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Spatiotemporal variations in aphid-parasitoid relative abundance patterns and food webs in agricultural ecosystems

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Abstract. Understanding the stability of communities is fundamental in theoretical and applied ecology. Organisms atop trophic chains are particularly sensitive to disturbance, especially when they are dependent on a specific trophic resource subject to strong fluctuations in density and quality, which is the case of parasitoids. We investigated the (1) variability in spatiotemporal relative abundance patterns of a cereal aphid parasitoid community, determining at what scales such patterns vary in agrosystems. We also investigated whether (2) parasitoid relative abundances are strongly influenced by host relative abundances and if (3) different host species are exploited at distinct rates. Aphid parasitoid populations were monitored in three remote agricultural regions in France between 2010 and 2012. Five parasitoid species (Hymenoptera: Braconidae: Aphidiinae) and three aphid species (Hemiptera: Aphididae) were identified in each of those three regions. Fields sampled in one region in a single year exhibited similar relative abundance patterns, with aphid parasitoid communities varying across regions and years. All parasitoid species were able to exploit each monitored host species. *Metopolophium dirhodum* Wlk was consistently a more frequent species among parasitized aphids than among living aphids, indicating that this aphid species was exploited at a higher rate than the other two aphid species found (*Sitobion avenae* F and *Rhopalosiphum padi* L). Those findings suggest the cereal aphid-parasitoid network is not strictly determined by the intrinsic permanent environmental characteristics but partially varies from one year to another. The similarity in abundance patterns in different fields of a region in a given year suggests the existence of a mechanism allowing a rapid synchronisation of the relative abundance patterns at an intra-regional scale. This phenomenon could be useful in predicting host-parasitoid communities and bear important consequences for the ecosystem service provided by parasitoids.

Key words: Aphididae; Aphidiinae; biodiversity; Braconidae; community structure; Hemiptera; host-parasitoid interactions; Hymenoptera.

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INTRODUCTION

Evaluating the importance of factors that drive the structure of communities is an important objective of both theoretical and applied ecology (Nowicki et al. 2009). In agricultural ecosystems, human activities have led to an increase in the amount of habitat disturbance events affecting the structure of resident communities. Species face locally frequent cycles of extinction-recolonization following disturbance events, persisting in the landscape as a metapopulation (Hanski 1998). Those species respond to a number of environmental filters which apply at different spatial scales, thus shaping the structure of metacommunities (Leibold et al. 2004, Schweiger et al. 2005). The dynamic instability in local populations could lead to a high importance of environmental stochasticity in determining community structure and dynamics, especially in cultivated areas. Environmental stochasticity is generally believed to be the main driving force influencing the dynamics of insect populations (Nowicki et al. 2009). Upper trophic level organisms can be particularly affected by disturbance events and environmental changes, as predicted by the trophic rank hypothesis, due to cumulative bottom-up effects influencing those organisms (Holt et al. 1999, Tscharntke and Brandl 2004). In highly disturbed agroecosystems, host-parasitoid systems are particularly interesting to investigate variations in insect community structures, as parasitoids are subject to the expansions and regressions of the spatial distribution of their insect hosts (Folcher et al. 2011). Several studies have focused on the influence of land cover patterns (Coll and Hopper 2001, Kruess 2003, Costamagna et al. 2004, Bennett and Gratton 2012) or climate (Stireman et al. 2005) on the species richness, abundance and diversity of parasitoid communities (Folcher et al. 2011), but few studies have considered the large scale spatiotemporal variations in their relative abundances (e.g., Höller 1990, Gomez and Zamora 1994, Le Corff et al. 2000). Such investigation would help determining the extent to which environmental factors affect parasitoid communities and understanding the spatiotemporal dynamics of those organisms.

The fitness of parasitoids is linked to the availability of the host species they are able to exploit (Henry et al. 2008). Therefore, one can expect the specific composition of the community of hosts and their relative abundance to be a major factor explaining the relative abundances of parasitoids. Presumably, a high variance in the availability and the quality of host resources would be favorable for parasitoids presenting a generalist strategy. Similarly, a prevalence of specialist behavior could be expected in a stable environment (Peers et al. 2012). Furthermore, a decrease in preferred resources could lead to an expansion of niche breadth, as individuals tend to accept previously unutilized resources (Araujo et al. 2011). Consequently, frequent spatiotemporal variations in the quality and quantity of available resources would represent a favorable environment for jack-of-all-trades strategies, while a more predictable environment is expected to benefit specialists. In host-parasitoid communities, the fluctuations in the quality and quantity of host resources are expected to exert a strong influence on the resource exploitation strategy of parasitoids (Andrade et al. 2013).

In this study, we have investigated the relative abundances of the species in an aphid-parasitoid system in three remote areas in western France, during three consecutive years. Relative abundances of parasitoid species and their aphid hosts in cereal fields were determined in each of those regions during spring (i.e., a period when aphid hosts and their parasitoids increase in density in cereal fields compared to winter, and preceding the disturbance events linked to harvest in summer). We aimed at investigating (1) the degree of interannual, intra-regional and inter-regional variability in the relative abundances of parasitoids and their aphid hosts in order to assess at which spatial scale (inter-field, inter-regional) the structure of parasitoid-aphid networks is determined; (2) whether parasitoid relative abundances are mostly influenced by host species availability, or if relative abundance variations are mostly independent from the relative abundances of host species; (3) whether parasitoids exploit different host species at distinct rates, which could either indicate the occurrence of a partial specialization on host resources or whether available resources are equally exploited.

MATERIALS AND METHODS

Field data

Parasitoids and their host resources were monitored and sampled in host plants in cereal fields (a majority of winter wheat, as well as barley, oats, triticale) in three remote agricultural regions located in western France : the Long Term Ecological Research (LTER) site "Armorique" (48°29′, −01°35′) and the research sites "Plaine et Val de Sèvre" (46°12′, −0°28′) and "Vallées et Coteaux de Gascogne" (43°16′, 0°55′), referred to as "Ar", "PVS" and "VCG", respectively, from here on in this article. PVS is located roughly 300km south of Ar and 350 km north of VCG. Ar is composed of hedged farmlands, PVS is an open plain mostly dedicated to cereal crop production, and VCG consists of less intensified crop-livestock farmlands with a higher percentage of permanent grasslands. All three regions share a common characteristic in presenting a significant amount of cereal crops surrounded by local landscape contexts with varying degrees of agricultural intensification. All fields were conventionally managed, with insecticides being sprayed once in May 2011 and seeds treated with a fungicide as a measure of plant disease control. Field data were collected in May and June, when both parasitoid and aphid host populations are well-established in cereal fields in those regions and secondary parasitoids (hyperparasitoids) are found at very low frequencies. In addition, a large proportion of the aphid population in cereal fields in this period are the result of aphid population growth, while during earlier months in the year the proportion of wing aphids is high, indicating that a larger part of the population is the result of recent off-field migration. One region (Ar) was monitored in three consecutive years, 2010 to 2012, while the other two (PVS, VCG) were monitored in 2011 and 2012 only. In order to take into account intra-regional variations, 5–10 fields were monitored in each region and each year. The number of cereal fields monitored was: 6 in 2010, 10 in 2011 and 7 in 2012 for Ar; 5 in 2011 and 9 in 2012 for PVS; 5 in 2010 and 10 in 2011 for VCG. Distances between two fields within a single region varied from 0.5 to 14.8 km. In this study, cereal crops in different landscape contexts were monitored in order to assess the regional variability of parasitoid communities independently of locally deterministic factors.

To assess parasitoid diversity and abundance, fields were visited two times per month and an arbitrary number between 80 and 120 plants were thoroughly examined. All parasitized aphids (mummies) found were collected. Field borders were not prospected for aphid mummies. All parasitoids were sampled in the fields in order to avoid field margin effects and for standardization reasons. Each mummy was put in an individual gelatine capsule until parasitoid emergence. The species of emerging parasitoids and the species of the aphids from which those parasitoids emerged were identified based on morphology. Only primary parasitoids and their respective aphid hosts were considered. Emerging secondary parasitoids were excluded in this study due to their low frequency in the sampling period (a maximum hyperparasitism percentage of 22% was obtained in Ar in 2012, while in other years and regions hyperparasitism was lower than 15%).

To determine aphid host species availability and abundance, an independent protocol was used: three points were chosen randomly in each cereal field and 50 stems per point were thoroughly examined for aphid presence. The living aphids observed were counted and their species were identified based on morphological traits. Two surveys per month were carried out on each cereal field in May and June to account for population dynamics fluctuations. Relative abundances for each aphid species were calculated based on the aphid counts for each field, each of the three regions, and each year, to take into account field, regional and temporal scales respectively. Spring host resource availability was estimated through total aphid counts for the sampling period.

Data analysis

For the analyses of parasitoid communities, relative abundance data were considered. Dissimilarity of the parasitoid communities between samples (β-diversity) was quantified using a metric based on the abundance of each parasitoid species: the Bray-Curtis distance. Bray-Curtis dissimilarities between all pairwise combinations of samples were summarized as a matrix. To ordinate the Bray-Curtis dissimilarity matrix, we

used a non-metric multidimensional scaling (nMDS), a nonparametric ordination-based method using an iterative algorithm that takes the multidimensional data of the dissimilarity matrix and presents it in minimal dimensional space. The result of nMDS ordination is a map where the position of each sample is determined by its distance from all other points in the analysis. This method reduces ecological community data complexity and identifies meaningful relationships amongst communities. By using the matrix of Bray-Curtis dissimilarities between all pairwise combinations of parasitoid samples, an ANOVA was performed to test the effect of the geographical scale (within vs between regions) on the parasitoid community dissimilarities for each sampling year. The 'vegan' package was used to calculate Bray-Curtis dissimilarities and to perform the nMDS.

For each region and each year, the centroid of each monitored field was calculated using the GIS software Quantum GIS, v. 1.8.0. A matrix of linear distances between centroids was then calculated. In order to assess the occurrence of spatial autocorrelations between fields, spline correlograms were performed using the geographical coordinates of those centroids and the relative abundance of each species of parasitoids. Spline correlograms were executed on the data corresponding to all fields in each individual region, and secondly on the field data belonging to all three regions. Ninety-five percent bootstrap intervals were calculated with a number of 1000 resamples for each spline correlogram.

Quantitative food web graphical representations (Memmott et al. 1994) were made based on the identified aphid mummies and their respective emerging parasitoids for each region and each year, in order to illustrate the degree to which relative abundances of aphids and parasitoids are linked. To test whether the different aphid species are exploited at similar rates, the relative abundances of the living aphids found and collected as well as the relative amount of mummies corresponding to each of those species were compared through chi-squared tests of independence, for each region and each year. The frequencies corresponding to each parasitoid species resulting from each aphid species (mummies) were also compared through chi-squared tests of independence for each region and each

year, in order to identify whether aphid species was a determinant factor in structuring parasitoid relative abundance patterns. In order to evaluate trophic interaction overlaps between different parasitoid species, the Pianka index formula (O) was applied to quantitative food web data, considering the dietary interactions of each parasitoid species in all three regions and years (Pianka 1973, Posluszny et al. 2007). Pianka index values were calculated for all combinations of two different parasitoid species.

All statistical analyses were performed with R version 2.13.2 (R Development Core Team 2014). Multivariate analyses were done with the R package "FactoMineR" (Lê et al. 2008) and spline correlograms were performed with the R package "ncf" (Bjornstad and Falck 2001). The Bray-Curtis cluster analysis was performed with the R package "vegan" (Oksanen et al. 2013).

RESULTS

Spatiotemporal structure of parasitoid communities

Among the parasitoids sampled (N = 2419), five parasitoid species (Hymenoptera: Braconidae: Aphidiinae) were identified: *Aphidius avenae* Haliday, *A. ervi* Haliday, *A. rhopalosiphi* De Stefani-Perez, *Ephedrus plagiator* Nees, *Praon volucre* Haliday. No other species were identified. Less than 2% of all samples were not identified due to damaged morphological characters (e.g., loss of antennae or wings). Each of the five identified species occurred in each sampled region at least once during the three-year period corresponding to this study (Table 1). *Aphidius avenae* (2010, 2012) and *A. rhopalosiphi* (2011) were the dominant species in the region Ar. *Aphidius rhopalosiphi* was also present at high frequencies in the other two regions, while *A. avenae* either occurred at low numbers or was absent in those regions. *Praon volucre* represented a large part of the parasitoids sampled in PVS in both 2011 and 2012, but was not as frequent in the other two regions. *Ephedrus plagiator* was generally the least frequent parasitoid species, except for Ar in 2010 and VCG in 2011 (Table 1).

The non-metric MDS analyses showed separate clusters of parasitoid relative abundance patterns for different regions and years (Fig. 1). For both sampling years where an inter-regional comparison between parasitoid communities

Table 1. Data corresponding to the regions "Armorique" (Ar) (2010, 2011, 2012), "Plaine et Val de Sèvre" (PVS) (2011, 2012) and "Vallées et Coteaux de Gascogne (VCG) (2011, 2012). N = 2419. The rows correspond to the relative abundances of each parasitoid species sampled, and to the total number (N) of samples, in each region and each year.

Site/Year	A. avenae	A. ervi	A. rhopalosiphi	E. plagiator	P. volucre	N
Ar 2010	71.4	11.8	3.4	10.4	3.1	654
Ar 2011	16.9	16.6	60.4	0.0	6.0	331
PVS 2011	0.0	16.7	21.7	3.3	58.3	60
VCG 2011	0.0	10.8	49.2	30.8	9.2	65
Ar 2012	73.4	14.6	8.3	1.8	1.9	623
PVS 2012	3.9	12.5	40.4	1.2	42.0	255
VCG 2012	1.9	32.5	60.8	1.2	3.7	431

was performed (2011 and 2012), the dissimilarities between parasitoid communities were higher between regions than within the regions sampled (Fig. 2; 2012: ANOVA, $F_{5, 319} = 159.4$, p < 0.001; 2011: ANOVA, $F_{5, 184} = 37.49$, p < 0.001).

The spline correlograms performed to test for the occurrence of spatial correlations in each region for the relative abundances of each
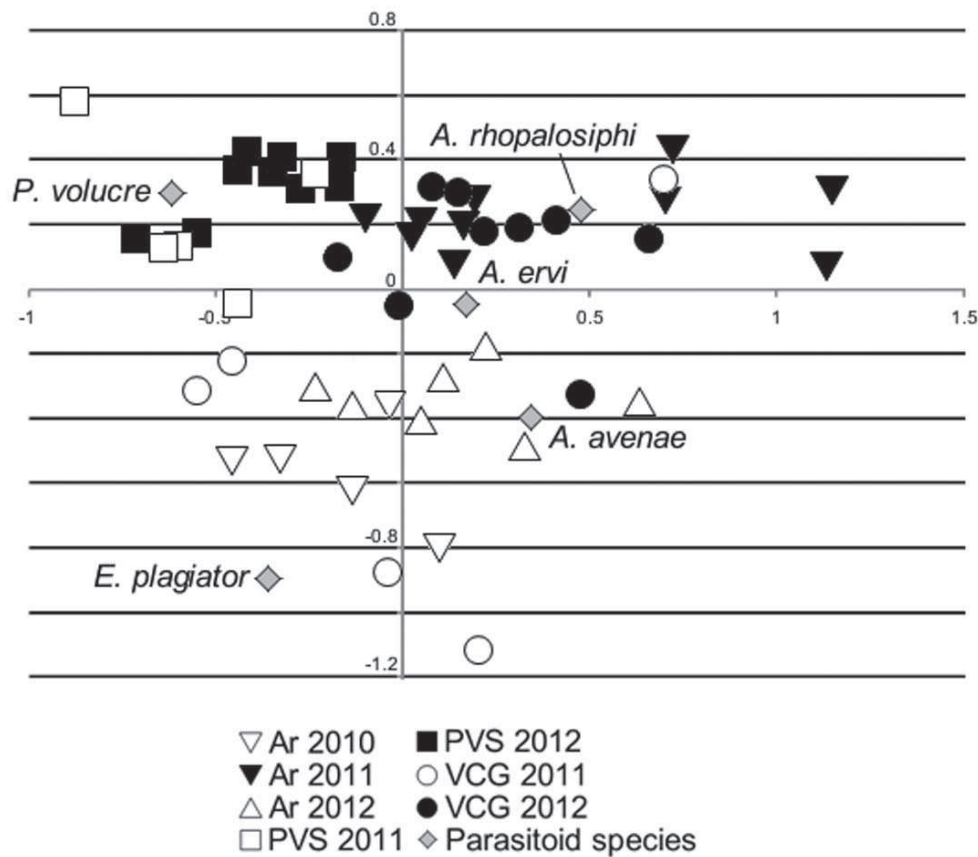

Fig. 1. The non-metric MDS ordination plot comparing parasitoids communities from different cereal field samples. Each data point in nMDS plot represents the parasitoid community identified from a single field sample. The Bray-Curtis dissimilarity index was used to rank distances calculated using the abundance community data. Stress of the nMDS = 0.130.
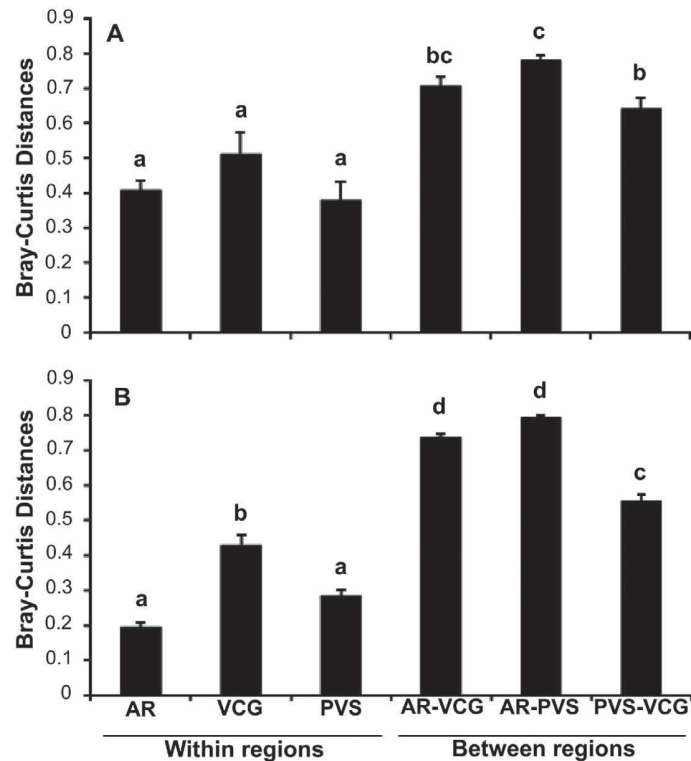
Fig. 2. Effect of the geographic scale (within vs between sampling regions) on parasitoid community dissimilarity. (A): 2011; (B): 2012. Average Bray-Curtis dissimilarity values of parasitoid communities from specimens within region sampled and among region sampled. Errors bars represent standard error. Statistics results: ANOVA.

parasitoid species were non-significantly different from the zero according to the bootstrap intervals. Therefore, in the scale of a single region, relative abundance patterns of different fields were not significantly different than a by-chance-alone geographical distribution of relative abundance patterns. This indicates the absence of an intra-regional geographical compartmentalization of parasitoid communities and the occurrence of a synchronization (i.e., a standardization of abundance patterns across fields) at the intra-regional scale. Spatial autocorrelations were significantly different from by-chance-alone relative abundance patterns at inter-region scales for the parasitoid species *A. avenae, A. ervi, E. plagiator* and *P. volucre* (Fig. 3). This suggests a non-random distribution of parasitoid species across regions, even with interannual variations taken into account. Indeed, in this study two species were found at high frequencies in a single

region (*A. avenae* in Ar, *P. volucre* in PVS) while the other three had less contrasted geographical distributions among the three regions.

Host resource availability and host-parasitoid trophic interactions

Among the living aphids (Hemiptera: Aphididae) counted and identified in the fields monitored in this study (N = 13943), three species were found: the English grain aphid *Sitobion avenae* F., the rose grain aphid *Metopolophium dirhodum* W. and the bird cherry-oat aphid *Rhopalosiphum padi* L. *Sitobion avenae* and *M. dirhodum* were the most abundant for the sampling period in this study, representing, respectively, 81.8% and 16.5% of the total living aphids counted, while *R. padi* represented only 1.7% of those living aphids. In 2010 (for Ar) and 2011 (for all three regions), *S. avenae* was the dominant aphid species, while *M. dirhodum* was
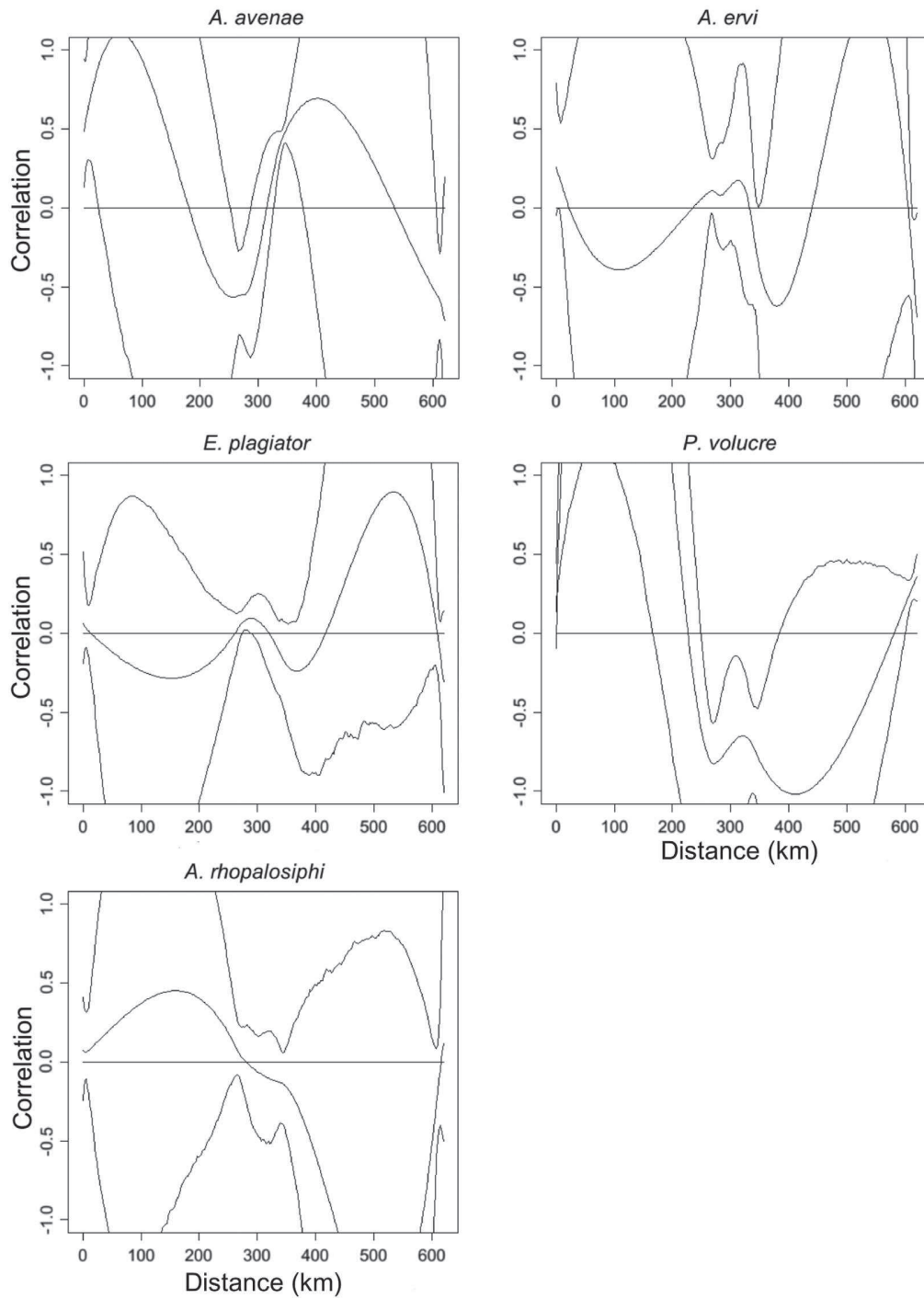
Fig. 3. Spline correlograms on parasitoid relative abundance data corresponding to all fields and each of the five parasitoid species monitored. The x axis represents the distance between monitored fields and the y axis represents the positive and negative correlations of parasitoid relative abundances between fields. Outer lines represent 95% bootstrap intervals and the x-intercept represents the distances at which the fields are no more similar than expected with a by-chance-alone structuring.

Table 2. Data corresponding to the regions "Armorique" (Ar) (2010, 2011, 2012), "Plaine et Val de Sèvre" (PVS) (2011, 2012) and "Vallées et Coteaux de Gascogne" ("VCG") (2011, 2012). *Notes:* Rows 2 to 5 show the results corresponding to the living aphids counted and identified (N = 13943), while rows 6 to 9 represent the results obtained by sampling parasitized aphids (mummies) (N = 2419). The last column shows the significance (NS, non-significant; *P < 0.05; **P < 0.01; ***P < 0.001) of the chi-squared test of independence performed between the relative abundances among living aphids and aphid mummies.

	Living aphids (%)				Aphid mummies (%)				Chi-squared significance
Site/Year	S. avenae	M. dirhodum	R. padi	N	S. avenae	M. dirhodum	R. padi	N	
Ar 2010	100.0	0.0	0.0	1124	94.5	5.5	0.0	654	***
Ar 2011	66.5	31.9	1.6	6737	55.3	44.7	0.0	331	***
PVS 2011	84.2	5.9	9.9	608	85.0	10.0	5.0	60	NS
VCG 2011	98.4	1.0	0.6	2322	87.7	9.2	3.1	65	***
Ar 2012	41.6	25.0	33.3	24	11.7	88.1	0.2	623	***
PVS 2012	9.8	51.2	39.0	123	13.3	86.3	0.4	255	***
VCG 2012	99.3	0.7	0.1	3005	91.0	8.8	0.2	431	***

more frequent in 2012 in Ar and PVS (Table 2). High interannual and inter-regional variability was also observed in the relative abundances of each aphid species among parasitized aphid samples (Fig. 4). The points on the ternary plot (Fig. 4) corresponding to a single region in one given year are generally regrouped in function of the fluctuating ratio between the populations of *S. avenae* and *M. dirhodum*, as only the region Ar in 2011 presented a high intra-regional variability in *M. dirhodum* and *S. avenae* relative abundances. Similarly to the parasitoid community data, intra-regional relative abundance variations were lower than inter-regional or interannual ones, with the exception of Ar in 2011 (Fig. 4).

For the quantitative food web analysis, a total of 2419 aphid mummy-emerging parasitoid pairs were identified (Fig. 5). The parasitoid species *A. avenae*, *A. rhopalosiphi* and *P. volucre* were able to parasitize all aphid species found, while *A. ervi* and *E. plagiator* were found parasitizing the two most common aphid species (*S. avenae*, *M. dirhodum*).

In each region and each year, the predominant parasitoid species found emerged from multiple aphid species. In Ar in 2010 and 2012, two similar parasitoid relative abundance patterns (chi-squared p-value < 0.001) resulted from contrasted proportions of the aphid species among the mummies collected (*S. avenae* representing, respectively, 94.5% and 11.7% of those mummies, which were all identified). Similar aphid species relative abundance patterns (VCG in 2011 and 2012, chi-squared p-value > 0.05; Ar and PVS in 2012, chi-squared p-value > 0.05) resulted in

contrasting parasitoid relative abundance distributions, indicating the importance of interannual and inter-regional variability in aphid-parasitoid interactions.

Host species exploitation

The aphid mummies collected and identified all belonged to the three aphid species found in the living aphid counts. However, the proportions of each aphid species in mummies was not
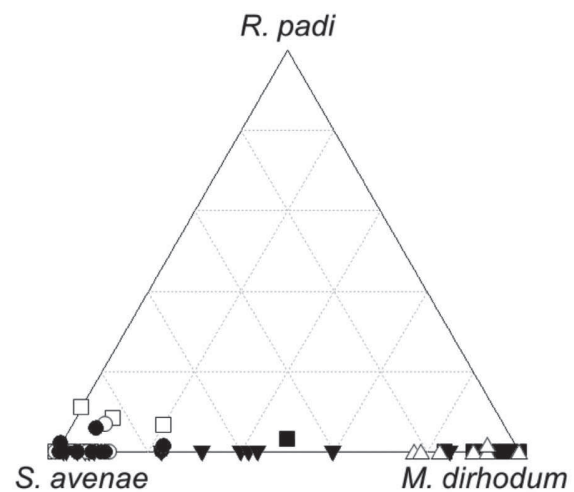

Fig. 4. Parasitized aphid relative abundances for the regions "Armorique" (Ar) (2010, 2011, 2012), "Plaine et Val de Sèvre" (PVS) and "Vallées et Coteaux de Gascogne" (VCG) (2011, 2012). Each point on the ternary plot represents a sampled field. The axes represent the relative abundance of each parasitized aphid species. Symbols are the same as in Fig. 1.
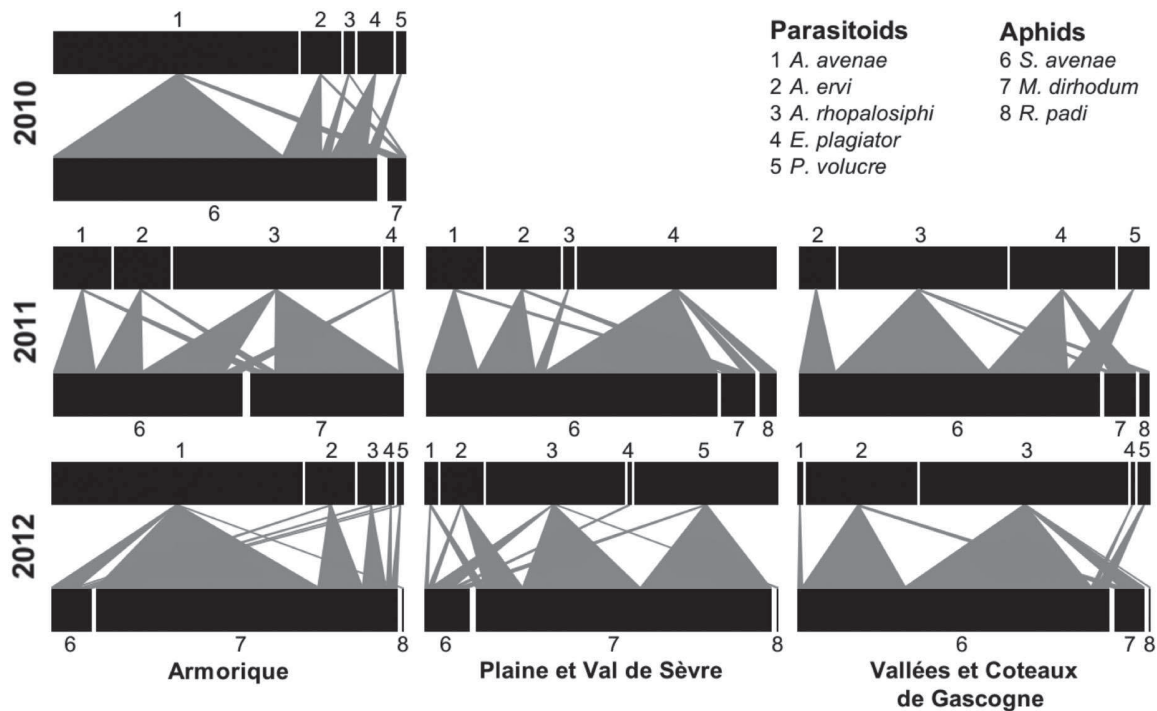
Fig. 5. Quantitative food webs for the regions "Armorique" (Ar), "Plaine et Val de Sèvre" (PVS) and "Vallées et Coteaux de Gascogne" (VCG) (columns) and each year (rows). The upper bars represent parasitoid relative abundances and the lower bars represent aphid (mummies) relative abundances. N represents the total number of individuals in each trophic level for each region and each year. The thickness of the arrows between those two bars is proportional to the relative number of trophic interactions between each aphid species and each parasitoid species.

similar to the proportions observed in living aphids in the same regions and periods, except for "PVS" in 2011, as indicated by the chi-squared test significances (Table 2). In each region where the percentages of aphid mummies were statistically different to the percentages of living aphids, the frequency of *M. dirhodum* mummies was higher than the ratio observed for that species in the living aphids (Table 1). This indicates that this species of aphid was exploited more frequently than the other two species. Furthermore, this preferential *M. dirhodum* exploitation was found in communities dominated by different species of parasitoids (Fig. 5).

In Ar (2010, 2011) and PVS (2012), unequal relative abundances of each parasitoid species were found resulting from each of the most numerous aphid species (*S. avenae* and *M. dirhodum*), as shown by the chi-squared tests of independence (Ar 2010 p-value = 0.0329; Ar 2011 p-value < 0.001; PVS 2012 p-value < 0.001). In Ar (2010) and PVS (2012), parasitoid species exhibited no constant preference for a single aphid species, independently of regional and annual contexts. For example, *A. rhopalosiphi* exhibited higher frequencies when resulting from *M. dirhodum* hosts in Ar in 2011, but exploited *S. avenae* more frequently in PVS in 2012. Chi-squared parasitoid relative abundance tests for the two aphid species did not bear significant results for the Ar in 2012 (p-value = 0.1415) and VCG in 2012 (p-value = 0.5912). Those tests were not performed for VCG and PVS in 2011 due to the unreliability of comparing frequencies in lower sample totals for that year.

Pairwise Pianka index values (O) ranged from 0.78 between *P. volucre* and *E. plagiator* and 0.99 for three parasitoid species pairwise comparisons (*A. avenae* and *A. rhopalosiphi*, *A. avenae* and *P. volucre*, and *A. rhopalosiphi* and *A. ervi*). Such high

Pianka index values indicate similarity in host exploitation between parasitoid species, with a low degree of food web compartmentation.

DISCUSSION

Our first hypothesis aimed to identify the degree of variability the parasitoid community structure presents at intra-regional and inter-regional scales in multiple years, thus evaluating whether parasitoid relative abundances are indeed determined by local environmental filters (such as local agricultural practices, microclimatic factors, landscape context or local interspecific interactions) or whether those patterns occur at a broader scale. Our results showed a high degree of variability in the relative abundances of cereal aphid parasitoids, at both annual and interregional scales, but not at the local scale. The species richness (five species of parasitoids exploiting three species of aphids) was generally homogeneous at both the annual and the spatial scales, and the number of parasitoids was slightly lower than that of previous studies for the same host-parasitoid system in Europe (Vollhardt et al. 2008, Gagic et al. 2011, 2012). Rarer species were not found in this study, which could be a result of the sampling design, in which field borders were avoided. However, as the same five parasitoid species were consistently found across fields, regions and years, this could be an accurate perspective of this parasitoid community. At the local scale, inter-field differences in relative abundances were generally less marked, suggesting that the mechanisms driving the structure of the parasitoid community are regional context-dependent. Gagic et al. (2012) also demonstrated an intra-seasonal, intra-regional synchronisation of cereal aphid parasitoid abundances monitored in low and high agricultural intensification contexts, and the results of Vollhardt et al. (2008) also show no influence of local landscape complexity on the structure of those communities. Other studies on different host-parasitoid communities have demonstrated strong interannual species composition variations (Le Corff et al. 2000), significant parasitoid relative abundance variations at a local scale (10 km between monitoring points) (Craig 1994), or inter-regional, but not interannual variations in parasitism rates and diversity index (Folcher et al. 2011). These studies coupled to our results suggest that host-parasitoid communities consisting of different species are potentially structured at distinct spatiotemporal scales.

Concerning the host resources, high variations in the relative abundances of S. avenae and M. dirhodum were observed between years and regions. In Ar in 2011, a high discrepancy of aphid relative abundances was observed between fields, even between geographically close locations. These were also the region and year where the highest density of living aphids was observed in the field. On the other hand, low host density environments (Ar and PVS in 2012) exhibited a high degree of intra-regional homogeneity in the relative abundances of parasitized aphids, with a high percentage of M. dirhodum mummies collected. Studies have shown that locally deterministic factors, such as the presence of grassy strips or fertilizer effects, can skew the abundance of specific aphid species, potentially explaining relative abundance differences at the local scale (Garratt et al. 2010, Al Hassan et al. 2013). However, in most cases in this study, the intraregional homogeneity of relative abundance patterns indicates mitigated local-level factors (adjacent land use, employment of pesticides) in comparison to regional-level ones such as climate or shared general agricultural management policies in those areas. The local use of pesticides in particular could be a key factor in interrupting aphid-parasitoid dynamics. Nevertheless, according to our results, parasitoid relative abundance patterns seem to be defined at a larger scale.

In this study, our second hypothesis was to investigate whether parasitoid relative abundance patterns are strongly linked to availability of host species. This was not the case, according to the results obtained. Parasitoid relative abundance patterns were not heavily linked to aphid availability in this study. As the quantitative food web and the living aphid counts showed, fluctuations in the ratio between the aphids S. avenae and M. dirhodum (e.g., between 2011 and 2012 in two regions) and in the aphid density (higher living aphid counts in 2010 and 2011 compared to 2012, in the same two regions) did not clearly determine which parasitoid species were predominant. Contrasting aphid relative abundance patterns (such as those of Ar in 2010

and in 2012) were associated to similar parasitoid relative abundances. Indeed, dominant parasitoid species were able to exploit multiple aphid species independently of region and year, underlining their generalist strategy. All parasitoids monitored in this study are considered polyphagous, being detected on a large number of host species on different host plants, with the exception of *A. rhopalosiphi*, which is considered a Poaceae habitat specialist whilst still being a host resource generalist (Kavallieratos et al. 2004, Stilmant et al. 2008). In low host density situations, parasitoid species with superior competitive ability would be expected to thrive and be relatively more numerous than species presenting a high mortality when facing interspecific competition (Connell 1983). There is a scarce amount of information in the literature concerning competitive outcomes between the Aphidiinae species in this study, but our results show some indication that such interspecific interactions are not a major factor in determining relative abundance patterns. This can be due to resource partitioning, as Aphidiinae species have been known to exhibit distinct host resource exploitation strategies while exploiting the same host species, thus avoiding detrimental niche overlapping and allowing coexistence (van Baaren et al. 2004, Le Lann et al. 2012).

The discrepancies in relative abundance patterns observed in aphid-parasitoid networks did not seem to be largely determined by the heterogeneity in local environmental characteristics. Instead, the data suggest that the environmental factors driving differences in such patterns were probably at a larger geographic scale. These results agree with the findings of Vollhardt et al. (2008), who demonstrated a regional pattern of aphid parasitoid species diversity and relative abundances. However, in our study, some characteristics of the regional community patterns appeared to remain relatively constant from year to year despite the high relative abundance fluctuations: the cluster analysis shows a partition of relative abundance patterns in function of the regions, as fields pertaining to PVS in two years generally clustered together with and a similar result was observed for Ar in 2010 and 2012. *Aphidius avenae* and *P. volucre* presented significant positive spatial correlations at the intraregional level

(Fig. 3), between 0 and 50 km, which is due to the higher frequency of those species in specific regions (*A. avenae* in Ar, *P. volucre* in PVS). Due to that biogeographical structure, *P. volucre* also presented negative spatial autocorrelations corresponding to distances roughly between 250–300 km (Ar-PVS) and 300–350 km (PVS-VCG), while *A. avenae* frequencies were negatively correlated between Ar and PVS and positively correlated between PVS and VCG. Spatial autocorrelations also indicated a negative correlation between Ar and VCG for *A. ervi* and a positive one between Ar and PVS for *E. plagiator*. These tendencies point to a weighty regional influence on community patterns and to a non-random structure of parasitoid communities, considering that those populations face heavy disturbance events on a yearly basis. This regional pattern of parasitoid relative abundances may be linked to a similarity in environmental variables at a large scale. In other words, the Moran effect could be an important reason for the similarities in regional community responses. Spring parasitoid communities may also be closely linked to initial population numbers resulting from scarce aphid populations in winter (Höller 1990). Our results indicate that disparities in relative abundance patterns are minor at a scale from tens to hundreds of kilometers, and that increased differences in such patterns at a broader scale may be related to regional environmental factors.

Our third hypothesis was to investigate whether parasitoids exploit host species at distinct rates. Among the monitored aphid species, *M. dirhodum* was present at a higher frequency among the mummies collected than the living aphids found, in 6 out of 7 region and year combinations, both in low and high host density situations. Therefore, the parasitoids monitored considered as a whole exploited *M. dirhodum* at a significantly higher frequency. The aphid *M. dirhodum* has been considered a "high cost" host compared to the smaller *S. avenae* for the parasitoid *Monoctonus paulensis* Ashmead, due to its higher likelihood of behavioral defences upon facing the parasitoid, escaping or causing injury to the ovipositing female (Chau and Mackauer 2001). On the other hand, *M. dirhodum* was reported to represent a higher nutritional value for the generalist linyphiid spider *Erigone atra* Blackwall (Bilde and Toft

2001), thus potentially consisting of a "high risk, high reward" type of host. One potential explanation for the disparity of frequency of *M. dirhodum* among aphid mummies and living aphids is a general parasitoid exploitation preference, but this hypothesis cannot be confirmed based on field data only. This overexploitation of *M. dirhodum* by aphid parasitoids should be taken into consideration in biological control programs, as previous studies have demonstrated that *S. avenae* induces more damage in cultivated winter wheat than *M. dirhodum* (Niehoff and Stablein 1998) and that *S. avenae* populations possess a higher intrinsic rate of increase than *M. dirhodum* at a wide range of temperatures (Asin and Pons 2001). In this study, high host density situations were only observed with a marked increase in *S. avenae* populations; when *M. dirhodum* was the more frequent aphid species, host density was low. It is also noted that host exploitation rates seemed to vary from year to year and between regions for each parasitoid species, and no parasitoid species exhibited a clearly defined exploitation specificity for any of the aphid species, which is in agreement with aphid relative abundances not being a determinant factor in cereal parasitoid relative abundance patterns. Furthermore, trophic overlap (Pianka index O) values were generally high between different parasitoid species, indicating that host exploitation was similar for different parasitoid species. The high abundance of aphid hosts in spring could favor a low degree of compartmentation in host-parasitoid food webs.

Understanding how environmental changes affect communities is a key challenge in the conservation of biodiversity. This study provides insight on the structure of aphid-parasitoid communities by assessing the degree of variability in parasitoid and host relative abundances. The regional and annual homogenization of relative abundance patterns observed in this study could also prove to be useful information in agroecosystem management, as local sampling should help predict large-scale patterns relevant to biological control. This sustains the possibility of an agroecological crop management limiting pest outbreaks by contributing to the stability of communities at a territory scale.

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