al., 2018). This knowledge is critical for developing conservation measures to halt the loss of semi-natural grasslands and decline in pollinating insects. We also identify species of conservation concern in this landscape as species that only occur in semi-natural grasslands and none of the other habitats.

To investigate our main aim, we ask the specific research question: (1) How can widespread habitats function as potential alternative habitats for the conservation of species associated with rare and fragmented semi-natural grasslands in a landscape? (2) What part of the species communities associated with semi-natural grasslands are present in alternative habitats? (3) What are the functional traits of plants species present in semi-natural grasslands and alternative habitats? (4) How does semi-natural grasslands and alternative habitats contribute to supporting resource plants for pollinators?

2 | MATERIALS AND METHODS

2.1 | Study area and sampling

The study was carried out in two municipalities in Norway (Figure 1), Rauma in western Norway (62.297899N, 8.119213E) and Trondheim in central Norway (63.394698N, 10.375063E). The agricultural landscapes in Rauma and Trondheim are representative for Norway with small-scale farms and heterogeneous landscapes and represent
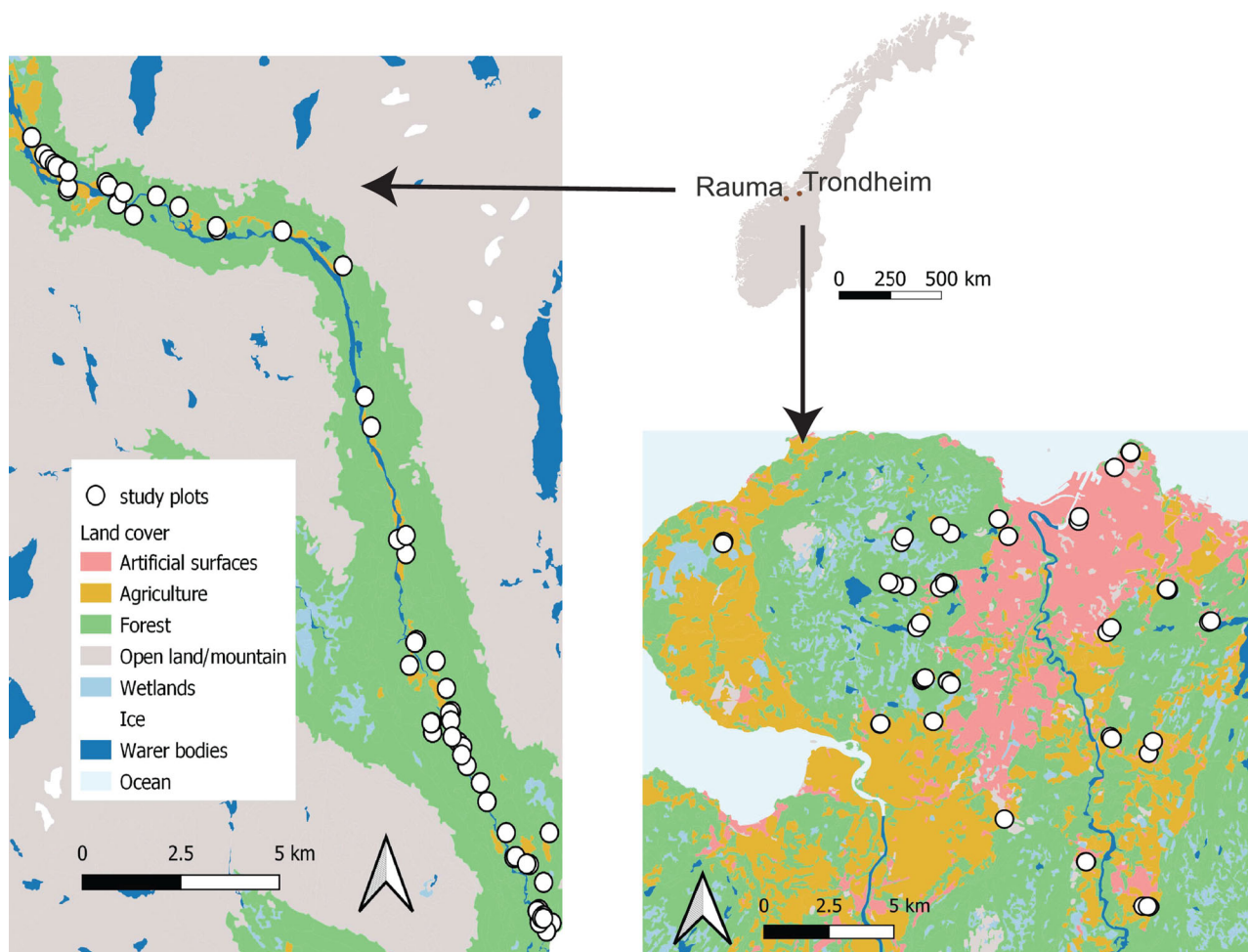
FIGURE 1 The two studied municipalities Rauma and Trondheim in Norway

land-use changes including intensification and abandonment that drive changes in biodiversity in semi-natural grasslands in western Europe (Veen et al., 2009). In Rauma, agriculture is declining (Wehn et al., 2018) and the landscape is at present dominated by boreal coniferous and deciduous forest (Table S2). The Trondheim area, on the other hand, is dominated by expanding urban areas surrounded by a rural persistent agricultural landscape that mainly include intensive managed crop fields as well as boreal coniferous and deciduous forest (Table S2). Within both municipalities, there are few and fragmented semi-natural grasslands and the number of registered semi-natural grasslands (The Norwegian Environment Agency, 2022) in Rauma is 95 (mean size: 13,931 m^2) and in Trondheim 107 (mean size: 22,192 m^2). In Norway, no monitoring data of the loss of semi-natural grasslands exist. The climate in Rauma is wetter than that in Trondheim (annual precipitation, Rauma: 1500–2000 mm, Trondheim: 1000–1500 mm), whereas the mean annual temperatures in the boreal agricultural landscapes studied are comparable across the two study areas (for both municipalities: 4–6°C) (The Norwegian Meteorological Institute, 2019). Gneiss is dominating the bedrock in Rauma, while the bedrock in Trondheim includes gneiss, granite, schist, amphibolite, limestone and grit (Geological survey of Norway, 2019).

In both study municipalities, we recorded occurrence of all vascular plant species in semi-natural grassland (meadows/pastures not ploughed, artificially fertilized or reseeded) and four alternative habitats, permanent grassland (meadows/pastures not reseeded, rotated or fertilized regularly), abandoned (encroached) semi-natural grassland, forest (mixed with boreal tree species) and road verges (established vegetation along single-lane roads) (Table 1). Habitat types selected as potential alternative habitats for semi-natural grasslands species were either widely distributed or had high cover in both study areas (Table S2). Permanent grasslands not considered as semi-natural were not identified in Rauma.

To select study plots, we used a combination of open-access spatial data (area resource maps: AR5 [NIBIO, 2021], habitat maps in Norway: Naturbase [The Norwegian Environment Agency, 2022]) and aerial photos before fieldwork was initiated. Forest, road verges and permanent grasslands were selected randomly within these AR5 categories. We used a stratified sampling approach to identify study plots in semi-natural grasslands and abandoned semi-natural grasslands because very few records of these habitat types exist in spatial databases. For these two habitat types, study plots were identified using semi-natural grasslands registered in the Naturbase database and on aerial photos.

TABLE 1 Definitions of the habitat types and number of plots (*n*) sampled across the types and municipalities

Habitat type	Definition	n_{Rauma}	$n_{Trondheim}$
Semi-natural grassland	Meadows or pastures managed by low intensive agricultural practices. Not ploughed, artificially fertilized or reseeded. Include mainly a native species composition. Low disturbance.	23	18
Permanent grassland	Meadows or pastures managed by medium intensive agricultural practices. Not reseeded, rotated or fertilized regularly. Medium disturbance.	0	8
Abandoned semi-natural grassland	Encroached grasslands that less than 40 years ago were open grassland but where the species composition and ecological processes typical of forest are not developed. No/low disturbance.	7	5
Forest	Continuous area where the coverage of tree crowns is at least 10%. Mixed forest of boreal tree species No/low disturbance.	24	14
Road verge	Low intensive managed (not fertilized or sown, cut once or twice in late summer) road verges with established vegetation along single lane asphalt or gravel road that is wider than 1 m. Low disturbance.	8	8

Aerial photos were used to identify encroachment by bushes and trees and thereby separate managed semi-natural grasslands from abandoned semi-natural grasslands using methods developed in Johansen et al. (2017). Quality control of all selected study plots was done in field and study plots were replaced if there was a mismatch in habitat type between field observations and available spatial data (AR5, Naturbase) or if we did not get permission from landowners to access the area. We got permission from all landowners to perform fieldwork in all study plots.

The study plots were 16 m², 4 m × 4 m in forests, abandoned semi-natural grasslands, semi-natural grasslands and permanent grasslands and 1 m × 16 m in road verges and the study plots were located at least 20 m apart. The number of plots per habitat type (Table 1) is a result of the relative cover of each habitat type in the municipalities (Table S2), except from semi-natural grasslands that are overrepresented according to the relative cover. Study plots in road verges were located at least 0.5 m form the road and all other study plots were located at least 2 m away from habitat edges. Each plot was placed in an area within the selected habitat patch that represented the dominating environmental gradients. GPS coordinates of plot centres were recorded. We conducted the survey and fieldwork in Rauma in July and August 2015 and in Trondheim between June and August 2018. Each plot was visited once by experienced botanists that surveyed the plot systematically in parallel 1-m transects covering the entire plot. All vascular plant species were recorded without time limitation.

2.2 | Functional traits

A semi-natural grassland specialist was defined as a native vascular plant species with its main distribution in semi-natural grasslands based on information provided by Halvorsen et al. (2016). Information on plant pollen vectors was extracted from the ecoflora database (Fitter & Peat, 1994) to determine which plants were insect-pollinated and therefore assumed to provide food resources for pollinators. Information at the genus level was used for species where pollen vector information was missing. For all vascular plant species, we extracted information about growth forms (dwarf shrubs, graminoids, trees/ shrubs, herbs) from Lid and Lid (2005) and lifespan (annual, perennial) from the LEDA database (Kleyer et al., 2008) and Lid and Lid (2005).

2.3 | Statistical analysis

2.3.1 | Species richness

The potential of forest, road verge, abandoned grassland and permanent grassland to function as alternative habitat was determined by first comparing mean local richness per plot with that of semi-natural grassland plots for each of three groups of plants: all vascular plants, insect-pollinated plants and semi-natural grassland specialists. For each plant group, a model was fit with plant richness as response, habitat type as a categorical predictor and municipality as a covariate. To assess model fit, models were compared to a null model containing only an intercept. Models were fit as generalized linear models (maximum likelihood) with Poisson error distribution and log link function suitable for count data. Model diagnostics were checked visually and overdispersion of the data was ruled out.

For each habitat type, total regional observed richness was quantified for the three plant groups in each municipality. Since sampling effort was unevenly distributed across habitat types and municipalities, we also estimated total regional richness (including unobserved species) using the Chao2 richness estimator which estimates richness based on sample size (i.e. number of plots), observed richness and the number of times species occurred in only one or two samples (uniques and duplicates, respectively; Colwell & Coddington, 1994). Compared to other richness estimators, Chao2 richness assigns a relatively high weight to rare species in the system (Gotelli & Colwell, 2001).

2.3.2 | Functional traits

To understand how different habitat types were related to the functional traits of the species assemblages and further investigate the

suitability of habitats as alternative, we used an RLQ test. With the RLQ test, we evaluated the relationship between environmental variables at each plot (R: a plot by habitat type matrix) and the traits of each species (Q: a species by traits matrix) based on the correlation of species across plots (L: a presence/absence plots by species matrix) (Dray & Legendre, 2008). First, the matrices were evaluated independently with a correspondence analysis for the presence–absence data in matrix L and multiple correspondence analyses for both matrices R and Q that contained categorical variables only (i.e. habitat types for R and semi-natural grassland specialists, insect-pollinated plants, growth forms and lifespans for Q). The three matrices were then combined in the RLQ analysis to assess the association between habitat types and species traits and the significance of the functional trait–environment relationship was tested in a fourth corner max test with 10,000 permutations (Ter Braak et al., 2012).

To better understand the dependence of individual species on different habitat types, the distribution of species in the five habitat types was illustrated visually as a network of nodes (habitat types and plant species) connected by links (observed presence of species in each habitat type). The strength of the links was quantified as the number of plots each species was observed in weighted by the relative sampling effort (i.e. proportion of all sampled plots) per habitat type.

Statistical tests were performed in R 3.5.2 (R Core Team, 2018). Spatial autocorrelation between plots within municipalities was tested and ruled out with Moran's I tests of model residuals in the vegan package (version 2.5-3; Oksanen et al., 2018). The Chao2 richness estimate was also calculated in the vegan package. Variance explained by generalized linear models was calculated as McFadden's pseudo-R^2 (McFadden, 1973). Post hoc tests for pair-wise comparisons of predicted means (averaged across regions) between habitat types were performed in the emmeans package (Lenth, 2018). The RLQ test was performed in the ade4 package (version 1.7-13; Dray & Dufour, 2007). Network of links between species and habitat types was visualized in the circlize package (version 0.4.5; Gu et al., 2014).

3 | RESULTS

3.1 | Species richness

A total of 228 vascular plant species were observed including 33 semi-natural grassland specialists, 145 insect-pollinated plants and five alien species. No red listed species were found.

Local richness of all plant groups varied with the habitat type (Table 3) and all models were a better fit for the data than null models (all vascular plants: $\Delta AIC = 105.3$; insect-pollinated plants: $\Delta AIC = 109.0$; semi-natural grassland specialists: $\Delta AIC = 178.3$; Table S1). Richness in road verges was at least as high as in semi-natural grasslands across all plant groups (Figure 2). For all vascular plants and insect-pollinated plants, richness in abandoned semi-natural grasslands was similar to semi-natural grasslands, while it was significantly lower for semi-natural grassland specialists. Richness in both forests and permanent grasslands was consistently lower
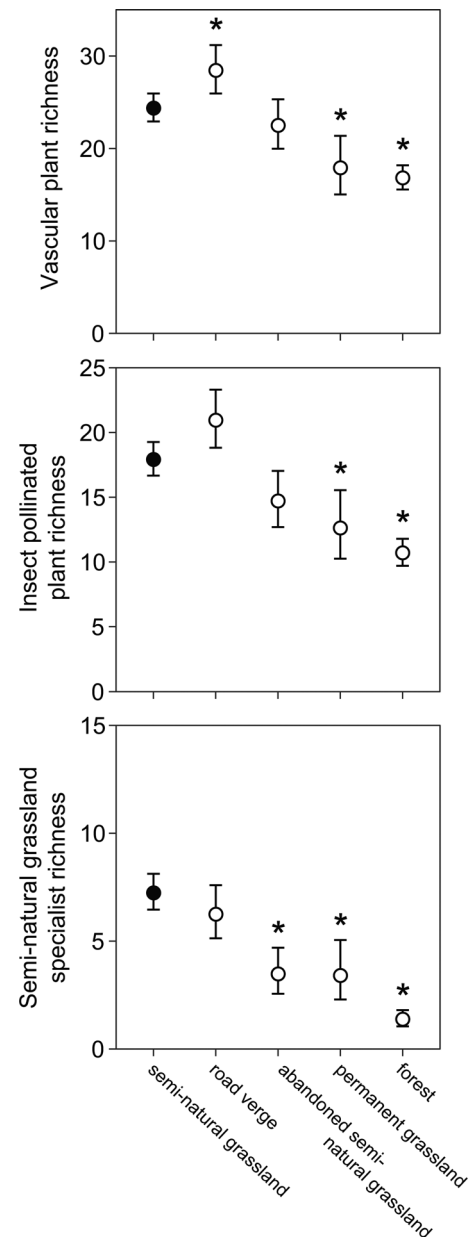

FIGURE 2 Predicted mean richness (± 95% CI) across habitat types. Asterisks indicate significant differences between potential alternative habitats and semi-natural grasslands (filled circles) according to post hoc tests of predicted means.

than that in semi-natural grasslands across all three plant groups (Figure 2).

Semi-natural grassland was the most species-rich habitat type across the two municipalities when considering both observed and estimated total regional richness of all vascular plants (observed richness: 122 in Rauma and 93 in Trondheim; estimated richness ± SE: 195.7 ± 32.1 in Rauma and 127.9 ± 16.9 in Trondheim; Table 2). As expected, estimated total richness of semi-natural grassland specialists was also consistently higher in semi-natural grassland across municipalities (27.8 ± 5.1 in Rauma and 26.9 ± 7.2 in Trondheim), whereas estimated richness of insect-pollinated plants was highest in

TABLE 2 Observed (and Chao2 estimated ± SE) total richness per habitat type

Municipality	Habitat type	All vascular plants	Insect-pollinated plants	Semi-natural grassland specialists
Rauma	Semi-natural grassland	122 (195.7 ± 32.1)	78 (99.6 ± 13.3)	24 (27.8 ± 5.1)
	Abandoned semi-natural grassland	92 (149.9 ± 22.0)	55 (121.7 ± 35.2)	11 (18.7 ± 8.8)
	Forest	92 (120.9 ± 14.6)	59 (97.7 ± 23.6)	9 (14.8 ± 6.8)
	Road verge	98 (128.2 ± 12.9)	65 (74.3 ± 5.7)	19 (26.9 ± 9.0)
Trondheim	Semi-natural grassland	93 (127.9 ± 16.9)	63 (76.4 ± 8.9)	21 (26.9 ± 7.2)
	Permanent grassland	63 (97.0 ± 16.0)	47 (76.6 ± 15.9)	12 (17.3 ± 5.7)
	Abandoned semi-natural grassland	53 (72.2 ± 10.6)	38 (54.2 ± 10.4)	8 (8.0 ± 0.0)
	Forest	76 (107.6 ± 14.7)	49 (66.1 ± 9.8)	6 (6.9 ± 2.1)
	Road verge	84 (123.1 ± 16.9)	64 (92.1 ± 13.8)	14 (16.3 ± 3.1)

Note: Habitat types are ordered within municipalities by estimated richness of all vascular plants. Total observed richness in Rauma is 186 and in Trondheim 165.

TABLE 3 Relationship between plant richness and habitat type and municipality

Model	Predictor	df	Chi square	*p*-value	Pseudo-R^2
All vascular plants	Habitat type	4	95.9	<**0.001**	0.43
	Municipality	1	18.6	<**0.001**	
Insect-pollinated plants	Habitat type	4	111.7	<**0.001**	0.45
	Municipality	1	8.2	**0.004**	
Semi-natural grassland specialists	Habitat type	4	187.9	<**0.001**	0.56
	Municipality	1	1.1	0.30	

Note: Significant main effects ($p < 0.05$) are highlighted in bold.

abandoned semi-natural grassland in Rauma (121.7 ± 35.2) and road verge in Trondheim (92.1 ± 13.8) (Table 2).

3.2 | Functional traits and species composition

A large proportion of the overall variation was explained by the first axis in the RLQ (covariance explained between plant traits and habitat type was 92.67% for axis 1 and 4.14% for axis 2) and plant species traits were significantly related to habitat type (*p*-value < 0.001) (Figure 3). Along axis 1, explaining most of the overall variation, the habitat with species composition most similar to semi-natural grassland was permanent grassland, followed by road verge, while species composition in forest was least similar to semi-natural grassland (Figure 3a). Semi-natural grassland specialists, graminoids and herbs were associated with semi-natural grassland, permanent grassland and road verge habitats along the first axis (i.e. habitats and functional identities with positive values along the first RLQ axis; Figure 3a,b). This included semi-natural grassland specialists such as *Sagina procumbens*, *Plantago lanceolata*, *Plantago media* and *Hieracium lactucella* (Figure 3a,c). As expected, dwarf shrubs, ferns, trees/shrubs and non-specialist plants were most strongly associated with forests and abandoned semi-natural grasslands (i.e. habitats and functional identities with negative values along the first RLQ axis; Figure 3a,b). Plants associated with these habitats included species in the Salix genus (e.g. *Salix arbuscular*, *Salix caprea*, *Salix hastata*, *Salix myrsinifolia*, *Salix phylicifolia*; Figure 3a,c). The pollen vector characteristics were only weakly related to habitat type along both axis of the RLQ (Figure 3b). Annual plants were most strongly associated with semi-natural grasslands as the only habitat present in the upper right quadrant of the plot (Figure 3b).

High overlap in occurrence of semi-natural grassland specialists between semi-natural grassland and road verge (Figure 4) illustrates the importance of road verges as alternative habitat for these specialists. Widespread specialists (i.e. occurring across many plots as indicated by size in Figure 4) were more commonly found in semi-natural grasslands and road verges than any other habitat type, including several insect-pollinated plants (e.g. *Achillea millefolium*, *Bistorta vivipara*, *Campanula rotundifolia* and *Knautia arvensis*; Figure 4). Twenty-seven species were only found in semi-natural grasslands (Table S3) including seven semi-natural grassland specialists (*Euphrasia frigida*, *Sagina procumbens*, *Plantago lanceolata*, *Plantago media*, *Thymus pulegioides*, *Thlaspi caerulescens* and *Hieracium lactucella*) that only occurred in few plots (Figure 4). The occurrence of insect-pollinated plants in semi-natural grasslands and road verges is illustrated in Figure S1.
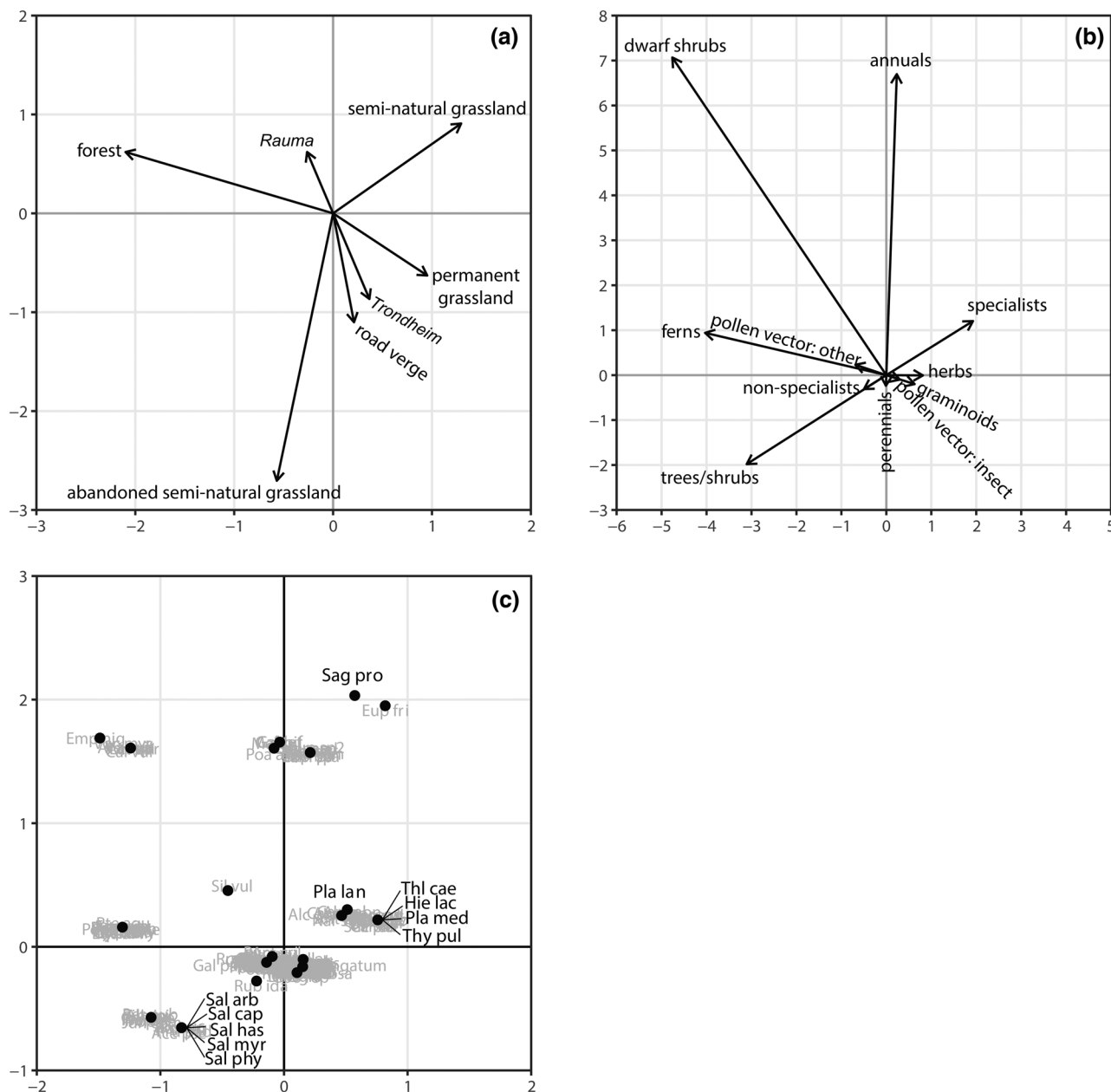
FIGURE 3 Coefficients for (a) environmental and (b) plant characteristic variables and (c) species scores along the first two RLQ axes. There is a high overlap in the occurrence of plants in relation to environment and traits (overlapping black points with species names illustrated in grey) due to the many categorical variables included in the analysis. Select species names are highlighted in black. See Table S3 for explanation of abbreviated plant names.

4 | DISCUSSION

About 10% of the vascular plants, including several semi-natural grassland specialists, were present only in semi-natural grasslands. Our results therefore suggest that no wide-spread, alternative habitat can fully substitute semi-natural grasslands, a rare and fragmented habitat type, because they do not host all the plant species associated with semi-natural grassland. However, species composition in semi-natural grasslands was most similar to composition in permanent grasslands and road verges. This indicates that these habitats can act as alternative habitat for some of the vascular plants associated with semi-natural grasslands. In contrast to permanent grasslands, road verges had a high richness of both semi-natural grassland's habitat specialist and insect-pollinated plants and is therefore the most promising alternative habitat for the plant community. We found semi-natural grasslands specialist species in all habitats studied. This means that even if some habitats only host few habitat specialists from a threatened habitat, the combination of different habitats in a heterogenous landscape may be important for metapopulation dynamics of habitat specialists.
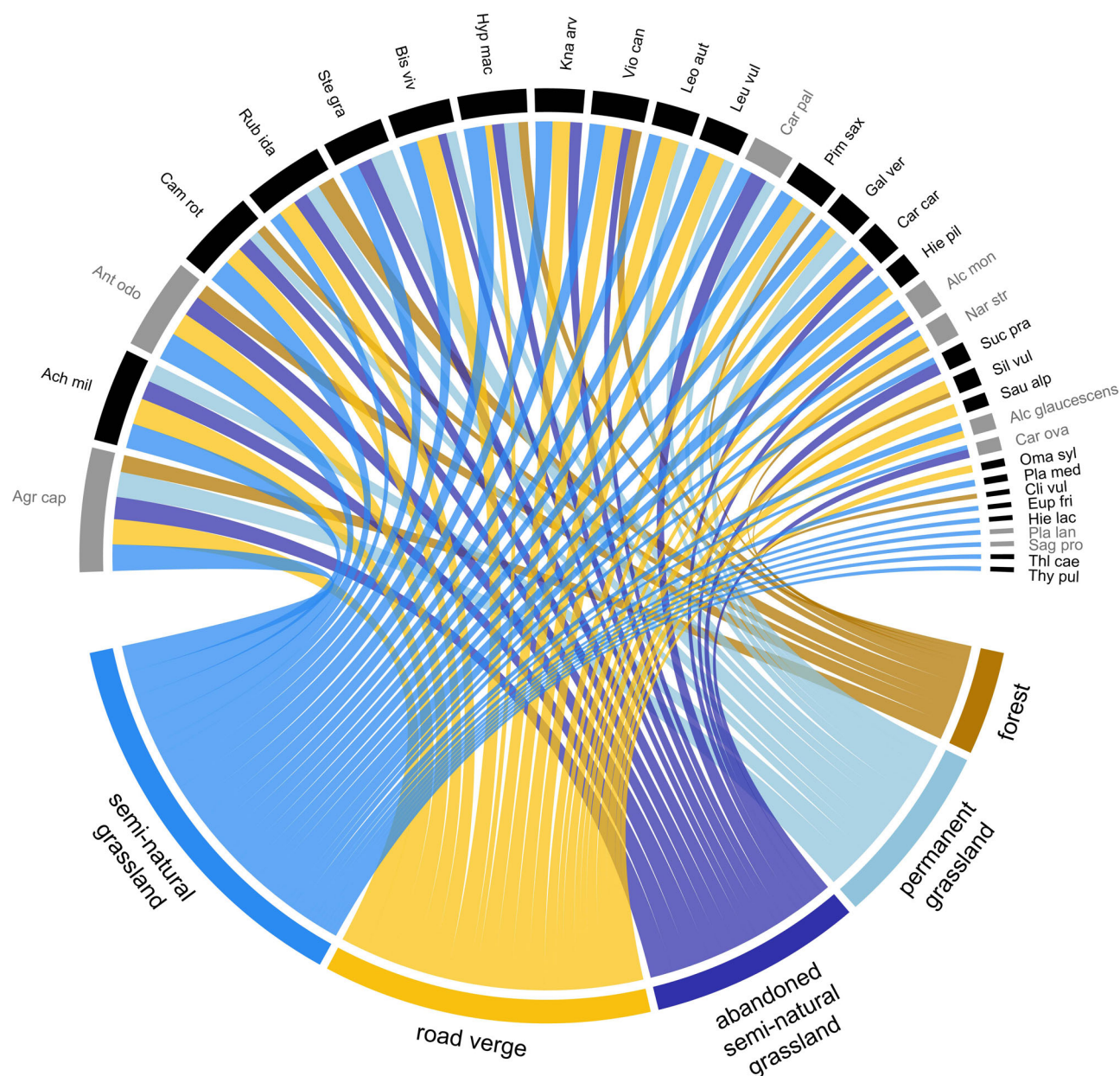
FIGURE 4 Occurrence of semi-natural grassland specialists (top) in five habitat types (bottom) illustrated visually as a network of interactions between habitats and plants. Insect-pollinated plants are indicated in black. Bars and links are sized by the square root of the relative occurrence of species per habitat type (i.e. how many plots a species occurred in) weighted by the relative sampling effort in each habitat type. The square root was used to make rare occurrences more visible. See Table S3 for explanation of abbreviated plant names.

Permanent grasslands had a low total species richness across the landscape but a high overlap in species composition with semi-natural grasslands which indicates that permanent grasslands due to homogenization only function as alternative habitat for a fraction of plant species. The main reason for the difference in species composition between semi-natural grassland (extensive management) and permanent grassland (intensive management) is different management between the habitats. Habitat requirements for grasslands species are fulfilled by pre-cultural disturbances such as fire and large ungulate grazing. Traditional agriculture in semi-natural grasslands mimics this disturbance that is now lost and carries biodiversity forward

(Middleton, 2013). High species richness in semi-natural grasslands is therefore a result of the long history of traditional agriculture with extensive management of grazing, haymaking and burning that has created this ecosystem (Crumley et al., 2018). Instead of an extensive management regime with one or two usages (grazing or cutting) per year, as in semi-natural grassland, the high intensity management in permanent grasslands with several usages, more fertilization and re-seeding are leading to lower stand height and reduced structural diversity. This prevents several plant species from flowering and setting seeds (Dengler & Tischew, 2018). There has been a strong trend in Europe toward changes from extensive to intensive management,

resulting in loss of semi-natural grasslands and establishment of the more intensified permanent grasslands (Veen et al., 2009). Land-use intensification is one of the largest threats toward local biodiversity and is causing multitrophic homogenization of grasslands communities and a loss of specialist species (Finderup Nielsen et al., 2019; Gossner et al., 2016).

Road verge habitats had the highest richness of vascular plants, even higher than semi-natural grasslands that are usually regarded as biodiversity hotspots (Öckinger & Smith, 2007; Squires et al., 2018; Veen et al., 2009; Wilson et al., 2012). The higher species richness in road verges compared to semi-natural grasslands can be attributed to more forest species (trees/shrubs, ferns and dwarf shrubs) occurring in road verges than in semi-natural grasslands where trees and shrubs are browsed or manually removed to increase fodder quality (Wehn et al., 2017). Similar richness and, more importantly, a large overlap in composition of semi-natural grassland specialists between semi-natural grasslands and road verges indicate that road verges are suitable as alternative habitat. Other studies have also shown new, open green infrastructure such as road verges, forest clear-cuts and power line corridors to function as alternative habitats or refuges for several species groups including birds, butterflies, insect and plants typically associated with agricultural landscapes and grasslands (Auestad et al., 2011; Auffret & Lindgren, 2020; Berg et al., 2016; Eldegard et al., 2017; Oki et al., 2021; Ram et al., 2020; Steinert et al., 2020; Villemey et al., 2018). High species richness of both plants (Auestad et al., 2011; Auffret & Lindgren, 2020; Jantunen et al., 2007) and insects (Phillips et al., 2019; Valtonen et al., 2006) in road verges is a result of low-intensity management, creating open, treeless vegetation resembling semi-natural grasslands. In addition, Auffret and Lindgren (2020) showed that road verge plant diversity is related to road age and reported long time lags in establishment of grasslands communities in road verges. Road verges in our study were not fertilized or sown and were only cut once or twice in late summer. Proper management effort is necessary for road verges and other successional habitats to have nature conservation potential for farmland species (Auestad et al., 2011; Auffret & Lindgren, 2020; Steinert et al., 2020).

The advantage of road verges, and other green infrastructure habitats, is that they are widespread and provide a large total area available for semi-natural grassland specialists and insect-pollinated plants in the landscape. They can also be important corridors that can increase connectivity between remaining semi-natural grasslands and contribute to metapopulation dynamic. As proposed by Lindborg et al. (2014), species-rich habitats such as road verges should be regarded as part of the semi-natural grassland network analogues to metapopulations. Road verge management should therefore be considered in conservation measures that safeguard biodiversity associated with semi-natural grasslands.

When extensive management in semi-natural grasslands ceases, the species composition will change with succession from semi-natural grassland, over abandoned semi-natural grasslands, toward forest (Dengler & Tischew, 2018). Here, we found abandoned semi-natural grasslands to have few semi-natural specialists compared to semi-natural grassland. Other studies have reported a high richness of semi-natural grassland specialists in both abandoned grassland (Cousins, 2006; Cousins & Eriksson, 2001; Hamre et al., 2010; Waldén et al., 2017) and forest (Edvardsen et al., 2010; Hamre et al., 2010). This difference is likely a result of varying land-use history and succession stages in the transition from semi-natural grassland to forest habitat where early successional stages have a larger number of remaining semi-natural grassland species compared to late successional stages. Forests in our study had both a low species richness and a low overlap in species composition and functional traits with semi-natural grasslands and are not a likely candidate as alternative habitats. However, late succession forest should not be overlooked as important for species adapted to open agricultural landscapes because this habitat can have other ecological functions such as nesting sites for pollinators (Proesmans et al., 2019).

In this study, we have explored species patterns and not the distribution mechanism that must take place for habitats to function as stepping stones. To what extend grassland species use alternative habitats to move between fragmented semi-natural grasslands is therefore not determined. Dispersal from source populations in primary habitats are important for establishment of specialist species in alternative habitats (Matsumura & Takeda, 2010; Winsa et al., 2015). Given that road verges in the study areas were not sown with semi-natural grasslands specialist species when the roads were established, these species will have dispersed from other patches to establish there over time. This indicates that there is movement of individuals between semi-natural grassland and road verges in the study areas and that road verges contribute to metapopulation dynamics in the landscape, functioning as stepping stones for the semi-natural grassland specialists.

Richness of insect-pollinated plants was similar in semi-natural grasslands, road verges and abandoned semi-natural grasslands. Whether this also results in high abundance of floral resources will depend on local environmental conditions and management practices. Road verges can contain abundant floral resources for pollinators (Phillips et al., 2019) and may even have higher richness and abundances of pollinators than semi-natural habitats (Cole et al., 2017). Their quality as habitat, however, depends on management practices including mowing regime (Phillips et al., 2019). In abandoned semi-natural grasslands, the occurrence of early flowering trees and shrubs can provide important resources in spring, for example for bumblebee queens (Inari et al., 2012). Alternative resources, such as nesting and overwintering sites, may also influence pollinator populations at a landscape scale (Thomson & Page, 2020). Hence, a heterogenous and dynamic landscape including both open managed habitats rich in flowering plants and early successional habitats rich in shrubs and trees provides floral resources throughout the season, as well as hiding places. Both seasonal variation in floral resources and spatial variation in nest sites need to be considered to fully evaluate the quality of these wide-spread, alternative habitats for pollinator communities. While road verges are recognized for their potential to contribute to pollinator conservation (Phillips et al., 2020), less attention has been given to semi-natural grasslands that have lost their quality due to abandonment or intensification. There is, however, a restoration potential of

abandoned semi-natural grasslands (Waldén et al., 2017) and targeted management effort to restore plant communities in this habitat could contribute to pollinator conservation in this type of landscape in the future.

5 | CONCLUSION

In a changing modern agricultural landscape, there are few isolated and fragmented habitats available for farmland and grassland species. A study by Aune et al. (2018) showed that almost half of the semi-natural grasslands in a boreal landscape in Norway were lost during the last 55 years. We will never return to the agricultural landscape of 55 years ago which had a high abundance and frequency of semi-natural grasslands (Aune et al., 2018). We therefore need conservation actions that are in line with societal and agricultural transformation and to gain knowledge about how available habitats in agricultural landscape can contribute to biodiversity conservation.

The results highlight that semi-natural grasslands, a threatened habitat, have a unique species composition and certain species are exclusively associated with this habitat in the landscape. Road verges were the most promising alternative habitat for species associated with semi-natural grasslands including habitats specialists and insect-pollinated plants. Widespread alternative habitats, such as road verges, can mitigate the negative effects of land-use change by increasing landscape connectivity and thereby play a crucial role for persistence of habitat specialists associated with threatened and fragmented habitats. Holistic conservation approaches are therefore needed for biodiversity associated with a threatened habitats that include management of the remnant primary patches in combination with conservation practises where potential alternative habitats are prioritized. However, for semi-natural grassland species, the most important conservation action is to implement legislation and manger advice that stop further loss of semi-natural grasslands by either supporting extensive agriculture or management measures that mimic such disturbances when agricultural practices are lost.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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PEER REVIEW

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SUPPORTING INFORMATION

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

Figure S1. Occurrence of insect pollinated plants (top) in road verge and semi-natural grassland (bottom)

Table S1. Model fit (AIC) for the three plant groups. Best fit models are highlighted in bold

Table S2. The percentage cover of area resource classes in the studied municipalities

Table S3. Plant species names and abbreviations with observed occurrence across five habitat types