RESEARCH ARTICLE

Temporal and spatial heterogeneity of semi-natural habitat, but not crop diversity, is correlated with landscape pollinator richness

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Abstract

1. Enhancing the diversity of mass-flowering crops (i.e. crop diversity) in agricultural landscapes is often proposed as a measure to favour pollinators and pollination, but it is uncertain whether crop diversity enhances pollinator richness on the wide landscape level.

2. Here, we surveyed pollinator communities in semi-natural habitats and mass-flowering crops throughout the whole growing season in 26 agricultural landscapes to examine how the temporal and spatial heterogeneity in semi-natural habitats and crop diversity support pollinator species richness.

3. Crop diversity was unrelated to pollinator richness in the wider landscape, and temporal and spatial heterogeneity in semi-natural habitats were equally important in determining pollinator richness. Surprisingly, the crop pollinator species pool size was a fixed proportion of the landscape pollinator species pool along a 0%–72% semi-natural habitat cover gradient.

4. *Synthesis and applications.* Our results suggest that increasing crop diversity alone does not contribute to maintaining diverse wild pollinator communities in agricultural landscapes and emphasize the key role of temporally stable habitats such as semi-natural habitats to maintain rich pollinator communities.

KEYWORDS
crop diversity, pollinator species richness, mass-flowering crops, pollinator conservation, spatial stability, temporal stability

1 | INTRODUCTION

Agricultural expansion and loss of (semi-)natural habitats are major drivers of pollinator declines (Potts et al., 2010), with associated threats to the pollination services these species provide to wild plant populations (Clough et al., 2014; Martins et al., 2015; Pauw & Bond, 2011) and crop yields (Fijen et al., 2018; Sritongchuay et al., 2020; Webber et al., 2020). However, reversing these trends by converting agricultural fields to semi-natural habitat comes with high opportunity costs (smaller surface productive land) that may not outweigh the benefits of increased productivity (Kleijn et al., 2019). Increasing the diversity of mass-flowering crops is often raised as a promising strategy to complement resources to semi-natural habitats, which ultimately could benefit pollinator biodiversity levels in agricultural landscapes (Fahrig et al., 2011). Whether this approach could work likely depends on the capacity of different crops to sustain complementary diverse pollinator communities, or to supplement the characteristics of semi-natural habitats. However, we know surprisingly little about the potential of mass-flowering crop diversity to support rich pollinator communities (but see Raderschall et al., 2021; Sirami et al., 2019) and about the characteristics in semi-natural habitats that make them so relevant for pollinators. For instance, is semi-natural habitat the main determinant of the diversity of pollinator communities or can (diversity in) flowering crops boost pollinator diversity by adding new and abundant resources? Does this vary over space and time? Do different crop types complement each other and partially provide for different species?

Ecological theory suggests that niche diversity or habitat heterogeneity is a key driver of species coexistence and therefore species diversity (Benton et al., 2003; Chesson, 2000; Reverté et al., 2019). Compared to crops, semi-natural habitats are generally much more heterogeneous, both within and between landscapes, and vary, for example, in the composition of flowering plants and availability of nesting substrates (Williams & Kremen, 2007). In addition to this spatial heterogeneity, the same semi-natural habitats also vary markedly in floral composition across the growing season as early flowering species senesce and are replaced by later flowering species (CaraDonna et al., 2017). This may not only imply that these habitats provide resources for species with different host plant preferences and phenologies (Mallinger et al., 2016), but also results in continuity of resources over time for generalist species that accept a wide range of host plants (Schellhorn et al., 2015). The relative role of temporal and spatial heterogeneity in resource supply in semi-natural habitats is virtually unexplored.

A higher within and between habitat heterogeneity could explain why species diversity in semi-natural habitats is generally higher than in crops (Fijen et al., 2019). Nevertheless, even though the spatial and temporal heterogeneity of floral resources is inherently very limited in crops, each new insect-pollinated crop that is introduced into an agricultural landscape provides a potential new niche. This could mean that agricultural landscapes with insect-pollinated crops support richer pollinator communities than similar agricultural landscapes without insect-pollinated crops. Hence, promoting the

cultivation of different mass-flowering crop types in agricultural landscapes might represent a strategy to boost insect pollinator communities in agricultural landscapes. Indeed, growing a single mass-flowering crop has been found to increase pollinator abundance and richness both locally (Diekötter et al., 2014; Holzschuh et al., 2013) and at the landscape scale (Beyer et al., 2020; Westphal et al., 2003). More recent studies have examined how pollinator abundance and diversity in one insect-pollinated crop depends on presence of other crops with responses differing between pollinator species groups (Aguilera et al., 2020; Martins et al., 2018). Whether flowering crop diversity increases landscape-level pollinator diversity and how this compares to the contribution of semi-natural habitat remains untested.

Here, we address these questions using a dataset of pollinator communities occurring in South-Italian agricultural landscapes in two types of semi-natural habitats and 15 different crops across the entire growing season.

In this study, we evaluate the relative importance of crop diversity and sources of heterogeneity in semi-natural habitats to promote insect pollinator richness in agricultural landscapes. To this aim, we sampled pollinator communities occurring in South-Italian agricultural landscapes in two types of semi-natural habitats and 15 different crops across the entire growing season (i.e. 4 months). We monitored pollinator communities in 26 agricultural landscapes along a gradient of increasing semi-natural habitat cover. We specifically asked (a) Does diversity of insect-pollinated crops contribute to pollinator diversity in agricultural landscapes? (b) How important is temporal heterogeneity in resources compared to spatial heterogeneity in driving pollinator species richness in agricultural landscapes? and (c) Does semi-natural habitat cover moderate pollinator richness similarly in semi-natural habitats and adjacent crops? We addressed these questions using a resampling approach, in which we analysed whether different sampling scenarios (e.g. sampling pollinators in one crop type vs. sampling different crop types; sampling pollinators in different landscapes at the same time vs. sampling pollinators at different times in the same landscape) would result in significant differences in the cumulative species numbers. We mainly focused on cumulative species numbers rather than species densities as this more accurately reflects the landscape-level species pool and enables a better understanding of the contribution of each site or habitat type.

2 | MATERIALS AND METHODS

2.1 | Study design and landscape characterization

The study was conducted in a Mediterranean agricultural landscape located in southern Italy, in the same general region as the study of Fijen et al. (2018). The study area covered approximately 1,400 km² and is dominated by wheat cultivation, but many other crops are cultivated, such as olive, faba bean and chickpea for food and feed, and onion and leek for seed production. In total, 26 study landscapes

(750 m radius) were selected within the region based on a wide gradient of insect-pollinated crop types (0–8 per landscape) and semi-natural habitat cover (from *c.* 0.2%–72% semi-natural area; Table S1). Landscapes were separated from each other by 19 ± 18 km (mean ± 1 *SD*), except for one landscape pair where the borders of the landscape slightly overlapped. However, the radii of the landscapes were above the mean maximum foraging range of most solitary bees, *c.* 200–300 m c.f. (Zurbuchen et al., 2010). Therefore, we decided to keep that landscape pair in the analyses. The centre of 22 landscapes was a mass-flowering focal crop (18 leek hybrid seed production fields and four onion [hybrid] seed production fields). Four landscapes contained no mass-flowering crops. The semi-natural habitat cover for each landscape was quantified via Google earth aerial imagery and initial classifications were validated through field visits. Grasslands, woodlands, fallow arable fields and road verges (i.e. estimated as 1 m wide area along each side of roads) were considered as semi-natural habitats. The sampled herbaceous semi-natural habitats were mostly located at road verges with annual ruderal plants, while woody semi-natural habitats were usually forest edges or hedgerows. The most abundantly flowering species in herbaceous transects consisted of ruderal species of Brassicaceae (e.g. *Diplotaxis erucoides*, *Sinapis arvensis*, *S. alba*), Malvaceae (e.g. *Malva sylvestris*), Papaveraceae (e.g. *Papaver rhoeas*, *Fumaria officinalis*), Asteraceae (e.g. *Anthemis tinctoria*, *A. arvensis*) and Boraginacea (e.g. *Echium plantagineum*, *Borago officinalis*). Flowering woody plants consisted mostly of *Prunus spinosa*, *Crataegus monogyna* and several species of wild roses (*Rosa* sp.). Access to fields was kindly granted by the company Nunhems Netherlands BV (BASF).

2.2 | Pollinator surveys

In each landscape, two important pollinator groups (bee and syrphid pollinators) were surveyed every 2 weeks in semi-natural habitats and each blooming mass-flowering crop during the main growing season (end of March to end of July 2018), resulting in eight rounds per landscape. Standardized transects of 150 m long and 1 m wide (150 m^2) that were subdivided in three 50 m^2 subareas were used, to ensure an even time distribution across the whole transect. Transects were monitored for 15 min pure observation time (i.e. excluding handling time). During surveys, we visually recorded all the observed species interacting with flowers. The pollinator species that could not be recognized in situ, were caught using butterfly nets and identified to species or morphospecies level in the laboratory. For this study, we discarded all the individuals that had not been identified to (morpho) species level (*c.* 6% of individuals). We ascertained that these unidentified individuals did not influence the results because they were few and evenly distributed across habitat types and landscapes (Figure S1). Surveys were conducted with temperatures above 18 degrees Celsius, on sunny and calm days (<5 bft wind), and roughly between 8 a.m. and 5 p.m. (c.f. Fijen & Kleijn, 2017). Days and times of the surveys were randomized across landscapes. This study did not require ethical approval for sampling pollinators.

Within each landscape, semi-natural areas were sampled in each round with two transects in flowering herbaceous vegetation (including pioneer vegetation, grasslands and ruderal vegetation), and with a varying number of transects in woody vegetation (including shrubs and trees). Herbaceous transects were always located in focal areas containing flowers whenever these were locally present. This was achieved by slightly shifting, from one round to the next, the exact location of the transects up to 50 m to the right or the left to avoid sampling sites without flowers and therefore pollinators. The number of woody transects depended on the availability of flowering woody vegetation, and therefore varied between 0 and 2 transects per landscape per round. In total, nine landscapes had no woody vegetation and hence no transects in woody vegetation. During each round, all flowering insect-pollinated crops were surveyed when at least 10% of the flowers were open as even a small percentage of crop flowers represent large numbers of flowers. If there were multiple fields of the same crop in a landscape, we only sampled only one of the fields. For each flowering crop type, we selected one crop field close to the centre of the landscape and located one fixed 150 m^2 transect starting at least 20 m from the edge of the field. Transects in crops were not moved, as variation in flowering stage within crop fields was negligible. Overall, this sampling provided data from 416 transects in herbaceous semi-natural habitats, 179 transects in woody semi-natural habitats and 122 transects in the 15 following insect-pollinated crop types (see also Table S2). The sampled crop types were as follows: basil *Ocimum basilicum*, broccoli *Brassica oleracea* var. *italica*, cauliflower *Brassica oleracea*, chickpea *Cicer arietinum*, dill *Anethum graveolens*, faba bean *Vicia faba*, leek *Allium porrum*, flax *Linum usitatissimum*, lucerne *Medicago sativa*, onion *Allium cepa*, rucola *Eruca vesicaria*, sulla *Hedysarum coronarium*, sunflower *Helianthus annuus*, clover *Trifolium* sp. and vetch *Vicia* sp. All these crops were flowering because they were either used for vegetable/herb seed production (e.g. leek and onion), oil-seed production (e.g. sunflower and flax), for food or feed (e.g. faba bean and chickpea), or because they had not yet been harvested for animal feed (e.g. sulla, clover and vetch).

2.3 | Analysis

To analyse the data, we used a resampling approach. This was necessary because all our variables of interest had been sampled with different intensities and replication. Not correcting for these differences could result in the variable with the largest sample size being most strongly related to species richness, only because of the wider environmental gradient sampled. In contrast, using a method with, for example, sample size as an offset would not account for the fact that with an increasing number of samples the probability of finding new species decreases, which would lead to underestimated species richness in more sampled sites. Our robust resampling with replacement approach allowed us to correct for differences in sample size but still use all the data in our extensive dataset and estimate confidence intervals from which infer significance.

In this study, we used four sets of analyses. To compare the diversity of pollinators supported by crops and semi-natural habitats, we compared the total number of pollinator species observed in herbaceous and woody semi-natural habitats with (a) a mix of 12 different crop types, (b) faba bean, the most frequently occurring early flowering crop type and (c) leek, the most frequently occurring late-flowering crop type. Mean estimates of accumulated species richness and 95% confidence intervals were obtained by randomly resampling 250 combinations of 12 transects in each habitat type or crop (mixture). Twelve was the highest number of transects we considered acceptable for estimating the cumulative number of species by means of resampling because the maximum number of crops was restricted at 15. The cumulative species numbers in the mixture of crops were estimated by selecting one transect each in 12 different crops in any landscape and round, thus maximizing the potential effects of crop diversity. This was compared with similarly obtained cumulative species numbers in herbaceous and woody semi-natural habitats from all landscapes and rounds. Because faba beans only flowered in rounds two/three and leek only flowered in rounds seven/eight, we compared cumulative pollinator species numbers of these crops with estimates from herbaceous and woody semi-natural habitats that were also based on resample analyses from these rounds only. To subsequently test for significant differences, we used linear models, with resampled cumulative species richness estimates as the response variables and habitat type as explanatory variable. We present the results as rarefaction curves to visualize differences in total richness, and different rates of species accumulation as the number of transects increases.

To test whether landscape-level pollinator diversity was influenced by the diversity of insect-pollinated crops, we also analysed whether the cumulative species richness in herbaceous semi-natural habitats across the eight sampling rounds was related to the number of crops grown in each landscape across the season ($n = 26$), using simple regression analysis. For this analysis, we focused on herbaceous semi-natural habitats only for several reasons. Sampling effort in herbaceous semi-natural habitats was completely balanced across landscapes, and 97% of all pollinator species were found in these habitats. Furthermore, including crop transects would lead to bias in this analysis, because landscapes with higher crop diversity had inherently more crop transects.

To better understand the relationship between crop diversity and pollinator diversity, we analysed for each pollinator species in how many different crops they had been observed and whether they had additionally been observed in herbaceous and/or woody semi-natural habitats.

To examine the importance of temporally stable habitats, we analysed the capacity of individual herbaceous semi-natural habitats to accumulate species richness across the season and compared it to the richness accumulated in multiple herbaceous semi-natural habitats from different landscapes in a single round (i.e. same site different times vs. same time different sites). We refer to these two different drivers of species richness as temporal heterogeneity and spatial heterogeneity in resources, respectively. Although other stressors such as competition or diseases might contribute to species

spatial/temporal turnover, resource heterogeneity is expected to be the main limiting factor, and the main differentiating characteristic of semi-natural habitats compared to coexisting crops.

We first pooled each pair of transects in herbaceous semi-natural habitats within each landscape and round to increase sampling effort/precision. Then, we calculated species richness accumulated in herbaceous semi-natural habitats across the eight rounds within each landscape (26 data points; one per landscape). We also calculated species richness accumulated in herbaceous semi-natural habitats from eight different landscapes within the same round. We resampled eight random landscapes 10 times and averaged the results to provide stable estimates that are representative for all spatial samples per round. This was done 26 times within each round to run balanced models, as we have 26 replicates in the temporal heterogeneity dataset. To test for significant differences, we fitted two separate linear models, in which accumulated species richness was the response variable, and the source of heterogeneity (temporal/spatial) was the explanatory variable. In the first model, we tested for general differences in accumulated species richness due to spatial and temporal heterogeneity. For this analysis, we selected three random samples in each of the eight rounds from the spatial heterogeneity data pool ($n = 24$) to more or less balance the temporal heterogeneity data pool ($n = 26$). For the second model, we compared the accumulated species richness due to temporal heterogeneity to that of spatial heterogeneity in each round (i.e. temporal heterogeneity compared to spatial heterogeneity in each round). Groups were compared using post-hoc Tukey tests.

To study whether landscape semi-natural cover moderates the distribution of pollinator species over semi-natural habitats and crops, we analysed how the number and percentage of shared species between semi-natural habitats and nearby crops were influenced by semi-natural cover in the landscape. We first calculated the number of species in herbaceous semi-natural habitats in each landscape (throughout the whole season). Then, we calculated the number and percentage of these species that were also found in a single transect of each crop sampled in that same landscape. We fitted two general linear models with number and percentage of shared species as response variables, and crop type and percentage of semi-natural habitat in the landscape as explanatory variables.

The Gaussian error structure of the models was chosen based on model fit and performance of the residuals. All models were checked for outliers and for normal distribution of the residuals. We conducted all the analyses in R (R Core Team, 2019). We used the package STATS (base R) to run the linear models, *dplyr* to manage data (Wickham et al., 2021), *ggplot2* to create the graphs (Wickham, 2016), *vegan* for species accumulation curves (Oksanen et al., 2020) and *spadeR* to count the number of shared species (Chao et al., 2000). Code and data are freely available (see corresponding section).

3 | RESULTS

In total, 26,123 individuals belonging to 49 genera and 372 different species or species complexes were found in the 717 surveyed

transects (see Table S3 for a species list). The most frequently observed species were *Sphaerophoria scripta* complex (35% of transects), *Apis mellifera* (32%), *Andrena flavipes* (25%), *Lasioglossum villosulum/medinai* (22%), *Syritta pipiens* (21%) and *Eristalis tenax* (20%).

Herbaceous semi-natural habitats consistently hosted more diverse pollinator communities than the two most frequently cultivated crops or, perhaps more interesting, any combination of 12 different crops (Table 1; Figure 1). Herbaceous semi-natural habitats furthermore supported more species-rich pollinator communities than woody semi-natural habitats. The cumulative number of species observed on leek crops alone was higher than the cumulative number of species observed on a sample combining 12 different crops (non-overlapping confidence intervals; Figure 1 and Table 1). Flowering leek fields were particularly attractive and hosted a rich community of pollinators (mean 42.40 ± 0.37 *SE* species per 12 crop fields). In contrast, faba bean fields were visited by a relatively small number of species (mean 19.97 ± 0.36 *SE*).

Crop diversity was not related to pollinator richness in herbaceous semi-natural habitats (Figure 2A; $t_{24} = -0.092$, $p = 0.927$). A total of 236 pollinator species were exclusively encountered in semi-natural habitats, and 13 only in crops. Crops were visited by 136 species, of which 90% were also observed in semi-natural habitats. Most crop visiting species visited only a few crops (1–3) but 20 species were observed in more than three crops (Figure 2B). The

honeybee was the most ubiquitous species in crops, visiting 13 of the 15 crop types (Figure 2B). Because this species is managed by farmers in these landscapes, it is a poor representative of how most pollinators use crop resources.

Temporal heterogeneity was at least as important as spatial heterogeneity for pollinator species richness ($t_{48} = 0.946$, $p = 0.349$; Figure 3A). The species richness due to spatial heterogeneity varied strongly between sampling periods, being highest in mid-season (May) and lower in early/late season (Figure 3B).

The number of shared species between semi-natural habitats and nearby mass-flowering crops increased roughly from five to nine along a gradient of 0%–72% semi-natural cover scale ($t_{105} = 3.725$, $p < 0.001$, $\beta = 0.059$; Figure 4A). This was in line with a general increase in species density with increasing cover of semi-natural habitats at the landscape scale (Figure S2). However, the percentage of shared species (8.3% ± 4.9; mean ± 1 *SD*) remained stable along this landscape gradient ($t_{105} = 0.705$, $p = 0.482$, $\beta = 0.015$). These differences were fairly stable across crop types (Tables S4 and S5).

4 | DISCUSSION

Understanding what habitat and landscape characteristics determine the size of the pollinator species pool in agricultural landscapes

TABLE 1 Summary of linear models explaining differences in richness between different crop types and semi-natural habitats (SNHh for herbaceous and SNHw for woody), for the period when faba bean is flowering (Faba), when the leek is flowering (Leek) and a mixture of 12 different crops throughout the whole season (Crop Mixture). ΔAIC_{null} shows the difference in AIC between the model including habitat type as an explanatory variable and a null model. All estimates show significant differences ($p \ll 0.05$) except leek versus SNHw

| Model	Terms	Estimate	SE	R^2	ΔAIC_{null}
Faba bean	Intercept (faba)	19.97	0.36	0.84	956
	SNHh	32.78	0.51		
	SNHw	18.92	0.51		
Leek	Intercept (leek)	42.40	0.37	0.89	366
	SNHh	9.98	0.52		
	SNHw	0.19	0.52		
Crop Mixture	Intercept (mixture)	39.46	0.45	0.67	831
	SNHh	24.72	0.64		
	SNHw	9.06	0.64		
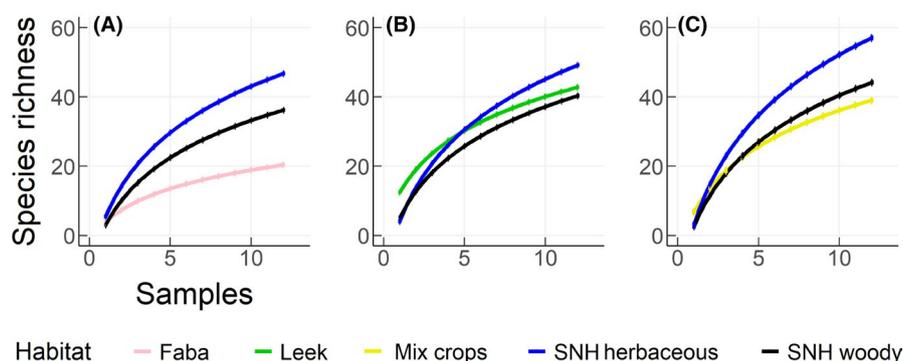
FIGURE 1 Species accumulation with increasing number of samples in different habitats. (A) In faba bean crops and semi-natural habitats (SNH) for the period when faba bean flowers (early season). (B) In leek crops and semi-natural habitats for the period when leek flowers (late season). (C) In a mixture of 12 different crops (Mix crops), and semi-natural habitats across the whole season. Error bar shows 95% CI. Differences in accumulated species richness between groups are significant when confidence intervals do not overlap
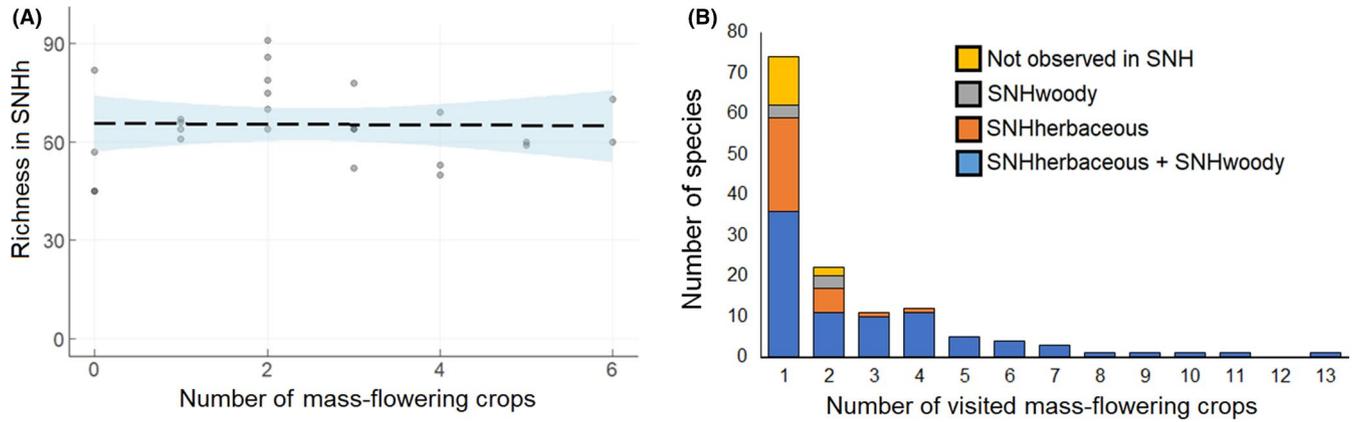
FIGURE 2 (A) Variation in pollinator richness in herbaceous semi-natural habitats with increased number of crop types in the landscape. The dashed line represents the linear model, showing non-significant differences. (B) Number of species that visit different number of crops and different habitats in which they appear. For instance, blue (SNHherbaceous + SNHwoody) shows the number of species that appear in 1–13 crops and in both semi-natural habitat types
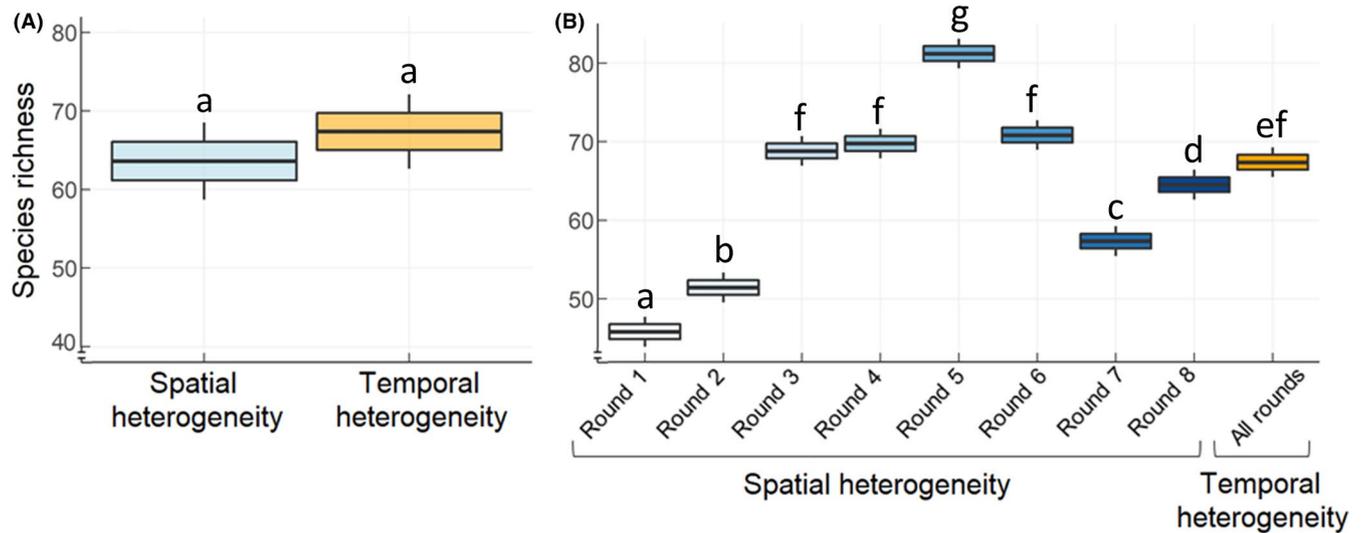
FIGURE 3 (A) Accumulated species richness in eight herbaceous semi-natural habitat transects due to spatial heterogeneity (between landscapes for the same period) and temporal heterogeneity (within landscape in different times), not significant differences ($p = 0.26$). (B) Mean accumulated species richness due to spatial heterogeneity in eight random transects in herbaceous semi-natural habitats. Spatial heterogeneity is decomposed for each round (boxes in blue gradient), from round one to round eight. The orange box shows mean accumulated richness due to temporal heterogeneity. Boxes represent estimated mean ± 1 *SE* and whiskers show 2*SE. Letters correspond to groups obtained by Tukey post-hoc multiple comparisons at the level of $\alpha = 0.05$
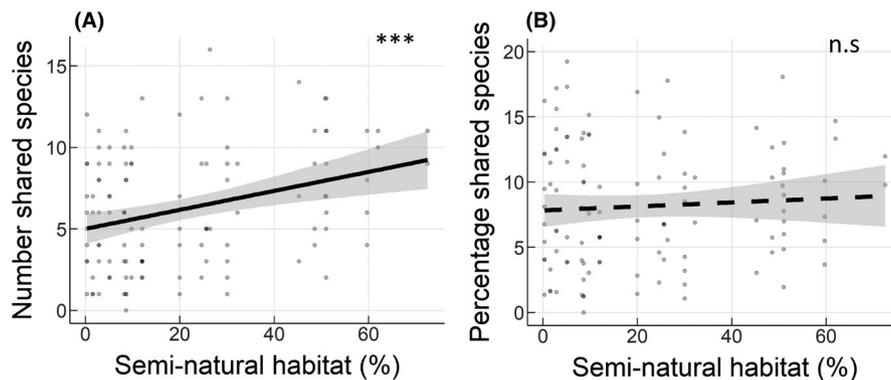
FIGURE 4 The effect of semi-natural habitat cover (%) on (A) the number of shared species, and (B) the percentage of shared species between the whole pollinator community found in semi-natural habitats and single transects in adjacent crops. The slope in A is significant ($p < 0.01$; *R*-squared = 0.03) while the slope in B is not (n.s.). See Tables S4 and S5 in Supporting material for model estimates including crop types as covariable

is important for the development of productive agroecosystems that support high diversity of pollinators. In this study, we compared the relative importance of different habitat types for determining pollinator species richness. We found that the capacity of croplands to support pollinators seems to depend more on crop identity than on crop diversity, as a single crop hosted more pollinator species than a mixture of 12 different crops. In addition, pollinator richness in semi-natural habitats was not influenced by the number of flowering crop types in that landscape. We also found that semi-natural habitats generally hosted a richer pollinator community than individual crops or mixtures of crops. Furthermore, only few species visited more than two different crops, probably because crops offer a limited set of resources and provide suboptimal habitat conditions for most pollinators (e.g. disturbed ground or use of pesticides). The temporal continuity and heterogeneity in resources provided by semi-natural habitats was at least as important as spatial heterogeneity for determining pollinator species richness, highlighting the value of habitats that provide resources throughout the season. Lastly, our results suggest that landscape-moderated increases in crop pollinator diversity are driven by more complex habitats supporting larger pollinator species pools because the percentage of shared species between crops and semi-natural habitats was stable across a landscape complexity gradient.

Pollinator richness in landscapes was not related to crop diversity. This indicates that other landscape characteristics, such as landscape composition (i.e. what specific habitat types compose a landscape) or edge density (i.e. amount of very small semi-natural habitats) might be more important for pollinators (Hass et al., 2018). The most likely explanation for this is that mass-flowering crops are only temporally available habitats, and therefore do not provide a permanent niche for pollinators (Schellhorn et al., 2015). Most pollinator species probably cannot complete their life cycle in crop habitats (e.g. they need above ground cavities) and visit crops only to forage. Furthermore, only a subset of pollinator species makes use of crops (Kleijn et al., 2015; Senapathi et al., 2015), and these are usually generalist species that can readily exploit abundant resources when they become available (Fijen et al., 2019). We show that most crop pollinators visit only one or two crops, with the exception of honeybee that was abundant in most crops. This suggests that even these generalist species have preferences or are constrained in the floral resources they can use and thus remain partially dependent on semi-natural habitats for foraging, not only for reproduction and shelter. Whether pollinators make use of crops probably depends on flower morphology and crop phenology (i.e. crop identity). For example, the highly attractive leek crop has open flowers and blooms in June when many pollinator species are active but nectar is scarce (Timberlake et al., 2019). Leek fields hosted twice as many species as the early flowering faba bean that has complex flowers that are not accessible to many insect pollinators. Crop diversity can, therefore, probably at best increase pollinator abundance, as demonstrated for faba bean pollinators (Raderschall et al., 2021), and, indeed, some studies have shown that cultivation of a single mass-flowering crop such as faba bean, red clover or oilseed rape can also (temporarily)

increase abundances (but see Riggi et al., 2021 for bumblebee diversity) of crop pollinators (Beyer et al., 2020, Westphal et al., 2003, Westphal et al., 2003) by providing temporally abundant floral resources (Holzschuh et al., 2013).

Ninety-seven percent of all observed pollinator species were found in semi-natural habitats. This highlights that semi-natural habitats, particularly herbaceous semi-natural habitats, are the main source of pollinators and effectively determine how many species can exist in agricultural landscapes. Crops generally supported high densities of less species than semi-natural habitats, but the right crop can temporarily attract a large proportion of the local species pool, as illustrated by leek in our study, since it hosted a similar number of species as woody semi-natural habitats in the time when leek bloomed. In our study, we found surprisingly few crop pollinator species that were only found in woody habitats, suggesting that woody habitat mainly provides resources that are complementary to herbaceous semi-natural habitat but offer few unique niches for pollinators (Eeraerts et al., 2021; Rivers-Moore et al., 2020). These complementary resources most likely include nesting sites for cavity nesting species (Rivers-Moore et al., 2020), that are not available in herbaceous habitats or crops.

Semi-natural habitats contain many different niches and the resources that pollinators need are therefore temporally and spatially spread out (Schellhorn et al., 2015). Our study assessed the relative importance of the commonly studied spatial heterogeneity (number of bee species supported by multiple habitats in a specific period during the growing season) with the importance of the rarely studied temporal heterogeneity (one habitat repeatedly sampled throughout the growing season) and found that temporal heterogeneity was just as important for species richness as spatial heterogeneity. This suggests that most work on the contribution of semi-natural habitats to crop pollination underestimate the total number of species that rely on these semi-natural habitats because they are generally done during a small period around crop flowering (see Kleijn et al., 2015). Importantly, the richness accumulated due to temporal turnover might be even stronger than shown here, because the richness accumulated through different landscapes (spatial heterogeneity) also includes some temporal heterogeneity due to topographic and phenological mismatches between these landscapes (Olliff-Yang & Ackerly, 2020). In conclusion, the combination of temporal and spatial heterogeneity in the resources (e.g. flowers and nesting sites) that semi-natural habitats provide is likely the main reason why they can support richer pollinator communities than a combination of many different flowering crops.

Pollinator richness increased in landscapes with more semi-natural habitat cover, which supports the widely accepted view that landscape simplification jeopardizes pollinator communities (Kennedy et al., 2013). This has well-known pernicious effects for the provision of pollination services at the landscape scale. Interestingly, our results provide a key nuance, since small semi-natural habitats in very simplified landscapes hosted a decent density of different pollinator species (c. 11 species vs. 15 species in patches of the same size in highly naturalized landscapes). Hence,

these (stable) small semi-natural patches in highly intensified landscapes might be very important for pollinator conservation, acting as refuges where pollinator species concentrate (Boetzl et al., 2021; Li et al., 2020; Martínez-Núñez et al., 2020; Redhead et al., 2020). Maintaining even small patches of semi-natural habitat can therefore help conserving pollinator populations in simplified landscapes.

The number of shared species between semi-natural habitats and nearby crops increased with landscape complexity, yet the proportion of shared species remained constant across landscapes. This suggests that the proportion of pollinators that can use crops and non-crop pollinators is rather similar in simple and complex landscapes. This apparently goes against ecological theory that suggests that specialist bee species have higher extinction rates in highly fragmented landscapes (Harrison et al., 2017; Redhead et al., 2018), but the equal proportion across the landscape complexity gradient may at least partly be explained by the fact that many pollinator species only opportunistically make use of crop resources (Fijen et al., 2019; Senapathi et al., 2015). Whether pollinator species visit crops is strongly limited by the species' tolerance to crops, or, conversely, their preference for semi-natural habitats, and our results show that this tolerance/preference is proportionally constant along a landscape complexity gradient. This strongly supports the concept of ecological intensification, because it shows that by increasing the cover of semi-natural habitats at the landscape level it simultaneously and proportionally increases the crop and non-crop pollinator species pools (Bommarco et al., 2013; Kleijn et al., 2019), with subsequent benefits for ecosystem services and crop pollination (Morandin & Kremen, 2013).

5 | CONCLUSIONS

We show that increasing crop diversity cannot be used as a strategy to maintain species-rich pollinator communities in agricultural landscapes. Instead, promoting spatially and temporally heterogeneous habitats is key to increase the availability of niches and support a high number of pollinator species throughout the season. Conservation of semi-natural habitat, and the restoration or promotion of set-aside small patches of semi-natural habitat can contribute to maintaining relatively rich pollinator communities, and helps to keep the proportion crop and non-crop pollinator species fairly stable across wide landscape complexity gradients.

CONFLICT OF INTEREST
None of the authors have a conflict of interest.

AUTHORS' CONTRIBUTIONS
T.P.M.F. and D.K. designed the sampling and led the project; T.P.M.F., D.K. and C.M.-N. conceived the main ideas of the manuscript; C.M.-N. analysed the data and wrote the first draft of the manuscript with inputs from T.P.M.F. and D.K.; C.G., D.H., W.V. and T.P.M.F. conducted the fieldwork; I.R. identified species in the laboratory. All authors contributed significantly to the final version of the manuscript.

DATA AVAILABILITY STATEMENT
Data and code available via the Figshare https://doi.org/10.6084/m9.figshare.19153214.v1 (Martinez-Nuñez et al., 2022).

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