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Changes in Overwintering Arthropod Assemblages across and within Varying Habitats of a Swiss Agricultural Landscape

Summary:

Determining which habitats and features of those habitats are important for supporting biodiverse overwintering arthropod communities which is important for land management in agricultural landscapes. Emergence traps were used to sample overwintering arthropod communities across the five most prevalent habitat types in Swiss agricultural landscapes; crops, meadows, flower strips, forests, and hedgerows. Habitat trait and arthropod trait data were used to explain variation in overwintering arthropod communities across the different habitat types. Forests and hedgerows supported the highest levels of abundance and diversity of overwintering arthropods, followed by meadows and flower strips, while crops were the least productive. Soil bulk density and functional ground cover richness appeared to be the most influential habitat traits affecting overwintering arthropod communities. Wing morphology and size were important arthropod traits useful in explaining overwintering arthropod assemblages across a highly fragmented agricultural landscape. Findings in this study should be taken into consideration for land management seeking to optimize pest control by predators in agricultural landscapes.

Introduction:

Agricultural land use accounts for roughly 40% of the earth's land surface (Owen, 2010), therefore research in sustainable land management of agroecosystems is a major objective of global conservation of biodiversity. Biodiversity in agroecosystems is negatively affected by the degree of agricultural intensification (Billeter et al., 2008), which can vary a great deal amongst different land management regimes. Agricultural land management is commonly geared to consider only the effects of practices on crops, disregarding impacts on surrounding semi-natural habitats (SNHs; defined as habitats in which "there has been minimal disturbance, thus allowing the continued existence of natural communities in a relatively unchanged form" (Calow, 2009)) (Pimentel et al., 1992). Pesticide application is common practice, which imposes one of the greatest hazards to diversity of arthropod communities (Pimentel et al., 1992). Application of herbicides and fertilizers is also common practice, and can negatively impact plant species densities (Kleijn et al., 2006). Furthermore many pesticides and herbicides may have negative side effects on human health (Male et al., 1976; Garry, 2004; Pimentel et al., 1992; Lu et al., 2000).

Fostering biodiversity in agricultural landscapes present direct economic opportunities by increasing crop production, and decreasing the necessity of costly inputs like pesticides and fertilizers. For example, presence of stable tree communities reduces erosion, which helps to maintain nutrient rich topsoil, a critical and expensive component for agriculture (Mathews, 1989). Diverse functional groups of arthropods may also provide increased ecosystem services, such as pollination services resulting in increased output, with respect to seed and fruit production of crops and wild plants (Hoehn et al., 2008; Albrecht et al., 2012). Wild relatives of crops provide genetic information useful in resolving issues relating to inbred crops experiencing genetic bottlenecks (Tanksley & McCouch, 1997). Due to reduction of biodiversity, crops have experienced a reduced ability in autonomous pest regulation (Altieri,1999). Maintaining a diverse community of arthropods in agroecosystems has been shown to be advantageous for controlling pest insects (Balvanera et al., 2006). As a result, the main objective of this project is to determine which habitats, and their traits, promote high numbers of individuals and diversities of overwintering arthropods, especially those which are of functional significance to agriculture, such as predators of pests.

Large polyphagous beetles can be extremely voracious predators, and have occasionally been documented preying on invertebrates (Bernard & Samolag, 2014). Other beetles, like lady bugs (Coleoptera: Coccinellidae) or hairy-horned spring tail hunters (Carabidae: Loricera) are specialized in preying upon specific prey such as aphids (Hemiptera: Aphdidae) or springtails (Hexopoda: Collembola). Spiders (Arachnida: Araneae) make up a diverse group which prey on a number of arthropod species including many pest insects (Marc & Canard, 1997). It has been suggested that activity levels of certain arthropods, such as ground beetles (Coleoptera: Carabidae), may be closely related to overwintering sites (Collins et al., 2003). Understanding which habitats and/ or environmental traits are associated with increased abundance and diversity of overwintering arthropods is a critical component in providing increased pest control within agricultural landscapes, however has yet been thoroughly investigated. It has been documented that lowest overwintering survival rates of beetles existed in bare soil, a prevailing feature of crops during off season (Dennis et al., 1994). A number of species are only known to overwinter in SNHs while few exist only in crops (Pfiffner & Luka, 2000). Woody habitats such as hedgerows may prove to provide higher overwintering densities of species and individuals of coleopterans and spiders (Pywell et al., 2005).

A number of factors are known to contribute towards general composition of arthropod communities on a local scale such as habitat fragmentation (Schweiger et al., 2005), intensity of agricultural land management (Hendrickx et al., 2007), landscape complexity/ heterogeneity (Gonzalo et al., 2014) or migration as a result of competition (Vandermeer et al., 1980). Agroecosystems exist as a mosaic of crops and SNHs and it is known that predators of pests migrate from SNHs to crops during spring and summer months (Anderson, 1997) contributing to pest control. In many cases carabids are used to model the interactions of anthropogenic changes on the environment, such as land fragementation, due to their efficiency of consuming pest insects and because they are often viewed as bioindicator species, but it may however make more sense to recognize them instead for their ability to reflect changes in small spatial scales (Pearce & Venier, 2006). Therefor carabid beetles were used as model taxa and analyzed in more detail than other arthropod groups.

The following research questions were addressed in this study:

1) How does overwintering of functionally important arthropod groups differ among and within different types of SNHs compared to crops in agricultural landscapes?
2) Which are the key SNH traits driving overwintering in different taxonomic and functional arthropod groups? To what extent do traits predicting the overwintering of different functional groups of arthropods overlap?
3) How important are plant diversity and structural heterogeneity of SNHs in predicting overwintering arthropod biodiversity?
4) How do arthropod traits shape overwintering arthropod assemblages, i.e. how are different ecological species groups of carabids linked to different SNH types?

Hypotheses:

1) Overall arthropod diversity and abundance (as well as carabids) will be positively affected by increasing botanical heterogeneity.
2) A negative relationship will exist between overwintering of arthropods and soil bulk density.
3) Significant differences between abundances of various arthropod groups will exist in the majority of cases between crops and SNH types.
4) Crops will prove inefficient at harboring overwintering of carabids and other predators of pest arthropods.
5) Forests will support the highest abundances and diversities of overwintering arthropods, mostly due to their size and lack of disturbance.

Methods:

Study area:

Study sites were located within rural agroecosystems in bordering cantons Zürich and Aargau, Switzerland. Eight sectors, with a gradient of landscape complexity, were established, each encompassing the five investigated habitat types within a one km radius from a randomly selected midpoint. SNHs consisted of sown flower strips, grasslands of varying management intensity, hedgerows, and forests. Crops, or arable land, were also sampled however not regarded as SNHs. Four sampling points were established in each SNH, with two situated on the habitat`s edge and two within the interior. Within the confines of this study, edge is defined as the first two meters inside

the SNH from the crop field. Interior for linear elements (hedgerows and flower strips, narrower than 25 m) was in the middle of the SNH as regarded from the two opposing borders. Within aerial elements (forests and meadows wider than 25 m), distances between traps were kept for internal reference. Crops received two traps each where no edge effect was tested. Traps were placed on bare patches within the crops rather than clearing bare patches, out of respect to farmers. A total of 144 traps were distributed across all sectors, resulting in eight replicates for each distance and habitat combination.

Sampling method:

Emergence traps (Fig. 1.), designed to capture arthropods emerging from the substratum/ leaf litter layer, were used to sample overwintering arthropods. Trap frames (50 x 50cm) were constructed with sheet metal. One rod ascended from each frame corner, converging 50 cm above the center of the trap frame to create a tent like structure. Mesh was utilized as a semi-permeable barrier, allowing air flow but restricting dispersal of surfacing arthropods. One pitfall (plastic cup, diameter 6.5cm) was inserted into a single corner of each trap for collecting epigeous arthropods. An initial cup was dug in so that its` crest rested slightly under ground level.  A hole was poked in it to allow for water drainage and prevent an air vacuum with the second cup, which needed to be removed and emptied every other week.  The second cup laid flush with ground level and was filled up to roughly one third of its` height with a 25% propylene glycol solution. A couple drops of detergent were also added to reduce surface tension. At the top of each emergence trap, a plastic jar containing a narrow entrance from the tent like structure opened upwards into a wider chamber, also partially filled with propylene glycol solution with the intention of capturing aerial arthropods. Black weed block was fitted around the mesh portion of each trap to create a light gradient and promote upward movement of flying insects towards incoming light of the translucent jars.

Fig. 1. Photo of emergence trap used during study.

A robust metal frame, flat on top but reaching 8 cm deep with sharp edges, was used to slice the ground open merely wide enough to allow to emergence traps to slide in. The frame had to be welded as it was repeatedly hammered into the ground which often contained rocks or roots. Emergence traps needed to penetrate the ground deep enough to prevent escape via burrowing of arthropods after emerging into traps and to ensure trap stability.

Samples were collected every two weeks starting at the beginning of March and finished in early June, with six sub-samples per trap. Propylene glycol solution was replaced upon every visit and arthropods were placed in 70% ethanol solution for identification. Precautionary repairs to traps were made often during trips to field sites as rain, sun, and wind all contributed to slow but steady deterioration of trap conditions. On two occasions traps had to be replaced as they had been trampled, seemingly by deer based on tracks. Two meadow sites were lost to cows and were not replaced because of persisting cattle presence. In spite of electric fence barriers, traps still managed to provoke curiosity from cows resulting in decimation of all on site traps.

Arthropod sorting:

A total of 38,714 arthropods were sorted into 53 groups ranging in their taxonomic levels from order to species (Appendix A). Data were organized in a nested hierarchical format. In most cases specimens were identified to the family. As predators are of particular significance to this project, carabids, rove beetles (Coleoptera: Staphylinidae), and spiders (Arachnidae: Araneae) had been stored as separate groups. Carabids were then identified to species (Müller-Motzfeld, 2004, Appendix B), while staphylinids and araneae were not, due to time constraints. Carabid species only found within one habitat type have been classified as stenotopic, within the confines of this study (Fig. 4.).

Assessment of habitat traits:

Soil bulk density was calculated from one liter soil core samples procured from the surface of each trap location. They were taken after the field season was finished to avoid creating disturbances during emergence periods. Samples were dried in an oven at 100 C° for three days, weighed, and recorded. Bulk density was determined as the ratio of weight in grams to volume in milliliters. Ground cover was also documented on the trap level. Recorded percent cover included bare soil, litter, herbaceous growth, dead herbs, tussock grass, fine grass, dead grass, moss, and wood. Coefficient of variation values were calculated on the site level by dividing standard deviation with mean values of all traps within a site to represent site wide ground cover values.

Sites from a previous study, in which plant species data were compiled, were utilized in this project, allowing for the opportunity to use these data as traits for habitats in order to explain arthropod community composition. For all expected one site botanical surveys were performed in the summer preceding the period of investigation. Ground cover of all plants was estimated in percentage for each sampling point on 5 single squares of 1m ^{2} for each habitat around the area where the trap would be located.

Statistical analysis:

To test whether abundance and diversity of overwintering arthropods differed among and within habitats, linear mixed effect models (LMMs, response variables summarized in Table 3.) were used. Generalized linear mixed effect models (GLMMs, response variables summarized in Table 3.) were used when residual errors were not normally distributed and assumptions of normality could not be met by transforming the response variable. Mixed effects models included habitat type as fixed factors and site ID as random effects nested in landscape sector ID. To account for overdispersion, negative binomial distribution families were used in all GLMMs with the glmmADMB function of the glmmADMB package (Fournier et al., 2012) in R (R Core Team, 2013). LMMs were performed with the lmer function in the package lme4 (Bates et al., 2014) in R (R Core Team). To test for differences among edge and interior parts of semi-natural habitats (hereafter referred to as "distance") and potential interactive effects with habitat type, distance (factor with levels edge or interior) and its interaction with habitat type were included as fixed factors in the models described above. Crops were not included in these models because edge and interior were not separated for the placement of traps. The interaction term habitat x distance was significant in each model, thus the full model was consistently the minimum adequate model. Statistical inference for explanatory variables was based on log-likelihood ratio tests (Zuur et al. 2013), and Tukey's HSD post-hoc tests,

performed with the R package multcomp (Hothorn et al., 2008), were used to test for significant differences among factor levels.

To explore which traits explained arthropod overwintering across habitats and distances:

Small-scale traits within habitats were examined as driving factors of arthropod diversity and abundance. Traits initially included all ground cover categories as well as their coefficients of variation, however models quickly became overly complex resulting in consolidation of ground cover values to include all grass categories together. The same was done for herbaceous categories while moss and wood were dropped. Wood and moss values were extremely low and insignificant and dropping them helped to ease the complexity of the models. In addition to ground cover (bare soil, leaf litter, herbaceous, grass, CV bare soil, CV leaf litter, CV herbaceous, and CV grass), soil bulk density, plant species richness (PSR), plant species evenness (PSE), and functional ground cover richness (FGCR) values were also selected. Pearson correlation coefficients (Table 1.) were obtained for pairwise comparison of explanatory variables and weakly correlated variables (0.6) were included in the model (Zuur et al., 2005). Model selection for response variables using mixed effects models have been described in the previous section. Habitat traits were then added to these models as covariates. Decisions for which traits to add to which models were made through backward elimination stepwise AIC model selection. Minimum adequate models are summarized in Table 3. In order to explain significant effects, if habitat traits had a negative or positive impact on response variables, scatterplots for response variables against soil bulk density (Fig. 5.), functional ground cover (Fig. 6.), grass cover (Fig. 7.), bare soil (Fig. 8.),percent herbaceous cover (Fig. 9.), plant species evenness (Fig. 9.), and leaf litter layer (Fig. 9.) were created. Soil bulk density scatterplots were fit with smooth curves in order to illustrate the negative relationship between extremely low and high values with overwintering of arthropods.

Table 1. Summary of estimated pair-wise Pearson correlation coefficient values for habitat traits.

Covariate	Bulk denstiy	Bare soil	Litter	Herbcaeous	Grass	CV litter	CV herbaceous	CV grass	PSR	PSE	FGCR
Bulk denstiy	1	0.18	-0.48	0.18	0.08	-0.05	-0.15	-0.18	-0.01	-0.07	-0.07
Bare soil	0.18	1	-0.31	-0.33	-0.42	-0.37	-0.08	-0.55	-0.18	-0.6	-0.55
Litter	-0.48	-0.31	1	-0.24	-0.39	-0.1	0.3	0.26	-0.06	0.04	-0.13
Herbcaeous	0.18	-0.33	-0.24	1	-0.26	0.02	0.03	0.32	-0.01	0.17	0.18
Grass	0.08	-0.42	-0.39	-0.26	1	0.41	0.35	-0.23	0.24	0.4	0.45
CV litter	-0.05	-0.37	-0.1	0.02	0.41	1	0.38	-0.13	0.11	0.38	0.34
CV herbaceous	-0.15	-0.08	0.3	0.03	0.35	0.38	1	0.4	0.2	0.46	0.32
CV grass	-0.18	-0.55	0.26	0.32	-0.23	-0.13	0.4	1	0.03	0.3	0.15
PSR	-0.01	-0.18	-0.06	-0.01	0.24	0.11	0.2	0.03	1	0.13	0.27
PSE	-0.07	-0.6	0.04	0.17	0.4	0.38	0.46	0.3	0.13	1	0.56
FPR	-0.07	-0.55	-0.13	0.18	0.45	0.34	0.32	0.15	0.27	0.56	1

Results:

Overwintering of arthropod groups among and within different habitat types:

Surprisingly few differences existed between abundances of overwintering arthropods between crops and SNHs, except for araneae where crops differed from meadows (Fig. 2.), hedgerows (Fig. 2.), and forests (Fig. 2.). Arthropod diversity also varied in comparison with crops across flower strips (Fig. 2.), hedgerows (Fig. 2.), and forests (Fig. 2.). Analysis of SNHs included the interaction of habitat x distance (edge effect) in all cases, as interactions were found to be significant through log-liklihood ratio tests (Table 2.). In most cases habitat edges did not differ from their corresponding interior. The exception to this case were forests, where differences between trap distances existed for overall arthropod abundance (Fig. 2.), arthropod order diversity (Fig. 2.), total predators (Fig. 2.), total herbivores (Fig. 2.), araneae (Fig. 2.), and for carabids (Fig. 2.). Forest edges always harbored a higher abundance and diversity of arthropod groups (Fig. 2.).
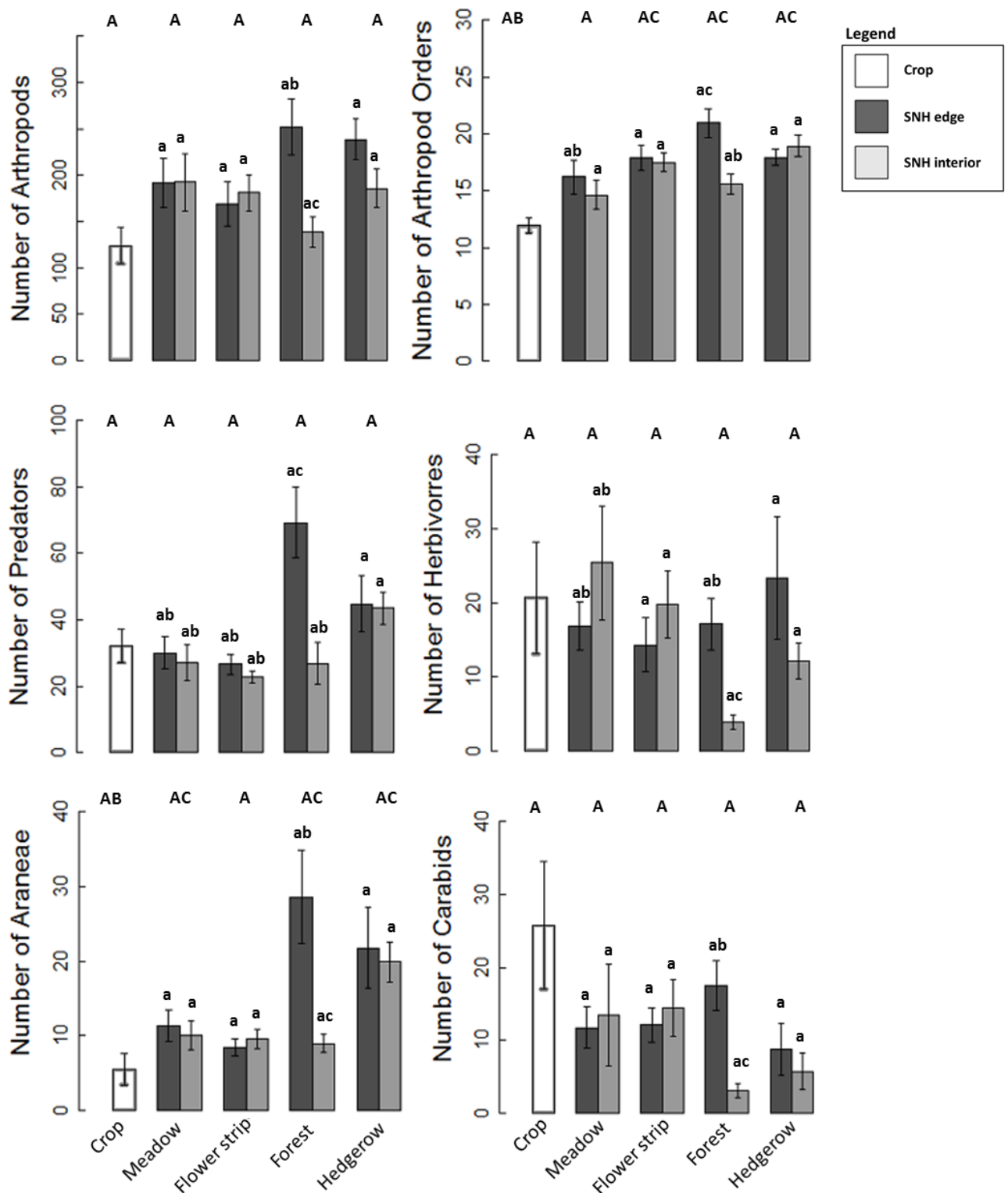
Fig. 2. Mean (± 1 standard error) (a) number of arthropods, (b) number of arthropod families, (c) number of predators, (d) number of herbivores, (e) number of araneae, and (f) number of carabids per trap overwintering in edges (<2 m from adjacent arable crop) and interior (2-12.5 m from adjacent crops for hedgerows and flower strips; 12.5 m for forests and meadows, see methods section) of semi-natural habitats compared to arable crops (winter oil-seed rape) (N = 8). Different lower case letters represent significant differences ($P ≤ 0.05$; Tukey's HSD post-hoc tests) among SNHs (separated in edge and interior habitat); different capitalized letters represent significant differences among habitats of the pooled data across trapping locations.).

Table 2. Significance (95% confidence interval) of fixed effects are summarized.

Response group	SNH Habitat df	χ²	p	SNH Distance df	χ²	p	SNH Habitat * Distance df	χ²	p	Total habitats Habitat df	χ²	p
Total arthropods	3	1.548	0.671	1	8.342	0.004	3	18.969	<0.0001	4	5.716	0.221
Arthropod diversity	3	4.122	0.249	1	7.131	0.007	3	18.379	0.0003	4	18.127	0.001
Total predators	3	10.114	0.0176	1	9.503	0.002	3	15.934	0.001	4	12.238	0.016
Total Herbivores	3	7.496	0.058	1	5.18	0.022	3	26.084	<0.0001	4	6.308	0.177
Araneae	3	11.464	0.009	1	6.128	0.013	3	15.048	0.002	4	25.22	<0.0001
Carabidae	3	5.886	0.117	1	7.022	0.008	3	21.384	<0.0001	4	8.9	0.063
Carabid predators	3	9.516	0.023	1	13.48	0.0002	3	11.282	0.0102	4	13.288	0.009
Carabid Omnivore	3	6.19	0.103	1	0.166	0.684	3	11.506	0.009	4	8.178	0.085
Carabid Herbivore	3	3.088	0.378	1	2.808	0.094	3	19.146	0.0003	4	2.852	0.583
Carabid Species Richness	3	9.497	0.023	1	7.687	0.005	3	26.581	<0.0001	4	10.941	0.027
Carabid Species Evenness	3	9.728	0.021	1	6.688	0.01	3	28.959	<0.0001	4	10.086	0.039

With 1,802 occurrences in 92% of the traps, carabids prevailed as one of the most abundant families. They were split according to diet and analyzed separately as distinct groups then were examined for differences between total habitats and then further investigated amongst SNHs, as previously done. Crops supported the highest densities of carabids, over twice the abundance of the most individual-rich SNH (forests). However, no significant difference existed between crops compared to SNHs, which was most likely due to the high level of variation in abundance. The only significant habitat wide difference was concerning carabid species richness between flower strips and hedgerows (Fig. 3.). Generally herbaceous habitats appeared to support higher densities and diversities of carabids than woody habitats did. Abundance of stenotopic species (Fig. 4.), which were highest in forests, were virtually absent in crops, and did not reflect upon species richness.
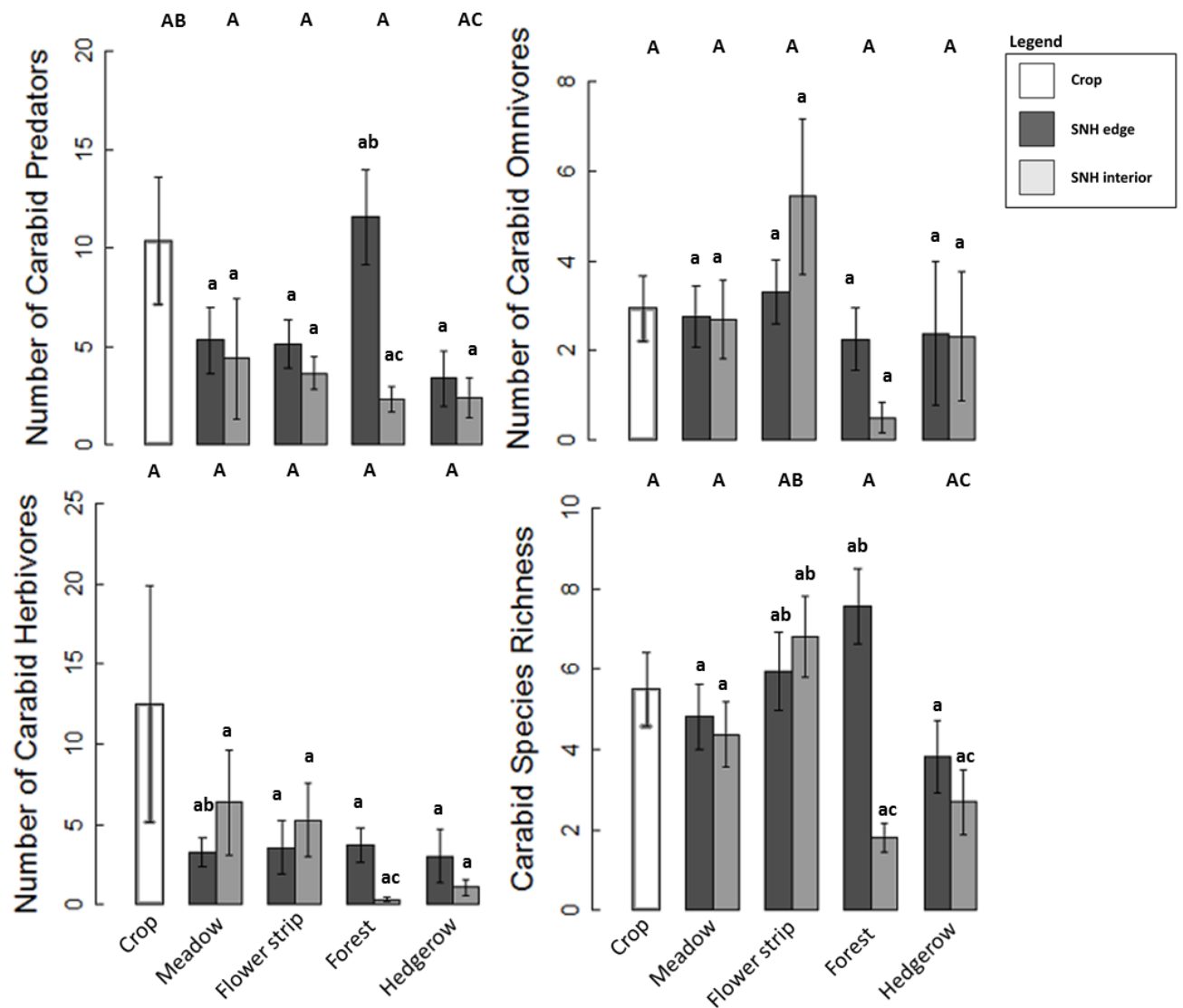
Figure 3. Mean (± 1 standard error) (a) number of carabid predators, (b) number of carabid omnivores, (c) number of carabid herbivores, and (d) species richness of carabids per trap overwintering in edges (<2 m from adjacent arable crop) and interior (2-12.5 m from adjacent crops for hedgerows and flower strips; 12.5 m for forests and meadows, see methods section) of semi-natural habitats compared to arable crops (winter oil-seed rape) (N = 8). Different lower case letters represent significant differences ($P \leq 0.05$; Tukey's HSD post-hoc tests) among SNHs (separated in edge and interior habitat); different capitalized letters represent significant differences among habitats of the pooled data across trapping locations.).
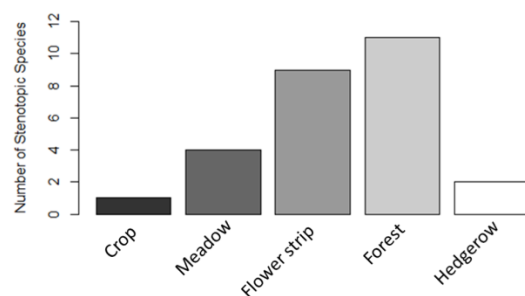

Fig. 4. Abundances of stenotopic species, found only within only one habitat type, across all habitats.

SNH traits driving overwintering in different taxonomic and functional arthropod groups:

SNH traits were examined for influence on arthropod abundances and diversities across habitat types as well as trap distances. Soil bulk density ranging from 1.0 – 1.4 appeared to support the highest levels of overwintering arthropod abundance and diversity (Fig. 5.). Bulk density influenced total arthropod abundance (Table 3.), carabid abundance (Table 3.), carabid species richness (Table 3.), and carabid species evenness (Table 3.) across all habitat types. It was also important in explaining arthropod diversity, carabid species richness, and carabid species evenness (Table 3.) within SNHs. Bulk density ranged from 0.5247 to 1.5417 and was lowest in forests (Fig. 10.). Functional ground cover was a further important driver of arthropod overwintering abundances, which was found to influence arthropod and carabid abundances (Table 3.) across all habitat types as well as in SNHs (Table 3.). While overwintering arthropods responded positively to increasing functional ground cover richness, carabids did not (Fig. 6.). Diversity within arthropod groups was better explained by plant species evenness rather than functional ground cover (Table 3.). A positive relationship existed between plant species evenness and diversity of total arthropods (Fig. 9.) across all habitats. Carabid predators surprisingly responded negatively to increasing grass (Fig. 7.) and herbaceous cover (Fig. 9).

Only certain effects have been mentioned in the results. Full models have been summarized in Table 4. Stepwise AIC model selection resulted in covariates occasionally being accepted into models despite their statistically insignificant effect on response variables and may be interesting to examine.

Table 3.1. Minimum adequate models for overwintering of (a) total arthropod abundance, (b) total arthropod (family) diversity, (c) carabid abundance, (d) carabid predator abundance, (e) carabid omnivore abundance, (f) carabid herbivore abundance, (g) total herbivore abundance, (h) total predator abundance, (i) carabid species richness, (j) carabid species evenness, and (k) araneae abundance are summarized below. Two models are used for each response variable, where ALL habitats include crops, but not edge effect. SNH includes the interaction of habitat x distance but excludes crops. Degrees freedom, chi square, and p values (95% confidence interval) are listed for covariates selected for specific models (backwards elimination AIC stepwise procedure.

Distribution	Response group	Habitats	Bulk density			Bare soil			Litter			Herbaceous			Grass		
			df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P
LME Gaussian sqrt	Total arthropods	All	1	6.314	0.012												
		SNH	1	2.885	0.089												
LME Gaussian	Arthropod diversity	All				1	6.78	0.009	1	4.196	0.04	1	5.393	0.02	1	9.653	0.002
		SNH	1	7.345	0.007	1	2.926	0.087	1	3.847	0.05	1	2.064	0.15	1	5.398	0.02
GLMM NB	Carabidae	All	1	16.29	<.0001												
		SNH	1	7.816	0.005												
GLMM NB	Carabid predators	All	1	23.412	<.0001	1	6.49	0.011	1	2.572	0.109	1	6.818	0.009	1	4.166	0.041
		SNH	1	12.794	0.0003	1	1.396	0.237				1	1.82	0.177			
GLMM NB	Carabid omnivores	All	1	8.96	0.003												
		SNH	1	4.884	0.027												
GLMM NB	Carabid herbivores	All															
		SNH				1	2.464	0.116									
GLMM NB	Herbivores	All	1	2.996	0.083												
		SNH				1	1.662	0.197									
LME Gaussian sqrt	Predators	All	1	5.1025	0.024	1	2.609	0.106	1	3.221	0.073	1	6.538	0.01	1	5.956	0.015
		SNH															
LME Gaussian ln	Carabid species richness	All	1	13.67	0.0002												
		SNH	1	3.831	0.051												
LME Gaussian	Carabid species evenness	All	1	14.716	0.0001												
		SNH	1	4.057	0.044												
GLMM NB	Araneae	All	1	2.996	0.083												
		SNH															

Table 3.2. Minimum adequate models for overwintering of (a) total arthropod abundance, (b) total arthropod (family) diversity, (c) carabid abundance, (d) carabid predator abundance, (e) carabid omnivore abundance, (f) carabid herbivore abundance, (g) total herbivore abundance, (h) total predator abundance, (i) carabid species richness, (j) carabid species evenness, and (k) araneae abundance are summarized below. Two models are used for each response variable, where ALL habitats include crops, but not edge effect. SNH includes the interaction of habitat x distance but excludes crops. Degrees freedom, chi square, and p values (95% confidence interval) are listed for covariates selected for specific models (backwards elimination AIC stepwise procedure.

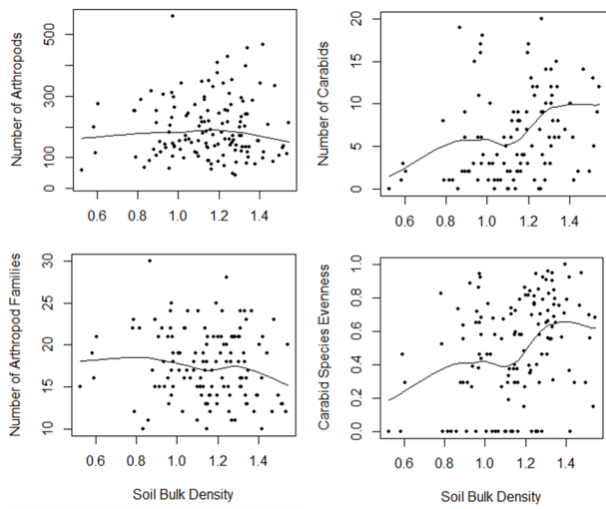|			CV litter			CV herbaceous			CV grass			Plant species evenness			Functional plant diversity		
			df	χ^2	p	df	χ^2	P	df	χ^2	P	df	χ^2	P	df	χ^2	P
LME Gaussian sqrt	Total arthropods	All				1	0.177	0.674							1	4.536	0.033
		SNH				1	0.675	0.411				1	1.769	0.183	1	5.034	0.023
LME Gaussian	Arthropod diversity	All							1	7.37	0.007	1	5.074	0.024	1	0.188	0.665
		SNH							1	6.173	0.013	1	11.148	0.0008			
GLMM NB	Carabidae	All	1	1.502	0.22										1	6.002	0.014
		SNH	1	2.384	0.122	1	1.018	0.313	1	1.564	0.211				1	5.13	0.023
GLMM NB	Carabid predators	All													1	1.734	0.188
		SNH															
GLMM NB	Carabid omnivores	All	1	9.712	0.002	1	2.098	0.147							1	7.062	0.008
		SNH	1	9.774	0.002	1	3.134	0.077							1	5.908	0.024
GLMM NB	Carabid herbivores	All													1	5.698	0.017
		SNH													1	4.458	0.035
GLMM NB	Herbivores	All													1	2.516	0.113
		SNH							1	2.73	0.098				1	2.59	0.107
LME Gaussian sqrt	Predators	All													1	5.028	0.025
		SNH													1	3.063	0.08
LME Gaussian ln	Carabid species richness	All										1	2.978	0.084	1	2.403	0.121
		SNH															
LME Gaussian	Carabid species evenness	All										1	3.413	0.0647			
		SNH															
GLMM NB	Araneae	All															
		SNH										1	2.362	0.124	1	1.894	0.169

Fig. 5. Scatter plots with soil bulk density against (a) number of total arthropods, (b) number of carabids, (c) number of arthropod families, and (d) carabid species evenness. Scatter plots have been fitted with a smooth curve to illustrate the negative relationship between low and high bulk density values with overwintering arthropod abundances and diversities.
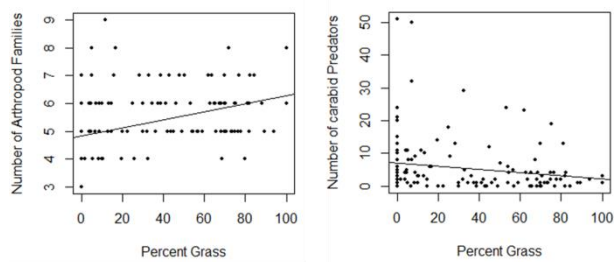

Fig. 6. Scatter plots with functional ground cover richness as an explanatory variable against (a) number of total arthropods, (b) number of total carabids, and (c) number of total predators with lines of best fit.

Fig. 7. Scatter plots with percent grass cover as an explanatory variable against (a) number of arthropod families and (b) number of carabid predators with lines of best fit.
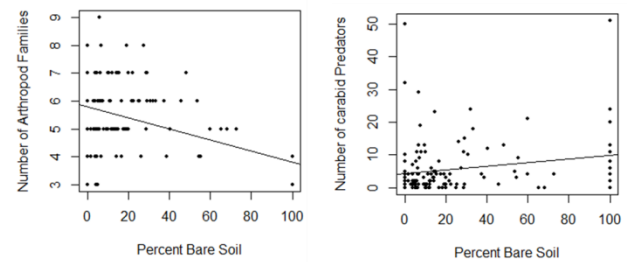
Fig. 8. Scatter plots with percent bare soil as an explanatory variable against (a) number of arthropod families and (b) number of carabid predators with lines of best fit.
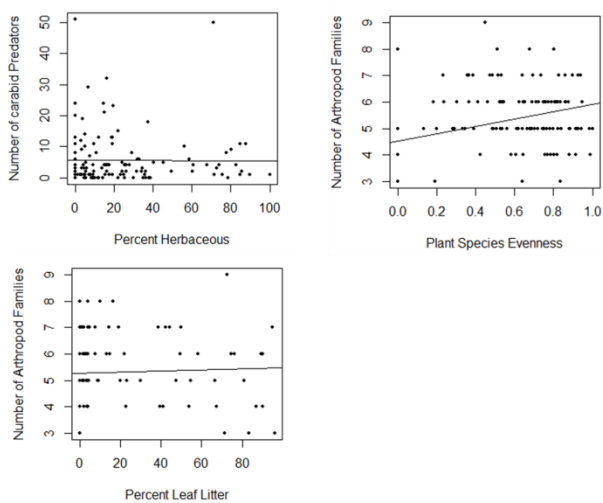

Fig. 9. Scatter plots with (a) percent herbaceous cover against number of carabid predators, (b) plant species evenness against number of arthropod families, and (c) percent leaf litter against number of arthropod families fitted with lines of best fit.
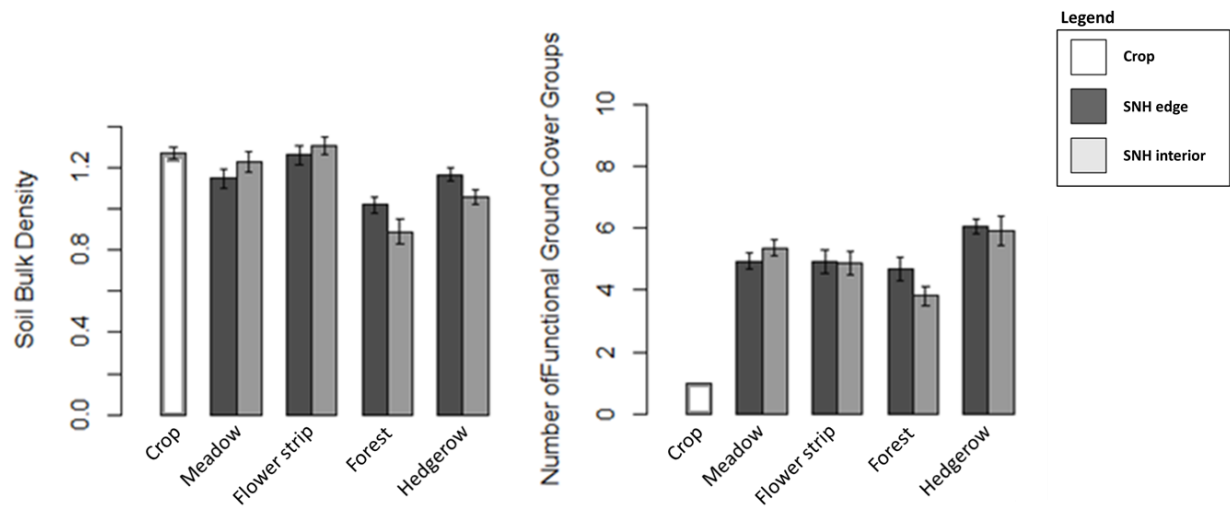
Fig. 10. Mean (± 1 standard error) (a) soil bulk density and (b) number of functional ground cover groups per trap in edges (<2 m from adjacent arable crop) and interiors (2-12.5 m from adjacent crops for hedgerows and flower strips; 12.5 m for forests and meadows, see methods section) of semi-natural habitats compared to arable crops (winter oil-seed rape) (N = 8).

Influence of arthropod traits on overwintering arthropod assemblages:

Wing morphology and diet data were used to explain responses in arthropod assemblages. Again, SNHs were analyzed separately from total habitats. The interaction of habitat and distance with arthropod traits were found to impact response variables in all instances (Table 4.) quite possibly attributed to by immense contrast between forest trap distances. Habitat alone was found only to influence wing morphology. The interaction of habitat traits with arthropod traits was found to affect all response groups amongst SNHs (Table 4.), with much variance occurring between forest trap distances. Once more habitat without the interaction was found only to influence wing morphology of carabids(Table 4.). There were no differences between trap distances in herbaceous habitats. Predator abundance (Fig. 11.) and carabid species richness (Fig. 11.) contrasted greatly between forest edges and interiors. Omnivores were relatively balanced amongst habitat edges and interiors while herbivores did vary between meadow edges and forest interiors (Fig. 11.). Edge effect differences were far more prominent amongst carabid species richness opposed to the three dietary groups. Flower strip interiors differed from forest (Fig. 11.) and hedgerow interiors (Figure x) while flower strip interiors varied from forest interiors (Fig. 11.). Forest edges supported higher diversities of carabids than hedgerow interiors (Fig. 11.).

Table 4. Degrees freedom, Chi ², and p values (95% confidence interval) are summarized for fixed factors (arthropod trait data) and their effects on (a) number of arthropods grouped by diet, (b) number of carabids grouped by diet, (c) number of carabids grouped by wing morphology, and (d) number of carabids grouped by size. Mixed effects models (family of distribution and model corresponding to response variable seen in Table 3.) with the fixed factors were compared to models without the corresponding fixed factor using ANOVAs in order to determine effects.

Response group	Factor x	SNH Factor x			SNH Habitat			SNH Distance			SNH Factor x * (Distance + Habitat)		
		df	χ^2	p	df	χ^2	p	df	χ^2	p	df	χ^2	p
Total arthropods	Diet	1	71.381	<0.0001	3	2.106	0.551	1	8.949	0.003	4	25.516	0.0004
Carabidae	Diet	1	7.394	0.006	3	4.028	0.258	1	13.98	0.0001	4	12.6	0.013
Carabidae	Wing morphology	2	124.33	<0.0001	3	14.528	0.002	1	5.572	0.018	8	67.396	<0.0001
Carabidae	Size	2	95.832	<0.0001	3	5.384	0.148	1	8.844	0.003	8	19.28	0.013

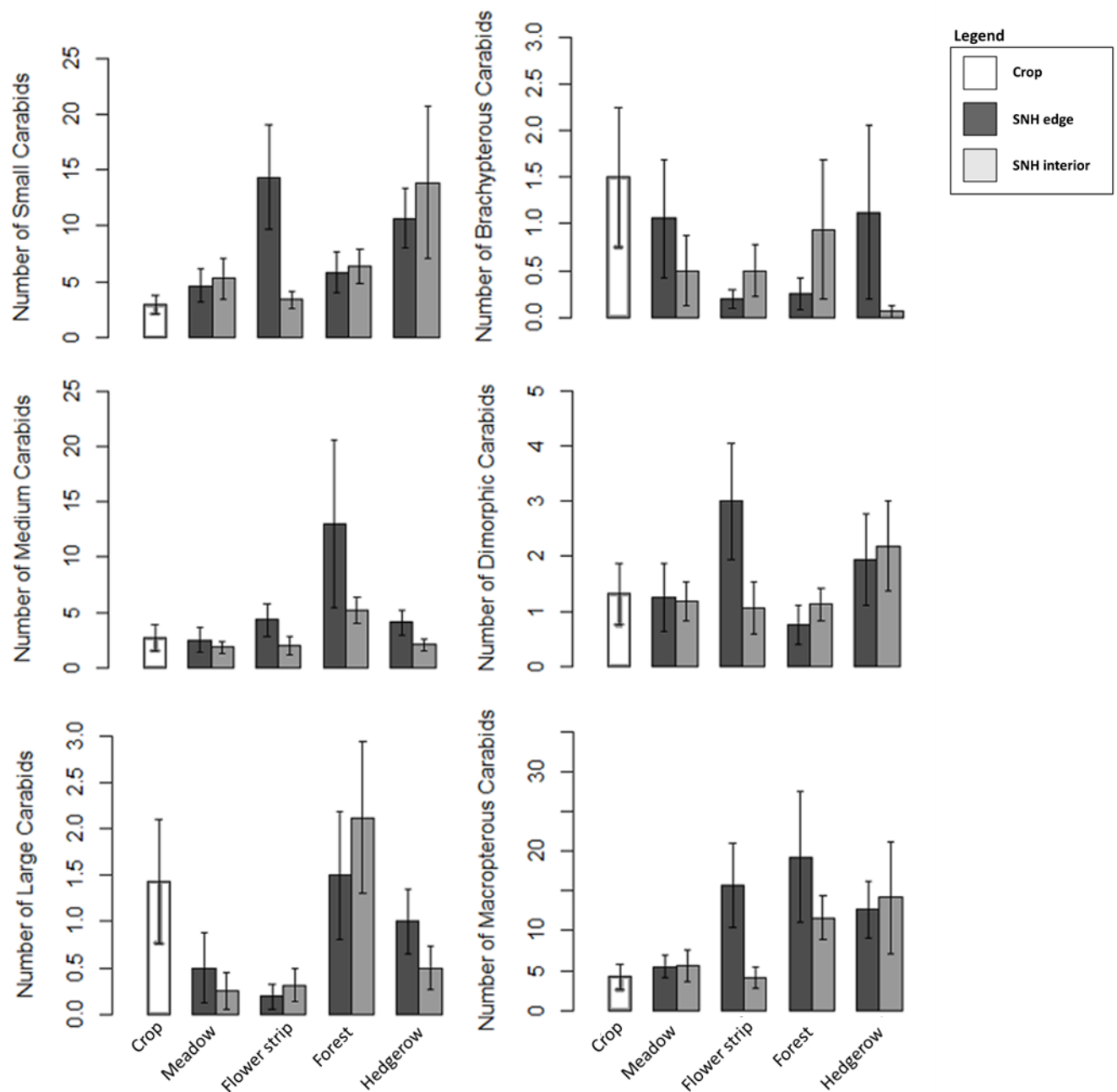| Response group	Factor x	Total habitats Factor x			Total habitats Habitat			Total habitats Factor x * Habitat		
		df	χ^2	p	df	χ^2	p	df	χ^2	p
Total arthropods	Diet	1	77.754	<0.0001	4	1.9216	0.75	4	23.807	<0.0001
Carabidae	Diet	1	9.522	0.002	4	7.11	0.13	4	10.758	0.029
Carabidae	Wing morphology	2	161.8	<0.0001	4	15.956	0.003	8	75.288	<0.0001
Carabidae	Size	2	120.03	<0.0001	4	6.472	0.167	8	28.376	0.0004

Fig. 11. Mean (± 1 standard error) (a) number of small carabids, (b) number of brachypterous carabids, (c) number of medium carabid, (d) number of dimorphic carabids, (e) number of large carabids, (f) number of macropterous carabids overwintering in edges (<2 m from adjacent arable crop) and interior (2-12.5 m from adjacent crops for hedgerows and flower strips; 12.5 m for forests and meadows, see methods section) of semi-natural habitats compared to arable crops (winter oil-seed rape) (N = 8).

Discussion:

How do overwintering arthropod taxa and functional groups vary among different types of SNHs compared to crops in agricultural landscapes?

This project highlights distinct differences in overwintering arthropod assemblages across habitat types in an agroecosystem. In this study woody habitats (forests and hedgerows) predominantly supported the highest levels of overwintering diversity and abundance followed by herbaceous habitats (meadows and flower strips) (Fig. 2. and Fig. 3.). Arable land harbored the lowest quantities of overwintering arthropods with roughly two thirds the diversity and abundance found in woody habitats. Intense land management practices are major factors contributing to low arthropod diversity in crops (Schmidt et al., 2003). Thorbek and Bilde, 2004 observed negative impacts of soil tillage and weed removal, which both lead to direct mortality of carabids and araneae, while this study observed an increased abundance of carabids in crops (Fig. 3.), araneae were particularly scarce in arable land. Weed removal contributed to habitat homogenization of crops (Fig. 10.), reducing the likelihood of providing suitable microclimates for various arthropods (Kroos and Schaefer, 1998). Evidence of poor climactic conditions on crops were shown as Pfiffner and Luka (2000) found that the top five centimeters of soil samples they took from arable fields (in a nearby canton to where this study occurred) were frozen, which was not the case for bordering SNHs. Arable fields in this study had been tilled and planted before winter, leaving only bare soil present, eliminating any insolation properties provided by vegetation and reducing ovipositing suitability for arthropods as native flora is often preferred for ovipositing (Landis et al., 2000). In addition to homogenization of habitat and diminishment of favorable microclimatic conditions required to support healthy arthropod assemblages, pesticides impose a negative impact on arthropod communities (Pimentel et al., 1992). Application of pesticide was routinely witnessed during sampling, possibly leading to a decline of arthropods and modification of arthropod community structure (Lee et al., 2001). The cumulative effects of management on arable fields lead to low biodiversity and abundance of overwintering arthropods in agroecosystems (Fig. 2. (a) and (b)).

Presence of SNHs in agroecosystems provide refuges for fauna which can not survive the intense management regimes of arable fields (Thorbeke & Bilde, 2004, MacLeod et al., 2004). Woody elements sheltered the most valuable arthropod communities, throughout the investigated agroecosystems, in terms of biodiversity and predation on pest insects. Forests also supported the highest amount of stenotopic species in this study (Fig. 4.) coinciding with Diekötter et al. (2008), who showed that woody and protected habitats contained higher biodiversity than anthropogenic habitat types. In some senses structural features of woody habitats are what protect them from disturbances. Hedgerows were virtually impassable and forests remained relatively untraveled except for trails and dirt roads. Reduced traffic as well as accumulation of leaf litter may be reflected in lower soil bulk density (Fig. 6. (a)), which are both characteristic of undisturbed landscapes. Disturbances in forests consisted mostly in the form of recreational activities such as dog walking or bike riding (Angold et al., 2006) in comparison to the heavy mechanical and chemical disturbances experienced in arable fields. High habitat heterogeneity of hedgerows, not observed in forests, (Fig. 6. (b)) is another essential factor related to their high productivity. Tall, diverse vegetation with the presence of bare ground in hedgerows, compared to field margins, provide greater suitability for overwintering of beetles and spiders (Pywell et al., 2005).

While it came as no surprise that woody elements supported the highest diversity of overwintering arthropods, one might have expected herbaceous elements to support higher abundances (Gardner et al., 1995) which was not corroborated in this study (Fig. 2. and Fig. 3.). Herbaceous habitats incorporated into arable field systems are often rotated with crops on a multiple year cycle. This was evident within the study sites as maps from previous years showed chronological changes in flower strip, meadow, and crop locations which may contribute to their reduced ability to harbor lower overwintering diversities and abundances. Frank and Reichhart (2004) found a positive relationship between age of flower strip and species richness/ abundance of overwintering adult carabids and staphylinids. This could indicate that reduced overwintering of arthropod abundance and diversity in herbaceous habitats compared to woody may be partially related to young age of herbaceous habitats. Changes in carabid and staphylinid assemblages can possibly be attributed to changes in botanical structure associated with age such as increases in forb cover, soil organic content matter, as well as height and diversity of vegetation (Pywell et al., 2005).

How important are edge effects, if even present, of different SNH types for the overwintering of arthropods if?

Abundance and diversity of arthropods in herbaceous habitats were not affected by trap distances. The opposite was observed for woody habitats with major divisions in forests and minor ones within hedgerows. It has been proposed that starkest degrees of contrast can be observed at the landscape level, in certain biogeographic regions, and in agroecosystems (Chalfoun et al., 2002). Varying organisms will respond to edge effects differently, some negatively and some positively (Fahrig, 2003), but carabid species richness was significantly higher in forest edges than interiors largely due to herbaceous cover, or lack thereof (Magura, 2000). Abiotic and biotic differences existed between forest edges and interiors resulting varying microclimates, which are important for explaining different carabid assemblages. Forest canopies do not permit much sun from reaching forest floors resulting in gradients, reaching perpendicular from the forest edge to the center where herbaceous cover becomes scarce, and relative air moisture increases (Magura et al., 2001). Forest interiors repeatedly supported low overwintering abundances and diversities (Fig. 2. and Fig. 3.) with only a few exceptions of sparsely populated carabids grouped by ecological traits (Fig. 11.).

Which are the key SNH traits driving overwintering in different taxonomic and functional arthropod groups?

Bulk density was influential in distribution of arthropod assemblages (Table 3.), yet very little research has been published to determine the effects of soil bulk density on overwintering arthropod populations. Soil is compacted when heavy machinery, as in tractors, repeatedly operate over a landscape. Soil may be loosened but effects of compaction will not be reversed by repeated soil tillage (Horn et al., 1995), however may be through earthworm activity (Beare et al., 1997). Soil compaction reduces biotic activity and constrains root elongation (Whalley et al., 1995). It can also lead to decreased ability of soil to withhold water and nutrients (Hamza & Anderson, 2005) further restricting plant growth. Physical characteristics of extremely compacted soil may directly affect overwintering arthropods in a negative way, or indirectly through a trickledown effect of a degraded

plant community. Extremely loose soil also had a negative impact on overwintering arthropods (Fig. 5.), perhaps due to reduced insulation.

How important are plant diversity and structural heterogeneity of SNHs in predicting overwintering arthropod biodiversity?

Grassy and herbaceous ground covers were found to be important for abundance and diversity of specific arthropod groups (Table 3.). These effects were however, not witnessed across multiple groups, but indicate that diverse or functionally diverse plant groups are important for supporting a wide array of overwintering arthropods. Functional plant richness and species evenness seemed to account for much more of an all-encompassing explanation to arthropod assemblages. Functional ground cover over botanical diversity was a major influence in arthropod abundances contrary to literature (Siemann et al., 1988). Functional ground cover richness was high in hedgerows (Fig. 6.), and coincided with high overwintering arthropod abundances and diversities (Fig. 2.). Low functional ground cover richness of forests (Fig. 6.) however, did not help to explain their high overwintering productivity. Plant species evenness seemed to affect overwintering arthropod diversity rather than abundance (Table 3.). High botanical diversity is important for supporting diverse herbivore populations, which in turn promotes high predator diversity (Siemann, 1998).

How do carabid traits shape overwintering carabid assemblages?

Intense land management regimes of agricultural landscapes are reflected across carabid assemblages (Chapman et al., 2005). As Ishitani et al. (2003) also observed, disturbed sites such as crops were often characterized by a proportionally high abundance of relatively few generalist species. These less specialized species may benefit from extreme conditions, which would not normally be available to them in nature (van Straalen, 1998) but in order to recolonize those ephemeral habitats, dispersal ability is crucial. Consequently wing morphology may be the most effective trait at explaining carabid distribution in relation to a highly fragmented agroecosystem. Macroptery is a common trait for carabids which are prone to extinction (Liebherr,1988). As a result macropterous and dimorphic species tended to dominate crops and herbaceous habitats (Fig. 11), which were prone to imminent disturbances. Lacking high dispersal abilities, brachypterous species were almost exclusively found in forests.

Large predatory carabids are strongly affected by land management practices (Cole et al., 2002) and were only found to overwinter in forests in extremely low abundances within this study. Large carabids in general were relatively absent from crops and meadows. It may be because smaller carabids and generalists tend to be winged more often than larger ones that they are more capable of recolonizing unbalanced habitats (Ishitani et al., 2003) and due to an abundant availability of unbalanced habitats are able to exist in such high abundances.

Conclusion:

Management of SNHs in agricultural landscapes should seek to increase arthropod diversity and optimize ecosystem functioning and services, such as natural pest control through high predator

abundances. Woody habitats, especially forests, were the most productive landscapes in promoting overwintering of predators. Herbaceous habitats supported lower biodiversity, lower predator abundances, and higher herbivore abundances while crops supported the lowest densities and diversities of overwintering arthropods. Soil bulk density and functional ground cover richness were found to have all encompassing effects on response groups/ overwintering arthropods with respect to abundance and diversity. Low soil bulk density helped to explain high overwintering productivity in forests, but low functional ground cover richness did not help to describe rich production of forests. Dispersal ability is a limiting factor for migration of many large predatory carabids (Chapman et al., 2005), which were almost exclusively found in forests. Providing more connectivity of SNHs and crops with forests may improve biodiversity and pest control services in agricultural landscapes.

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Appendix A) List of all individuals and abundances (*n*) sampled and identified, to various taxonomic levels, throughout the project.

Taxon	*n*	Taxon	*n*
Acrididae	17	Ichneumonidae	237
Aphididae	590	Isopoda	2045
Araneae	1983	Ixoidea	51
Asilidae	51	Lepidoptera adults	73
Blattoidea	98	Lepidoptera larvae	301
Bombus	13	Meligethes	409
Brachycera	1930	Mecoptera	107
Buprestidae	5	Megadrilacea	211
Cantharidae	37	Meloidae	18
Carabidae	1802	Muscidae	103
Chilopoda	60	Nematocera	5771
Chrysididae	63	*Oulema melanopus*	49
Chrysomelidae	114	Opiliones	22
Chrysopidae	12	Oribatida	476
Cicadellidae	375	Pentatomidae	26
Coccinellidae	54	Pseudoscorpionida	25
Coleoptera	257	Reduviidae	35
Collembola	6899	Scarabaeidae	84
Curculionidae	703	Sphecidae	156
Dermaptera	366	Staphylinidae	2067
Diplopoda	1459	Stratiomyidae	176
Elateridae	200	Syrphidae	50
Formicidae	4702	Tipulidae	412
Gastropoda	3018	Trichoptera	86
Gryllidae	13	Trombidiformes	480
Hemiptera	124		

Appendix B.1) List of all carabid species and abundances (*n*) sampled throughout the project.

Species	*n*
Abax (Abax) ovalis (Duftschmid, 1812)	9
Abax (Abax) parallelepipedus parallelepipedus (Piller &Mitterpacher, 1783)	5
Abax (Abax) parallelus parallelus (Duftschmid, 1812)	15
Acupalpus meridianus (Linné, 1761)	1
Agonum (Agonum) muelleri (Herbst, 1784)	48
Amara (Amara) aenea (De Geer, 1774)	40
Amara (Curtunotus) aulica (Panzer, 1796)	2
Amara (Amara) convexior Stephens, 1828	38
Amara (Amara) familiaris (Duftschmid, 1812)	22
Amara (Zezea) fulvipes (Audinet-Serville, 1821)	6
Amara (Zezea) kulti Fassati, 1947	4
Amara (Amara) lunicollis Schiødte, 1837	8
Amara (Amara) montivaga Sturm, 1825	1
Amara (Amara) ovata (Fabricius, 1792)	92
Amara (Zezea) plebeja (Gyllenhal, 1810)	3
Amara (Amara) similata (Gyllenhal, 1810)	31
Anchomenus (Anchomenus) dorsalis (Pontoppidan, 1763)	241
Anisodactylus (Anisodactylus) binotatus (Fabricus,1787)	117
Anisodactylus (Anisodactylus) nemorivagus (Duftschmid, 1812)	1
Anisodactylus (Pseudanisodactylus) signatus (Panzer, 1796)	152
Asaphidion curtum curtum (Heyden, 1870)	2
Asaphidion flavipes (Linné, 1761)	4
Badister (Badister) bullatus (Schrank, 1798)	10
Bembidion (Metallina) lampros (Herbst, 1784)	91
Bembidion (Phyla) obtusum Audinet-Serville, 1821	1
Bembidion (Metallina) properans (Stephens, 1828)	8
Bembidion (Bembidion) quadrimaculatum quadrimaculatum (Linné, 1761)	21
Bembidion (Peryphus) tetracolum tetracolum Say, 1823	16
Brachinus (Brachinus) crepitans (Linné, 1758)	16
Brachinus (Brachynidius) explodens Duftschmid, 1812	45
Callistus lunatus lunatus (Fabricius, 1775)	2
Carabus (Tachypus) auratus auratus (Linné, 1761)	1
Carabus (Morphocarabus) monilis Fabricus, 1792	2
Carabus (Archicarabus) nemoralis nemoralis O. F. Müller, 1764	2
Clivina collaris (Herbst, 1784)	3
Clivina fossor fossor (Linné, 1758)	45
Cychrus caraboides (Linné, 1758)	1
Demetrias (Demetrias) atricapillus (Linné, 1758)	6
Diachromus germanus (Linné, 1758)	33
Dromius quadrimaculatus (Linné, 1758)	1
Harpalus (Harpalus) affinis (Schrank, 1781)	76

Appendix B.2) List of all carabid species and abundances (*n*) sampled throughout the project.

Species	*n*
Harpalus (Harpalus) anxius (Duftschmid, 1812) / (s. str.) subcylindricus Dejean, 1829	6
Harpalus (Harpalus) dimidiatus (P. Rossi, 1790)	12
Harpalus (Harpalus) distinguendus distinguendus (Duftschmid, 1812)	26
Harpalus (Pseudoophonus) griseus (Panzer, 1796)	1
Harpalus (Harpalus) latus (Linné, 1758)	8
Harpalus (Harpalus) luteicornis (Duftschmid, 1812)	65
Harpalus (Harpalus) rubripes (Duftscmid, 1812)	2
Harpalus (Pseudoophonus) rufipes (De Geer, 1774)	76
Harpalus (Harpalus) tardus (Panzer, 1796)	5
Loricera pilicornis pilicornis (Fabricu, 1775)	11
Microlestes maurus maurus (Sturm, 1827)	1
Molops piceus piceus (Panzer, 1793)	37
Nebria (Nebria) brevicollis (Fabricus, 1792)	14
Nebria (Nebria) salina Fairmaire &Laboulbéne, 1854	27
Notiophilus biguttatus (Fabricius, 1779)	1
Notiophilus palustris (Duftschmid, 1812)	9
Ophonus (Metophonus) cf melletii (Heer,1837)	1
Ophonus (Metophonus) puncticeps Stephens, 1828	2
Paradromius (Manodromius) linearis linearis (Olivier, 1795)	1
Parophonus maculicornis (Duftschmid, 1812)	12
Platynus (Platynus) assimilis (Paykull, 1790)	8
Poecilus cupreus cupreus (Linné, 1758)	144
Poecilus lepidus lepidus (Leske, 1785)	1
Poecilus versicolor (Sturm, 1824)	3
Pterostichus (Pseudomaseus) anthracinus anthracinus (Illiger, 1798)	7
Pterostichus (Cheropus) burmeisteri burmeisteri Heer, 1838	2
Pterostichus (Steropus) madidus (Fabricius, 1775)	16
Pterostichus (Morphosoma) melanarius melanarius (Illiger, 1798)	2
Pterostichus (Platysma) niger niger (Schaller, 1783)	3
Pterostichus (Bothriopterus) oblongopunctatus oblongopunctatus (Fabricius, 1787)	7
Pterostichus (Phonias) ovoideus ovoideus (Sturm, 1824)	6
Pterostichus (Phonias) strenuus (Panzer, 1796)	1
Pterostichus (Cryobius) unctulatus (Duftschmid, 1812)	2
Pterostichus (Argutor) vernalis (Panzer,1796)	35
Stenolophus teutonus (Schrank, 1781)	12
Stomis pumicatus pumicatus (Panzer, 1796)	1
Trechoblemus micros (Herbst, 1784)	1
Trechus (Trechus) quadristriatus (Schrank, 1781)	10
Trichotichnus laevicollis (Duftschmid, 1812)	2