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Yannick Outreman, Thiago Oliveira Andrade, Philippe Louâpre, Liliane Krespi, Cyrille Violle, et al.. Multi-scale and antagonist selection on life-history traits in parasitoids: a community ecology perspective.. Functional Ecology, 2018, 32 (3), pp.736-751. 10.1111/1365-2435.13007 . hal-01742069

HAL Id: hal-01742069

<https://hal.science/hal-01742069>

Submitted on 8 Jun 2018

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Article type : Research Article

Section: Evolutionary Ecology

Editor: Hefin Jones

**Multi-scale and antagonist selection on life-history traits in parasitoids:
a community ecology perspective**

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Running title: Ecological drivers of parasitoid traits

Data archival location: databases will be submitted to DRYAD once the paper accepted

Keywords: ecological drivers, external/internal filters, guild, insect parasitoids, phenotypic evolution, trait-based community study

Abstract

- 1) Life-history traits within ecological communities can be influenced by regional environmental conditions (external filters) and community-wide density-dependent processes (internal filters). While traits in a regional context may converge to a narrow range of values because of environmental filtering, species belonging to a guild may present contrasting traits as a means of niche differentiation, allowing coexistence whilst exploiting the same resources.
- 2) To disentangle the role of external and internal filters on phenotypic diversity within ecological communities, we examined the patterns of life-history trait variation within a guild of insect parasitoids during two successive years across three contrasted regions in relation to several ecological factors.
- 3) By combining a mean-field approach and an analysis of phenotypic variance across organizational levels (from individual to guild), we showed that the patterns of life-history

trait variation across regions are consistent with local adaptation or adaptive phenotypic plasticity while the patterns of phenotypic variation within regions suggested how coexistence modulates life-history traits expression through niche differentiation.

- 4) Within a given region, phenotypic pattern of parasitoid life-history traits may also arise from bottom-up effects of trophic webs: insect host species could also control parasitoid life-history traits in nature. Our results also showed that parasitoid life-history traits presented contrasting variation patterns according to the sampling year, suggesting temporal variations in evolutionary and ecological dynamics of parasitoid species.
- 5) The application of such trait-based studies to insect parasitoids has the potential to provide further insight on how agricultural environments contribute to differential diversification among natural enemies guilds, highlighting the main role of agricultural landscape management for organisms' responses.

Introduction

Phenotypic variation observed within populations arises from various and interacting ecological and evolutionary forces (Antonovics & van Tienderen, 1991; Kingsolver & Pfennig, 2007; McGill, Enquist, Weiher & Westoby, 2006; Weiher et al., 2011; Enquist et al., 2015). Since wild populations are not isolated, biotic interactions between species, including competitive and trophic interactions, have long been recognized as a major source of phenotypic adaptation and diversification (e.g., Roughgarden, 1972). Surprisingly though, the studies focusing on biotic factors have been interested by simple bipartite interactions, notably when examining the phenomenon of character displacement (Pfennig & Pfennig, 2009). The ecological community represents a study unit of choice to improve our

understanding of phenotypic variation (e.g., community-wide character displacement - Dayan & Simberloff, 2005) because it results from both abiotic and biotic factors.

Environmental filtering theory states that regional environmental conditions should induce phenotypic convergence at the community level, i.e. by reducing the range of trait values among coexisting individuals (Weiher et al., 2011; Violle et al., 2012; Enquist et al., 2015). Such phenotypic convergence is expected when regional environmental conditions exert strong pressure on species (Weiher et al., 2011). Inversely, phenotypes are expected to diverge in competitive contexts as a result of niche partitioning (MacArthur & Levins, 1967), which should consequently favour stable species coexistence under limiting resource conditions (MacArthur & Levins 1967; Grant & Grant, 2003; Losos, 2009). That being so, a central challenge is to disentangle the various abiotic and biotic factors that drive local patterns of phenotype variation within communities.

Violle et al. (2012) proposed a spatially explicit framework that defines two operational groups of agents of phenotypic diversification within communities: ‘external’ and ‘internal’ filters. These authors did not try to decipher abiotic and biotic factors because they often both act at the same time and at the same place, but rather highlighted the key role of scale-dependent community assembly processes. External filters include all pressure agents outside the community whereas internal filters include all the selection agents within the community. External filtering can be a product of the interplay of both abiotic and biotic factors such as climate conditions, landscape structure, and the composition or global availability of food resources (Diaz & Cabido, 2001; White, 2008; Aparicio, Hampe, Fernandez-Carrillo & Albaladejo, 2012). The internal filtering represents all processes within a community such as competition, parasitism or intra-guild predation (Violle et al., 2012). As agents of pressure, both external and internal filters may have opposite effects on trait variation within communities. In a community, more or less similarity in trait values among co-occurring

organisms can thus be observed depending on the type and strength of selective pressures generated by external and/or internal filters (Violle et al., 2012). Figure 1 summarizes different phenotypic variation patterns within a community depending on the ecological filtering processes at play.

In the last decades, the linkage between ecological filtering processes and phenotypes has been one of the main research questions in community ecology, in an effort to understand community responses to environmental changes and subsequent impacts on ecosystem functions (Lavorel & Garnier, 2002). Community-level trait responses to ecological filters have been mostly studied in plants (e.g., Weiher, Clarke & Keddy, 1998; Grime, 2006; Lebrija-Trejos, Perez-Garci, Meave, Bongers & Poorter, 2010; Bernard-Verdier et al., 2012; Tomlinson et al., 2013), which implies a focus on basal levels of trophic webs. However, all species are not affected by ecological filters equally in a trophic web: the trophic rank hypothesis predicts that upper-trophic level organisms should be more harshly affected by environmental changes and disturbance (Holt, Lowton, Polis & Martinez, 1999; Tscharnkte & Brandl, 2004). As a result of the difficulty of establishing causality relationships in traits in complex food webs (Lavorel, 2013; Gravel, Albouy & Thuiller, 2016), studies on the effects of filtering processes on upper-trophic level organisms are scarce (e.g., Farias & Jaksic, 2011; Mouillot et al., 2005).

We conducted a community-wide approach to life-history trait variation using insect parasitoids as biological models. These organisms occupy high levels in trophic webs and are intimately influenced by their insect hosts. A number of interspecific trait studies have been done on parasitoids suggesting that interspecific phenotypic variation is often related to interspecific competition and host use strategy (Jervis & Ferns, 2004; van Baaren et al., 2004; Le Lann, 2009; Andrade et al., 2015; Andrade, Krespi, Bonnardot, van Baaren & Outreman, 2015). For instance, variability in the competitive pressure within an aphid parasitoid guild

due to seasonality has been linked to a higher level of food web compartmentalization as well as contrasted life-history traits such as body size and emergence rate (Andrade et al., 2015; Andrade et al., 2016). Laboratory studies have measured the effect of ecological factors such as host species (Bilu, Hopper & Coll, 2006; Henry, Roitberg & Gillespie, 2006; Andrade, Hervé, Outreman, Krespi & van Baaren, 2013; Mayhew, 2016), host size (Colinet, Salin, Boivin & Hance, 2005; Harvey, 2005; Mayhew, 2016), host instar (Sequeira & Mackauer, 1992; Cloutier, Duperron, Tertuliano & McNeil, 2000), host plant species (Bilu et al., 2006), or temperature (Hance, van Baaren, Vernon & Boivin, 2007), among others, on fitness components. These ecological factors influence several life-history traits, such as body size, egg load, longevity, which are known to be fitness proxies (Godfray, 1994; Roitberg, Boivin & Vet, 2001). Although trait differentiation within habitats may likely be driven by divergent evolutionary responses to the various selection pressures operating in the local environment (e.g., McArthur & Levins, 1967), there are some evidences that intra-guild interspecific competition and host-parasitoid interactions would be major factors in explaining trait dissimilarity. However, to our knowledge, no studies have taken an interest in the overall ecological factors that shape such life-history traits in the field. In fact, field conditions encompass a number of factors that are difficult to disentangle.

Our investigation aimed to quantify the relative importance of external and internal filters in driving the variation of parasitoid life-history traits. We hypothesized that life-history traits of parasitoid species are driven by various filtering processes and that the strength of those filters may vary in space (i.e., at the biogeographic scale) but also in time (i.e., temporal variation of habitat properties). To investigate this question, we measured traits that are tightly related to fitness through their effects on survival and reproduction in a guild of aphid parasitoids sampled in three contrasted French regions during two successive years. Two complementary statistical strategies have been used to establish the presence/absence of

external and internal filtering processes. In trait-based community ecology, the mean field theory has been widely adopted (McGill et al., 2006; Weiher et al., 2011) where the focus is on mean trait differences among co-occurring species. Because interactions with the local environment are ultimately based at the individual level (Bolnick et al., 2003), intraspecific trait variation has been shown to be critical for responding to key questions in community ecology (Bolnick et al., 2011, Violle et al., 2012, Escudero & Valladares, 2016). Here we study the parasitoid guild by analysing both mean trait values of different species and the decomposition of phenotypic variances across hierarchical levels (individual, population, community).

Materials and methods

Studied regions

To carefully examine a broad spectrum of environmental external filters, we selected three research sites presenting contrasted local conditions and far enough apart so that no gene flow was expected. In sum, we generated three contrasted and independent external filtering study cases. The three Long Term Ecological Research (LTER) sites located in western France were considered for this study: “Armorique” (48°29', -01°35'), “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 in this article. “PVS” is located roughly 300km south of “Ar” and 350km north of “VCG” and these sites present different climate conditions because of their latitude. The three research regions display contrasted agricultural landscapes. “Ar” presents a gradient of agricultural intensification and hedgerow density (Burel et al., 1998), with sectors dominated by grasslands, hedgerows and fodder crops, and other sectors marked by a higher density of cultivated areas. “PVS” is mostly dedicated to cereal crop production, its open landscapes bearing low percentages of semi-natural elements

such as permanent grasslands or woods. “VCG” is composed of mixed crop-livestock farmlands, with a moderate amount of semi-natural landscape elements throughout the research area. In order to study how filtering processes can vary over time, we performed a two-year sampling in the three research sites. Given that two years represent a large time window for the studied parasitoid species characterized by a short generation time (ca. 20 days depending on temperature, Le Lann et al., 2011a), we expected important temporal changes in trait distribution within the sampled populations at a given site.

Parasitoid sampling

In 2011 and 2012, primary parasitoids (Hymenoptera: Braconidae) of cereal aphids (Hemiptera: Aphididae) were monitored in cereal fields (a majority of winter wheat, as well as barley, oats, triticale) in the three research regions from May to June. Five to ten fields were selected in each research region to capture the gradient of within-site landscape complexity, while maintaining field area uniformity. The number of cereal fields monitored in each research region was: 10 in 2011 and 7 in 2012 in “Ar”; 5 in 2011 and 9 in 2012 in “PVS”; 5 in 2011 and 10 in 2012 in “VCG”. Each field was sampled twice a month. For each sampling session, an arbitrary number (no less than one hundred) of plants randomly chosen in the field were thoroughly examined and all parasitized aphids (mummies) found were collected. Each aphid mummy was put in an individual gelatine capsule until parasitoid emergence. New parasitoid emergences were checked twice a day (at 9:00 and 18:00). Life-history trait measurements were measured on these emerging parasitoids (see below). Whenever possible, the aphid species from which each parasitoid emerged was identified based on the morphology of the aphid mummy.

Life-history trait measurement

The longevity of the emerged parasitoid individuals under starvation conditions was measured as an estimation of the amount of energy stocked in larval development and of the rate of energy consumption after emergence (Ellers, van Alphen & Sevenster, 1998). Parasitoid longevity was calculated by placing parasitoids in 2.0 ml Eppendorf tubes containing a wet cotton ball (with water being administered daily to avoid desiccation) without any food. This procedure was performed at a room temperature of $20\pm 1^{\circ}\text{C}$ and a 16:8-h photoperiod. Parasitoid deaths were checked twice a day (at 9:00 and 18:00). After their death, taxonomic identity and sex of parasitoids were determined and their body size was estimated, by using the left hind tibia length as a body size indicator (Godfray, 1994; Ellers et al., 1998 ; Cohen, Jonsson, Müller, Godfray & Savage, 2005; Ameri, Rasekh, Michaud & Allahyari, 2013). In parasitoids, the left hind tibia length is a well-known proxy for body size, itself positively correlated with several indicators of individual's fitness including longevity, mating preference, fecundity, reproductive longevity, progeny emergence and sex-ratio (Collins & Dixon, 1986; Sagarra, Vincent & Stewart, 2001). Hind tibia length was measured by analysing pictures taken with a binocular (6.3x, Olympus SZ-CTV) linked to a video camera (JVC KY-F50) using ImageJ 1.41o (Schneider, Rasband & Eliceiri, 2012). Lastly, using ImageJ 1.41, we measured forewing area. Forewing area can be considered as a trait potentially linked with flight ability (Kingsolver, 1999).

Statistical analyses

Our objective is to determine which evolutionary scenarios explain life-history trait variations within the studied parasitoid guild (see Figure 1). The first analysis aims at identifying the different factors driving the species mean-trait values. The second analysis studied the external and internal filtering processes more specifically by considering the trait

variation at different organisational levels (i.e. a variance decomposition approach). Finally, we quantified phenotypic space of each species and their overlapping within communities.

Drivers of parasitoid life-history trait variation: a mean-field approach

We used mixed models in order to compare mean trait values of different species between sites while accounting for multiple sources of variation, thus the overall effect of internal and external filters on these mean trait values. A model was created for each life history trait (i.e., tibia length, forewing area, longevity and sex-ratio), including the following fixed factors: the ‘research region’ (i.e. the environmental context-external filters), the ‘parasitoid species’ (i.e. internal filters related to interspecific mean trait values differences), as well as the interaction between those two factors (i.e., if the strength of the interspecific mean trait values differences varied according to the environmental context; see Scenario ‘IF×EF’, Figure 1).

In addition to the inclusion of internal/external filtering processes in mixed models, other factors have been considered. Given that the life-history traits in aphid parasitoids depend on the sex of individuals, this fixed factor was included in the statistical modelling. The host species has also been added in the modelling as a bottom-up effect on life-history traits in order to link traits across trophic guilds. To consider allometric constraints, tibia length was tested as a covariate in the forewing area modelling. Finally, as some individuals originated from the same cereal field and each cereal field within a remote region were selected at random, ‘field’ was included as random factor in models. Precise details about the explanatory variables initially included in the models are given in Table 1. The effect of these explanatory variables on each life-history trait was tested by using generalized linear mixed modelling (R packages ‘nlme’ by Pinheiro, Bates, DebRoy, Sarkar & R Core Team 2015 and ‘lme4’ by Bates, Maechler, Bolker & Walker, 2015) considering either a normal error (dependent variables: tibia length, forewing area and longevity) or a binomial error (dependent variable: sex-ratio). The significance of each model term was determined by a

Wald χ^2 test using the *Anova* function of the *car* R package (Fox & Weisberg, 2011).

Residuals of fitted models were visually inspected (quantile-quantile plot and residuals vs. predicted values plot) and all were approximately normal, i.e. unimodal and symmetric.

External and internal filtering processes: a variance decomposition approach

We used the classical permutation framework earlier proposed in community ecology to determine the effects of internal and external filtering processes on community-wide phenotypic variation. In this framework, permutations of traits are carried out on the hierarchical level below the one of interest – e.g., means of communities are permuted to test for regional differences. To account for the importance of individual variation that partly regulates community assembly processes (Bolnick et al., 2011, Enquist et al., 2015), we used a variance decomposition approach from individuals to region. More precisely, used the ‘T-statistics’ method that decomposes the sources of phenotypic variances within a community relative to the regional phenotypic variance (Violle et al., 2012). We partitioned the trait variances among the four hierarchical levels involved in community assembly (i.e., individual level (I), population level (P) (i.e. the community-specific species), the community level (C) (i.e. the guild) and the regional level (R)). This allowed us to detect phenotypic convergence in response to external drivers (e.g., climate, landscape structure) but also within-community phenotypic divergence in response to density-dependent processes such as intra-guild competition. The calculation of two T-statistics indices was implemented to quantify the relative amount of intra- to interspecific variation, and of within-community to regional variation. First, we calculated the $T_{IC/IR}$ index that is the ratio of community-wide variance (i.e. variation of trait values among individuals within a particular community) to total trait variance (i.e. variation of trait values among individuals (I) sampled in all regions(R)), assessed at the individual level. By calculating the $T_{IC/IR}$ index for each trait, we measured the strength of the inter-regional phenotypic divergence (i.e. external filters) when accounting for

individual differences. The lower $T_{IC/IR}$, the stronger external filters on the community. Second, we calculated the $T_{IP/IC}$ index that is the ratio of the within-population variance (i.e. variation of trait values among individuals within a single species) averaged across all species co-occurring in a community to the total within-community variance (i.e. variation of trait values among individuals within a community). By calculating the $T_{IP/IC}$ index for each trait, we measured the strength of the phenotypic divergence (i.e. internal filters) within a parasitoid guild. The lower $T_{IP/IC}$, the higher phenotypic divergence among coexisting species.

To test the significance of the observed $T_{IC/IR}$ and $T_{IP/IC}$ values, a null modelling approach (i.e. a comparison of observed values compared to randomized situations as classically performed in community ecology) is required (Gotelli & McCabe, 2002). More specifically, we used the null model (i.e. for $T_{IC/IR}$: no external filtering; for $T_{IP/IC}$: no internal filtering) of the *cati* package (Taudiere & Violle, 2015) in which individual trait values are randomized (200 permutations) at the community and regional scales. The departure of the $T_{IC/IR}$ and $T_{IP/IC}$ values from the randomized distributions was calculated using the standardized effect size (SES) as $SES = (T^{obs} - T^{null})/sd^{null}$ where T^{obs} is the observed T-value and T^{null} and sd^{null} are the mean and standard deviation, respectively, of the null distribution (see e.g. Jung, Violle, Mondy, Hoffmann & Muller, 2010; Taudiere & Violle, 2015). A significant $T_{IC/IR}$ means that two individuals belonging to a particular guild have more-similar trait values than two individuals drawn randomly from different regions and a significant $T_{IP/IC}$ means that two individuals belonging to the same species have more-similar trait values than two individuals drawn randomly from the guild. T-statistics and their respective SES were calculated for the three quantitative life-history traits (i.e., tibia length, forewing area, longevity).

Quantifying species' phenotypic space

Finally, we applied a multi-trait analysis to approach the phenotypic space of each species (as a proxy for species niches, Violle & Jiang, 2009) and the overlap between these species-specific phenotypic spaces. This is a means to better evaluate the role of internal filtering on phenotypic divergence among coexisting species. For each species of a guild, we estimated its trait multidimensional space. This notion refers to the concept of the Hutchinsonian multidimensional niche: Hutchinson (1957) first proposed that niches can be quantified by assessing the life-history trait hypervolumes that characterize trait multidimensional space occupied by a set of species (Blonder, Lamanna, Violle & Enquist, 2014, Blonder, 2016; see also Lamanna et al., 2014 for an application). By considering only parasitoid individuals on which the three quantitative life-history traits were measured (i.e., tibia length, forewing area and longevity), we quantified and represented the trait hypervolume using the ‘*hypervolume*’ R package (Blonder et al., 2014). These algorithms infer the shape, the volume and the intersection of high-dimensional objects via a thresholded kernel density estimate. To estimate niche differentiation between species within the guild, all possible pairwise hypervolume overlaps between species pairs were calculated. We defined overlap as the hypervolume in common divided by the mean volume of the two hypervolumes. A full description of the algorithms can be found in Blonder et al. (2014).

All the statistical analyses were performed using R 3.1.2 (R Core Team 2015).

Results

Aphid parasitoid taxonomic diversity: sampling year and geography matter

A total of 1905 primary parasitoids (Hymenoptera: Braconidae) were sampled. Five parasitoid species were identified: *Aphidius avenae* Haliday, *A. ervi* Haliday, *A. rhopalosiphii* De Stefani-Perez, *Ephedrus plagiator* Nees and *Praon volucre* Haliday (Table 2). The

diversity of the guild strongly varied between years and regions. In 2012, all five species were found in the three studied regions. In 2011, *A. avenae* was not found in both “PVS” and “VCG” and *E. plagiator* was not found in “Ar”. The relative frequencies of the parasitoid species within the guild varied strongly between regions and years. For example, *A. avenae* represented 15.5% of the parasitoid guild in “Ar” in 2011, and 73.5% in 2012 in this same region, while occurring at very low frequencies in the other two research regions for the two years. From these results, the parasitoid species to include in data analyses were determined (see Table 2 for details about criteria used for specimens’ selection).

A total of 1765 aphid mummies were identified: 967 individuals corresponding to the aphid species *Metopolophium dirhodum* Walker, 790 individuals to the aphid species *Sitobion avenae* Fabricius, and 8 individuals to *Rhopalosiphum padi* Linneaus. These three aphid species are used as hosts by the five parasitoid species found in our collections (Andrade et al., 2015). Given their low number, the 8 parasitoid specimens that emerged from *R. padi* were excluded from all data analyses. Similarly to the parasitoid guild, parasitized aphid relative abundances varied strongly from year to year and between the research regions (Table 2).

Drivers of parasitoid life-history trait variation: the mean-field approach

By using mixed models, we assessed the main driving factors of the mean traits values within the parasitoid guild. The significance of the different explanatory variables on the parasitoid life-history traits is detailed in Table 3. Figure 2 presents the mean of the life-history traits for the different parasitoid species sampled in the three regions in 2011 and 2012, respectively.

The effect of the region and the parasitoid species on the parasitoid life-history traits varied from year to year. In 2011, these two factors affected significantly the two morphometric traits (i.e. tibia length and forewing area). The non-significance of the

interaction term between these factors indicated that guild-wide interspecific trait differences were not affected by the regional factors (scenario 'IF + EF' of Fig. 1). Overall, parasitoid specimens in "Ar" had the longest tibias and the largest forewing areas and *A. rhopalosiphii* presented the shortest/smallest organs (i.e. tibia/forewing area) among all parasitoid species (Figure 2). Neither geographical variation nor interspecific variation was found in parasitoid longevity (scenario 'NV', Figure 1) and the sex-ratio in the studied guilds varied between species only (scenario 'IF', Figure 1): the *P. volucre* populations presented fewer females in the three regions.

Compared to 2011, the statistical modelling retained more significant terms in 2012. The two morphometric traits (i.e., tibia length and forewing area) still varied between regions and parasitoid species. The interaction term was also now significant, indicating that the interspecific trait differences changed with the environmental context (scenario 'IF×EF', Figure 1): interspecific variations for tibia length and forewing area were more pronounced in "Ar" (Figure 2). In 2012, the longevity of parasitoids differed between species and regions (scenario 'IF+EF', Figure 1): parasitoids lived longer in "VCG" and the *A. avenae* species presented the longest lifespan. Concerning the sex-ratio within the guild, it varied between species and these interspecific differences in sex-ratio changed according to the environmental context (scenario 'IF×EF', Figure 1): in "Ar", the *A. ervi* populations presented the lowest proportion of females while in "VCG", this sex-ratio bias was observed in *A. avenae* populations (Figure 2).

Finally, the effects of individual sex and host species on the parasitoid life-history traits were similar in both sampling years (Table 3). In all guilds sampled, parasitoid males and females presented contrasted life-history traits: male specimens had shorter tibias, larger forewing areas and lived longer than females. In 2011 and 2012, the host species affected parasitoid longevity only: parasitoids resulting from *S. avenae* presented a higher longevity

(all parasitoid species considered together; in 2011: *S. avenae*: 3.97 days \pm 0.12; *M. dirhodum*: 3.17 days \pm 0.09; in 2012: *S. avenae*: 4.71 days \pm 0.08; *M. dirhodum*: 3.88 days \pm 0.05).

External and internal filtering processes: a variance decomposition approach

The comparison of the departure of the T-statistics from randomized situations (through SES values) is plotted in Figure 3. The results are not consistent among life-history traits and years. In 2011, $T_{IC/IR}$ values significantly departed from the null model for tibia length in “Ar” and longevity in “PVS” suggesting a parasitoid phenotypic convergence in these regions for those two traits as a result of the local environmental conditions. In “PVS”, $T_{IP/IC}$ value was low compared to randomized situations for two life-history traits (tibia length and forewing area) suggesting significant morphometric divergence among coexisting species in this region. In “Ar”, two individuals belonging to a particular species displayed more similar forewing area than two individuals drawn randomly from the guild (see Fig.3). In 2012, the three traits displayed significant pattern for $T_{IC/IR}$, particularly the morphometric traits (i.e., tibia length and forewing area). This result suggests there was external filtering for these traits, possibly because of strong environmental differences between the sampled regions. Concerning the $T_{IP/IC}$ results, significant phenotypic divergence among the species of the guild was observed for the three traits: the two morphometric traits strongly diverged between parasitoid species in “Ar” while in the “PVS” guild, phenotypic divergence between parasitoid species concerned longevity only. From all the results, only two traits presented both significant $T_{IC/IR}$ and significant $T_{IP/IC}$ values: tibia length and forewing area measured on parasitoids sampled in “Ar” in 2012. This suggests that the individual morphometry within this guild was governed by both specific regional conditions and intra-guild ecological processes.

A quantification of species' phenotypic space

Considering the three quantitative life-history traits simultaneously, the species hypervolumes were constructed and represented in order to visualize phenotypic divergence within the parasitoid guilds (Figure 4). Overlap in trait hypervolumes was variable, ranging from 23% to 67.5% (Table 4). In 2011, the narrowest volume and a low degree of hypervolumes overlap between species in “PVS” confirmed phenotypic divergence within the guild in this region. In 2012, both shape and volume of the species hypervolumes in “Ar” were highly contrasted, confirming the phenotypic divergence between parasitoid species living in this region. The hypervolume overlap estimates indicate that the phenotypic space of *P. volucre* differed from those of the two dominant parasitoid species of the guild in this region.

Discussion

We examined the patterns of life-history trait variation within a guild of insect parasitoids across three different regions in relation to several ecological factors and hypothesized whether such phenotypic patterns reflect adaptation to local conditions and species coexistence processes. In doing so, our results showed that (1) patterns of life-history trait variation across regions suggest a directional environmental filtering and (2) patterns of phenotypic variation within regions emphasize how local coexistence could modulate the expression of life-history trait through niche differentiation processes. Interestingly, our study indicates that the phenotypic variation pattern in a given region may change with time and that bottom-up effects within trophic webs can mediate life-history traits at a given upper trophic level.

External filtering and parasitoid life-history traits

In the parasitoid guild, most of the life-history traits differed between sampled regions. In 2011 and 2012, parasitoids sampled in the northernmost region (i.e. “Ar”) were larger and had broader wings, whereas longevity under starvation was longer in the individuals sampled in the southernmost region in 2012 (i.e. “VCG”). The significant reduction of variance for most of the traits (see $T_{IC/IR}$ values) highlighted a phenotypic convergence in each region suggesting that life-history trait variation is a product of the guild response to regional environmental conditions as a whole. The interregional trait differences may be a result of the different climate conditions linked to the contrasted latitude of the three sampled regions, the difference in agricultural landscapes and practices, the differences in regional aphid host quality/abundance/diversity or a combination of those environmental factors. The observed variation in sex-ratio within the guild should also be related to the regional environmental conditions. In arrhenotokous parasitoids (i.e., species in which unfertilized eggs produce haploid males and fertilized eggs produce diploid females), there can be a high occurrence of sib-mating, especially when hosts are patchily distributed, which is often the case in aphids (Völkl, Mackauer, Pell & Brodeur, 2007). As a result of this type of mating and to consequent local mate competition, most theoretical models on optimal sex allocation patterns in parasitoids predict female-biased sex-ratios (Hamilton, 1967; Charnov, Los-den Hartogh, Jones & van den Assem, 1981; Werren, 1983; West, 2009), but sex-ratios often decrease as a function of parasitoid and host densities (Meunier & Bernstein, 2002). Parasitoid density has been previously reported to increase with landscape complexity (i.e., percentage of arable land) (Thies, Roschewitz & Tschardtke, 2005). Since “PVS” is a region mostly dedicated to crop production and presenting low parasitoid abundances (Andrade et al., 2015), this could explain why the guild sex-ratio was more female-biased in this site.

Internal filtering and parasitoid life-history traits

Our results showed interspecific contrasts in parasitoid life-history traits, indicating differentiation in niche spaces. Globally, *A. avenae* and *A. ervi* presented the highest values for tibia length, forewing area, and longevity. There were also interspecific differences in sex-ratio, which could be linked to contrasting population densities and local mate competition (Charnov, 1982; Godfray, 1994). The degree of niche differentiation between species varied across the environmental context: phenotypic divergence was mostly observed in “Ar” (2012) and “PVS” (2011) regions whereas phenotypic convergence has been found in “VCG”. In the latter regional environmental context, interspecific trait differences were low and the multidimensional phenotypic spaces overlapped.

Given that interspecific competition for limiting resources may generate divergence in life-history traits among species, niche differentiation would be more pronounced in habitats with highly diverse and abundant guilds. Interestingly, we found no correlation between the degree of trait divergence and species abundance in the different regions. Consequently, using a trait-based analysis to predict a guild composition and diversity would be challenging. Recent researches show, however, that the ability to predict community composition increases rapidly with the number of phenotypic traits included in the model (Laughlin, Joshi, van Bodegom, Bastow & Fulé, 2012; Laughlin, 2014).

Life-history traits in food webs

We asked whether/how host species control parasitoid life-history traits in nature (bottom-up effects), taking into account that both host absolute and relative abundances are affected by the environmental context (Thies et al., 2005; Aqueel & Leather, 2011; Andrade et al., 2015). In our study, host species influenced parasitoid longevity but not their body size, forewing area nor sex allocation. In relation to longevity, it is possible that the energy reserve accumulated and/or the energy consumption rate would differ between parasitoids emerging

from the two cereal aphid host species, *S. avenae* and *M. dirhodum*. The interspecific differences in energy consumption rates may be linked to differences in metabolic rates of adult parasitoids (Le Lann et al., 2011a): both *A. avenae* and *A. rhopalosiphi* display contrasted metabolic rates and lifespans but accumulate a similar amount of energy resources when exploiting *S. avenae* (Le Lann, Visser, van Baaren, van Alphen & Ellers, 2012).

Through these effects on parasitoid traits, a host species could modulate both the shape and volume of the phenotypic space of a parasitoid species and hence the overlap between species trait spaces. The phenotypic space packing would then depend on the host selection behavioural strategies in each species of the guild. Some studies conducted on the selection of host species by aphid parasitoids have suggested some host preferences (Andrade et al., 2013, Eoche-Bosy, Outreman, Andrade, Krespi & van Baaren, 2016). So, the hypervolumes estimated here depended on the host species used by the parasitoids collected and this behavioural effect on niche differentiation must be included in the set of features driving phenotypic evolution.

In conclusion, knowledge of the divergence in host/prey traits among sites, the abundance and distribution of hosts/prey across the landscape, as well as the population density and parasitism/predation rate within sites, are all important for the correct interpretation of trait variation patterns.

Differential response of the life-history traits

Ecological filters may affect distinct traits differently. In the fruit fly parasitoid *Leptopilina heterotoma* (Hymenoptera: Figitidae), no differences were found between populations from four sites along a 300 km gradient for several fitness traits, including longevity under starvation conditions (Vuarin, Allemand, Moiroux, van Baaren & Gilbert, 2012), but there were interregional intraspecific differences in wing load, a morphometric trait linked to dispersal (Gilchrist & Huey, 2004). Similar patterns of trait responses were

found here: the studied life-history traits resulted from different evolutionary patterns, and the two morphometric traits (i.e., tibia length and forewing area) were generally governed by more complex evolutionary scenarios than for longevity (Figures 2, 3 and 4). Tibia length is a good estimate of specimen's fitness: in females, tibia length is positively correlated with mating preference, fecundity, reproductive longevity and progeny emergence (e.g., Collins & Dixon, 1986; Ellers et al., 1998); in males, there is also some evidence that large males have greater mating success (Godfray, 1994). The forewing area was used as a proxy for dispersal ability. In parasitoids, dispersal ability strongly influences the host searching performance of the female and mating success of the male individuals (Zepeda et al., 2015). Our results underlined that as phenotypic differences between guild members may not express themselves equally across all traits, it is important to study multiple traits.

Temporal variation in phenotypic variation patterns

Our findings show that analysing the sources of phenotypic variation over time is crucial for our understanding of the ecological and evolutionary processes shaping phenotypic diversification within the communities. In our study, life-history traits presented contrasting variation patterns according to the sampling year, suggesting variations in evolutionary dynamics of parasitoid species from year to year. Actually, we consider our study as a 'proof of concept' of the importance of temporal monitoring in trait-based community ecology. The observed temporal variation can be interpreted as the outcome of the change in the diversity and/or in the strength of internal and external filters. For instance, we noted a variation in guild diversity between the two sampling years (i.e. more species within the guild in 2012) and the internal filters would be harsh when a guild is more diverse. Also, this temporal variation could be a result of differences in climate conditions between years since climate conditions can alter parasitoid life-history traits directly or indirectly. Emergence rate, development time, growth rate, fecundity, metabolic rate and longevity in aphid parasitoids

vary significantly according to temperature variations in the range of 10 to 25 degrees (Le Lann, Wardziak, van Baaren & van Alphen, 2011b). By altering aphid populations (Dedryver et al., 2008), climate conditions can modify the parasitoid host resource pool qualitatively and quantitatively. In addition, multiparasitism and hyperparasitism are ecological factors that can partly explain trait differentiation, although these factors tend to increase in importance as aphid populations' crash towards the summer season (Traugott et al., 2008). The sources of temporal phenotypic variation are obviously numerous and further work is needed to decipher them.

Mechanisms of phenotypic evolution

Two non-exclusive mechanisms operating at the level of the individual allow the adaptation of a population to the local environment: natural selection and phenotypic plasticity. Divergent selection between sites will result in local adaptation through genetic differentiation (Kawecki & Ebert, 2004). Genotypes subjected to local selection will exhibit higher fitness in their own environment compared with those from other environments and the trait differences among populations will be genetic in origin. Phenotypic plasticity is defined as the ability of a single genotype to produce multiple phenotypes (morphological, physiological and behavioural) in response to varied environmental conditions, allowing organisms to adapt to the specific conditions in their local environment (Schlichting 1986; Davidson et al. 2011). Selection on genetic variability and phenotypic plasticity can be complementary mechanisms adjusting organisms to local conditions (Grenier, Barre & Litrico, 2016). In parasitoids, some studies showed how life-history traits are plastic (e.g., Godfray, 1994). There is however a shortage of studies testing the role of phenotypic plasticity in the field. Here, we selected three sites presenting contrasted environmental conditions and far enough apart so that no gene flow was expected and local selective pressure varied spatially. This low gene flow among populations may be a prerequisite for

local adaptation but it does not necessarily indicate that the phenotypic differences among populations are genetic-based. For example, some differences could be simply be due to differences in host quality among the different regions (i.e. trophic-mediated phenotypes). Similarly, deviations among species within sites may well be due to different plastic responses (i.e., different reaction norms) or possibly to divergent evolutionary responses to the various selection pressures operating in the local environment rather than to niche divergence (e.g., MacArthur & Levins, 1967).

To test whether there is a genetic component to differences in populations, further investigations should therefore be addressed in regards to the reasons behind this trait variation. Identifying the evolutionary mechanisms would require culturing specimens in different environments to test for different phenotypic outcomes (reciprocal transplant experiments).

Conclusion

By combining complementary analytical approaches to regional and local life-history trait variation, our study highlights evidence that phenotypic adaptation within communities is complex and community-specific: evolutionary patterns of life history traits could vary dramatically among communities. The application of such trait-based studies to insect parasitoids has the potential to provide further insight on how agricultural landscapes contribute to differential diversification among evolutionary lineages. As insect parasitoids are the dominant parasites of aphids on crops worldwide, there is a growing concern about the functioning of their guilds and we have shown that the inclusion of life-history traits in determining parasitoid responses to agricultural landscapes may be important for future management decisions.

Acknowledgments

This study was funded by the French National Research Agency (ANR) Landscaphid program (ANR-09-STRA-05) and by Région Bretagne and was supported by the LTER France Zone Atelier Armorique. CV was supported by the European Research Council (ERC) Starting Grant Project ‘Ecophysiological and biophysical constraints on domestication in crop plants’ (Grant ERC-StG-2014-639706-CONSTRAINTS). All field and laboratory work conducted in this study complies with French legal requirements. We are grateful to V. Briand, S. Chicher, H. Deraison, D. Eoche-Bosy, C. Gérardin, M. Granger, V. Guyot, H. Mahé, L. Martin, C. Nicolai, C. Puech, M. El-Souki and J. Yvernault for their technical support. Finally, two anonymous referees are also acknowledged for their perceptive and helpful comments on an earlier draft. The authors declare no conflict of interest.

Data availability

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.85s4m> (Outreman *et al*, 2017)

Author contribution statement

Y.O, T.O.A., L.K. and J.v.B conceived the study and Y.O., L.K. and J.v.B. supervised it. T.O.A. performed the insect sampling and T.O.A. and P.L. conducted traits measurements. Y.O., T.O.A. and C.V. analyzed the data. Y.O. led the writing of the manuscript and all authors contributed critically to the drafts and gave final approval for publication.

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Table 1. Description of the explanatory variables tested for their effect on the life-history traits of different parasitoid species composing a guild. (FF): fixed factor; (RF): random factor; (C): covariate. Checkmark: explanatory variable considered in the statistical modelling.

<i>Explanatory variables</i>	<i>Dependent variables</i>			
	Tibia length	Forewing area	Longevity	Sex-ratio
Region (FF): the geographical site of a parasitoid individual	✓	✓	✓	✓
Parasitoid species(FF): the species of a parasitoid individual	✓	✓	✓	✓
Region:Parasitoid species	✓	✓	✓	✓
Aphid host species(FF)	✓	✓	✓	✓
Parasitoid sex(FF)	✓	✓	✓	
Tibia length (C)		✓		
Field (RF): the field of a parasitoid individual	✓	✓	✓	✓

Table 2: Total number parasitoids and their aphid hosts sampled in 2011 and 2012 in three research regions (Armorique: “Ar”, Plaine et Val de Sèvre: “PVS”, Vallées et Coteaux de Gascogne: “VCG”). ^a Specimens considered in the mixed models (as we tested the interaction term between the parasitoid species and the research sites, we included in the analyses any species sampled in the three research sites); ^b Specimens considered in the $T_{IC/IR}$ and $T_{IP/IC}$ values estimate (any species presenting a sampling size greater than 5 individuals for the quality of the intra-species variance estimates); ^c Specimens considered in the hypervolume approach (parasitoid individuals on which the three quantitative life-history traits were measured).

	2011			2012		
<i>Parasitoid species</i>	Ar	PVS	VCG	Ar	PVS	VCG
<i>Aphidius avenae</i>	64 ^{b,c}	0	0	465 ^{a,b,c}	11 ^{a,b,c}	7 ^{a,b}
<i>Aphidius ervi</i>	67 ^{a,b,c}	12 ^{a,b,c}	9 ^{a,b,c}	92 ^{a,b,c}	33 ^{a,b,c}	143 ^{a,b,c}
<i>Aphidius rhopalosiphi</i>	251 ^{a,b,c}	15 ^{a,b,c}	36 ^{a,b,c}	53 ^{a,b,c}	107 ^{a,b,c}	268 ^{a,b,c}
<i>Ephedrus plagiator</i>	0	3	23 ^{b,c}	11 ^{b,c}	3	5
<i>Praon volucre</i>	31 ^{a,b,c}	48 ^{a,b,c}	6 ^{a,b}	12 ^{a,b,c}	112 ^{a,b,c}	18 ^{a,b,c}
Total parasitoids	413	78	74	633	266	441
<i>Aphid host species</i>						
<i>Metopolophium dirhodum</i>	148	6	6	549	220	38
<i>Rhopalosiphum padi</i>	0	3	2	1	1	1
<i>Sitobion avenae</i>	183	51	57	73	34	392
Total aphids	331	60	65	623	255	431

Table 3: Generalized linear mixed models on the effect of different explanatory variables on the life-history traits of different parasitoid species composing a guild.

	2011				2012			
	Dependent variables				Dependent variables			
	Tibia length	Forewing area	Longevity	Sex-ratio	Tibia length	Forewing area	Longevity	Sex-ratio
Explanatory variables	χ^2 d f p	χ^2 d f p	χ^2 d f p	χ^2 d f p	χ^2 d f p	χ^2 d f p	χ^2 d f p	χ^2 d f p
Region	28.32 <0.001	<0.05	0.52 0.75	4.22 0.1	<0.05	12.92 <0.005	12.92 <0.005	4.22 0.1
Parasitoid species	46.62 <0.001	13.62 <0.005	4.62 0.098	6.52 <0.05	61.63 <0.001	14.33 <0.005	13.43 <0.005	36.53 <0.001
Region:Parasitoid species	4.14 0.399	0.432	5.34 0.58	5.14 0.76	12.86 0.05	15.96 0.05	6.96 0.33	23.96 <0.005
Aphid host species	2.61 0.102	0.163	18.81 <0.001	0.11 0.67	0.631 0.31	0.51 0.54	10.01 <0.005	2.41 0.22
Parasitoid sex	32.91 <0.001	16.21 <0.001	4.11 <0.05	- - -	16.21 <0.001	112.91 <0.001	25.91 <0.001	- - -
Tibia length	- - -	22.92 <0.001	- - -	- - -	- - -	141.25 <0.001	- - -	- - -
Field	0.00029	0.000016	0.000016		0.00045	0.00024	0.056	

(variance value)								
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Table 4: Hypervolume overlap between each pair of different species within a parasitoid guild sampled in three regions (“Ar”, “PVS”, “VCG”) in 2011 and 2012.

2011

"Ar"

	<i>A. ervi</i>	<i>A. rhopalosiphi</i>	<i>P. volucre</i>
<i>A. avenae</i>	0.478	0.483	0.675
<i>A. ervi</i>		0.538	0.566
<i>A. rhopalosiphi</i>			0.581
Overlap mean \pm s.d.	0.551 \pm 0.08		

"PVS"

	<i>A. rhopalosiphi</i>	<i>P. volucre</i>
<i>A. ervi</i>	0.347	0.362
<i>A. rhopalosiphi</i>		0.312
Overlap mean \pm s.d.	0.340 \pm 0.02	

"VCG"

	<i>A. rhopalosiphi</i>	<i>E. plagiator</i>
<i>A. ervi</i>	0.484	0.369
<i>A. rhopalosiph</i>		0.473
Overlap mean \pm s.d.	0.442 \pm 0.06	

2012

"Ar"

	<i>A. ervi</i>	<i>A. rhopalosiphi</i>	<i>P. volucre</i>
<i>A. avenae</i>	0.605	0.494	0.230
<i>A. ervi</i>		0.516	0.286
<i>A. rhopalosiphi</i>			0.435
Overlap mean \pm s.d.	0.428 \pm 0.14		

"PVS"

	<i>A. ervi</i>	<i>A. rhopalosiphi</i>	<i>P. volucre</i>
<i>A. avenae</i>	0.467	0.424	0.429
<i>A. ervi</i>		0.572	0.643
<i>A. rhopalosiphi</i>			0.692
Overlap mean \pm s.d.	0.538 \pm 0.14		

"VCG"

	<i>A. rhopalosiphi</i>	<i>P. volucre</i>
<i>A. ervi</i>	0.576	0.426
<i>A. rhopalosiphi</i>		0.391
Overlap mean \pm s.d.	0.463 \pm 0.09	

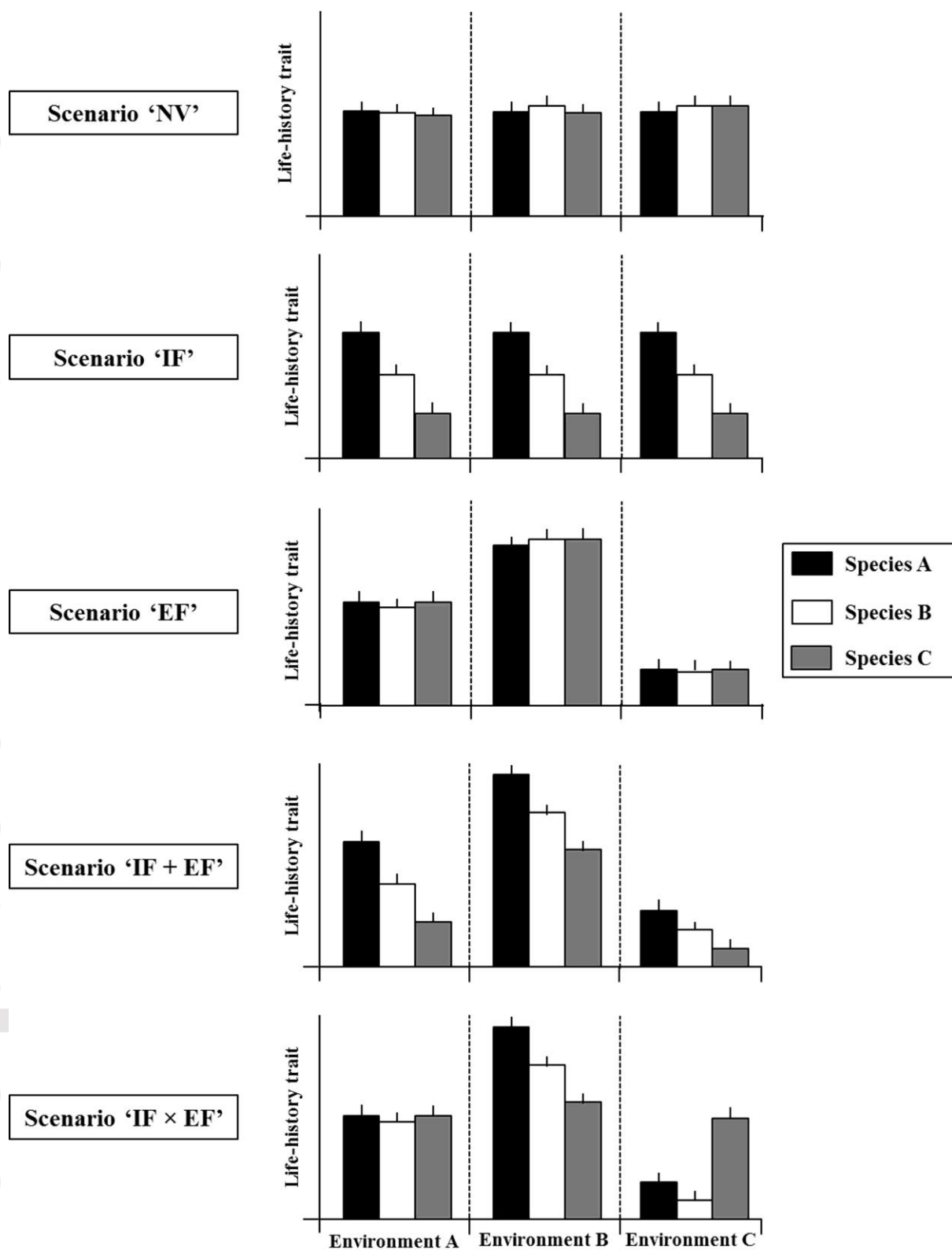
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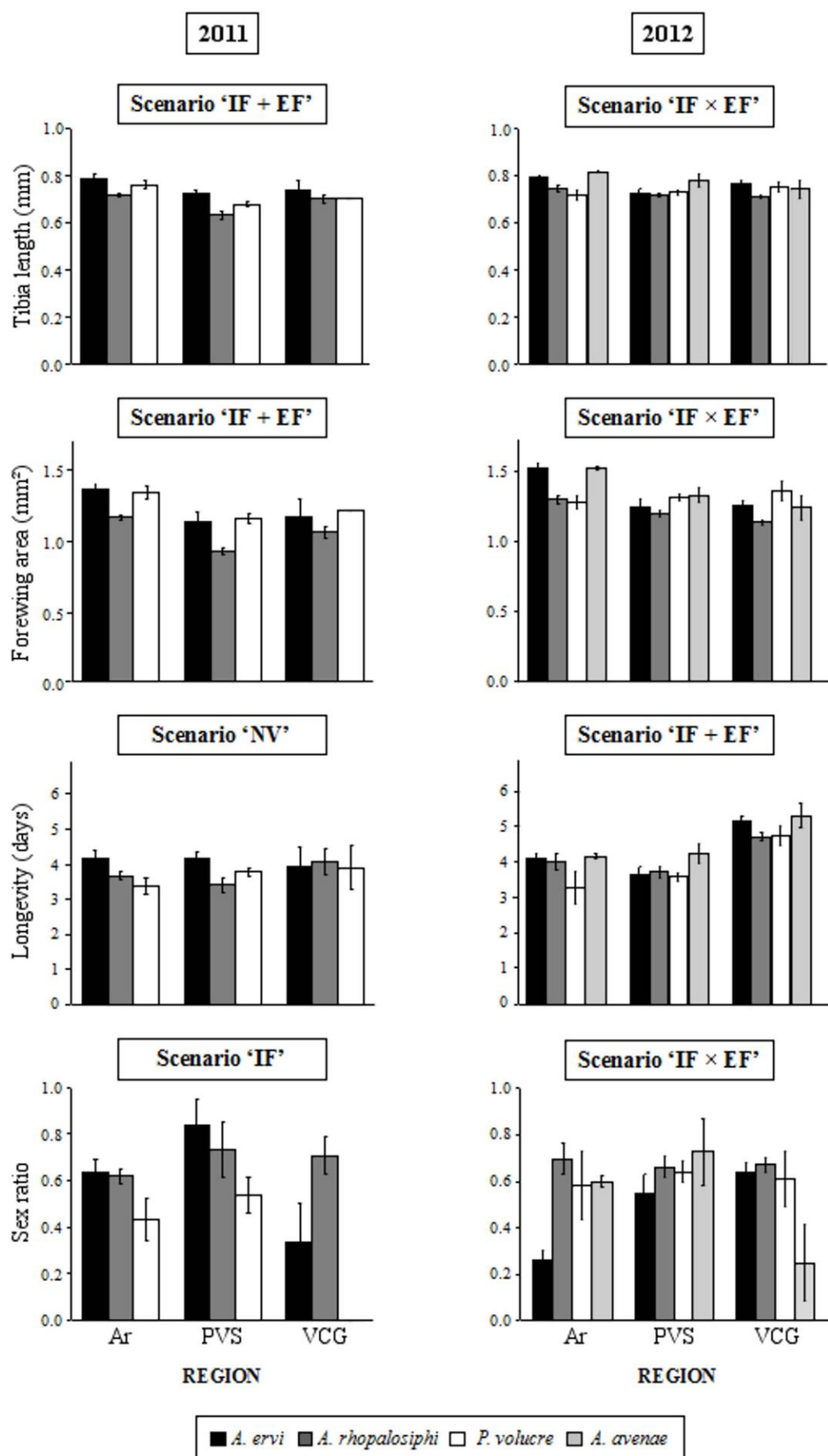
Figure 1. The theoretical framework of the present study: the different patterns of life-history trait variation within a parasitoid guild. **Scenario ‘NV’:** No life-history trait variation between species and regions; **Scenario ‘IF’:** Internal filters (IF) induces trait divergence between the different species of the guild; within each species, the environmental context does not influence the mean trait value; **Scenario ‘EF’:** External filters (EF) induce convergence in the trait between the different species of the guild; for all species, the mean trait value varies similarly according to the environmental contexts; **Scenario ‘IF + EF’:** Internal filters induces divergence in the trait between the different species of the guild; for all species, the environmental context influences similarly the mean value of the trait; **Scenario ‘IF × EF’:** The contribution of both internal and external filters in the variation of life-history trait values depends on the environmental context.

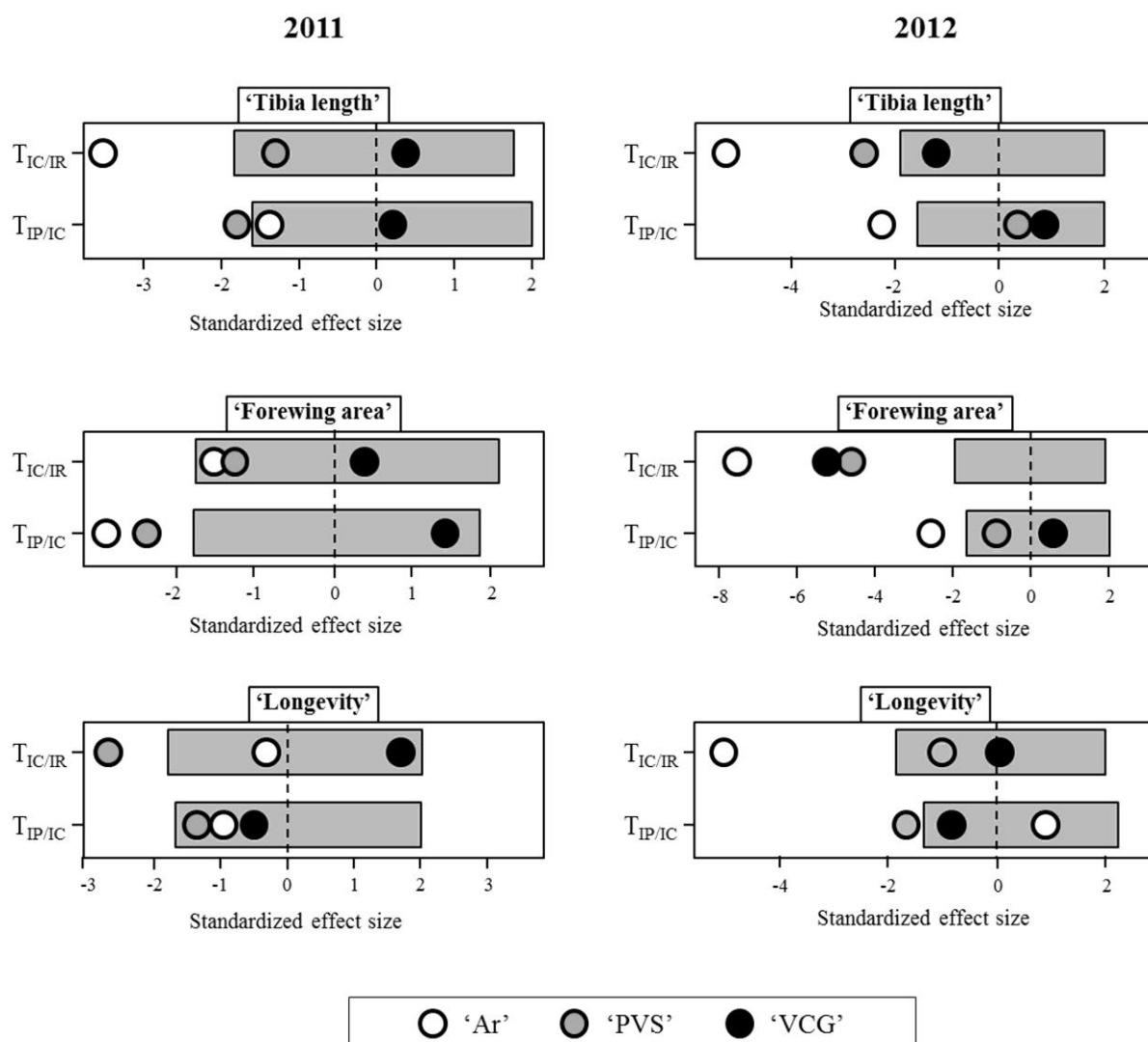
Figure 2. Life-history traits (mean value \pm standard error) of different species within a parasitoid guild sampled in three regions (“Ar”, “PVS”, “VCG”) in 2011 (left panel) and 2012 (right panel). The scenario indicated at the top of each graph refers to the evolutionary scenarios described on Figure 1 and is suggested from the statistical analysis described in the Table 3.

Figure 3. Standardized effect size (SES) of $T_{IC/IR}$ and $T_{IP/IC}$ values for the life-history traits (tibia length, forewing area and longevity) of different species within a parasitoid guild. For a given trait, a dot represents the $T_{IC/IR}$ or $T_{IP/IC}$ SES value for the parasitoid guild in a given region. When a SES value presents a negative value and is not embedded within the grey coloured bar, the value significantly departs from the null distribution.

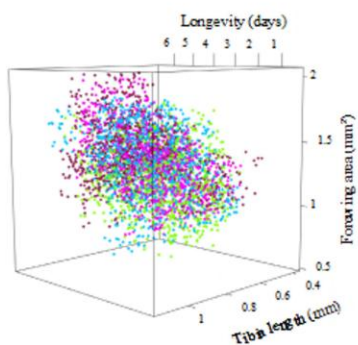
Figure 4. Hypervolumes considering the life-history traits (tibia length, forewing area and longevity) of different species within a parasitoid guild sampled in three regions (“Ar”, “PVS”, “VCG”) in 2011 (left panel) and 2012 (right panel).



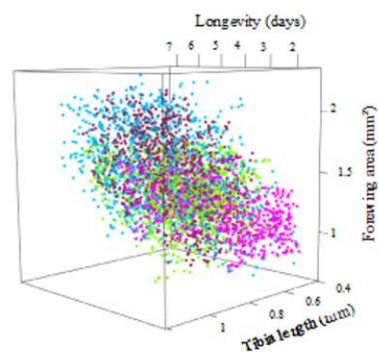




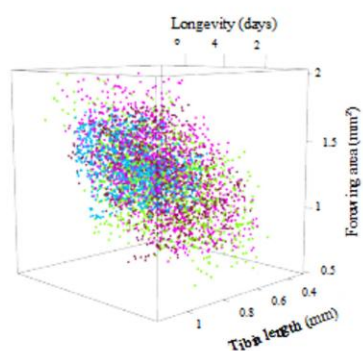
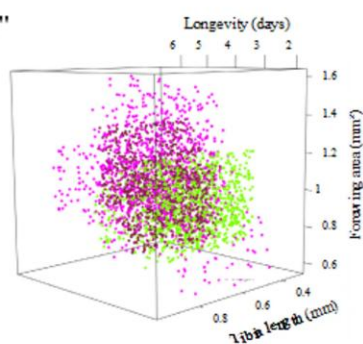
(a) "Ar"



2012



(b) "PVS"



(c) "VCG"

