The potential of different semi-natural habitats to sustain pollinators and natural enemies in European agricultural landscapes

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ABSTRACT

Semi-natural habitats (SNH) are vital to sustain pollinators and natural enemies, and the ecosystem services they provide in agroecosystems. However, little is known about the relative importance of different SNH types and their vegetation traits for pollinators and natural enemies. Yet, such knowledge is essential for effective habitat management to promote both functional arthropod groups and associated multiple ecosystem services. We quantified vegetation traits and abundances of pollinators (bees) and natural enemies (predatory flies and parasitic wasps) in 217 SNH differing in type (woody or herbaceous) and shape (linear or areal habitats), for edge and interior locations within each SNH patch with respect to adjacent crops, across 62 agricultural landscapes in four European countries. Pollinators and natural enemies responded distinctively to major SNH types and within-habitat location of SNH: abundance of natural enemies (predatory flies and parasitic wasps) was higher along woody habitat edges than herbaceous SNH or the interior of woody habitats. In contrast, bee abundances, especially of honey bees, were generally higher in areal herbaceous compared to woody SNH. Abundances of both wild bees and managed honey bees were lowest for the interior sampling location in areal woody habitats. These findings reflected divergent key vegetation traits driving pollinator and natural enemy abundances across SNH: bee pollinators increased with herbaceous plant cover and were well predicted by SNH type and the floral abundance of identified key plant trait groups. In contrast, floral abundances of these plant groups were poor predictors of the studied natural enemies, which were better predicted by SNH type and sampling location within SNH. Our findings stress the need to move beyond the simplistic pooling of SNH types and highlight the importance of considering their vegetation traits to more reliably predict pollinators and natural enemies in agroecosystems. They suggest that the floral abundance of key groups of flowering plants is crucial for habitat management to promote bee pollinators, while vegetation-structural traits appear more important for predatory flies and parasitoids. The distinct importance of different SNH types and associated vegetation traits for pollinators and natural enemies calls for agroecosystem management ensuring diverse SNH with complementary vegetation traits to concomitantly foster pollination and pest control services.

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1. Introduction

Semi-natural habitats (SNH) play a vital role for sustaining plant and animal populations in agricultural landscapes and the functioning of agroecosystems (Tscharntke et al., 2012). They provide essential food resources, shelter and hibernation habitat for beneficial organisms such as pollinators and natural enemies of crop pests (hereafter natural enemies) delivering key regulatory ecosystem services in agricultural landscapes (Holland et al., 2016). Optimizing the potential of SNH to sustain pollinators and natural enemies is therefore one of the central pillars of ecological intensification to maintain or enhance agricultural production and food security through maximizing ecosystem service provision (Bommarco et al., 2013; Tittonell, 2014). A primary goal of agroecosystem management for jointly maximizing pollination and pest control services must therefore be to identify key SNH types and vegetation traits driving different pollinator and natural enemy functional groups. In fact, SNH in most agricultural landscapes greatly differ in type, shape and vegetation traits (e.g. Holland et al., 2016). Moreover, important vegetation traits potentially driving pollinator and natural enemy abundances can also vary considerably within an SNH, in particular between the edge and the interior parts (Albrecht et al., 2007; Pfister et al., 2017; Schirmel et al., 2018). It is therefore important to overcome the simplistic pooling of SNH and to better understand to what extent pollinators and natural enemies respond similarly or distinctively to SNH and associated traits (Shackelford et al., 2013). Such knowledge is a prerequisite to guide habitat management strategies for maximizing the value of SNH for pollinators and natural enemies and the multiple ecosystem services they provide in agroecosystems (Birkhofer et al., 2015; Sutter and Albrecht, 2016). This is also highly relevant for future iterations of the Common Agricultural Policy and the design and implementation of agri-environment schemes (Veres et al., 2013; Holland et al., 2017).

Bees and other pollinators, as well as many of the most important natural enemies of crop pests, such as parasitoids or predatory flies, feed on floral resources (nectar and/or pollen) provided by flowering plants, either as a sole food source (bees) or as an important complementary component of the diet during life-history (e.g. parasitoids and predatory flies; Isaacs et al., 2009; Wäckers and van Rijn, 2012). Hence, the availability of adequate floral resources provided by different types of habitats is considered as a key driver of pollinator and natural enemy populations, and the provision of pollination and pest control services in agroecosystems (Wäckers and Van Rijn, 2012; Carvell et al., 2017). In fact, tailored measures to enhance the availability of floral resources according to dietary requirements of target groups of beneficial insects can be highly effective to promote pest control (Tschumi et al., 2015) and pollination services (Blaauw and Isaacs, 2014). It has been proposed that floral enhancement measures targeted at pollinators should concomitantly generate similar benefits to other functional groups of flower-visitors, such as parasitoids or predatory flies (Wratten et al., 2012). However, accessibility, consumer-flower trait matching and preferences may vary considerably between pollinators and natural enemies (Campbell et al., 2012), and between different taxa within these functional groups (Sutter et al., 2017a). To what extent pollinators and natural enemies respond similarly or distinctively to floral traits associated with different SNH remains poorly explored.

Obtaining detailed information about floral and other vegetation traits is, however, expensive in terms of resources and time. An important question is therefore whether simple and easily obtained habitat and vegetation descriptors are instead sufficient to predict the potential value of SNH for pollinators and natural enemies compared to more detailed predictors that are more resource-intensive to obtain. We therefore developed a hierarchical modeling approach aimed at comparing the performance and predictive power of simple predictors, such as the type, and distance to crop fields structure of SNH vegetation, compared to more refined predictors considering increasingly detailed information regarding other vegetation traits.

Here, using quantitative assessments of 217 patches of SNH across 62 agricultural landscapes and four European countries, we address the following research questions:

(i) How do abundances of different groups of pollinators and natural enemies differ across edge and interior parts of major SNH types in European agricultural landscapes?

(ii) Which distinct or shared habitat and vegetation traits drive abundances of pollinators and natural enemies across SNH?

(iii) What level of resolution of habitat and vegetation traits is required to adequately predict pollinators and natural enemies across SNH?

2. Materials and methods

2.1. Study design

The study was conducted in 2013 and 2014 in a total of 62 agricultural landscape sectors of 1 km radius (hereafter landscapes) in four European countries: Italy (Pisa Plain, N: 43°39′39.12″, E: 10°27′17.96″; 15 landscapes), Switzerland (northern part of the central plateau, N: 47°29′59.37″, E: 8°27′3.75″; 17 landscapes), Germany (upper Rhine valley, N: 49°16′27.31″, E: 8°15′58.44″; 18 landscapes) and UK (southern England, N: 51°6′55.96″, W: 1°23′39.88″; 12 landscapes). Landscapes were selected based on aerial photographs along a gradient of landscape complexity (proportion SNH) to ensure that landscapes reflected the typical range of landscape complexity in each study region: 4–61% in Italy, 12–75% in Switzerland, 1–64% in Germany and 4–54% in the UK; see Pfister et al., 2017 for more detailed information). Thus, our findings should hold for these typical ranges of agricultural landscape complexity, and not only for simple or complex landscapes. Furthermore, it was ensured that landscapes did not (or in a few cases only minimally) overlap. In all study regions, agricultural landscapes were characterized by a mosaic of crops, as well as areal and linear patches of herbaceous semi-natural vegetation (e.g. extensively managed grasslands or grassy strips, uncropped or extensively managed herbaceous field margins) as well as woody areal (e.g. forest remnants, woodlots) or linear woody vegetation (e.g. hedgerows). Hence, SNH could be classified into four major types (hereafter SNH type): herbaceous areal (HA), herbaceous linear (HL), woody areal (WA) and woody linear (WL) habitats (see Table A.1 for more detailed description of SNH types including definitions of areal/linear and woody/herbaceous). In each landscape sector, one SNH patch (hereafter SNH) of each SNH type was randomly selected, but with a minimum distance of 200 m to any other selected SNH and a minimum surface of 150 m² for each SNH type. Each SNH patch was bordering an arable crop field. Herbaceous areal SNH were not a major SNH type in the UK study region and therefore not sampled there. In total, 217 SNH –38 herbaceous areal (HA), 61 herbaceous linear (HL), 55 woody areal (WA) and 63 woody linear (WL) SNH– were sampled.

2.2. Assessing vegetation composition, floral abundance and plant species traits

Vegetation surveys (assessing plant species composition and cover of each species) were performed in each of three separate vegetation layers: tree (height > 4 m), shrub (1–4 m height) and herbaceous (0–1 m) layer. Percentage vegetation cover and type of management ('managed' or 'not managed') were assessed at the SNH level for the first two layers (if present). In the herbaceous layer, vegetation surveys were performed in two subplots (5 × 1 m, at least 10 m apart from each other) randomly placed along two parallel belt transects (50 × 1.5 m); one transect was located right at the border of SNH to the adjacent crop (approx. 1 m distance from the crop border: "edge") and one at a distance of 12.5 m from the crop border ("interior") of areal habitats. This distance was chosen because according to our definition of an "areal"

(compared to a "linear") its width had to be ≥ 25 m (Table A.1; Pfister et al., 2017). Hence, 12.5 m is identical to center of the narrowest areal SNH patches in our study. In fact, many areal SNH patches in the studied regions were rather narrow and thus 12.5 m transect was in the central zone of these areal SNH patches. In order to standardize sampling distance and avoid variation in sampling distance from the crop edge of the more interior transect, it was fixed to 12.5 m in all areal SNH. In narrow linear SNH (< 3 m width) both transects were arranged in line rather than parallel (see Pfister et al., 2017 for more details). Subplot data was pooled at the transect level for analysis.

In order to estimate the floral abundance of species and trait groups of plants in all SNH types, the number and type of flower units (following Pywell et al., 2006) of all vascular flowering plant species were recorded in 10 cubes (ground surface 1×1 m, 2 m height) randomly distributed within each belt transect (abundance of flowers of plants above a height of 2 m could not be assessed). Flower abundance of each species was estimated as the number of flower units multiplied by their dimension per m^2 (retrieved from floral trait information from Naturgate (http://www.luontoportti.com/suomi/en), E-Flora BC (Klinkenberg, 2013), Flora d'Italia (Pignatti, 1982), New South Wales flora online (http://plantnet.rbgsyd.nsw.gov.au/floraonline.htm) and Flora of China (http://www.efloras.org); Table A.3). For plant species that were not present in any of the trait-databases, flower unit size was estimated based on direct measures of herbaria specimens. Flower abundance, cover of the herbaceous vegetation and management were assessed at the start of the vegetation period (T1), in May/June (T2), July (T3) and six weeks before the end of the vegetation period (T4) (Note: T1 was not assessed in Italy). Species composition and cover of all plants (vegetation survey mentioned above) and management of the trees and shrubs were measured once (T2).

In order to be able to assess the importance of plant traits, and in particular floral traits, to adequately predict pollinators and natural enemies across SNH, the following traits were extracted from trait-databases using the *R* package 'TR8' (Bocci, 2015) for each recorded plant species: floral reward ('nectar', 'pollen' or 'nectar and pollen'), pollen vector ('insect pollinated' or 'other'), flower class according to Müller (1881), flower color, months of flowering, Raunkiaer life form and mean height (see Tables A.2 and A.3 for flower classes and sources). Flowering period was subdivided into 'early' (January to April), 'middle' (May to June), and 'late' (July to December). For plants identified to the genus level, the chosen value for the trait was the most abundant value among the recorded species belonging to that genus.

2.3. Sampling of pollinators and natural enemies

In the present study we focus on several taxa that have been identified as important pollinators and natural enemies of crop pests in European agroecosystems: bees (Hymenoptera: Apoidea), hoverflies (Diptera: Syrphidae), predatory flies (dipteran families Empididae and Dolichopodidae), and parasitic wasps (Hymenoptera: Chalcidoidea, Braconidae and Ichneumonidae). Insects were sampled using a set of standardized pan traps of different UV-reflecting colours (yellow, white and blue; Westphal et al., 2008); this sampling method has been demonstrated to be effective for the studied insect groups (e.g. Stephens et al., 1998; Westphal et al., 2008; Pfister et al., 2017). Pan trap triplets consisted of three 500-ml plastic bowls (Pro-Pac, Vechta, Germany) sprayed with UV-reflecting paint (SparvarLeuchtfarbe, Spray Color GmbH, Merzenich, Germany) and filled with 300 ml of water with scentless detergent to reduce surface tension. Pans were mounted on wooden posts at an average height of c. 1.5 m (range 1–1.8 m) according the predominant flowering zone of the sampled vegetation type, i.e. herbaceous or shrubby/woody, in a randomly selected location within each of the two belt transects for vegetation surveys (see above) of each sampled SNH. They were active during four consecutive days during each of the four rounds the vegetation was assessed (see above). For bees, standardized transect walks were used as an

additional sampling method. It has been shown that the two methods effectively complement each other (Westphal et al., 2008) and they are recommended in combination for bee sampling and monitoring programs (e.g. LeBuhn et al., 2003). Bees were recorded for a maximum of 5 min in two subdivisions of 25 x 1.5 m of each of the vegetation transects (50 × 1.5 m). Bees that could not be identified in the field were captured for later identification in the laboratory. Transect walks were carried out when climatic conditions followed the standard described by Pollard and Yates (1994). Collected insects were stored in 70% ethanol for preservation and identified at the family (but not species) level in the laboratory.

2.4. Statistical analysis

To test for the effects of SNH type and sampling location within SNH (edge or interior area) on the abundance of the two functional groups pollinators and natural enemies, and the abundance of the different studied taxonomic groups within these two functional groups, (research question (i)), generalized linear mixed models (GLMMs) with negative binomial error distribution (to account for the overdispersion in the data) were fitted. The first model with the response variable insect abundance contained the fixed effects SNH type, sampling location and functional group (pollinator or natural enemy), and the two and three-way interactions among factors and SNH nested within landscape nested within country crossed with sampling round and sampling round per country as random effects. Analogous models were used to test for potentially distinct responses of taxonomic groups within pollinators (response variable pollinator abundance, fixed explanatory factor pollinator group (factor levels: wild bee or honey bee)) and natural enemies (response variable natural enemy abundance, fixed explanatory factor predator group (factor levels: predatory fly or parasitic wasp)). Neither the area of SNH nor its interaction with SNH type had any significant effect on bees or natural enemies (see Table A.4 for results), and were therefore not included in the models described above.

To identify key floral and other vegetation traits and their role in driving pollinator and natural enemy densities in SNH (research question (ii)), GLMMs with the fixed explanatory variables floral abundance (log-transformed) of identified key "trait groups" of flowering plants (see below), as well as percentage cover of herbaceous plants, shrubs and trees, and the same random structure as described above were fitted.

In order to identify distinctive "plant trait groups" of flowering plant species with similar floral and other traits that are systematically associated with SNH type, within-habitat location and other higher-level SNH descriptors (research questions (ii) and (iii)) RLQ analysis was used (Dolédec et al., 1996). This analysis recognizes the associations between species data (L table: floral abundance of each plant species of each SNH in each landscape), traits data (Q table: life form, mean height, pollen vector, floral reward, flower colour, flower class, flowering duration and flowering period) and "higher-level" structural descriptors of SNH (usually referred to as "environmental variables" in RLQ analyses; R table: type of SNH, the location within SNH, SNH management and perimeter-area ratio; Fig. A2). First, we performed an ordination analysis of the R, L and Q tables: for the L table, a correspondence analysis was performed, while for the R and Q tables, the Hill-Smith method was used since it allows for the analysis of both continuous and categorical variables (Dray et al., 2014). Secondly, the results of these ordinations were used as input for the RLQ analysis. Finally, the species scores on the first two RLQ axes (which preserved 91.4% of the variance of the environmental scores and 69.8% of that of the plant traits compared to simple principal component analysis) were used for a Ward-distance based clustering procedure. The optimal number of clusters (i.e. trait groups of plants) was calculated via the function K-means with the Kalinski-Harabasz criterion (Oksanen et al., 2016). The RLQ analysis was combined with fourth corner method to test the significance of bivariate associations between traits and

environmental variables as recommended by Dray et al. (2014); for more detailed information see description in caption of Fig. A.2).

In order to assess what level of resolution of habitat and vegetation traits is required to adequately predict the abundance of pollinators and natural enemies across SNH (research question (iii)), we built three different models with the same random structure, but with increasingly refined level of information with respect to vegetation traits of predictors. The simplest model (level 1) included only SNH type, location,

and their interaction as predictors. The more complex level 2 model included refined vegetation predictors: vegetation-structural traits of SNH (cover of trees, shrubs and herbs) as well as flowering species richness. Because flowering species richness and total flower abundance were strongly positively correlated (n = 1737, Pearson's r = 0.87, $P < 0.001$), only the flowering species richness but not total flower abundance was included in level 2 models. The most complex model (level 3) included structural SNH traits and flower abundance of each
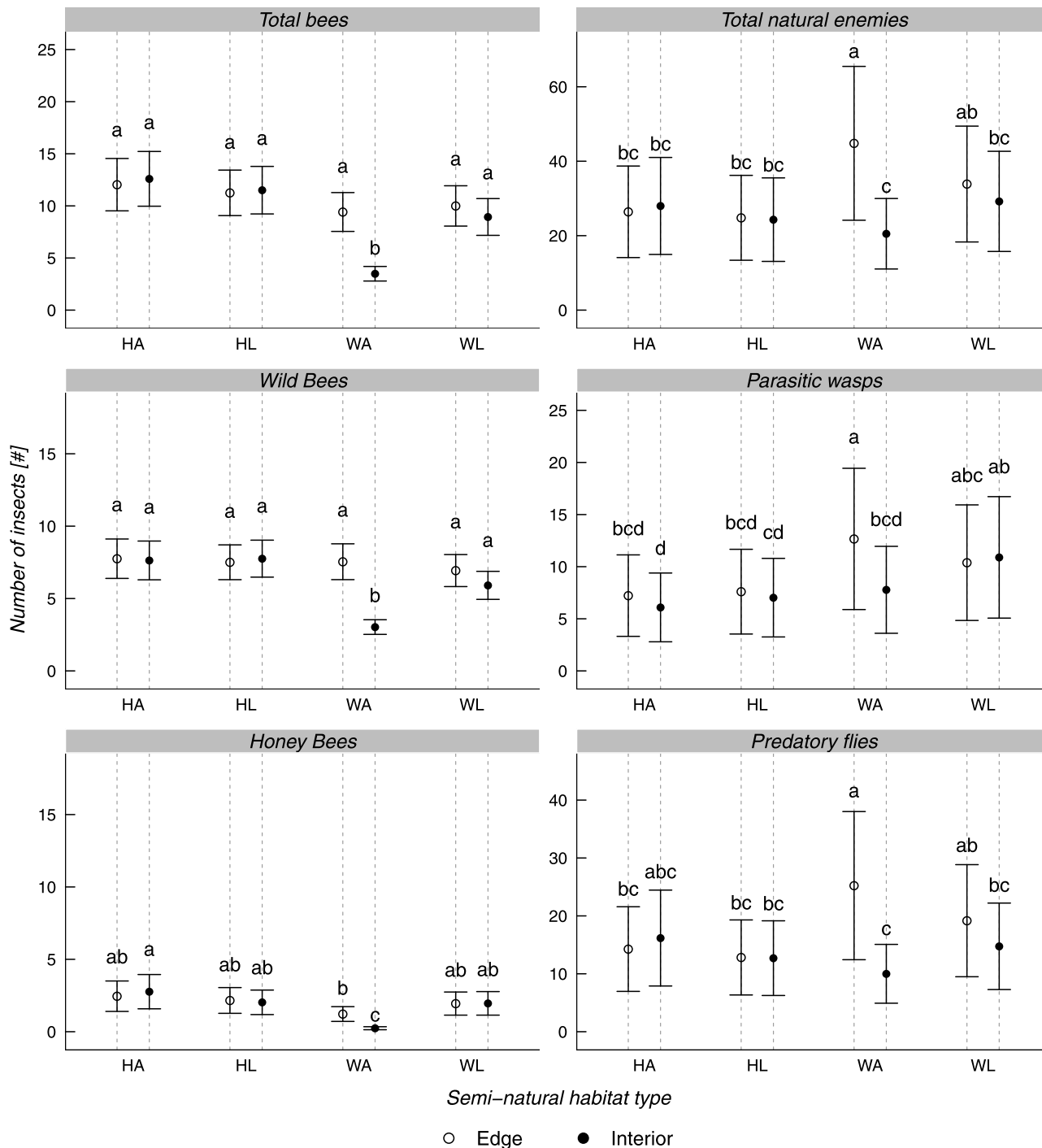

Fig. 1. Number of insects across SNH types ('HA': herbaceous areal; 'HL': herbaceous linear; 'WA': woody areal; 'WL': woody linear) and within-SNH locations ('Edge' ; 'Interior'). Results are shown for wild bees, honeybees and their combined number ('total bees'), as well as for parasitic wasps, predatory flies and their combined number ('total natural enemies'). Bars represent standard errors. Different letters indicate significant differences among insect groups (Tukey's adjusted P-values ≤ 0.05. Although error bars of different groups may overlap on the linear scale on the transformed scale (where posthoc comparisons where applied) group levels are different (according to the lettering.) For easy interpretation the results are presented in on the linear scale (as recommended by Menge et al., 2018).

Table 1

Results of Wald chi-square tests to investigate differential responses of two functional groups of insects (bees and natural enemies) and taxonomic groups of bees (honey bees and wild bees) and natural enemies (predatory flies and parasitic wasps) to SNH type (herbaceous areal, herbaceous linear, woody areal, woody linear) and within-habitat location (edge or interior zone) in generalized linear mixed models (see Material and Methods section). Significant interactions of group with SNH type and/or within-habitat location ($P(\chi^2) \leq 0.05$) indicate differential responses of groups to these predictors.

Response variable	Fixed model component	Df	LRT	$P(\chi^2)$
Total insect abundance (groups: bees and natural enemies)	SNH:location:group	3	1.32	0.723
Total insect abundance (groups: bees and natural enemies)	SNH:location	3	118.97	**< 0.001**
Total insect abundance (groups: bees and natural enemies)	SNH:group	3	59.91	**< 0.001**
Total insect abundance (groups: bees and natural enemies)	location:group	1	0.07	0.798
Bee abundance (groups: wild bees and honey bees)	SNH:location:group	3	13.32	**0.004**
Natural enemy abundance (groups: predatory flies and parasitic wasps)	SNH:location:group	3	15.04	**0.002**

plant trait group identified by the RLQ analysis described above (Table 2). Separate models were run for pollinators and natural enemies. For level 3 models, no strong correlation among explanatory variables was present (highest Pearson's r = 0.28), therefore all explanatory variables were included in the model.

All models were GLMMs with a negative binomial error distribution; they were compared using the Akaike information criterion corrected for small sample sizes (AICc). Model assumptions were checked adopting the graphical validation procedures recommended by Zuur et al. (2009). Collinearity among explanatory variables was assessed using the corvif function (Zuur et al., 2009). The effect of predictors was tested with type II analyses of deviance with Wald chi-square tests. Multiple pairwise comparisons were carried out on least-square means with Tukey's adjustments of *P*-values. Statistical analyses were performed in R 3.3.1 (R Core Team, 2017) using the packages lme4 (Bates et al., 2015), ade4 (Dray and Dufour, 2007), MuMIn (Barton, 2016), lsmeans (Lenth, 2016) and vegan (Oksanen et al., 2016).

3. Results

3.1. Response of pollinators and natural enemies to SNH type and within-habitat location

In total, 21,772 bees (pan traps: 13,974; transect walks: 7,798) were captured (14,519 wild bees and 7,253 honey bees). Furthermore, 58,777 predatory flies and 20,087 parasitic wasps were sampled. The number of bees was not significantly different between SNH types or between edge and interior parts of SNH, except for a 3.1 fold reduced number of bees in the interior of woody areal habitats compared to edges of woody areal habitats or other SNH (Fig. 1; Table 1), which was reflected by a significant SNH type × within SNH location interaction (χ^2 = 84.98, df = 3, P < 0.001; Table 1). This pattern was consistent for both wild bees and honey bees (Fig. 1; Table 1). The variation of natural enemy numbers between SNH types depended on within SNH location (SNH type × within SNH location interaction: χ^2 = 49.30, df = 3, P < 0.001; Table 1). In contrast to bees, natural enemy numbers were significantly increased at the edge of woody habitats compared to herbaceous habitats or the interior of woody habitats (Fig. 1; Table 1). Patterns of predatory flies and parasitic wasps were similar to each other (Fig. 1; Table 1).

3.2. Vegetation traits across SNH affecting pollinator and natural enemy abundance

The number of wild bees and honey bees increased with the cover of herbaceous plants (Fig. 2a; Table A.5), while only the honey bees decreased with the cover of trees (Table A.5). Numbers of natural enemies were, however, positively related to the cover of trees and herbaceous vegetation (Fig. 2b; Table A.5), and those of parasitic wasps (but not those of predatory flies) also with the cover of shrubs (Table A.5).

Cover, floral abundance and floral traits of a total of 393 flowering plants species (plus 22 plants identified at genus level) were analysed.

Cumulative inertia of the first two RLQ axis was 87.1% and nine distinct trait groups of flowering plants were identified (Fig. A.l).

Irrespective of whether wild bees, honey bees or pooled numbers of bees were analysed, they increased with floral abundance of functional trait groups 1, 3, 5, 6 and 7, with the strongest increases in bee numbers correlating with floral abundance of plants belonging to trait group 5, followed by 1 and 3 (Fig. 3; Table A.6). Group 1 was characterized by tall woody species (trees, shrubs and woody creepers) with predominantly white flowers and early, relatively short flowering period, whereas group 3 contained almost exclusively herbaceous species, most of them mid-season flowering with hidden-nectar flowers (Fig. 4). Group 5 was a heterogeneous trait group containing both herbaceous and woody species containing a relatively high proportion of pollen-flower plants (according to Müller, 1881; Fig. 4). Most abundant plant genera in terms of floral abundance of group 5 were *Rubus* (32.4%), *Hypericum* (19.8%) and *Papaver* (11.1%); *Sambucus* (21.8%), *Prunus* (16.1%), *Crataegus* (11.3%) and *Rosa* (10.8%) for group 1; *Achillea* (11.9%), *Ranunculus* (11.8%), *Trifolium* (9.3%) and *Leucanthemum* (7.5%) for group 3 (see Table A.7 for a complete list of plant species in each group). In contrast, no significant correlation could be detected between the floral abundance of any of the plant trait groups and the studied natural enemies, either for predatory flies or for parasitic wasps (Table A.6). For RLQ results regarding associations (co-correlations) of plant traits with higher-level SNH structural traits ("environmental variables") across SNH see Fig. A.2.

3.3. Level of vegetation trait information needed to predict pollinators and natural enemies

Bee abundance was best predicted by the most complex model (model 3) with the most refined level regarding flowering vegetation trait information: floral abundance of plant trait groups in addition to vegetation-structural traits (conditional R-squared estimating variation of fixed and random effects = 0.549, marginal R-squared estimating variation explained by fixed effects (without random effects) = 0.151) and had a significantly lower AICc value compared to the less complex models (model 1, conditional R-squared 0.533, marginal R-squared = 0.106) (Table 2). Conversely, for natural enemies (predatory flies and parasitic wasps), the simplest model (model 1 including only SNH type, within-habitat location and their interaction) was identified as the best model in terms of parsimony (lowest AICc, conditional R-squared = 0.659, marginal R-squared = 0.026; Table 2).

4. Discussion

4.1. Differential response of pollinators and natural enemies across SNH in Europe

Our study of 217 semi-natural habitats (SNH) across four countries reveals distinct abundance distributions of key functional groups of pollinators and natural enemies across different types of SNH in European agricultural landscapes. The edge zones of woody habitats

Table 2
Comparison of models with increasing level of detail of SNH characteristics ('Level') predicting abundance of bees and natural enemies. Rank function: AICc. 'Loc.': position within SNH (edge or interior); 'SNH': SNH type; 'Herb cover': cover of the herbaceous layer; 'Shrub cover': cover of the shrub layer; 'Tree cover': cover of the tree layer; 'Plant richness': number of flowering species; 'G n': flower abundance of plant trait group n; 'ΔAICc': delta AICc; 'Marg. R²' and 'Cond. R²': marginal and conditional R², respectively. Empty cells stand for parameters not included in the models; see Materials and Methods section for more information about SNH traits and statistical analysis.

Group	Level	Intercept	Loc.	SNH	Loc.::SNH	Plant Richness	Herb cover	Shrub cover	Tree cover	G 1	G 2	G 3	G 4	G 5	G 6	G 7	G 8	G 9	df	ΔAICc	Marg. R²	Cond. R²
Bees	1	2.49	+	+	+		0.63	−0.09	−0.24										14	0	0.106	0.533
	2	1.53		+		0.09	0.58	−0.16	−0.23										11	−33.94	0.124	0.533
	3	1.6								0.08	0.03	0.07	0.01	0.16	0.04	0.05	0.02	−0.03	19	−81.73	0.151	0.549
Natural enemies	1	3.27	+	+	+		0.76	0.16	0.37										14	0	0.026	0.659
	2	2.56		+		0.01	0.79	0.18	0.39										11	25.88	0.024	0.669
	3	2.55								0.01	−0.02	0.03	−0.02	−0.02	−0.01	0.01	0.01	−0.06	19	34.93	0.027	0.672

supported higher densities of parasitic wasps than herbaceous SNH, while bee densities were generally similar across these SNH. However, consistently across taxonomic and functional insect groups, we found considerably lower abundances of bees, predatory flies and parasitic wasps at the more internal sampling location of 12–13 m distance to the adjacent crop border in woody habitats (i.e. forests and woodlots). These findings highlight the importance of moving beyond the pooling of SNH by taking differences among SNH types and within-habitat variation into account to improve assessments, predictions and management recommendations with respect to the valued SNH for pollinators and natural enemies. It is important to note that the pronounced difference in abundance we report here reflect differences in "activity-density" and preference rather than mobility, which is likely due to the markedly lower floral resource availability of the woodland understory compared to other SNH and less favourable microclimatic conditions (Fig. A.3; Hannon and Sisk, 2009). However, in the present study, as in most other studies where insects were sampled in agricultural landscapes, we could not sample insects directly in the canopy layer of forests, which may offer additional floral resources to pollinators and natural enemies (Rollin et al., 2013; Requier et al., 2015; Persson et al., 2018), although for example Wood et al. (2016), analyzing pollen collected by solitary bees in the UK study region, did not find trees to be important pollen sources. In any case, our findings suggest that the understory edge vegetation of areal woody habitats directly adjacent to crops can be highly valuable for pollinators and in particular natural enemies, but that this zone is restricted to a few meters from the crop edge. As our sampling design ensured that in each country broad and typical ranges of agricultural landscape complexity were covered, our results should not only hold for simple or complex landscapes, but rather for these broad ranges of European agricultural landscapes (but not necessarily for more diverse landscapes such as tropical ones, see e.g. Henri et al., 2015). However, further research is required to gain a better understanding of how the composition and spatial distribution of SNH of differing in type and vegetation traits shape the distribution of multiple functionally important insect groups at the landscape scale.

Although average abundances of bees did not significantly differ across the other studied SNH types, both honey bee and wild bee numbers strongly varied within habitat types (Fig. 1; Table 1), primarily due to variation in the cover of herbaceous vegetation and the availability of important floral resource plants (Fig. A.3 and discussion below). We could not assess to what extent the spatial distribution of hives may have affected honey bee densities in our study, but is highly unlikely it significantly contributed to this observed variation in honeybee densities within habitat types. Rather, our findings suggest that for bees, habitat quality in terms of key resource availability is particularly important (Pywell et al., 2006; Wood et al., 2017). Hence, "functional habitat maps" (Lausch et al., 2015) of resource gradients in agricultural landscapes based on more refined vegetation and floral resource traits could be a promising approach (Vanreusel and Van Dyck, 2007) to assess the spatial distribution of the potential of pollinators and pollination services in agricultural landscapes.

In contrast to bees, forest edges, hedgerows and other woody linear habitats sustained higher abundances of predatory flies and parasitic wasps than herbaceous SNH. These habitats can harbour high levels of densities of prey and hosts for predators and parasitoids, respectively (e.g. Pollard and Holland, 2006; Schirmel et al., 2018), such as aphids and honeydew (e.g. Schirmel et al., 2018). Moreover, they are particularly valuable in providing shelter and overwintering habitat to most natural enemy taxa (Holland et al., 2016; Sutter et al., 2017b). These features together with potentially more suitable microclimatic conditions –e.g. for predatory flies (Röder, 1990; Pfister et al., 2017)– appear to be more important drivers of predatory fly and parasitic wasp densities than floral resource traits. This explanation is corroborated by the lack of predictive power of floral abundance or other floral trait predictors for natural enemies in our study (see 4.2). The differences among SNH types and within-SNH zones in sustaining pollinators and
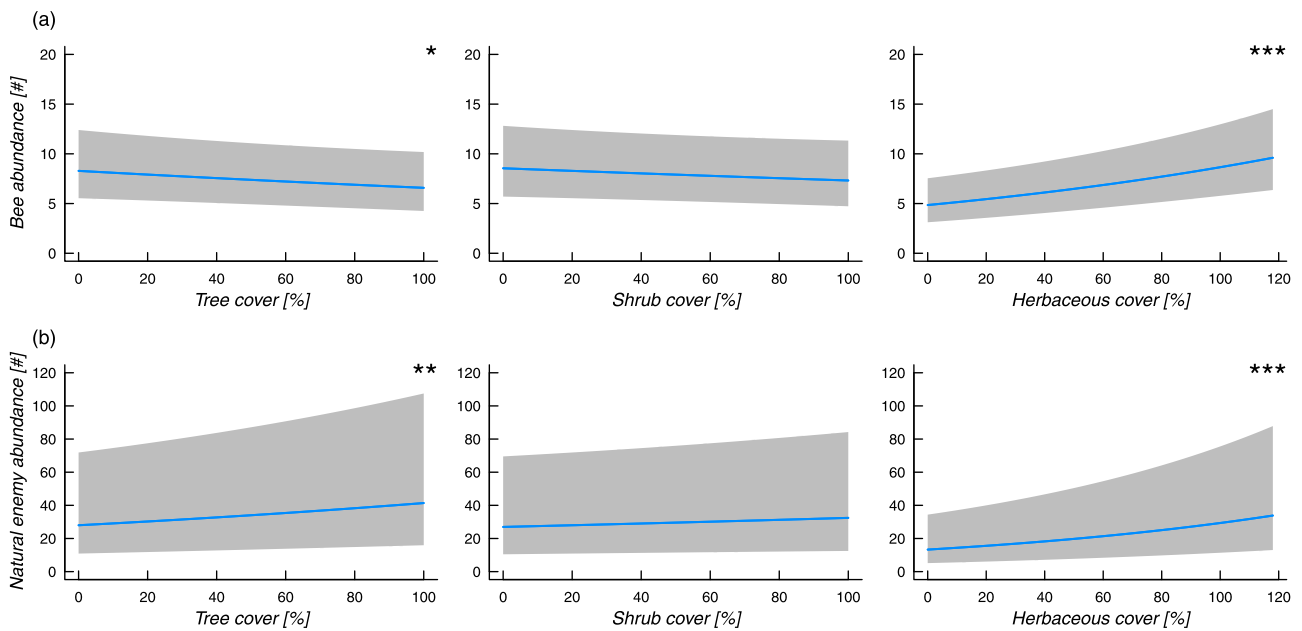
Fig. 2. Relationships between the cover of trees, shrubs and herbaceous vegetation and sampled insects across SNH: (a) number of bees (honey bees and wild bees); (b) natural enemies (parasitic wasps and predatory flies). Predicted relationships and confidence intervals at the 95% level based on generalized linear mixed effect models (at constant median of other explanatory variables) are shown (see Materials and Methods section and Table A.6 for detailed descriptions of methods and models, and model outputs, respectively). Note: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.
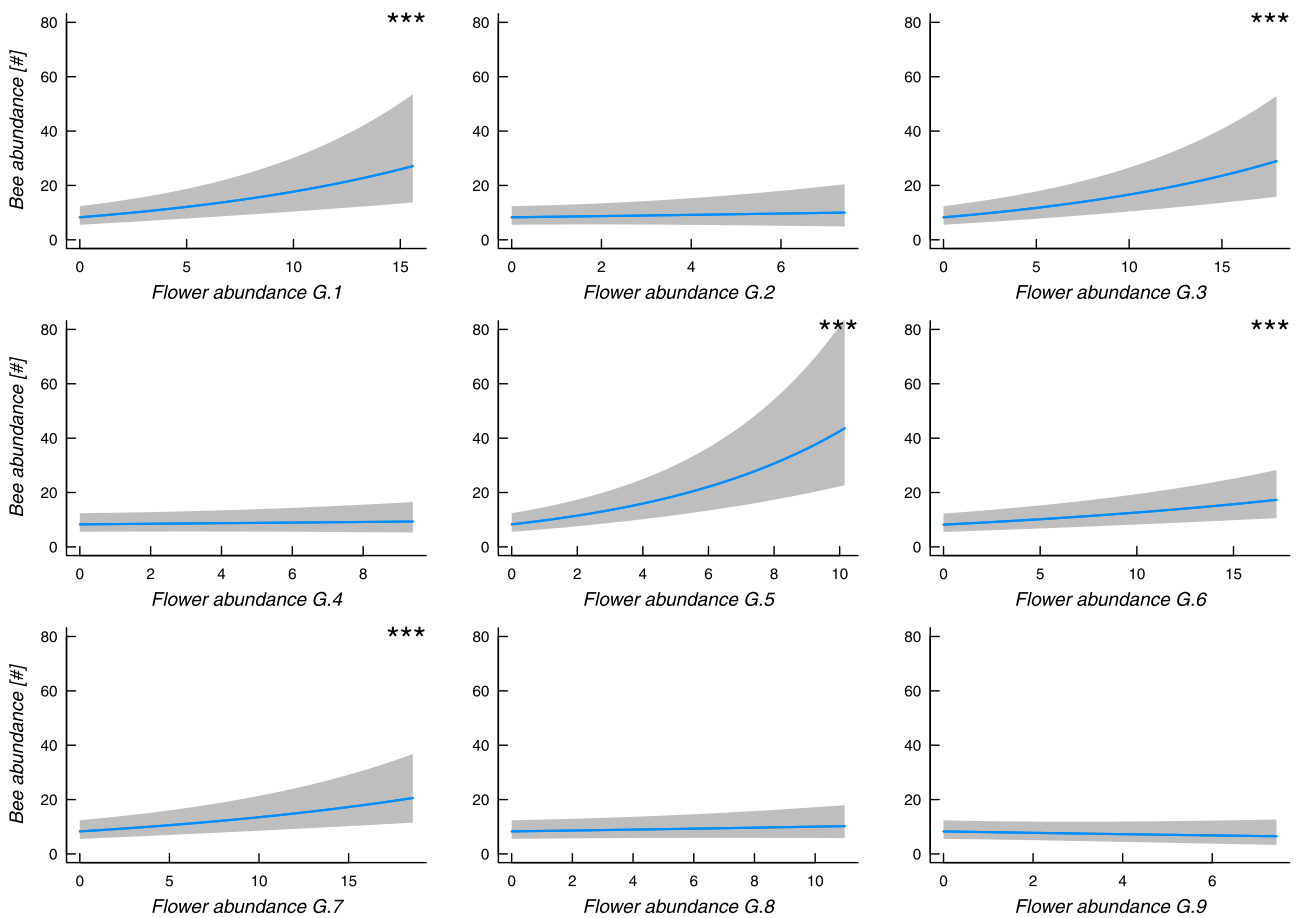

Fig. 3. Relationships between floral abundances of plant trait groups ('G'.1–9) and the number of sampled bees. Predicted relationships and confidence intervals at the 95% level based on generalized linear mixed effect models (at constant median of other explanatory variables) are shown (see Materials and Methods section and Table A.6 for detailed descriptions of methods and models, and model outputs, respectively). Note: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.
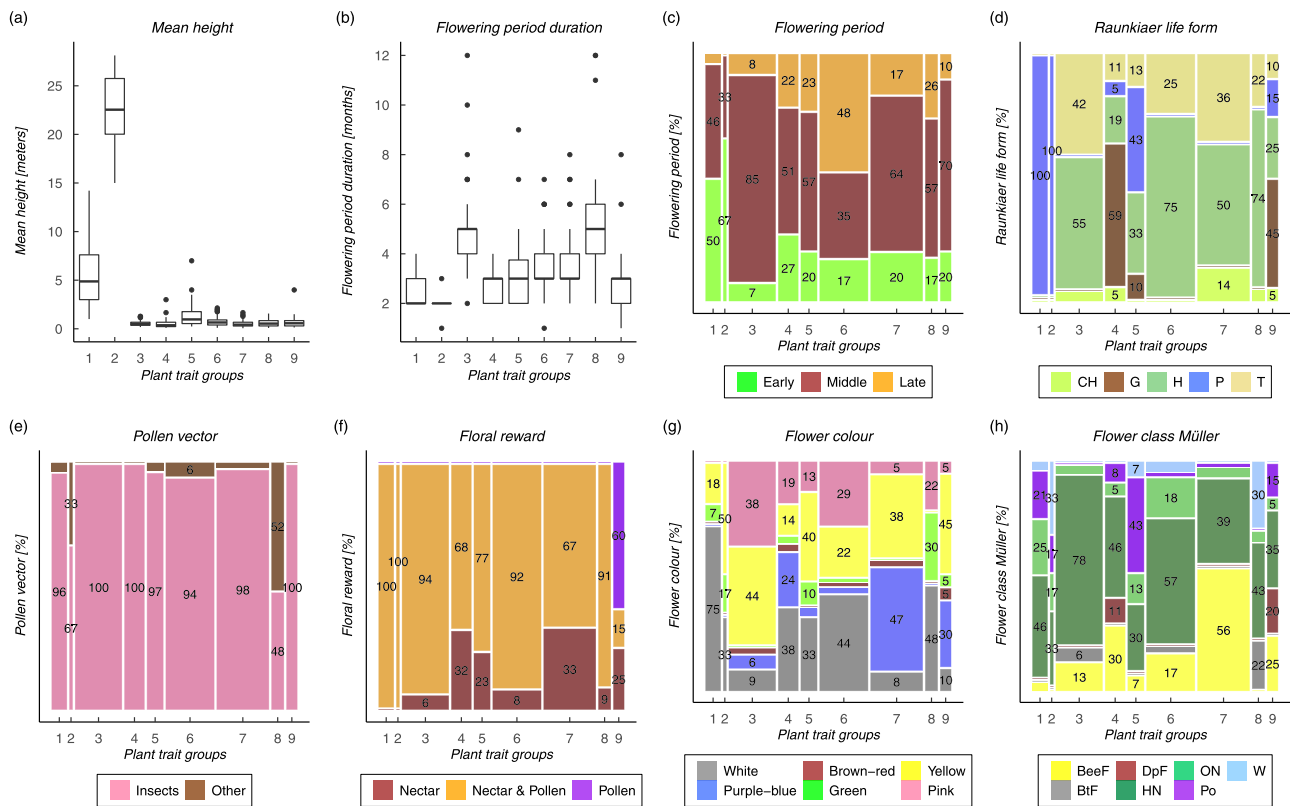
Fig. 4. Trait composition of distinctive plant groups (1–9) identified by the RLQ analysis: (a) mean height, (b) flowering period duration, (c) flowering period, (d) life form ['CH': Chamaephyte, 'G': Geophyte, 'H': Hemicryptophyte, 'P': Phanerophyte, 'T': Therophyte], (e) pollen vector, (f) floral reward, (g) flower colour, (h) flower class according to Müller ['Beef': Bee flowers, 'BtF': Butterfly-moth flowers, 'Dpf': Diptera flowers, 'HN': Hidden nectars, 'ON': Open nectars, 'Po': Pollen flowers, 'W': wind flowers]; see Tables A.2 and A.3 for a detailed description of flower classes and plant-trait database sources used. Trait composition across plant groups is expressed as boxplots (continuous traits) or mosaic plots (categorical traits: bars' height is proportional to trait dominance within a plant group, whereas their width represents the proportion of plant species belonging to that plant trait group [Group 1: 28 species; Group 2: 6 species; Group 3: 86 species; Group 4: 37 species; Group 5: 30 species; Group 6: 89 species; Group 7: 96 species; Group 8: 23 species; Group 9: 20 species]).

natural enemies revealed in our study may have important implications for the provision of pollination and pest control services in nearby crops. In fact, many studies have demonstrated functional spillover of pollinators and natural enemies from SNH into nearby farmland (e.g. Albrecht et al., 2007; Tschumi et al., 2015; Sutter et al., 2017c) resulting from increased abundances of pollinators and natural enemies in crop-bordering SNH (e.g. Tschumi et al., 2015; Sutter et al., 2017c). However, enhanced abundances of beneficial insects in SNH do not necessarily increase ecosystem service provision in nearby crops (Tscharntke et al., 2016). Moreover, diversity within and across functional groups of insects can play important roles for ecosystem service delivery, which could not be addressed in the present study. Further research is required to better understand these relationships.

4.2. Vegetation traits predicting pollinators and natural enemies across SNH

In the present study, we could identify several groups of flowering plant species whose floral abundances were predictive for the abundance of both wild bee and honey bee pollinators. Although variation explained by the studied fixed predictors was not very high (roughly 15% in the best model, Table 2), including the flower abundance of these key groups increased explained variation by 43% compared to the simplest model only considering SNH type and within-habitat location. In particular, floral abundances of trait groups 5, 1 and 3 were good predictors of bees across SNH. Key species of these groups were woody species of the genera *Rubus, Prunus* and *Crataegus*, and herbaceous species of the genera *Trifolium, Papaver* and *Hypericum*. These plant genera produce abundant nectar (e.g. *Trifolium, Prunus, Crataegus*; Baude et al., 2016) and/or pollen of high nutritional value (e.g. *Rubus*

and *Papaver*; Roulston and Cane, 2000). Some of these species have been suggested as important floral resource species in other European agroecosystems for bees (Carvell et al., 2006; Requier et al., 2015; Wood et al., 2017). Incorporating floral species richness and in particular floral abundance of these identified key flowering species groups substantially enhanced the predictive power of the models. The identified trait groups and key genera of flowering plants particularly valuable for bee pollinators include taxa such as *Rubus* and *Prunus* associated with woody SNH, taxa such *Trifolium* primarily associated with grasslands and taxa such as *Papaver rhoeas* and other annual herbaceous plants mainly associated with field margins or the crop edge that escapes herbicide application. This highlights the crucial role of maintaining a different semi-natural vegetation types associated with different vegetation traits and the presence of key floral resource plants in agricultural landscapes to support wild and managed bee pollinators.

For flower-visiting natural enemies (predatory flies and parasitic wasps), however, the patterns regarding the importance of floral and other vegetation traits differed from those observed for pollinators. While previous studies have shown that enhancing floral resource availability by plants targeted to the requirements of flower-visiting natural enemies of crop pests such as hoverflies, ladybeetles, lacewings or parasitic wasps can strongly increase their local availability and associated natural pest control services in nearby crops (Wäckers and van Rijn, 2012; Tschumi et al., 2015, 2016), floral species richness or floral abundance of distinctive plant trait groups were poor predictors of predatory fly or parasitic wasp density across SNH in the present study. In fact, they were most adequately predicted by SNH type and location within SNH. While variation in natural enemy numbers associated with variation in random effects (spatial and temporal variation

across sampled SNH, landscapes and countries) was relatively high, the explained variation by the studied fixed effects was, in all three models of different complexity, generally low –considerably lower than the explained variation of fixed effects of models predicting pollinators– (Table 2). Thus, other factors than SNH type, within-SNH location or floral resource availability associated with spatial and temporal variation across SNH in the different countries seem to be more important determinants to explain variation in natural enemy abundance.

The identified co-correlations of several of the identified plant trait groups with these higher-level structural SNH traits across SNH, such as positive associations of predominantly early flowering phanerophytes with woody SNH (Fig. A.2) may facilitate predictions of the potential of SNH for the studied functional insect groups. However, our findings highlight at the same time the complexity and heterogeneity involved in plant trait – structural ("environmental") SNH trait relationships, highlighting again the importance of assessing such predictive vegetation traits directly and illustrating the limitations of approaches to simply derive them from higher-level structural SNH traits.

5. Conclusions and implications

The findings of this study have several important implications for the management of agroecosystems aimed at promoting pollinators and natural enemies. First, the distinct responses of bee pollinators and the studied natural enemy groups to SNH types, within-habitat zones and vegetation traits highlight the crucial role of preserving and restoring high complementarity in floral and structural vegetation traits to synergistically promote these two important functional insect groups, and the ecosystem services they provide in agricultural landscapes. Edge zones of woody habitats appear to be particularly valuable for natural enemies (predatory flies and parasitic wasps). This calls for separating edge and interior of forests and woodlots in current pollination and pest control models, scoring the potential contribution of edges higher than the interior habitat (Rega et al., 2018), and for an emphasis on edge zones in woody SNH management. In contrast to natural enemies, our findings indicate that the cover of herbaceous vegetation and ecological quality in terms of availability of floral resources of key groups of flowering plants are important to consider when assessing the value of SNH for bees and designing effective SNH management schemes to promote bee pollinators as well as to improve models predicting bees in agroecosystems. Our results provide estimations of gained predictive power by including flowering plant information in such models. However, benefits of increased predictive power will have to be weighted against costs in terms of considerably higher investment in more detailed data collection. Recent work by Rega et al. (2018) illustrate how such data can be used to refine landscape models of pollination and pest control potential. Models that use uncropped vs. agricultural habitat dichotomy can indicate that SNH may be important, but are of less value for targeted measures to promote ecosystem services, for example agri-environment schemes or advising policy makers on management options. The generation of more refined information on vegetation traits and floral resource availability will help to maximise the returns from SNH and reduce the amount of land taken out of production to deliver such services (Gill et al., 2016). The identified groups of flowering plants in the present study should be helpful to inform targeted habitat management schemes to promote bees in agroecosystems.

Acknowledgments

Appendix A. Supplementary data

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