RESEARCH ARTICLE



Small habitats as sources of food for pollinators and frugivores in fragmented landscapes

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Abstract

Context Habitat loss and land use homogenization cause a decline in biodiversity in agricultural landscapes. Plant community in small landscape features which remain post-land use change (small natural or semi-natural habitats) may overlap with plant community in semi-natural grasslands and buffer species decline in landscapes where little or no grassland remains.

Objectives We explored if small natural or seminatural habitats buffer the decline of semi-natural grasslands when it comes to number of plant species

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Department of Ecology, Environment and Plant Sciences, Stockholm University, 106 91, Stockholm, Sweden e-mail: ove.eriksson@su.se with fleshy fruits and a variety of food resources for pollinators, throughout the vegetation season.

Methods We surveyed plants in grasslands and small habitats in five agricultural landscapes; 13 semi-natural grasslands (area 7016–85547 m²), 50 forest edges (area 145–1850 m²) and 130 midfield islets (area 17–4788 m²). We than explored how the richness of plants and plant traits (fleshy fruits, flower morphology and flowering period) are related to habitat type, landscape and canopy cover in the focal habitats.

Results Semi-natural grasslands and midfield islets had the highest richness of plant species and flower shapes compared to forest edges. In addition, midfield islets harboured more species with fleshy fruits. When comparing the plant community on midfield islets with the plant community in forest edges, midfield islets and semi-natural grasslands contributed equally with number of blooming plant species during the seasons. Landscapes that were less intensively used (less crop fields) provided food resources for a higher diversity of pollinators compares to less open landscapes, as there was a higher richness of plant species and flower morphologies. Forest edges were not as valuable to pollinators and frugivores as midfield islets.

Conclusions Small natural or semi-natural habitats can provide food resources to pollinators and frugivores at the landscape scale in fragmented landscapes. More crop field in the landscape had a negative impact on the richness of plants and flower morphologies in the habitats. Forest borders may not be as species rich as midfield islets but are still a part of the green infrastructure in the landscape. Particularly, in intensively managed landscapes, small natural habitats can contribute to landscape plant diversity and have a complementary function to each other, but this does not fully compensate for the loss of seminatural grasslands.

Keywords Floral traits · Forest edge · Functional diversity · Habitat complementary · Midfield islets · Small habitat · Green infrastructure

Introduction

Land use change is a major global threat to speciesrich habitats formed by human management regimes (Haddad et al. 2015; Jaureguiberry et al. 2022; Rockström et al. 2023). Changing agricultural practices and an increase in commercial forestry has led to a decrease in European semi-natural grasslands and deciduous forest habitats (Lindborg et al. 2012; Cousins et al. 2015; Schulp et al. 2019). The loss of open and semi-open areas and the resulting landscape homogenization has caused a change in landscape species composition in several taxa, including plants and important associated pollinators (Weibull et al. 2003; Butler et al. 2010; Cameron et al. 2011; Vanbergen et al. 2013; Berg et al. 2015).

Functional diversity is fundamental for ecosystem resilience to changes in environmental conditions (Mori et al. 2013). As an effect of diluted biodiversity and weakened connectivity between habitats, landscape changes, loss and fragmentation of habitats therefore weaken essential ecosystem functions such as pollination and seed dispersal (Tscharntke et al. 2005; Auffret et al. 2017). Loss of plant diversity in agricultural landscapes has been shown to reduce ecosystem functions provided by plant communities in the landscape, as multifunctionality depends upon high plant trait diversity (Hautier et al. 2018).

European agricultural landscapes often contain various small plant species-rich natural or seminatural habitats, such as midfield islets, forest edges, road verges, field and pasture margins, stone walls and hedgerows (Valdes et al. 2015; Poschlod and Braun-Reichert 2017; Smart et al. 2017; Brunet et al. 2021). Small natural habitats may act as refuges for plants which thrive in semi-natural grasslands e.g., many deciduous trees and shrubs (Smart et al. 2006; Lindgren and Cousins 2017; Hooftman et al. 2021), and for animals for foraging and nesting (Smart et al. 2000; Öckinger and Smith 2007; Auffret et al. 2017).

The contribution of such small natural habitats to the landscape functional diversity is poorly known. Available landscape floral resources have been related, for example, to pollinator richness (Balfour et al. 2018). If different types of small natural habitats support different subsets of semi-natural grassland plant communities, it is possible that a variety of small natural habitats may complement each other to maintain functional diversity at the landscape scale. Furthermore, there might be a seasonality of nectar/ pollen supply depending on habitat type, thus the value to pollinators might change during the growing season (Kudo et al. 2008; Eeraerts et al. 2021). For example, under a canopy of deciduous trees, many species flower early, before canopy closure, while plants in more open habitats flower later in season (Dion et al. 2017). Understanding the differences and similarities in functions provided by semi-natural grasslands and small natural grassland habitats will thus be helpful for future management of agricultural landscapes to prevent further loss of ecosystem functions.

Plants attract insects with flowers of different colors, scents and shapes, with higher plant species richness also increasing the richness of pollinating insects (Ebeling et al. 2008; Sutter et al. 2017; Wood et al. 2017). Hence, variations in flower morphology are vital for the type and diversity of the supported insect community (Zhang et al. 2016). This also generates positive feedbacks with biodiversity, since an increased richness of pollinators increases the possibility to promote viable plant populations and thus promote plant species diversity.

A functioning plant-dispersal vector interaction promotes connectivity between suitable habitats and is important for landscape biodiversity (Auffret et al. 2017). Co-evolutionary interactions between plants with fleshy fruits and frugivores has led to a dependence upon frugivorous animals for long distance seed dispersal (McConkey et al. 2012) and are hence crucial for the dispersal of fleshy fruit bearing plants in fragmented landscapes (Pérez-Méndez et al. 2017). The importance of an effective plant-dispersal vector interaction increases with isolation and loss of suitable habitats for the species in the landscape (McConkey et al. 2012). If the interaction between plants and frugivores or pollinators decreases to a certain level, e.g., by loss of habitat connectivity or dispersal vectors, this will affect seed and gene flow between landscape populations, increasing their vulnerability to stochastic extinctions (Naaf et al. 2021).

Additionally, the occurrence of plants adapted to open/semi-open conditions, including several trees and shrubs dispersed by species consuming fleshy fruits, requires the presence of suitable open/ semi-open habitat (McConkey et al. 2012; Cazetta and Fahrig 2021). Plants adapted to open/semi-open conditions will not grow optimally, and thus not set much fruit, in a dense forest as they need more light to thrive (Eckerter et al. 2019; Choi 2021). Hence canopy cover in the local habitat and openness in the surrounding landscape are expected to influence the species and trait composition from small natural habitats e.g., an increased species richness, with semiopenness, and therefore a greater trait diversity. With an increased trait diversity, more ecosystem functions can be expected in the landscape (Hautier et al. 2018).

In this study, we examined the plant community in semi-natural grassland and two types of small natural/ semi-natural habitats that are remnant from grasslands; midfield islets and forest edges in agricultural landscapes with little semi-natural grassland left. We specifically ask;

Does plant community (species richness, richness of different flower morphologies, and richness of species with fleshy fruits) in small natural/ semi-natural habitats overlap or complement each other and is the supported plant richness comparable to that of seminatural grasslands?

Does the richness of species flowering in different periods during the summer vary in the three habitat types?

Does landscape land use intensity (amount of crop field) and local habitat openness (canopy cover) affect the richness of plant species, including the richness of flowering morphologies represented in the communities, and the richness of species with fleshy fruits in the focal habitats?

We expect semi-natural grassland to have more plant species with more different flower shapes, compared to small natural/ semi-natural habitats. Midfield islets is expected to hold a higher species richness than forest borders as midfield islets are more open (but still semi-open) than forest edges. Forest edges may have more spring flowering plants and less flowering plants in mid and late season due to a denser canopy with less light reaching the ground, compare to semi-natural grasslands and midfield islets. In landscapes with more semi-open habitats, we expect species richness in small natural habitats to be richer in plants, morphologies and species with fleshy fruits as a larger amount of semi-open habitats enhance plant dispersal and hold more species compare to a landscape with less semi-open habitats.

Methods

Study region

The study region was located in south- Eastern Sweden (central point coordinates 59°35'09"N and 17°37'15" E). Mean annual temperature is 5-6 °C and mean annual precipitation in the region is 500-600 mm (SMHI 2017). The growing season in the study area is from late April to October-November. The region consists mainly of coniferous and mixed forest, arable land and lakes, where arable land occurs in valleys on finer soils and forest on coarser soils higher up in the terrain. The dominant tree species are Norway spruce (Picea abies ((L.) H. Karst), Scots pine (Pinus sylvestris L.), birch (Betula pendula and pubescens L.) and European aspen (Populus tremula L.). Most forests are managed coniferous forests where the field layer has few plant species (Cousins and Eriksson 2001).

The long continuity of livestock grazing and haymaking has had a large positive impact on the species pool of plants in the region (Eriksson and Cousins 2014). Since the late nineteenth century, a predominant part of pastures and meadows has turned into forest or crop field, and the landscape is now more homogeneous than 150 years ago (Cousins et al. 2015).

Today, only a fraction of species-rich semi natural grasslands remains resulting in fragmented landscapes with crop fields surrounded by planted coniferous forests (Cousins et al. 2015). Though, remining small natural or semi-natural habitats in fragmented landscapes, can host remnant plant populations long after grassland management ceases (Eriksson 1996; Cousins and Eriksson 2001; Lindgren and Cousins 2017; Deák et al. 2021).

In this study, we selected two different types of small natural habitats, common in the region, 'midfield islets' and 'forest edges'. Midfield islets are habitats with a thin soil layer on a core of bedrock and boulders surrounded by crop field. As such the soil is often nutrient poor and susceptible to drought. Midfield islets are small (less than 0.5 ha) and have therefore never been planted with trees but natural tree cover can range from relatively open to completely overgrown, with varying tree species composition.

Coniferous trees are usually planted adjacent to the crop field, with the edge consisting of a very homogeneous structure and with few tree species. Forest edges has varying soil moisture and soil depth, face open crop field on one side and dense, managed coniferous forest on the other side. In some locations however, edges contain naturally dispersed deciduous trees and shrubs and a varying proportion of gaps where more light demanding plants and shrubs may grow, creating more complex forest edges (Lindgren et al. 2018a, b). Both forest edges and midfield islets are sometimes managed, mainly by cutting down coniferous trees, to benefit deciduous trees, shrubs and herbs in the gaps.

Less than 100 years ago, forest and midfield islets were included in the farmers grazing system and managed by mowing or/ and grazing (Cousins and Eriksson 2001). Today, both habitat types are known to have remnant populations of typical grassland plant species (Lindgren and Cousins 2017; Lindgren et al. 2018a, b), and especially forest edges maintain a diversity of woody species with fleshy fruits (Arnell et al. 2019).

Vegetation sampling

Vascular plant species inventories were conducted in five landscapes of a 10 km radius (Fig. 1). Within the landscapes there is on average 58.0% (SD 4.8) forest, and 25.7% (SD 2.6) crop fields. In each landscape (n=5), 10 forest edges adjacent to crop-fields (Fig. 1), at least 50 m from forest clear-cuts, were randomly selected in ArcGIS 10.2 (ESRI, Redlands CA, USA). The forest edge was defined as the zone dominated by deciduous trees and shrubs between managed coniferous forests to the last shrub or tree before the crop field. Without a border with contrasting trees or shrubs to the planted coniferous forest, we consider the forest to lack a natural habitat in the forest edge and were not used in this study. Color infrared aerial photographs were used to identify the forest edges. The transects for the plant survey was placed in ArcGIS before field work was conducted. As sunlight affect species richness (Erdős et al. 2019; De Pauw et al. 2022) in forest edges we selected 3 forest edges facing south, 3 west, 2 north and 2 east in each landscape to even out the possible confounding effect of aspect between landscapes.

The goal was to sample the complete plant community within each border transect. In a 50-m

Fig. 1 Map showing the five study landscapes in south- central Sweden. The big circle shows one of the study landscapes (n=5) with a radius of 10 km. The small circle shows an example of midfield islet samples (radius 0.5 km) within the study landscape. In total 13 semi-natural grasslands, 50 forest edges and 130 midfield islets were included in the study



transect along each forest edge the presence of all trees and shrub species was recorded. To estimate the size of each forest edge, we measured the width of the habitat every 10 m by identifying the point where the composition of trees and shrubs transitioned from the adjacent forest plantation to the last tree or shrub near the open field. The average of the five sections was set as the depth of the forest edge and the area of the transect was calculated as the depth* 50 m (145–1850 m², mean = 568.6, SD = 408.4).

Within sections of 10 m, a 2×2 m plot was randomly placed to survey the field layer, resulting in five plots per forest edge. All additional plant species in the field layer not found in the plots within the 50-m transect, were noted when slowly walking around within each transect. The canopy openness of forest edge transects was visually classified in the field (4 classes). (1) > 50% canopy cover; (2) 25–50% canopy cover; (3) 10<25% canopy cover and (4)<10% canopy cover.

In each landscape (n=5, radius 10 km), three circular areas (radius 500 m) were randomly selected in areas with crop fields in which all midfield islets were inventoried, in total 130 midfield islets (area 17- 4788 m², mean=670.3, SD=896.2). The plant community in the field layer was sampled using 0.5×0.5 m plots with the number of plots adjusted to the size of each midfield islet (5–25 plots/ midfield islet). All additional plant species in the field layer not found in the plots were noted when slowly walking around the islet, including trees and shrubs. Habitat openness was recorded for each midfield islet using the classes of canopy cover stated above.

The nearest semi-natural grassland to each landscape circle was selected in the database TUVA (http://www.sjv.se/tuva) (area 7016–85547 m², mean 31,810.7, SD=23,845.6), and plant species were surveyed in 25 randomly placed plots $(0.5 \times 0.5 \text{ m})$ in each grassland (N=13 as two semi-natural grassland were shared by two circles). The plot species list was complemented by noting all additional plant species when slowly walking around each habitat, including tree and shrub species.

Habitat openness was recorded for each semi-natural grassland using the classes of canopy cover stated above.

Amount of crop fields in each landscape (n=5) was extracted from Swedish National Land Cover map in 10 m resolution (2018) and land use areas

were calculated in ArcGIS 10.6.1 (ESRI, Redlands CA, USA). The category semi- open land consists of midfield islets and semi-natural grasslands within the five landscapes.

Local canopy cover in the habitat, habitat area and amount of crop fields in the landscape were used as explanatory variables to assess the effects of local and landscape factors on the function of the plant community characteristic's associated with attracting pollinators and frugivorous. Amount of crop field in the landscape is used as a proxy for land use intensity.

Species traits

To attract pollinators a flower can offer nectar and/or pollen as a resource for bees, dipterans and butterflies (Stang et al. 2009). The architectural structure of the flower is often linked to insect pollinator groups that feed on nectar or pollen of that specific flower morphology (Stang et al. 2009; Stefanaki et al. 2015). Although this link is far from straightforward (Ollerton et al. 2009), we believe it reasonable to assume that a higher diversity of flower traits favors a larger range of insects (Zhang et al. 2016; Herrera 2020).

In this study three plant traits were selected; flower morphology, flowering time and production of fleshy fruits (yes or no). The traits were chosen for their potential ecological function of attracting pollinators and frugivores during different time-periods of the growing season. Each species was assigned to a shape according to flower morphology using the Biolflor database (Klotz et al. 2002). The flower morphologies of nectar offering flowers used were; lip, head, bell, funnel, disc, flag and brush. In addition, species noted in the Biolflor database to be pollen rewarding, were assigned to this category independent of flower shape. The number of different flower morphologies found in each sampling unit was used to represent the diversity of pollinator types supported within each habitat. Missing species in the database were given the same classification as species in the same genus. Where this was not available, flower morphology was visually assessed based on drawings and information in a local flora (Mossberg and Stenberg 2010).

Plant species trait databases can be used in conjunction with plant species occurrence data to assess the richness and variety of different traits (such as flower or fruit type) present in specific habitat types, and therefore compare characteristics of the plant community. For each sampling location, we calculated three trait compositional variables; the number of flower morphologies present (total unique flower types present in species found), the total number of species with fleshy fruits (a fruit containing a fleshy tissue, e.g. berries, drupes, rosehips and apples) (Eriksson and Ehrlén 1991; Bolmgren and Lönnberg 2005) (Online Appendix 1), and the number of species present which flower during each of the early (April-May), middle (June-July) or late (August-October) period of the flowering season according to Mossberg and Stenberg (2010). If a species flowers during multiple periods, the species was allocated to all appropriate time periods. Using these trait summary data, we assessed whether the richness of species with different flower shapes, fruit sources and flowering times differs between grasslands, midfield islets and forest edges during the vegetation season (i.e., whether habitat complementarity exists).

Statistical analyses

Plant community

To investigate the possible overlap in vascular plant communities (all species in the patch, trees and shrubs species) in semi-natural grassland and the small natural habitats visually, a non-metric multidimensional scaling (NMDS) in two dimensions with Bray–Curtis dissimilarity was used. Bray–Curtis dissimilarity considers differences in number of species in the proportions of patches in which the species occurs. NMDS uses ranked dissimilarities in the comparison of dissimilarities of samples.

Subsequent analyses were performed to determine whether there is a significant difference in species on alpha (plot) level between the three habitat types, Adonis (permutations=999, PERMANOVA, package; Vegan R) and "betadisper" (package; Vegan, R). Adonis is a method for comparing species distributions via community data matrices by analysing the variance within groups to compare between groups. This method calculates squared deviations from the centroids of the multivariate data set for each point and performs a significance test on sequential sums of squares from permutations of the raw data. "Betadisper" is a distance-based, multivariate test for homogeneity of multivariate dispersions (Anderson 2006), and checks for potential differences in the between-site variation in the plant community across habitat types.

Richness of plants, flower morphologies, and plants with fleshy fruits

To analyze differences in species richness, mean richness of flower morphologies, and fleshy fruits across different small natural habitat types and semi-natural grasslands, generalized linear mixed models using template model builder (GlmmTMB, glmmTMB; R package, CRAN) (Brooks et al. 2017, McGillycuddy et al. 2025), with landscape ID used as random factor, were used to create models for each morphology type, as well as one model for the richness of morphologies, with habitat type and habitat area (logtransformed) as explanatory variables. To be able to identify which habitat types differed in plant richness, morphology richness, richness of plants with fleshy fruits and each morphology type separately, post-hoc pairwise comparisons of means test were performed (emmeans; R package, CRAN). In the emmeans function for generalized models, the estimates of the contrasts between groups of habitats are calculated. As the habitat area and sampled area varied between sites and habitat type, habitat area (log transformed) was included as a predictor and sampling area (log transformed) was included as an offset term in the model.

The same method was used to investigate potential differences in the number of species flowering in different flowering times during the vegetation season between midfield islets, forest edges and semi-natural grasslands throughout the vegetation season.

Local habitat openness and amount of crop fields in surrounding landscape

Generalized linear mixed models using template model builder (GlmmTMB, *glmmTMB*; R package, CRAN), with landscape ID used as random factor, were used to investigate the effect of local canopy cover (class 1–4, see methods), focal habitat area (log- transformed), habitat type and amount of crop field in the surrounding landscape (n=5, radius 10 km), on richness of species, flower types and species with fleshy fruits in the habitats.

Variance inflation- tests (VIF) were used to test for multicollinearity between explanatory variables (Zuur et al. 2010). Maximum threshold value of VIF for explanatory variables to be included in the models was 2. All explanatory had VIFs below the threshold value and could be used in the same models. The error distribution model was defined as negative binomial as over-dispersion was detected in all models. As the sampled area varied between sites and habitat type, sampling area (log- transformed) was included as an offset term in the models.

Results

We found a total of 335 different plant species in the field layer (154 in forest edges, 273 on midfield islets and 272 in semi-natural grasslands), 29 shrub species (22 in forest edges, 23 on midfield islets, 22 in semi-natural grasslands) and 24 tree species (21 in forest edges, 19 on midfield islets, 22 in seminatural grasslands) (Table 1, see species list Online Appendix 1). Semi-natural grassland had the highest number of species with the flower morphologies bell, disc and lip and 39 pollen- or nectar rewarding plant species exclusively present in semi-natural grasslands. Midfield islets had the highest number of species with the flower morphologies flag and funnel (Table 1) and 34 pollen- or nectar rewarding plant species exclusively present in midfield islets. The number of pollen- or nectar rewarding plant species exclusively present in forest edges was 14. Semi-natural grasslands had the highest number of species flowering early in the season (April–May, average 32 species/ grassland) during mid-season (June-July, average 64 species/ grassland) and late season (August- October, average 40 species/ grassland). Midfield islets had nearly the same number of species flowering in early season (midfield islets average 11 species/ midfield islet and 10 species/ forest edges) more species flowering than forest edges during mid-season (27 species/ midfield islets and 11 species/ forest edges) and late season (17species/ midfield islets and 4 species/ forest edges).

Forest edges had the highest percentage of canopy cover comparing to semi-natural grasslands and midfield islets but the forest border had one species less with fleshy fruits than midfield islets and seminatural grasslands (Table 1).

Plant community

The plant community on midfield islets were more similar to the plant community in semi-natural grasslands than forest edges was, according to the NMDS (Fig. 2). The Adonis test ($R^2=0.21$, p=0.001) showed a difference in plant communities between the habitat types (multivariate dispersions among the habitat types betadisper; p < 0.001) among the habitat types were heterogeneous (betadisper; p < 0.001).

Flower morphology	Semi-natural grass- Midfield islets lands		Forest edges	
Bell	21	18	17	
Brush	3	3	3	
Disc	93	89	49	
Flag	19	21	15	
Funnel	2	4	1	
Head	39	42	25	
Lip	34	30	16	
Pollen rewarding	21	21	16	
No. species with fleshy fruits	31	31	30	
Habitat canopy cover				
1 (>50% canopy cover)	0	45	76	
2 (25-50% canopy cover)	23	11	16	
3 (10<25% canopy cover)	54	10	10	
4 (<10% canopy cover)	23	35	0	

Table 1 Number of species of specific flower shapes (bell, brush, disc, flag, funnel, head, lip and pollen rewarding), with fleshy fruits and percentatage of canopy cover in the habitats: semi-natural grassland (n = 13), mid-field islets (n = 130) and forest edges (n = 50) Fig. 2 The plant communities of semi-natural grassland, forest edges and midfield islets (NMDS, stress=0.18, dim=2, distance=Bray-Curtis dissimilarity) (Adonis, permutations=999, R^2 =0.21, p-value=0.001)





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Richness of plants, flower morphologies, and plants with fleshy fruits

When analysing differences in species richness between the habitat types with general linear models and pairwise comparisons of means, the average species richness did not differ in midfield islets and seminatural grassland. Forest edges had significantly less species that midfield islets and semi-natural grasslands for an equivalently sized area (Fig. 3, Online Appendix 2). Average richness of flower morphologies (lip, head, bell, funnel, disc, brush, flag and pollen rewarding) was lower in forest edges compared to midfield islets and semi-natural grasslands (Pairwise comparisons of means, Fig. 3, Online Appendix 2).

Semi-natural grasslands had on average more species with fleshy fruits (mainly trees and shrubs) when accounted for sampled area, compared to forest edges but midfield islets had even more plant species with fleshy fruits compared to forest edges and semi-natural grasslands (Fig. 3). A midfield islet is never larger than 0.5 ha which limit the contribution of midfield islets to pollinators and frugivore. The contribution of semi-natural grassland will be larger due to larger habitat area according the species-area relationship (Arrhenius 1921).

Semi-natural grasslands and midfield islets had the most diverse flower morphologies among the plant species (seven out of eight possible morphologies) (Fig. 4). Forest edges had fewest species of all morphologies except for funnels that were as few in forest edges as in semi-natural grasslands. Bell, disc, funnel, head shaped and pollen rewarding flowers were more frequent in midfield islets than in both semi-natural



-2

dictor and sampling area (log transformed) as offset. The letter above each box indicates significant differences between the habitat types according pairwise comparisons of means

2



Fig. 4 The three habitat types were holding different number of species with specific morphologies. Figures are based on pairwise comparisons of means on Generalized linear models with area of the habitat (log transformed) as a explanatory fac-

grasslands and forest edges. Disc was the most common flower shape among species in all three habitat types (Fig. 4, Online Appendix 3).

Seasonal variation in offering a diversity of flowering plant species

Semi-natural grassland and midfield islets had more flowering species compared to forest edges during the whole growing season (Fig. 5). Comparing the small natural habitats with each other, midfield islets were more important as a food resource compare to forest edges. Midfield islets and semi-natural grassland did not significantly differ in number of flowering species in any part of the growing season (Online Appendix 4) and were as important as semi-natural grassland when it comes to offer a richness of flowering plants in throughout the growing season.

Local habitat openness and crop field amount in surrounding landscape

We found that habitats in landscapes with more crop fields had a lower plant species richness and lower

tor in the model and sampling area (log transformed) as offset. and. The same letter above each box indicates significant differences (p < 0.005) between the habitat types according multiple comparisons of means (Online Appendix 2)

flower morphology richness (Table 2) than landscapes with less crop fields. All habitats in the study had more or less gaps in the tree cover but forest edges had the highest canopy cover of the survaed habitats. The amount of gaps in the tree canopy had no significant effect on richness of plants (Table 2) and flower shapes but had a negative effect on number of plants with fleshy fruits (Table 3).

Discussion

The loss and fragmentation of natural habitats causes losses of biodiversity in managed landscapes (Haddad et al. 2015; Jaureguiberry et al. 2022; Rockström et al. 2023). Grasslands with a long continuity of grassland management have some of the highest plant species richness that can be found in managed landscapes (Wilson et al 2012). Associated to the high plant richness are other organism groups and many ecosystem services. Ancient grasslands together with other natural or semi-natural habitats (Herzon et al. 2022) can form networks of green infrastructure in managed fragmented landscapes (Kimberley et al. 2021). The



Fig. 5 Plait trait distribution in forest edges, midfield islets and semi- natural grasslands based on number of plants species flowering during different times in the growing season (early,

mid- and late season). Pairwise comparisons on means were conducted between the habitat types (Online Appendix 3)

Table 2 Results from generalized linear mixed models using template model builder (GlmmTMB) models of plant species, number of flower morphology types (lip, head, bell, funnel, disc, flag, brush or pollen rewarding) and habitat type (semi-natural grassland (n=13), midfield islet (n=130) or forest edges (n=50)), the area of the focal habitats (log-

transformed), the class of gaps (class 1:>50% canopy cover; 2: $25 \le 50\%$ canopy cover; 3: 10 < 25% canopy cover and 4: <10% canopy cover) within the habitat, and amount of semi- open habitats in the five landscapes (hectars of midfield islets and semi-natural grasslands) within five landscapes

Number of plant species	Estimate	SE	z-value	p-value
Intercept	0.61	0.19	3.17	**
Habitat type midfield islet	2.92	0.05	55.25	***
Habitat type semi-natural grassland	2.72	0.11	24.26	***
Gaps in the focal habitat (%)	< 0.01	0.02	-0.23	n.s
Crop fields in the landscape (hectares)	< -0.01	< 0.01	-2.93	**
Area of focal habitat (hectares)	< 0.01	0.02	0.14	n.s
Number of flower morphologies	Estimate	SE	z-value	p-value
Intercept	- 1.69	0.31	-5.50	***
Habitat type midfield islet	2.44	0.08	28.74	***
Habitat type semi-natural grassland	2.35	0.18	13.15	***
Gaps in the habitat (%)	0.02	0.03	0.64	n.s
Crop fields in the landscape (hectares)	< -0.01	< 0.01	- 1.96	*
Area of surveyed habitat (hectares)	-0.21	0.03	-8.04	***

Landscape was used as random factor in the model. The habitat type forest edge is incorporated in the intercept, and the estimate for the midfield islet and semi-natural grasslands denotes the difference between forest edge and the semi-natural grasslands and midfield islets

*Indicates a significant effect of the variable (*** $p \le 0.001$), (* $p \le 0.01$), (* $p \le 0.05$)

amount of natural habitats (such as ancient grasslands, wetlands and deciduous forests) has decreased by 96% the last 150 years due to agricultural intensification and forestry (Cousins et al. 2015). The small semi-natural habitats can play an important role to uphold landscape diversity and function (Deák et al. 2021). We found that a larger amount of semi-natural habitat in the landscape increased the number of **Table 3** The relation between number of plant species with fleshy fruits in the habitat, and habitat type (semi-natural grassland (n=13), midfield islet (n=130) or forest edges (n=50)), the area of the focal habitats (log- transformed), the class of gaps (class 1:>50% canopy cover; 2: $25 \le 50\%$ canopy cover; 3: 10 < 25% canopy cover and 4: <10% canopy

cover) within the habitat and the hectars of crop field (in the landscapes (n=5)) represented by parameters estimate according to modelling using generalized linear mixed models using template model builder (GlmmTMB) with landscape used as random factor in the model

Number of plant species with fleshy fruits	Estimate	SE	z-value	p-value
Intercept	1.78	1.42	1.25	n.s
Habitat type midfield islet	1.94	0.10	19.72	***
Habitat type semi-natural grassland	0.75	0.25	2.98	***
Gaps in the habitat (%)	-0.18	0.04	-4.13	**
Crop fields in the landscape (hectares)	< - 0.01	< 0.01	-1.34	n.s
Area of habitat (hectares)	0.26	0.05	5.53	***

The habitat type forest edge is incorporated in the intercept, and the estimate for the midfield islet and semi-natural grasslands denotes the difference between forest edge and the semi-natural grasslands and midfield islets

*Indicates a significant effect of the variable (*** $p \le 0.001$), (** $p \le 0.01$), (* $p \le 0.05$)

flowers morphology in small habitats such as midfield islets and forest edges and also in semi-natural grasslands. The plant diversity observed on midfield islets closely resembles that of semi-natural grasslands rather than forest edges, indicating that these habitats are likely a more direct complement to traditional semi-natural grasslands in terms of food provision for a variety of pollinators. In contrast, the unique, nonoverlapping diversity found in forest edges underscores their potential role in supplying resources, within networks of natural and semi-natural green infrastructure. This highlights the importance of considering how multiple complementary habitat types can be managed together to enhance overall landscape diversity, especially in light of varying management practices, historical influences and abiotic conditions.

Species richness and flower morphology richness varied to some extent between the two small habitats. Midfield islets had a higher richness of flower morphologies and had a more similar plant community to semi-natural grasslands than to plant community in forest edges. Forest edges, on the other hand, supported less plant species richness plants, morphologies and plants with fleshy fruits compared to midfield islets, making them less important habitats for the diversity of pollinators and frugivores in agricultural landscapes with less semi-natural grasslands. However, less open forest edges had a higher richness of species with fleshy fruits.

Even though small natural or semi-natural habitats do not harbor as many species as semi-natural grasslands, the small habitats can buffer a decline in species to some extent in fragmented landscapes. For insect pollinated plant species in small habitats an increasing connectivity of habitats will prevent population extinctions, and the same holds for all plant species subject to dispersal limitation (Hooftman et al. 2016).

A community with more plant species, providing a diversity of nectar and pollen resources, has a greater potential to provide food resources to a more diverse insect community (Potts et al. 2003; Balfour et al. 2018). It is also important that there are plants flowering during the whole vegetation period to maintain plant- pollinator interactions. Therefore, a variation of the timing of peak flowering among plants in the landscape is essential. Contrary to our hypothesis, we found that forest edges had lower average number of plant species flowering in spring compared to midfield islets. Still, many of spring flowering plant species are trees and shrubs with a high abundance of flowers. Forest edges are therefore likely to provide an important source for pollen and nectar feeding insects early in the vegetation season, together with midfield islets and semi-natural grasslands. The high relative importance of midfield islets versus forest edges highlights the that some small natural or seminatural habitats may be more important than others, in managed landscapes. Although each of the habitats provide benefits to pollinators and frugivores, the presence of both habitat types together in a landscape is important for provision of food for pollinators and frugivores throughout the vegetation season in landscapes with less intact habitats of semi-natural grasslands.

Small natural habitats may play a supporting role for e.g., pollinators, in enhancing the contribution of species from semi-natural grasslands to the landscape's total species pool of plants by providing additional potential habitat area for different subsets of species affected by grassland loss. These habitats are also therefore likely able provide a possible additional food resource to pollinators and frugivores in fragmented agricultural landscapes. However, small habitats are still low in species density compared to semi-natural grasslands, and landscape diversity still likely depends heavily on intact grassland habitat both as a reservoir for more specialized species that rarely grow in small natural habitats and a source sustaining population in nearby small habitats. Nevertheless, dependent on the amount of small natural or semi-natural habitats left in the landscape and the management of them, small habitats may help conserve species and trait diversity at landscape scales.

Small natural or semi- natural habitats within a certain distance from each other is a condition for insects and animals to be able to link habitats together in fragmented landscapes with their function as seed dispersers and pollinators (Orlowski et al. 2016; Auffret et al. 2017). Habitat quality and landscape complexity will affect plant reproduction as the predominant part of plant species needs insects for pollination to avoid pollination failure and sets seeds (Potts et al. 2010; Chi and Molano-Flores 2015).

Recently there is an increasing awareness that small natural and semi-natural habitats can play an important role for preserving and increasing biodiversity and ecosystem services in intensively managed landscapes (Valdes et al. 2015; Lindgren and Cousins 2017; Lindgren et al. 2018b; Deák et al. 2021; Kimberley et al. 2021; Herzon et al. 2022). Small natural and semi-natural habitats have the potential to provide green infrastructure in the landscape that can enhance dispersal and ecosystem services albeit not for the highly specialized habitat specialists (Hooftman et al. 2023). We found that especially midfield islets can provide a richness of plant species and for support a high diversity of fleshy fruits, flower shapes and nectar accessibility during the vegetation season. However, small natural or semi-natural habitats may need to be managed to maintain their richness. By careful, low intensive management i.e., removing dense forest stands light can penetrate down to the field layer. In coniferous dominated landscapes such our study area deciduous trees and shrubs should be promoted which can also enhance the number of flowers as well as fruits and berries. Heterogeneity in the landscape, including different habitat types, but also heterogeneity in environmental conditions within habitats, can increase plant diversity (Brunbjerg et al. 2017; Deák et al. 2021). To reduce the decline of biodiversity in fragmented agriculture landscapes there is a need to increase functional connectivity and to protect the remaining semi-natural grasslands and small natural or semi-natural grassland habitats. A landscape with a diversity of habitat types with a variation in environmental conditions, e.g., openness, have a better chance to be a functioning green infrastructure. That possibility might decrease with time and most importantly, small natural or semi-natural habitats cannot fully replace the multiple functions of larger semi-natural habitats, such as ancient grasslands, wetlands, deciduous forests or other similar fragmented ecosystems.

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Author contributions Jessica Lindgren created the study conception and design. Material preparation, data collection and analysis were performed by Jessica Lindgren. The first draft of the manuscript was written by Jessica Lindgren and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript. The datasets analysed during the current study are available from the corresponding author on reasonable request.

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Data availability No datasets were generated or analysed during the current study.

Declarations

Conflict of interest The authors declare no competing interests. **Open Access** This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

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