



Pace of life and mobility as key factors to survive in farmland – Relationships between functional traits of diurnal Lepidoptera and landscape structure

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ABSTRACT

Agricultural intensification is known to lead to biotic homogenization by selecting against habitat and resource specialist species, but most studies on this phenomenon have been limited to certain parts of the landscape diversity gradient. We aimed to reveal the relationships between functional traits of diurnal Lepidoptera and landscape structure along a wide environmental gradient from nature reserves to intensive farmland in Baden-Württemberg, SW Germany. Butterflies and burnet moths were sampled along 1500 m long transects using ‘Pollard walk’ in 99 sites. Twenty nature reserves, 39 grassland-dominated and 40 arable-dominated agricultural landscapes were selected as study sites. Landscape structure was assessed within a 100 m buffer around each transect. The RLQ method and the ‘fourth-corner’ approach were combined to find statistical relationships between environmental factors and functional traits of Lepidoptera. We found a strong environmental gradient determined by landscape diversity and proportion of arable fields. Mobility, voltinism and overwintering stage were significantly correlated with these environmental variables. Butterflies with high mobility, high voltinism and non-larval overwintering stage were most abundant in landscapes with high proportion of arable fields and low landscape diversity. The second environmental gradient explained much less variance and separated less-intensively managed grasslands in nature reserves from conventionally managed grasslands in agricultural landscapes. Habitat specialization was correlated with this gradient as specialist butterflies were more abundant in grasslands in nature reserves. Larval diet breadth was not correlated with any environmental gradient or variable. We conclude that the mobility trait syndrome – comprising mobility, voltinism and overwintering stage – is independent from habitat and resource specialization and plays a primary role in shaping diurnal Lepidoptera communities in intensive agricultural landscapes with high cover of arable fields. We suggest that insect monitoring schemes should include some simple assessment of environmental variables to gain insight into the functioning of ecological communities beyond abundance trend estimations.

1. Introduction

Land use intensification and agro-economic pressure for land are causing habitat loss and degradation worldwide, and they are among the main drivers of vanishing biodiversity, including insect decline (Sala et al., 2000; Basset and Lamarre, 2019; Raven and Wagner, 2021). There

is a growing body of evidence that increasing disturbance of habitat and climate leads to functional homogenization of communities via the loss of specialist species (e.g. Rooney et al., 2004; Devictor et al., 2008; Habel et al., 2016; Habel et al., 2019a). This phenomenon can be explained using the concept of ecological niche (Hutchinson, 1957) as generalist species are expected to tolerate higher variation of

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environmental conditions, while species with narrower habitat requirements have less ability to escape from multiple pressures (Clavel et al., 2011; Cardoso et al., 2020). Among insects, declines of both habitat and resource specialists have been documented in many taxa (e.g. Koh et al., 2004; Bartomeus et al., 2013). Species with narrower feeding niche were found to be more negatively affected by habitat loss in wild bees (Bommarco et al., 2010) and butterflies (Öckinger et al., 2010), and selected against in simplified landscapes with intense management (Rader et al., 2014; Gámez-Virués et al., 2015). An increasing proportion of habitat generalist species was found in landscapes with high agricultural intensity in Finland (Ekroos et al., 2010) and the decline of butterfly species is also more pronounced in habitat specialists than in habitat generalists at different spatial and temporal scales in Germany (Filz et al., 2013; Habel et al., 2016, 2019a). Due to high land-use intensity in farmland, the turnover rate of habitat patches suitable for butterflies is very high, thus strong mobility and high development rate are important traits to cope with the rapidly changing environment (WallisDeVries, 2014). Accordingly, mobility and reproductive rate were also identified as key functional traits of insect communities affected by land-use intensity and landscape composition in farmland, sometimes independently from diet or habitat specialization (e.g. Jonason et al., 2012; Börschig et al., 2013; Hanspach et al., 2015), sometimes in addition to them (e.g. Bommarco et al., 2010; Ekroos et al., 2010; Archaux et al., 2018). However, the relative importance of these functional trait syndromes (specialization vs. mobility) in insect communities in agricultural landscapes is still unclear. Furthermore, in many studies on functional diversity of insect communities in agricultural landscapes, only some parts of the complete environmental gradient were sampled, for example only grasslands and/or croplands. We hardly found any studies in the literature where different habitat types were sampled along a wide gradient of landscape diversity (see e.g. Archaux et al., 2018; Harrison et al., 2018).

Insect decline has recently been the focus of much research effort worldwide. Several studies revealed a considerable decline of biomass, abundance and species richness of various insect taxa in different ecosystems mostly in North America and Europe (for reviews see e.g. Cardoso et al., 2020; Wagner, 2020; Warren et al., 2021). Among the most important findings of these investigations are that arthropod communities in forests suffer from similar declines as in grasslands (Seibold et al., 2019), that the loss of species is a long-term trend in Europe (Habel et al., 2016; Van Strien et al., 2019), that, at least in butterflies, mostly specialist species are lost (Wenzel et al., 2006; Filz et al., 2013; Habel et al., 2019a), and that even widespread and abundant species may show declines (butterflies: Van Dyck et al., 2009; hoverflies: Hallmann et al., 2021). There is a wide consensus that agricultural intensification is one of the main drivers of insect decline (Habel et al., 2019b; Raven and Wagner, 2021). Scientists have repeatedly stressed the importance of large-scale insect monitoring schemes in order to achieve biodiversity conservation targets (Dobson, 2005; Samways et al., 2020; Hausmann et al., 2020). However, existing large-scale butterfly monitoring programs mostly rely on volunteers, thus site selection is usually biased towards semi-natural habitats and/or sites are clumped around volunteers' residence. Hence the wider countryside, especially intensively used agricultural landscapes, might be underrepresented (Bretton et al., 2011). The State Institute for Environment Baden-Württemberg (LUBW) launched, therefore, in 2018 an insect monitoring scheme including butterflies and burnet moths, grasshoppers, ground beetles and moths in the Federal State Baden-Württemberg, Germany. In this monitoring scheme, butterflies and burnet moths are regularly sampled in randomly selected nature reserves, grassland-dominated and arable-dominated landscapes using counts ('Pollard walks') along 1500 m long transects. The sites are selected in a spatially balanced manner providing a representative sample in the whole state (Theves, 2018). The primary aim of this program is to provide reliable trend estimates on abundances of rare and common species both in nature reserves and in the wider countryside.

Here we analysed the abundance data of butterflies and burnet moths from the first two years of this large-scale insect monitoring program. Landscape composition and configuration were also assessed around the transects used for butterfly surveys. By examining landscapes with a wide range of proportion of natural biotopes vs. arable fields, we aimed to reveal relationships between functional traits of butterflies and burnet moths and environmental variables, especially landscape composition. Our predictions were that frequently disturbed landscapes with high proportion of intensively managed fields filter the butterfly community by (i) favouring habitat and host plant generalist species and (ii) selecting for species with high mobility and fast development. We also aimed to reveal the relative importance of different functional traits, environmental variables and their associations in shaping butterfly and burnet moth communities.

2. Material and methods

2.1. Study sites

For recording butterflies and burnet moths within the insect monitoring scheme of Baden-Württemberg, 201 sites: 40 nature reserves (NR) and 161 $1 \times 1 \text{ km}^2$ squares were randomly selected in a spatially balanced manner (Dröschmeister, 2001; Theves, 2018; Dolek et al., 2020). 80 squares were dominated by arable fields for representing arable landscapes (arable sites) and 81 squares were dominated by grasslands (grassland sites). The nature reserves were selected in the vicinity of arable and grassland sites to facilitate the comparison between them. The sites are sampled in a four-year rotational cycle. Each year 10 nature reserves, 20 arable and 20 grassland squares are sampled; thus each single site is sampled every four years (Theves, 2018).

Here we analysed the data from 2018 to 2019, the first two years of the monitoring program. Forty-nine sites were sampled in 2018 (10 NR, 19 grassland and 20 arable sites) and 50 in 2019 (10 NR, 20 grassland and 20 arable sites). These sites are distributed all over the Federal State of Baden-Württemberg between 110 m and 960 m elevation above sea level (Fig. 1).

2.2. Field survey

We implemented one 1500 m long transect in each sampling site with the aim to get a representative sample of landscape composition and butterfly community. In some cases, due to the vegetation structure, land use or infrastructure, we had to divide the transect into two or more sections. In nature reserves, the transects were laid in or at the edge of grasslands (i.e. non-forested habitats) as much as possible (see examples in SM Figs. S1-S3). Sampling was conducted following the well-established transect method (Pollard, 1977), with a recording range of 5 m on each side of the observer. Each observed butterfly and burnet moth was identified to species level (when possible) and the geographic coordinates of the observations were recorded using a GPS. Data were sampled with an Android application developed for this purpose. All transects were visited four times during the season: approximately, in late May, in early June, in late June and in July. Transect counts were conducted under favorable weather conditions, i.e. above 20 °C, low wind speed (<4 on Beaufort scale) and no rain. Data of the four visits were pooled for each site for the analysis.

Following the categorization system of biotopes in Baden-Württemberg (LUBW, 2016, 2018), we classified the habitat types and land use categories within a 100 m buffer around the butterfly transects based on own field surveys and aerial photographs using QGIS 3.4 (QGIS Development Team, 2019). We chose 100 m as a feasible distance within which landscape composition can be checked on the spot given the available labour. (We note that landscape composition was also calculated for 50 and 25 m buffers and showed very strong correlations with the 100 m.) From the proportions of these habitat types we calculated a Shannon index for landscape composition diversity (e.g. Archaux et al.,

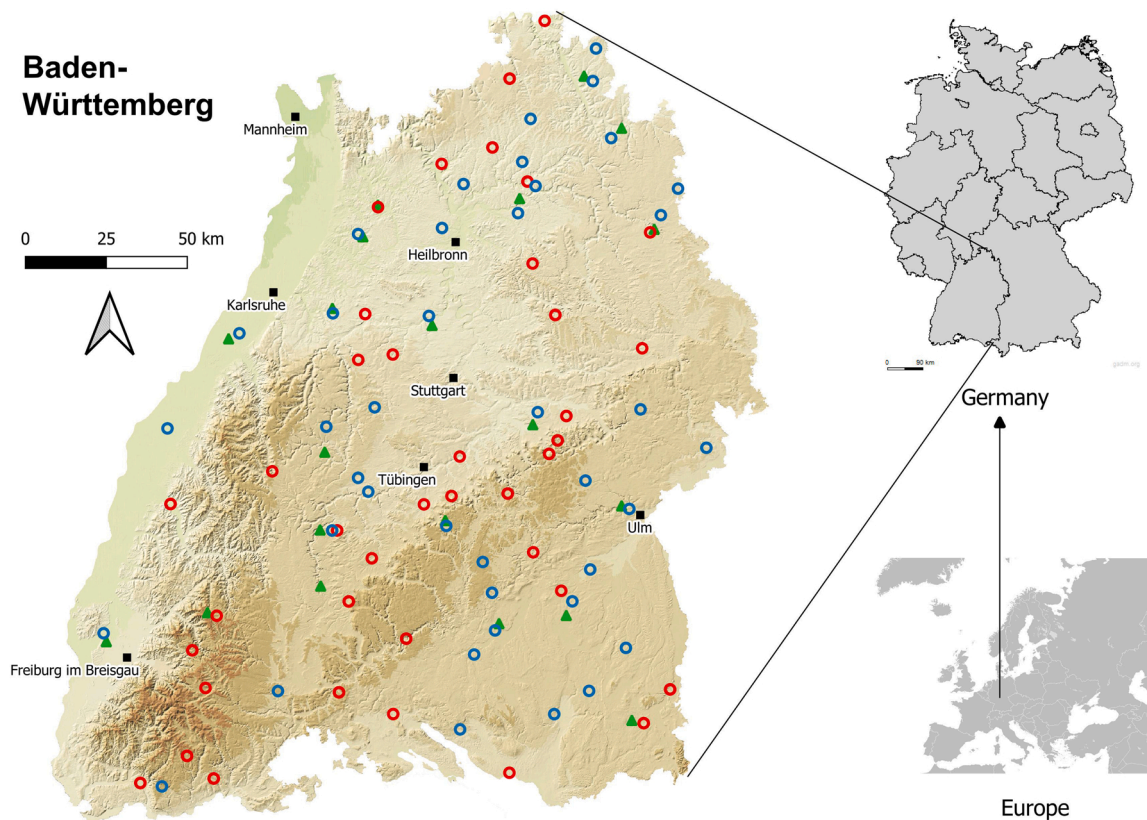


Fig. 1. Geographical location of sampling sites. Green triangles: nature reserves; red circles: grassland sites; blue circles: arable sites. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
Sources: blank map of Europe – Wikimedia Commons; map of Germany – © 2018 GADM <https://gadm.org>.

2018). We also applied a coarser classification consisting of the proportion of arable land, grassland, woodland and natural biotopes. The “grassland” category included conventional meadows and pastures. Intensively managed (sown and fertilized) grasslands and semi-natural grasslands, such as nutrient-poor dry calcareous grasslands or wet meadows, were excluded from this category, because they form quite different habitats from conventional grasslands and their cover was on average very low (<5%). For “natural biotopes” all habitat patches were pooled which are protected by national and federal legislation according to the biotope-mapping programme of Baden-Württemberg (LUBW, 2018), for example hedges, riparian forests, bogs, semi-natural grasslands etc. We also calculated the parameter to area ratio (PAR) for all habitat patches and used its mean in each buffer as a metric of landscape configuration (e.g. Perović et al., 2015).

2.3. Data preparation

We used only those observations where butterflies were identified at species level. We counted the *Leptidea juvernica/sinapis* species complex as one species, because genital inspections would be necessary for the species-level identification. Due to the high field abundance of *Pieris* spp., not every individual could be attributed to the species *P. napi* and *P. rapae*. The unidentified *P. napi/rapae* individuals were assigned to species according to the distribution of identified *P. napi* and *P. rapae* on the respective transect and date. We excluded all recordings of the Painted Lady (*Vanessa cardui*). Abundance of this migrant species is mostly affected by environmental conditions in Africa (Hu et al., 2021; Stefanescu et al., 2013), its occurrence is not indicative of habitat quality or landscape structure in Germany, hence not suitable to inform our study objectives. In total, the dataset contained 24 110 individual observations of 104 butterfly and burnet moth species. Fifteen species that

were recorded in only one site were dismissed, thus the reduced data set contained 24 053 observations of 89 species.

The type of sampling site (nature reserve, grassland or arable site), elevation, sampling year, the proportion of arable land, grassland, forest and natural biotopes, landscape diversity and PAR were used as environmental variables. Proportion of natural biotopes was square-root transformed. Butterfly trait variables (SM Table S1) were taken from the Fauna Indicativa (FI) database that was developed for the insect fauna of Switzerland (Klaiber et al., 2017a, 2017b). Categorical variables with four classes each were larval diet breadth (mono-, narrowly oligo-, oligo- and polyphagous) and overwintering stage (egg, larva, pupa, adult). Mobility was a quantitative variable ranging from one (very sessile) to four (migrant) with possible non-integer values. We derived this variable from the four-level habitat fidelity fuzzy variable of the FI database. We found strong positive correlations between our mobility scores and those used in earlier studies (also based on expert opinions: Bink, 1992; Cowley et al., 2001; Komonen et al., 2004) (SM Table S2). Voltinism (number of generations per year) was also a quantitative variable with possible non-integer values: data of the FI database were slightly adjusted using Settele et al. (1999) and the Distribution Atlas of Butterflies and Burnets in Germany (Reinhardt et al., 2020). Based on the FI database, we also calculated two quantitative variables for the habitat breadth of butterflies by summing the number of main habitat types (grasslands, forests/shrubs, wetlands and anthropogenic habitats; HAT) and subtypes (nine levels; HAST) where the species occur. These two variables ranged from one to four and from one to nine, respectively. We slightly adjusted the habitat use data of the FI database for 20 species based on our own field experience in Southern Germany. However, the analysis was conducted with both trait datasets and the difference in the results was negligible. For burnet moths, we got all trait variables from Reinhardt et al. (2020) and Ulrich (2018).

2.4. Data analysis

We combined the RLQ (Dolédec et al., 1996) and fourth-corner (Legendre et al., 1997; Dray and Legendre, 2008) methods to uncover the relationships between environmental variables and species traits following the approach proposed by Dray et al. (2014). The two methods have similar mathematical principles, but their objectives and output are quite different. RLQ analysis is a joint ordination that assigns scores to species traits, samples and environmental variables along orthogonal axes and maximizes the covariance between the traits and the environmental variables mediated by the species abundances. The fourth-corner method is based on permutations of the data matrices and calculates pairwise correlations between environmental and trait variables. RLQ summarizes multivariate structures but it does not provide significance tests, while the fourth-corner method only tests the significance of bivariate associations and it does not consider the covariation among traits or among environmental variables (Dray et al., 2014).

First, we carried out a Correspondence Analysis (CA) on the species abundance matrix. As both the environmental and trait data tables contained a mix of categorical and quantitative variables a Hill-Smith analysis (Hill and Smith, 1976) was conducted on both tables weighted by the sites and species weights derived from the previous CA. In the fourth-corner analysis, we used a sequential test proposed by ter Braak et al. (2012) to test if traits and environment influence species distributions. We applied 49 999 permutations in all randomization procedures and the false discovery rate method (FDR; Benjamini and Hochberg, 1995) to adjust P-values for multiple testing. We combined the two methods in three ways: first we performed a multivariate test, which is based on the total inertia of the RLQ analysis, to evaluate the global significance of the traits-environment relationships. Then we presented the significant relationships revealed by the fourth-corner method on a biplot where RLQ scores were used to represent traits and environmental variables. Finally, we tested directly the links between RLQ axes and traits and environmental variables using fourth-corner tests. These can be interpreted as correlation tests between environmental gradients and traits, and between environmental

variables and trait syndromes. Environmental gradients and trait syndromes are linear combinations of environmental variables and traits, respectively, which are found by the RLQ method by maximizing their cross-covariance (see more details in Dray et al., 2014). All analyses were made using the ‘ade4’ package 1.7–15 (Dray and Dufour, 2007) in R 3.6.3 statistical software (R Core Team, 2020).

3. Results

Environmental variables showed significant differences among the three site types (SM Fig. S4). Landscape diversity and proportion of grasslands was lower in arable sites, but there was no difference between grassland sites and nature reserves. Proportion of woodland and natural biotopes was higher in nature reserves than in the two other types, while proportion of arable fields was highest in arable sites and lowest in nature reserves. Elevation and PAR showed no significant differences. Although these results are not surprising, they provide important evidence on that landscapes in the three site types were basically different.

The first two RLQ axes explained 82.3% and 12.1% of the cross-covariance between traits and environmental variables. The environmental variables clearly diverged according to the three main types of sampling sites (Fig. 2a). Proportion of arable land was strongly negatively, while landscape diversity was positively correlated with the first axis. Proportion of forests and natural biotopes were positively correlated with the first axis and negatively with the second axis, while the proportion of grasslands was positively correlated with the second axis. Arable and grassland sites were highly correlated with proportion of arable fields and grasslands, respectively, while nature reserves were characterized by high proportion of forests and natural biotopes (see also SM Fig. S4). The two years, elevation and PAR did not explain much variance. The analysis revealed two environmental gradients: proportion of arable land and landscape diversity were strongly correlated with the first RLQ axis and arable sites and nature reserves were clearly separated along this gradient. Proportion of grasslands and woodlands were rather correlated with the second axis along which nature reserves and grassland sites were separated. Proportion of grasslands

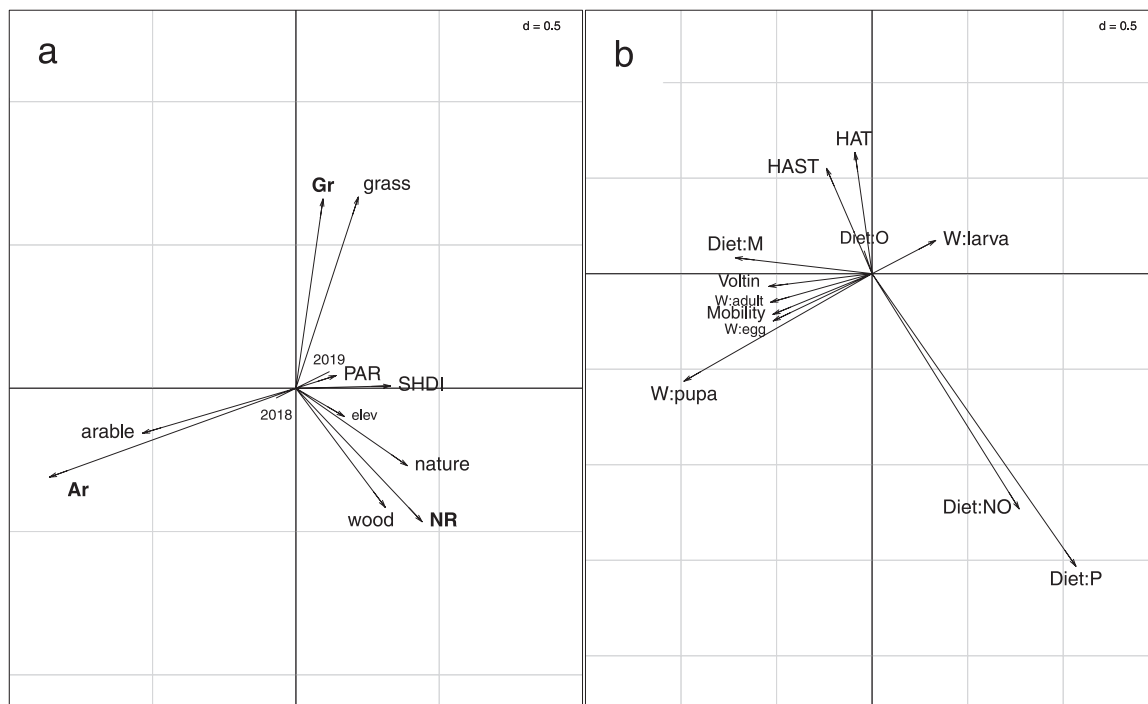


Fig. 2. Coefficients for (a) environmental and (b) trait variables along the two RLQ axes. (a) NR: nature reserves; Ar: arable sites; Gr: grassland sites; elev: elevation; SHDI: landscape diversity; PAR: perimeter-to-area ratio. (b) Diet: larval diet (M: monophagous, NO: narrowly oligophagous, O: oligophagous, P: polyphagous); HAT: number of used habitat types; HAST: number of used habitat subtypes; Voltin: voltinism; W: overwintering stage. See text for more details.

(conventional) was not significantly different between nature reserves and grassland sites, but proportion of woodland and natural biotopes was significantly higher in nature reserves (SM Fig. S4). Proportion of natural biotopes was positively correlated with the cover of semi-natural grasslands and high woodland cover often implies lower intensity of grassland use, thus we interpret this second environmental gradient as a grassland-use intensity gradient (see also Villemey et al., 2015; Archaux et al., 2018).

Butterflies related to arable landscapes usually overwinter not in the larval stage, but as eggs, pupae (e.g. *Pieris* spp.) or as adults (*Aglais* spp.), have higher mobility (e.g. *Vanessa atalanta*) and higher number of generations per year (e.g. *Pieris* spp.) (Fig. 2b and SM Fig. S5). Interestingly, monophagy was also correlated with these traits, which is related to monophagous nettle-feeding species such as *Aglais io*, *A. urticae* or *Vanessa atalanta*. These species are abundant in arable landscapes and are characterized by high mobility, higher voltinism and overwinter as adults. Two-third of our study species overwinter as larva (59 out of 89 species), they were positively related to the first axis and were dispersed along the second axis (Fig. 2b and SM Fig. S5). Habitat breadth was positively correlated with the second axis and with the proportion of grasslands indicating that species with larger habitat breadth were more abundant in grassland-dominated sites, such as *Aphantopus hyperantus*, *Maniola jurtina* or *Ochlodes sylvanus*. Finally, a large number of species occurring in nature reserves can be characterized by poly- or narrowly oligophagous larval feeding and low habitat breadth (high habitat specificity) (Fig. 2b and SM Fig. S5). Thus the analysis revealed roughly two trait syndromes: the ‘mobility’ syndrome including mobility, voltinism, overwintering stage and monophagy, and the ‘habitat specialization’ syndrome involving the number of used habitat (sub)types and polyphagous and narrowly oligophagous larval diet.

The global testing was significant for both permutation models

(Model 2 $p = 0.00001$, Model 4 $p = 0.001$) indicating a significant global relationship between species traits and environmental variables (Dray et al., 2014). We found ten significant pairwise associations after P -value adjustment using the fourth-corner approach (Table 1, Fig. 3). Mobility and voltinism were significantly positively related to arable sites and to the proportion of arable land, while they were negatively related to the proportion of natural biotopes. Mobility was also negatively associated with landscape diversity. In contrast, larval overwintering stage was positively correlated with landscape diversity and negatively with the proportion of arable land (Table 1, Fig. 3). We found a significant positive association between oligophagous larval diet and year 2018.

Finally, we found significant correlations between species traits and environmental gradients, and between trait syndromes and environmental variables (Fig. 4). The first trait syndrome (‘mobility’) was significantly negatively correlated with the proportion of arable land and arable sites and positively with landscape diversity, nature reserves and proportion of natural biotopes and forests. This means that landscapes with high proportion of arable fields are favored by rather mobile species that have several generations and overwinter not in the larval stage. (Note that mobility and voltinism were negatively correlated with the first RLQ axis, thus high voltinism and high mobility correspond to negative values in the mobility syndrome.) The second trait syndrome (‘habitat specialization’) was significantly positively related to grassland sites clearly indicating that these sites are mostly occupied by habitat generalist species (Fig. 4a, Table 2). Voltinism and mobility were negatively, while larval overwintering stage was positively related with the first environmental gradient, indicating again that butterflies overwintering in the larval stage occur rather in diverse landscapes, while simple landscapes with high proportion of arable fields are inhabited by highly mobile species with high voltinism and non-larval overwintering stages. Habitat breadth (HAT) was significantly positively correlated

Table 1

Results of the fourth-corner tests. Significant ($P < 0.05$) positive associations are represented by red cells, and significant negative associations correspond to blue cells, numbers indicate the association statistic. Nonsignificant associations are in gray. Black lines separate different variables; white lines separate different modalities for categorical variables. P -values were adjusted for multiple comparisons using the FDR (false discovery rate) procedure.

	Year		Site type				Landscape diversity (SHDI)	Perimeter to area ratio (PAR)	Proportion of			
	2018	2019	Arable (Ar)	Grassland (Gr)	Nature reserve (NR)	Elevation			arable fields	grass-lands	wood-lands	natural biotopes
Mobility			0.25				-0.17		0.27			-0.19
Larval diet	Monophagous											
	Narrowly oligophagous											
	Oligophagous											
	Polyphagous											
Overwintering stage	Egg											
	Larva						0.19		-0.29			
	Pupa											
	Adult											
Voltinism			0.25						0.28			-0.20
HAT												
HAST												

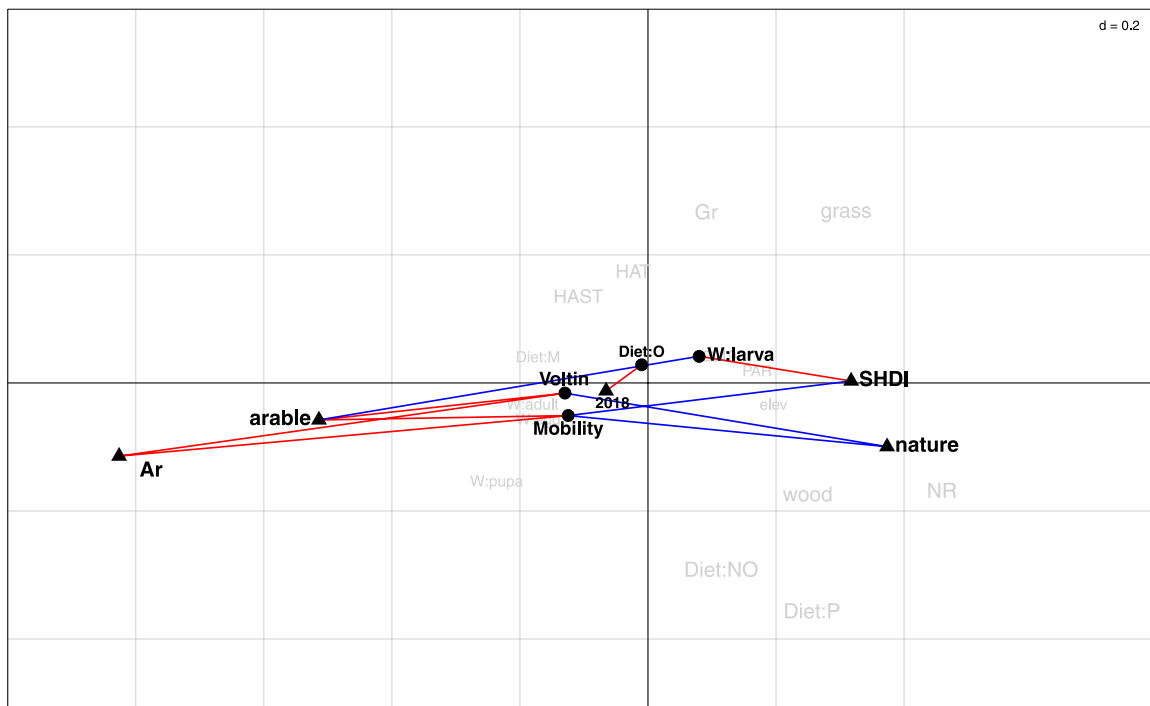


Fig. 3. Representation of significant ($P < 0.05$) associations between environmental variables (triangles) and traits (circles) identified by the fourth-corner method on the factorial map of RLQ analysis. Red lines indicate positive, blue lines represent negative associations.

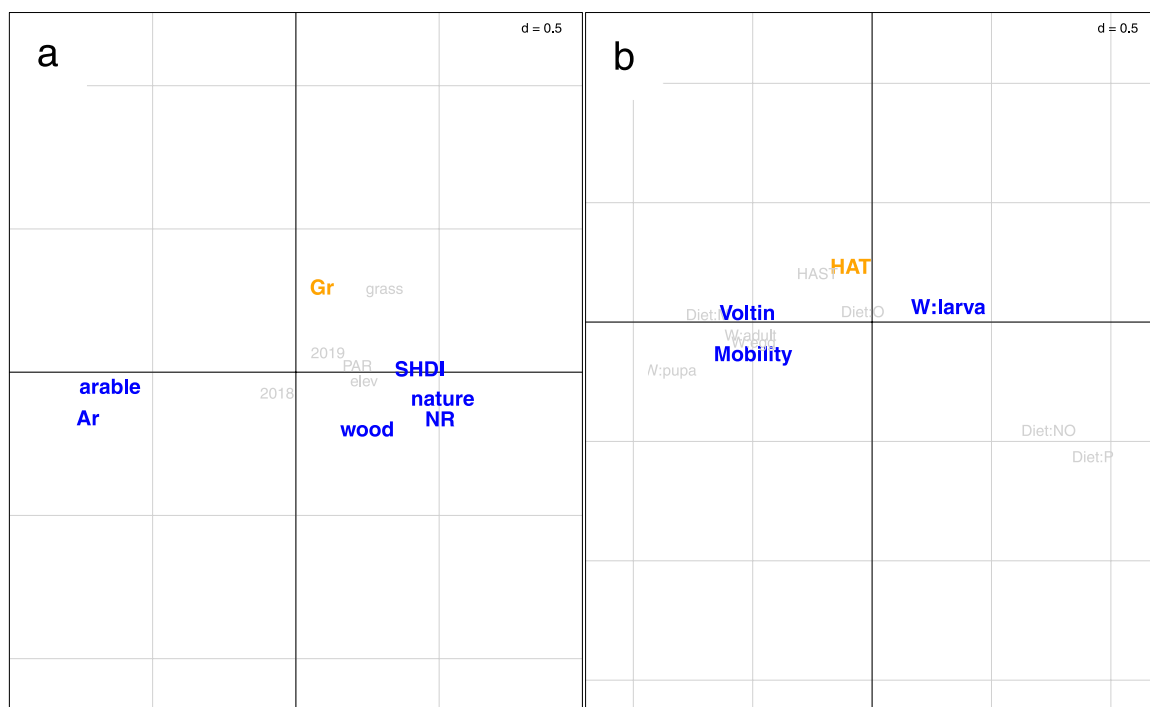


Fig. 4. Plot of (a) environmental and (b) trait variables on the RLQ factorial map. Variables significantly associated with the first axis are blue, with second axis are orange, variables with no significant associations are in light gray. (a) Fourth-corner tests between the first two RLQ-axes for trait syndromes (AxQ1 and AxQ2) and environmental variables. NR: nature reserves; Ar: arable sites; Gr: grassland sites; SHDI: landscape diversity; nature: proportion of natural biotopes; wood: proportion of woodland. (b) Fourth-corner tests between the first two RLQ axes for environmental gradients (AxR1 and AxR2) and traits. HAT: number of used habitat types; Voltin: voltinism; W: overwintering stage.

with the second environmental gradient (Fig. 4b, Table 3). Larval diet showed no significant correlations with the environmental gradients. Study year, PAR and elevation showed no significant correlations with trait syndromes.

4. Discussion

Functional diversity of a community forms the link between biodiversity and ecosystem functioning. As insects provide several ecosystem

Table 2

Results of the fourth-corner tests between the first two RLQ-axes for trait syndromes and environmental variables. Significant ($P < 0.05$) positive associations are represented by red cells, and significant negative associations correspond to blue cells, numbers indicate the association statistic. Black lines separate different variables; white lines separate different modalities for categorical variables. P -values were adjusted for multiple comparisons using the FDR (false discovery rate) procedure.

		Mobility trait syndrome	Habitat specialization trait syndrome
Year	2018		
	2019		
Site type	Arable (Ar)	-0.313	
	Grassland (Gr)		0.128
	Nature reserve (NR)	0.226	
Elevation			
Landscape diversity (SHDI)		0.216	
Proportion of	arable fields	-0.349	
	grasslands		
	woodlands	0.203	
	natural biotopes	0.254	

Table 3

Results of the fourth-corner tests between the first two RLQ axes for environmental gradients and traits. Significant ($P < 0.05$) positive associations are represented by red cells, and significant negative associations correspond to blue cells, numbers indicate the association statistic. Black lines separate different variables; white lines separate different modalities for categorical variables. P -values were adjusted for multiple comparisons using the FDR (false discovery rate) procedure. HAT: number of habitat types; HAST: number of habitat subtypes used by species.

		Environmental gradients	
		Arable vs. landscape diversity	Grassland use intensity
Mobility		-0.286	
Larval diet	Monophagous		
	Narrowly oligophagous		
	Oligophagous		
	Polyphagous		
Overwintering stage	Egg		
	Larva	0.284	
	Pupa		
	Adult		
Voltinism		-0.298	
HAT			0.189
HAST			

functions and are declining rapidly primarily due to intensive agriculture (e.g. Cardoso et al., 2020; Raven and Wagner, 2021), it is essential to reveal how functional traits are related to the environment in intensively managed agricultural landscapes. Here we demonstrated that in landscapes with a high proportion of arable field, butterflies with high mobility, high voltinism and non-larval overwintering stages were more abundant. Habitat specialization played a role in differentiating species between nature reserves and grassland sites as habitat generalists occurred in grassland sites in higher relative abundance. Larval diet specialization did not show any significant correlation with environmental gradients.

To interpret our results, we first highlight that the sampling protocol of our study was primarily designed for the purpose of a long-term, large-scale monitoring of butterflies and therefore it differs in many aspects from the sampling design of previous studies on insect communities in agricultural landscapes. The sampling unit in our study was a 1500 m long transect that traversed the landscape encompassing several different habitat patches. Thus we obtained a spatially more representative (or at least larger) sample of the butterfly community compared to earlier studies where usually single habitat patches had been considered. Furthermore, we selected both the sampling sites and their landscape context at a much wider range of habitats from species-rich, nutrient-poor grasslands in nature reserves to intensive agricultural landscapes with sometimes extreme high (>90%) proportion of arable fields. Butterfly and burnet moth communities have hardly ever been studied in arable fields (but see Kovács-Hostyánszki et al., 2011; Loos et al., 2014; Lang et al., 2016), most studies assessed them in semi-natural grasslands, a few studies involved arable field margins as well (e.g. Kuussaari et al., 2007). However, a large proportion of the countryside in Europe is arable land (Stoate et al., 2009), thus our approach provides a possibly more comprehensive picture on butterfly diversity in non-forested habitats than previous studies (although strictly speaking we did not sample the interior parts of arable fields, but the field margins).

Our results showed that arable sites and nature reserves were clearly separated from each other along the first RLQ axis that strongly correlated with landscape diversity and proportion of arable land. This is in concordance with that proportion of arable land is indeed a widely used proxy of landscape heterogeneity in ecological studies in farmland (e.g. Gabriel et al., 2006; Kormann et al., 2015; Jonason et al., 2017). The second axis explained much smaller amount of the total inertia indicating a weaker separation between nature reserves and grassland sites. Proportions of grassland and woodland were correlated with this axis, because nature reserves often consisted of meadows embedded in woodland, while grassland sites were usually covered with large contiguous meadows and pastures interspersed with arable fields.

Mobility has been identified as an important trait for the persistence of butterflies and other insects in agricultural landscapes in many cases. A positive relationship between butterfly mobility and arable land was found in traditional low-intensity farmland in Romania (Loos et al., 2014; Hanspach et al., 2015) and in lowland rural areas in France (Archaux et al., 2018). Butterflies with high mobility were disproportionately more abundant in landscapes dominated by arable land in Sweden (Jonason et al., 2012). High dispersal propensity of butterflies was correlated with high land use intensity (Börschig et al., 2013) and simplified landscape configuration (Perović et al., 2015) in grasslands in Germany. Increasing average mobility of butterfly communities in landscapes with high agricultural intensity was also proven in Finland (Ekroos et al., 2010). At larger spatio-temporal scales, it was also demonstrated that less-mobile species showed a more severe decline during the last centuries in southern Germany (Habel et al., 2016) and in Denmark (Eskildsen et al., 2015). Thus the positive relationship between butterfly mobility and proportion of arable land in our study corroborates these earlier results. Several studies emphasized the importance of functional grain of resources in the landscape as a determinant of animal dispersal (for a review see Baguette and Van Dyck, 2007). For example,

Fletcher et al. (2018) demonstrated that habitat fragmentation had the strongest effect on population size at the scale of dispersal in an insect herbivore, while a simulation study found that effects of habitat fragmentation on individual fitness interact with the spatial scale of movement behavior (Cattarino et al., 2016). Home range size of bats was negatively correlated with landscape diversity likely due to that diverse landscapes provide complementary resources within smaller distances (Laforge et al., 2021). That might also be an explanation to the negative relationship between mobility and landscape diversity in our present study as butterflies may need lower mobility to find suitable areas for foraging, oviposition, basking, shelter etc. in more diverse landscapes. We also note that higher mobility of butterflies may increase their detectability as well. Arable fields and their margins provide habitat for very few species and transient individuals of mobile species are more likely to be seen.

Voltinism was also shown to be linked to land-use intensity or landscape structure, but in fewer cases. Butterflies producing more generations were more abundant in arable fields in low-intensity farmland in Romania (Hanspach et al., 2015) and in more intensively used grasslands in Germany (Börschig et al., 2013), while species richness of univoltine butterflies declined with the proportion of cropland in France (Archaux et al., 2018).

Overwintering stage is a crucial life-history trait in holometabolous insects in the temperate zone. There is some evidence that butterflies overwintering in advanced stages can cope better with intensive land-use (Börschig et al., 2013), while species overwintering in earlier stages are often threatened or declining (Barbaro and Van Halder, 2009; WallisDeVries, 2014). In France, in sites with taller vegetation and low biomass removal butterfly communities were found to be dominated by species with long larval development (Van Halder et al., 2017), while species richness of butterflies overwintering as larvae declined strongly with the proportion of cropland (Archaux et al., 2018). We hypothesize that overwintering in the larval stage, which is the most common in butterflies and burnets in Central Europe, might make species vulnerable to habitat disturbances as larvae must feed both before and after winter implying a relatively long larval development during which mobility is very limited. Thus overwintering stage and voltinism are tightly coupled with mobility as they enable butterflies to maximize their time spent in the most mobile adult stage. This 'mobility' trait syndrome, which was clearly visible in our results as well, can be of crucial importance in arable landscapes that change dynamically during the season due to frequent disturbances such as plowing, harvesting, spraying or stubble breaking (Vasseur et al., 2013; WallisDeVries, 2014). Our results also demonstrate that butterflies in more diverse landscapes with more natural biotopes are more likely to overwinter as larvae and they can be characterized with slower movement and development.

Habitat specialization showed no significant correlation with any environmental variable, but it was significantly correlated with the second environmental gradient. This indicates that butterflies with broader habitat use (i.e. habitat generalists) were more abundant in grassland sites where the proportion of woodland was lower and land-use intensity was higher than in nature reserves (see above). These are mostly 'grassland generalist' species, such as *Aphantopus hyperantus*, *Maniola jurtina*, *Polyommatus icarus* or *Thymelicus lineola*, which occur in almost any kind of grasslands and can reach very high abundances. They represent only a small proportion of typical grassland species, such as those used for the European grassland butterfly indicator (Van Swaay et al., 2019). Many of these were rarely found on our randomly selected grassland sites indicating that these 'ordinary' grasslands are not suitable for many grassland species.

An increasing proportion of habitat generalist species was found in landscapes with high agricultural intensity in Finland (Ekroos et al., 2010). In calcareous grasslands in Germany, habitat specialist butterflies were found in higher numbers in habitat patches surrounded by forests, whereas habitat generalists were not affected by landscape structure (Krämer et al., 2012). Decline of butterfly species is also more

pronounced in habitat specialists than in habitat generalists at different spatial and temporal scales in Germany (Filz et al., 2013; Habel et al., 2016; Habel et al., 2019a). Our results are in concordance with these earlier studies and shed light on that more intensively used grasslands (regular N-input, frequent mowing), which are tending to be the standard nowadays, harbor a functionally impoverished butterfly fauna (see also Aviron et al., 2007; Marini et al., 2009). We also note that habitat specialization showed no correlation with the proportion of arable land or the first environmental gradient. This is because those butterfly species that successfully colonize arable landscapes are not necessarily habitat generalists. We argue, that the 'habitat specialization' trait syndrome that we found is independent from the 'mobility' trait syndrome and it plays a role in differentiating between butterfly species when only grassland-dominated habitats (semi-natural grasslands in nature reserves and conventional production meadows) are considered. Consequently, when arable-dominated landscapes are also investigated, as in our case, habitat specialization can explain only a minor part of the variation in relative butterfly abundances. We agree with WallisDeVries (2014) who argued that the currently prevailing categorisation of habitat specialist and generalist butterflies is ecologically misleading. In our view, butterflies (and other organisms) are rather specialized on resources and environmental conditions, and habitat is where the required resources and suitable conditions overlap in space and time (Dennis et al., 2003). Nonetheless, it is possible that our metric of habitat breadth was too coarse and some finer metrics on ecological/habitat specialization would provide a better insight into these trait-environment relationships (see e.g. Julliard et al., 2006; Devictor et al., 2010).

Some earlier studies found that species with specialized feeding habits are more threatened or more negatively affected by habitat loss in both mosaic landscapes and intensively used agricultural landscapes (Wenzel et al., 2006; Barbaro and Van Halder, 2009; Öckinger et al., 2010; Gámez-Virués et al., 2015; but see WallisDeVries, 2014). In our present study, we found only a hardly interpretable positive association between oligophagous diet and year 2018, which is probably due to that oligophagous species were the most numerous in both years in all types of sampling sites: 47 out of the 89 species and around 87% of all individuals were oligophagous and overall butterfly abundance was considerably higher in 2018 (15170 individuals) than in 2019 (8883 individuals). Note that larval diet breadth might still be related to landscape composition at larger spatial scales. Some species which were relatively widespread and abundant in arable landscapes are monophagous (e.g. *Aglais urticae*, *Vanessa atalanta*) as their larvae feed exclusively on nettle (*Urtica dioica*). These butterflies are also highly mobile, which explains the positive relationship between monophagous larval diet and mobility syndrome (Fig. 2b), and they provide an example of highly mobile resource specialists. Additionally, correlations between nature reserves and polyphagous (17 species) and narrowly oligophagous (23 species) species were clearly detectable on the RLQ biplots. These correlations were not significant, likely due to that most of these species occurred in nature reserves with much higher probability than in other sites, but their abundances were usually very low. We point out that the vectors of these two diet types showed in the opposite direction of the vectors of habitat breadth (Figs. 2 and 4). In other words, habitat specialist species were highly likely polyphagous or narrowly oligophagous.

Landscape configuration, quantified as perimeter-to-area ratio (PAR), also did not prove to be associated with any trait or trait syndrome. We did not find differences in PAR between the three site types indicating that size and shape of habitat patches showed less variation than landscape composition. This might also be partly due to that, in contrast to landscape composition, PAR is very sensitive to the grain of mapping: if, for example, narrow, elongated field margins are mapped as particular habitat patches or not, it can seriously influence the value of PAR, while it hardly affects landscape composition data. Furthermore, the 100 m buffer size might also be too small to detect variation in

landscape configuration.

In summary, our results show that the mobility trait syndrome (mobility, voltinism, overwintering) plays a much more important role in filtering butterfly communities than the specialization (habitat and larval diet) syndrome when the whole spectrum of habitats is inspected in an intensively managed agricultural landscape in western Central-Europe. Neither habitat nor larval diet generalists outperformed specialists in landscapes with high proportion of arable fields. Habitat specialization showed some relationship with the intensity of grassland management. We also found that the relationship between larval diet specialization and landscape composition is not as trivial as earlier studies suggested, and that resource specialization and habitat specialization are not necessarily related. Here we refer to the analysis of WallisDeVries (2014) who also found that mobility-related traits explained the largest, while food specialization traits the lowest proportion of trait variation in butterflies of NW Europe, while Red List status and recent population trends of Dutch butterflies showed the strongest relationship with phenology and development rate (cf. voltinism and overwintering stage in our case).

5. Conclusions

We conclude that our sampling approach provided valuable insights in how landscape structure affects the functional trait composition of butterflies and burnets in different landscapes. We identified a ‘mobility’ trait syndrome consisting of high mobility, high voltinism and non-larval overwintering stage that enables butterflies to persist in landscapes with high proportion of arable land. Habitat specialization was independent from the mobility syndrome, it explained much less variance and rather correlated with the extension and management intensity of grasslands, while larval diet breadth did not relate to any environmental gradient. Butterflies successfully inhabiting arable landscapes are neither habitat nor host plant generalists. Our results also show that the utility of insect monitoring datasets can be enhanced with little additional effort by mapping habitat type and land-use around sampling locations.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.agee.2022.107978](https://doi.org/10.1016/j.agee.2022.107978).

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