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Life history traits, but not phylogeny, drive compositional patterns in a butterfly metacommunity

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Abstract. Community assembly is a combination of ecological, evolutionary, and stochastic processes. Separating out the abiotic and biotic processes (such as limiting similarity or environmental filtering) from stochastic processes is central to developing a cogent approach for understanding patterns in ecological community structure and organization. Using butterfly communities in a fragmented landscape, we tested the hypothesis that local environmental filtering drives character convergences in traits of species belonging to different clades. We found that, while many traits were determined both by phylogeny and environment, trait convergence within the phylogeny was extensive and eroded the phylogenetic structure associated with habitat use. Traits associated with habitat use are shown to be only moderately phylogenetically conserved in chalk grassland butterfly assemblages, and further analysis revealed that traits associated with environmental filtering may be highly labile rather than phylogenetically conserved. In general, a significant phylogenetic signal is therefore neither sufficient to demonstrate a lack of trait convergence, nor to determine whether communities are likely to be phylogenetically structured. We conclude that explicit trait-based approaches should be used in preference to the more indirect approach based on phylogenetic conservatism for understanding metacommunity assembly processes.

Key words: assembly rules; butterflies; community assembly; community phylogenetics; European chalk grassland; fragmentation; functional diversity; habitat filters; phylogenetic diversity; phylogenetic signal.

INTRODUCTION

Metacommunity theory provides a conceptual foundation for elucidating and analyzing how patterns in local species composition are linked to the broader regional biotas in which they exist. This theory incorporates, in various different ways, how ecological processes such as limiting similarity, species turnover, and dispersal can maintain spatially extended communities (Holyoak et al. 2005). An important extension incorporates the role of evolutionary processes (Urban et al. 2008) by using phylogenies and functional traits (Webb et al. 2002, Ricklefs 2006, Westoby 2006) to understand biodiversity patterns in community and metacommunity assembly. Such approaches have highlighted two important processes that affect phylogenetic patterns and trait distributions in local communities: limiting similarity and environmental filtering (Webb et al. 2002).

Limiting similarity assumes that biotic forces like competition, mutualism, or facilitation tend to prevent similar species from coexisting (but see, e.g., Bonsall et al. 2004). In contrast, environmental filtering tends to favor the co-occurrence of species with similar traits. Both biotic interactions and environmental filtering effects are likely to act together to varying degrees as they facilitate coexistence via the two general mechanisms of stabilizing dynamics (limiting similarity) and fitness equalization (filtering) as developed in modern niche theory (Chesson 2000, Chase and Leibold 2003).

(Meta)community phylogenetics focuses on the degree of phylogenetic niche conservatism and hypothesizes that phylogenetic relatedness can serve as a surrogate for key life history traits without having to identify them per se (Losos 2008, Wiens et al. 2010). If generally true, then phylogeny could directly provide

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useful insights about (meta)community organization. However, the use of phylogenetic methods to evaluate species assemblage patterns depends on how trait evolution is manifest in the phylogeny. Traits that influence either environmental filtering or limiting similarity may or may not be phylogenetically conserved (Webb et al. 2002) and their evolution may or may not be associated with differential habitat use. Identifying specific traits related to either environmental filtering or limiting similarity can provide important insights into their ability to change and elucidate how strong phylogenetic structuring can occur in metacommunities. Indeed, although congruent functional and phylogenetic patterns due to phylogenetic conservatism have sometimes been observed (e.g., Willis et al. 2010), phylogenetic randomness has also been found in natural communities. For instance, in a long-term succession in arable to grassland ecosystems, Purschke et al. (2013) showed that, despite explicit changes in levels of plant (alpha) diversity leading to changes in functional turnover, phylogenetic diversity or phylogentic turnover did not contribute to the underlying plant assembly processes.

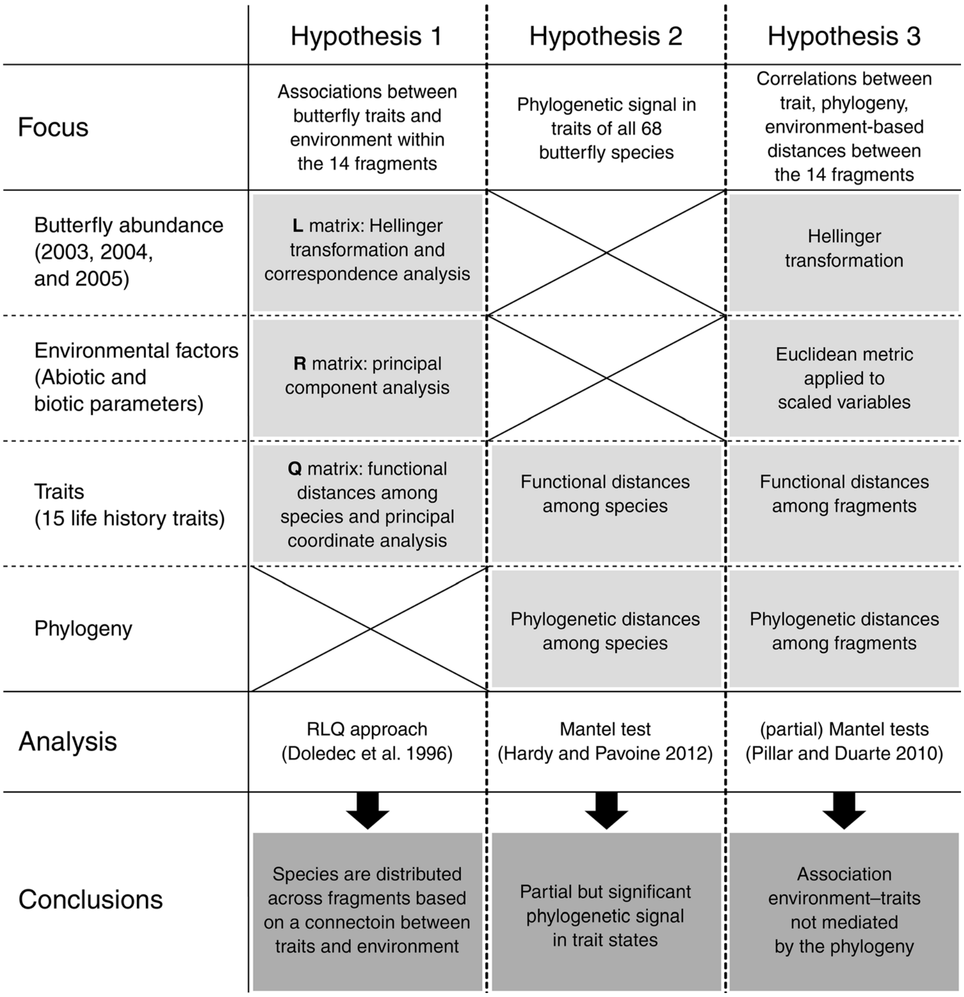
Differences between phylogenetic and functional patterns are more likely to be due to convergent trait evolution. While traits may have substantial degrees of phylogenetic signals (e.g., Blomberg et al. 2003), this need not be so for life history traits that influence environmental filtering or those that influence ecological interactions and hence limiting similarity (e.g., traits that affect fitness such as survival, reproduction, and dispersal). Such traits may be unusually labile in comparison to other traits that are less important in structuring ecological communities or driving ecological processes associated with limiting similarity (Pearman et al. 2008) and these traits may respond to either local environmental conditions (Gomulkiewicz and Holt 1995) or to the presence or abundance of other species (Thompson 2005). As such their evolution may be extremely rapid (Ellner et al. 2011).

In this study, we focus on the association between environmental filtering, traits, and evolutionary history in European butterfly communities of the Calestienne landscape in southern Belgium. Butterflies are a well-studied group in terms of both traits and their phylogenetic relationships (e.g., Bink 1992, Heikkilä et al. 2012), are of broad interest in understanding fundamental ecological processes (e.g., Dennis 2010), and are of high conservation interest due to habitat loss and fragmentation (Settele and Kühn 2009, Thomas et al. 2009). Despite all of this, they have rarely been studied in the context of community assembly rules. Understanding how communities organize in fragmented landscapes is of particular interest in the conservation of butterfly biodiversity. To explore the impact of environmental filtering and disturbance on butterfly communities, we contrast an analysis that is strictly focused on traits with one that explicitly examines evolutionary history to identify whether both approaches give similar results. Under the assumption of ecological niche conservatism, we expect that these effects would be similar, whereas they would differ if ecological niche evolution is labile and associated with habitat use. We tested three hypotheses about trait evolution in relation to environmental filtering (Fig. 1). Initially, we asked whether any similarity in trait states among co-occurring species is due to environmental filters (Hypothesis 1). Next, we explored if traits involved in environmental filtering have a phylogenetic signal (Hypothesis 2). We then examined if the environmental filters act on species traits independently of the phylogeny (Hypothesis 3). Our results show that, in general, species are distributed in the landscape according to an association between their traits and the environment. Nevertheless, this association results in a weak phylogenetic pattern (species that coexist in an environment are not particularly related to each other) involving independent convergence among species that occur in similar environments. This convergence thus weakens and erodes the signal from any possible overall phylogenetic effect.

MATERIALS AND METHODS

The Calestienne landscape in southern Belgium is characterized by chalk grasslands that are now reduced to small fragments (Appendix A). The area was probably naturally fragmented following succession to the climax forests assemblages after the last glaciation (e.g., through tree falls, cave-ins, and/or fires). European chalk grasslands are seminatural habitats, created by agro-pastoral activities after humans felled the primary forests in prehistoric times, ~7000 years before present (BP; WallisDeVries et al. 2002, Polus et al. 2007). Deforestation increased with the intensity of human activities. Since the Bronze Age, grazing by livestock, and since the Middle Ages, occasional mowing, prevented these grasslands from spontaneous afforestation (WallisDeVries et al. 2002). However, changes in land use (intensification of agriculture and afforestation) and major transformations in agro-pastoral methods (abandonment of grazing and mowing) have led to considerable fragmentation in chalk grasslands. From 1905 to 2005, the proportion of chalk grasslands decreased from ~15% (7.79 ha) to 0.7% (0.82 ha) (Polus et al. 2007). As a result, the butterfly community composition changed during the 20th century, with the disappearance of species either requiring large areas, or with specialized lifestyles (Polus et al. 2007).

We selected a total of 14 grassland fragments located on different hills of the Calestienne (see Appendix A). The area of the fragments varied from 3885 m^2 to 81 140 m^2 (mean of 24 360 m^2) with a perimeter varying from 384 m to 1712 m (mean of 886 m). These habitat fragments are close enough to allow butterfly dispersal among them (Vandewoestijne et al. 2008). Butterflies were identified to species along standardized transects on each fragment once every two weeks from April to September in 2003, 2004, and 2005, in optimal weather conditions (sunny days with no or light wind). A total of



	Hypothesis 1	Hypothesis 2	Hypothesis 3
Focus	Associations between butterfly traits and environment within the 14 fragments	Phylogenetic signal in traits of all 68 butterfly species	Correlations between trait, phylogeny, environment-based distances between the 14 fragments
Butterfly abundance (2003, 2004, and 2005)	**L** matrix: Hellinger transformation and correspondence analysis	×	Hellinger transformation
Environmental factors (Abiotic and biotic parameters)	**R** matrix: principal component analysis	×	Euclidean metric applied to scaled variables
Traits (15 life history traits)	**Q** matrix: functional distances among species and principal coordinate analysis	Functional distances among species	Functional distances among fragments
Phylogeny	×	Phylogenetic distances among species	Phylogenetic distances among fragments
Analysis	RLQ approach (Doledec et al. 1996)	Mantel test (Hardy and Pavoine 2012)	(partial) Mantel tests (Pillar and Duarte 2010)
Conclusions	Species are distributed across fragments based on a connectoin between traits and environment	Partial but significant phylogenetic signal in trait states	Association environment–traits not mediated by the phylogeny

FIG. 1. Hypotheses on testing phylogenetic effects on metacommunity structure. For each hypothesis tested (see *Introduction*), we summarize the factors studied, indicating the scale of the study (line designated "focus"), the data used (four types of data: butterfly abundance, environment, butterfly traits, butterfly phylogeny) and their potential transformation, the main analysis, and the main conclusion. A crossed-out cell indicates that the associated type of data was not used for the test of the hypothesis.

68 species were observed with a minimum of 32 species within a fragment, a maximum of 51 species, and a mean of 43 species (see Appendix B for a list of the species).

The matrix surrounding the fragments is composed of crops and forests. Only a few butterfly species (at very low densities) were occasionally observed in crops during our surveys. This is not surprising given the absence of suitable nectar resources in such areas. A few specialist species of forested areas and clearings may occur in the matrix, but these species were present in the forested borders of the fragments too, and were therefore integrated into the analysis. The matrix community is thus very poor for supporting butterflies, leading to highly restricted species overlap with the fragment communities.

Abundance data

Repeated surveys of these grasslands from year to year showed weak or no species temporal turnover, apart from the occurrence of vagrant species under particularly hot and dry conditions. However, given the high temporal variability in the abundance of the butterfly species (particularly observed with the hot 2003 summer that increased the abundance of most species), we used a weighed mean of the abundances across years. If n_{ijk} is the abundance of species i in grassland fragment j in year k and $n_{\cdot\cdot k} = \sum_{i,j} n_{ijk}$ the total number of individuals collected during the year k, then the index of abundance for species i in grassland fragment j is

$$N_{ij} = 1/3 \sum_{k=1}^{3} n_{ijk}/n_{\cdot\cdot k}.$$

Species abundances within local communities (N_{ij}) were then square-root transformed (Hellinger transformation; Rao 1995) to reduce undue bias due to the effects of very widespread and abundant species (such as *Maniola jurtina*, *Clossiana dia*, *Lysandra coridon*, and *Melanargia galathea*) (Appendix C).

Traits and phylogeny

Trait data for 15 life history characteristics were collated from Bink (1992): Beside body size, these include traits associated with (1) demographic strategies (potential fecundity, adult flight period [a proxy for adult survival]), (2) how demographic strategies are organized in time (larval growth rate, generation number, overwintering stage, female maturation, capital/income breeder), (3) how demographic strategies are organized in space (mobility), (4) adult behavior (male mate-searching behavior, female oviposition behavior), and (5) specialization (developmental flexibility, thermal tolerance of larvae, larval trophic group). This array of traits allowed us to capture many aspects of the different lifestyles of butterfly species (see Appendix C for a detailed description of these traits).

We constructed a molecular phylogenetic tree for the 68 species observed in our case study using 10 genes (for a total of 8646 bp with gaps): cytochrome oxidase subunit 1 (*CO1*), NADH dehydrogenase 1 (*ND1*) and 5 (*ND5*), elongation factor-1 alpha (*EF-1α*), *wingless* (a gene involved in wing pattern formation), ribosomal protein *S5* (*RPS5*), malate dehydrogenase NAD(P)-binding (*MDH*), glyceraldehyde-3-phosphate dehydrogenase (*GAPDH*), isocitrate dehydrogenase (IDH), and *CAD* gene. Sequences were aligned using MAFFT (Katoh and Toh 2008). We obtained maximum likelihood trees using RAxML (Stamatakis 2006) with integrated bootstrapped nodal values (using 1000 bootstraps). Relative divergence times were estimated using PATHd8 (Britton et al. 2007). The algorithms for sequence alignments, tree reconstructions, and relative divergence times were implemented in phyloGenerator (Pearse and Purvis 2013). A detailed description of the construction of the phylogeny is provided in Appendix D. We present the results obtained using the 10 genes and branch lengths expressed as relative divergence time. We found similar results with other estimations of both tree topology and branch length estimates (Appendix D).

Environmental data

Each grassland fragment was described by a series of both abiotic and biotic factors. Abiotic variables were the average altitude, the log-transformed slope (measured as difference in altitude), the closest distance to roads, the log-transformed area, the connectivity, and the fragment edge length (see Appendix C for details). Biotic variables were defined as the relative abundance of characteristic plant species associated with four main vegetation types (defined in the EUNIS classification of European habitat types; *available online*).[9] These were *Alysso alyssoides–Sedion albi*/rock debris swards (code EUNIS = E1.11), *Xerobrometum* (formations on superficial, rocky soil with flowering dicots; code EUNIS = E1.27), *Mesobrometum* (formations on deeper, humic soil with a majority of monocots; code EUNIS = E1.28), and forest habitats (combined codes EUNIS = E5.21, E5.22, and G1). Several vegetation samples were taken in each grassland fragment. In each sample, we calculated the relative abundance of each of the vegetation types as the sum of the abundance of all indicator species associated with a vegetation type divided by total abundance of all observed plants. The relative abundances of the vegetation types were then averaged across samples per fragment.

Statistical analyses

The statistical analyses were organized around our three main hypotheses (summarized in Fig. 1). Details of the analysis are given in Appendix C.

Hypothesis 1: Species are distributed across grassland fragments according to the association between their traits and the environment.—To analyze the association between environmental characteristics and species traits, we used an ordination approach (the RLQ method; Dolédec et al. 1996). The RLQ approach combines (1) the abiotic and biotic variables describing the grassland fragments (matrix **R** analyzed via principal component analysis), (2) butterfly species abundances within grassland fragments (matrix **L** analyzed by a correspondence analysis), and (3) trait-based distances among species (matrix **Q** analyzed via a principal coordinate analysis; see Appendix C). The RLQ approach measures the covariance between environmental attributes of grassland fragments and species traits. A test for the association between environmental attributes and species traits was derived by using the sum of all covariances between environmental attributes and traits (sum of eigenvalues in RLQ) and 1000 permutations of the trait states among species (following model 4 in Dray and Legendre 2008). The test was performed separately for the abiotic and biotic factors to separate out how species traits are associated with both these ecological factors. We provide the results in terms of P value and standardized effect size (SES). The standardized effect size indicates the strength of the link between traits and environments: $\mathrm{SES} = (X_{\mathrm{obs}} - \mathrm{mnX}_{\mathrm{the}})/\mathrm{sdX}_{\mathrm{the}}$, where X_{obs} is the observed value of the statistic, and $\mathrm{mnX}_{\mathrm{the}}$ and $\mathrm{sdX}_{\mathrm{the}}$ are the mean and standard deviation of the theoretical values obtained after permutations, respectively (here permuting the trait states among species; see Webb et al. [2002] for another example of use of SES in community ecology).

Hypothesis 2: Phylogenetic signal in life history traits is significant.—Given that traits were a mix of nominal, ratio-scaled, and ordinal variables, classical tests for Brownian-trait evolution model could not be used. Alternatively, a Mantel test (with 1000 permutations) was first applied to the trait-based distances among species using all traits combined (Appendix C), next to each trait separately, and finally to the square root of the phylogenetic distances among species (Hardy and

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[9] http://eunis.eea.europa.eu/about.jsp

Pavoine 2012). We provide the results in terms of *P* value, correlation, and SES (see Appendix E for further complementary analyses).

Hypothesis 3: The association between the environment and species traits is not influenced by the phylogeny.—Pillar and Duarte (2010) suggested two possible models for the role of the environment on species traits: The environment might influence traits with high phylogenetic signal, in which case, the correlation between the environment (E) and the traits (T) is mediated by the phylogeny (P) (model $1 = E \rightarrow P \rightarrow T$); or the environment and the phylogeny could both be correlated with species traits, but independent from each other (model $2 = E \rightarrow T \leftarrow P$). Following Pillar and Duarte (2010), we evaluated these two models using Mantel tests. Using the partial Mantel test, we tested the correlation between the distances among communities based on their composition in trait states (T) and the environmental distances (E) among communities, given the phylogenetic distances (P) among communities (H_0: $(E \rightarrow P \rightarrow T) = 0$) (see Appendix C for the calculation of the matrices of distances). Model 1 ($E \rightarrow P \rightarrow T$) is invalidated if this correlation is not equal to zero. Using the Mantel test, we tested the correlation between the environmental and phylogenetic distances among communities (H_0: $(E \rightarrow T \leftarrow P) = 0$). Model 2 is invalidated if this correlation is not equal to zero. Mantel tests were performed using 10 000 permutations incorporating Harmon and Glor's (2010) correction to control for inflated Type 1 errors. We provide the results in terms of *P* value, correlation, and standardized effect size (SES).

RESULTS

Phylogenetic tree

Placing the root node between 100 and 110 million years ago (Mya; Heikkilä et al. 2012), the structure of the phylogenetic tree (Fig. 2) agrees with rapid divergences among families within an approximate eight million-year period (Heikkilä et al. 2012). It also agrees with most within-family divergences of extant species occurring after the Cretaceous-Palaeogene (K-Pg) boundary, with the exception of Nymphalidae and Pieridae, where the divergence among several subfamilies might be older (Heikkilä et al. 2012).

Test for Hypothesis 1

Our RLQ analysis confirms the first hypothesis that there is an association between species traits and between biotic ($SES = 2.404$, $P = 0.025$) and abiotic variables ($SES = 3.106$, $P = 0.008$). The first two axes of the RLQ (Fig. 3) revealed the main types of associations between the biotic (plants) and the abiotic characteristics of the grassland fragments and the traits associated with the local butterfly assemblages. The RLQ analysis also revealed that one of the habitat (*Xerobrometum*) had a low correlation with species' traits and hence is absent from these associations. A principal gradient in Fig. 3A showed that species associated with the *Alysso–Sedion albi* vegetation type (located on small and elliptic fragments, close to the road, on higher altitude and higher slopes) contrast with those associated with the *Mesobrometum* habitat (round and elliptic fragments, far from the road, on lower altitude and lower slopes) according to most of the traits. Species associated with the *Mesobrometum* habitat were found to have lower generation number, tolerance, mobility, and developmental flexibility. These species also had slower larval growth rates, shorter flight period, earlier overwintering stages, weaker potential fecundity and mature egg loads, and random oviposition behaviors. Larvae of species associated with the *Alysso–Sedion albi* vegetation type were found associated with host plants in the Urticacae, Cannabinacae, Brassicacae, Fabacae, and Tropeolacae families. In contrast, larvae of those butterflies associated with the *Mesobrometum* habitat feed on other flowering plants and on monocots. The proportion of forest habitat constitutes a second gradient (Fig. 3A) where species associated with highest proportions of forest are distinguished by their larger body size, lower developmental flexibility, longer female maturity, and an absence of fully developed eggs when females emerge from the pupa (Fig. 3B–E; see also Appendix F).

Test for Hypothesis 2

Our results confirm a significant phylogenetic signal in the trait-based distances among species (Mantel test $n = 68$, $\rho = 0.309$, $SES = 11.406$, $P = 0.0001$). Analyzing each trait separately, we found that nine traits (adult size, male behavior, female oviposition, ripe egg load, potential fecundity, mobility, larval growth rate, larval trophic group, and overwintering stage) had a significant phylogenetic signal (Appendix E). Significant Mantel correlations ranged from 0.107 to 0.343. Nevertheless, even when the phylogenetic signal was significant, trait convergence was observed among species from different families (Fig. 2).

Test for Hypothesis 3

Our results confirm the third hypothesis that the association between the environment and species traits is only partially structured by the phylogeny. Analysis of the local butterfly assemblages revealed that phylogeny and environment were independently correlated with species traits. Model 1, which assumes that the correlation between environment (E) and traits (T) is mediated by the phylogeny (P) (model $1 = E \rightarrow P \rightarrow T$), was rejected ($\rho = 0.249$, $SES = 2.010$, $P = 0.0267$). In contrast, model 2 ($E \rightarrow T \leftarrow P$), which assumes that the environment and phylogeny could both be correlated with species traits, but independently from each other, was not rejected ($\rho = 0.132$, $SES = 0.848$, $P = 0.2059$).

DISCUSSION

Here we explored the effects of phylogeny and functional diversity on the structure of a butterfly metacommunity. We have shown that, in spite of a

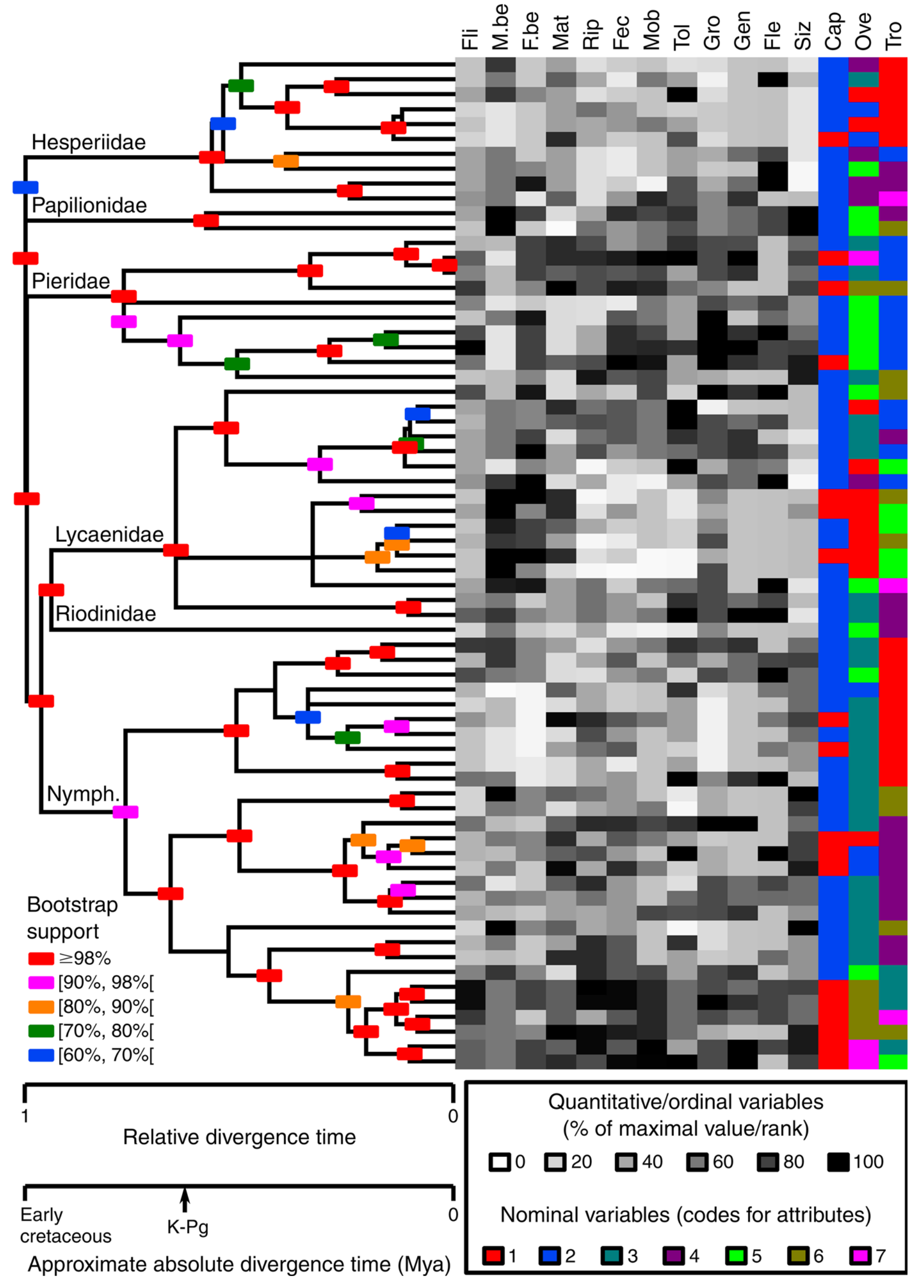

FIG. 2. Molecular phylogenetic tree of the 68-species RAxML maximum likelihood analyses (Stamatakis 2006) and life history traits. Branch lengths on the phylogenetic tree are expressed as relative divergence time as estimated by PATHd8 algorithm (Britton et al. 2007). An indication of the time periods under which speciation events occurred is given at the bottom of the tree (where Cretaceous-Palaeogene is shown as K-Pg, and Mya stands for million years ago; Heikkilä et al. 2012, Wahlberg et al. 2013). Support values were derived from 1000 bootstrap replicates. The divergences of the families are indicated (Nymph. represents Nymphalidae). The life history traits are given in front of the phylogeny with color scales. Quantitative and ordinal traits were divided by their maximum value and rank, respectively, to obtain variables bounded by 0 and 1. Trait codes (top of Fig.) are: Fli, adult flight period; M.be, male behavior; F.be, female oviposition behavior; Mat, female maturation; Rip, ripe egg load; Fec, potential fecundity; Mob, mobility; Tol, tolerance; Gro, larval growth rate; Gen, generation number; Fle, developmental flexibility; Siz, adult size; Cap, capital breeder; Ove, overwintering stage; and Tro, tropic group (larvae) (Appendix C). Codes for the attributes of the nominal variables for the capital breeder are: 1, no egg at the beginning of the female adult stage; and 2, eggs at the beginning of the female adult stage. Codes for the overwintering stage are: 1, eggs; 2, small larvae; 3, mean larvae; 4, large larvae; 5, pupae; 6, adults; 7, in warm countries. Codes for the trophic group are: 1, monocot (Cyperacae, Poacae); 2, Brassicacae, Fabacae, Tropeolacae; 3, Urticacae, Cannabinacae; 4, other flowering plants; 5, combination of herbs; 6, trees; 7, combination of herbs and trees (see Appendix B for the names of the species in the same order as in the phylogenetic tree and trait table, and see Appendix C for details on traits). Square brackets around the bootstrap support values designate intervals; i.e., they include the lesser value and go up, but do not include, the higher value.

significant phylogenetic signal on species traits, species with similar habitat preference also show substantial patterns of trait convergence. Contrasting environmental conditions among grassland fragments are the principal drivers of butterfly trait diversity and consequently of patterns of species coexistence in this metacommunity.

Environmental filters

Environmental filtering as a function of their traits is an important determinant of butterfly species distribution in the Calestienne landscape. This filter, mediated through biotic (e.g., plants) and abiotic factors, determines species distribution such that coexisting butterflies within a grassland fragment tend to have similar traits. Abiotic processes such as disturbance (indicated by the plant assemblages associated with the *Alysso–Sedion albi* habitat, which groups pioneer plant species dwelling on recently disturbed soil; European Commission 2007) favor the presence of ubiquitous species that have distinct traits that enhance their widespread distribution (e.g., high reproduction rates, high mobility, wide tolerance). These abiotic processes also act to filter specialist species with lower reproductive rates, mobility, and tolerance. In contrast, larger fragments characterized by the *Mesobrometum* habitat favor the presence of less tolerant, specialist species with less mobility and less flexibility in their reproduction strategy. Butterfly species in fragments associated with forest habitats had traits that allow them to cope with disturbance such as high mobility and high potential fecundity (although to a lesser extent than those species associated with the *Alysso–Sedion albi* habitat). However, they differed from species associated with disturbed grassland fragments by having low developmental flexibility and long female maturation. Both sets of traits might be expected to be favored by the stability and the predictability of the forest habitat where the need for fast adaptation to fluctuating conditions (developmental flexibility) or any constraints on the age at first reproduction (female maturation) are under weaker selection. Only a few species were associated with these fragments. In contrast, more species were associated with fragments with lower proportions of the forest habitat and a mix of *Mesobrometum*, *Xerobrometum*, and *Alysso–Sedion albi* habitats.

These differences between fragments, driven by biotic and abiotic factors, suggest that habitat stability is an important environmental filter driving trait evolution in this butterfly metacommunity. According to the shifting mosaic steady state concept (e.g., Pickett and White 1985), butterflies with high mobility, short generation time, high reproductive rates, and high tolerance are best able to track pioneer habitats created by disturbance in the landscape and complete their life cycles during a short time window. Host plants of these butterflies are ruderal species coping with such ephemeral habitats. Conversely, specialist butterflies require grasslands that offer a wide diversity of microhabitats, a large array of microclimatic conditions, and hence, a diversified flora of specialist plants. On these fragments, specialist butterflies require large and/or stable areas of habitat to complete their life cycle given their slow development, low mobility, low fecundity, and hence, low adult density. The increased loss of such grasslands in the Calestienne landscape during the last century thus threatens many of its specialist butterflies (Polus et al. 2007). Overall, butterfly species in the Calestienne landscape are distributed across the fragments by environmental filters on species traits driven by the dominant vegetation types, the distance to roads, and the size and shape of the fragments. As already noted, the *Alysso–Sedion albi* habitat is a pioneer habitat occurring after perturbation. Similarly, the proximity of roads is an indicator of higher human impact on habitats (e.g., by walkers, farmers, woodcutters, or hunters), and smaller habitat fragments are obviously more sensitive and less resilient to disturbances than larger ones.

Trait lability and random phylogenetic pattern

We found evidence for trait convergence despite a significant, moderate phylogenetic signal. Phylogenetic conservatism might be stronger at broader taxonomic (e.g., Lepidoptera, Insecta, Arthropoda) and geographic levels (see, e.g., Cavender-Bares et al. 2006 for plant communities). In addition, phylogenetic conservatism might be stronger in other biological traits of butterfly species than those included in our study, such as those involved in the plant defenses and butterfly counter-defenses (Wheat et al. 2007). The diversification period of the main lineages of butterflies, including those in our study, coincides with the first radiation of Angiosperm (125–90 Mya; Crane et al. 1995, Wahlberg et al. 2013). Following the events at the K-Pg boundary (~65 Mya), many angiosperm lines showed a rapid diversification at the genus and even family level, replacing some of the old lineages and filling empty niches. Most butterfly subfamily lineages might also have diversified after the K-Pg boundary (see also Fig. 2; Heikkilä et al. 2012). Climatic shifts after the K-Pg boundary might have influenced plant distribution and net diversification rates in different biomes across the globe, and this might have led to diversification of plant-feeding insects such as butterflies (Nyman et al. 2012). Large-scale ecological conservatism has been observed among plants (Crisp et al. 2009). Analyzing similar large-scale phylogenetic conservatism in butterflies might thus provide insights on the amount and origin of codiversification and coevolution among butterflies and plants (Nyman et al. 2012).

At the local scale of the Calestienne, we found that coexisting species are not particularly phylogenetically related, even though they have similar traits associated with the biotic and abiotic processes. This occurs as the connection between life history traits and the environ-

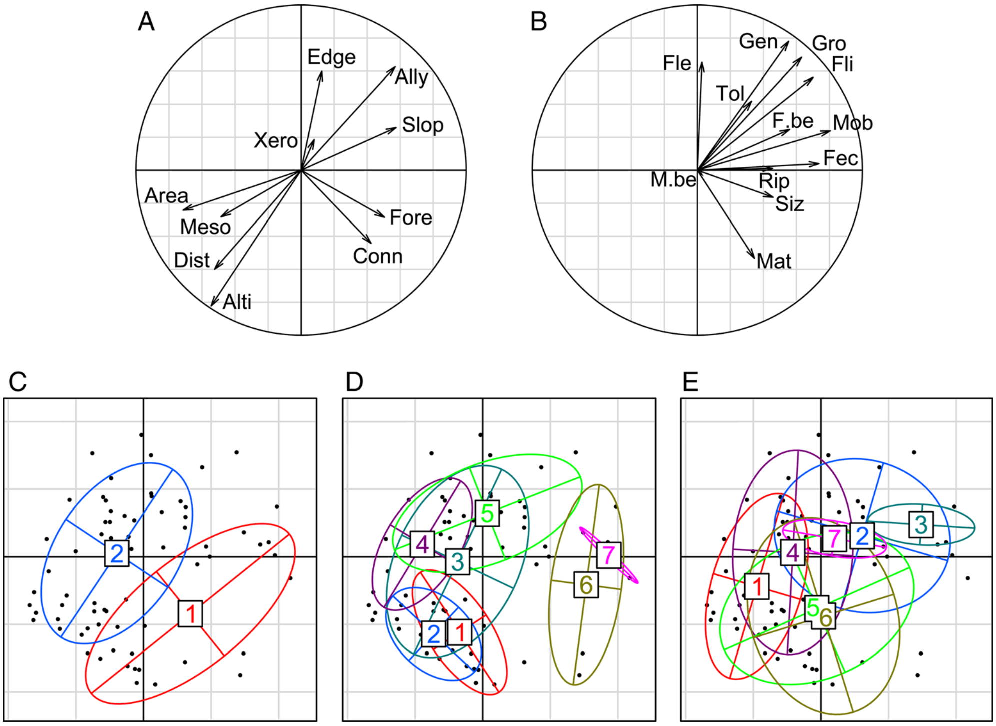

FIG. 3. Results of the RLQ approach. In all panels, axis 1 is horizontal and axis 2 is vertical. Axis 1 expressed 53% of the covariance between the environmental variables and species traits. Axis 2 expressed 30% of this covariance. Panel (A) displays a correlation circle where each arrow gives the Pearson correlations between an environmental variable and the two axes of the RLQ. Environmental variables included abiotic factors (Alti, averaged altitude; Area, log-transformed area; Conn, connectivity; Dist, distance to roads; Edge, edge length; Slop, slope, i.e., difference in altitude) and flora indicators (Ally, *Alysso–Sedion albi* habitat; Fore, forest habitats; Meso, Mesobrometum; and Xero, Xerobrometum) see *Materials and methods* for details. Panel (B) displays a correlation circle where each arrow gives the Pearson (Spearman) correlations between a quantitative (ordinal) trait and the two axes of the RLQ. Panels (C–E) display nominal traits. The attributes of the nominal traits are positioned at the center of the species that possess them, and an ellipse indicates the dispersion of species points around the center. Scales in all panels are given by a grid with cell side equal to 0.2 in panels (A and B) and to 1.0 in panels (C–E). Codes for all traits as in Fig. 2.

ment is largely independent of evolutionary history. Traits that influence environmental filtering are thus only partially phylogenetically conserved as their evolution is likely to be also associated with differential habitat use. For instance, rapid evolution of traits related to host plant fidelity has been observed in two lycaenid butterflies which recently diverged (Nice et al. 2002).

Phylogenetic divergence among broader butterfly families occurred over a period of a few million years in the Early Cretaceous (Heikkilä et al. 2012, Wahlberg et al. 2013), and many phylogenetic speciation events within families are old (starting mostly after the K-Pg boundary; see also Fig. 2; Heikkilä et al. 2012). In contrast, these chalk grassland ecosystems were created much more recently (∼7000 years BP; WallisDeVries et al. 2002). There is also substantial intraspecific biogeographic variation in ecological traits across different biomes in Europe (Bink 1992, Stevens et al. 2010). The patterns of convergence and divergence we observed in this butterfly metacommunity are thus more likely to be due to population differentiation within species rather than during speciation events. This presumably reflects the role of within-biome adaptive evolution. Our finding is supported by the emerging theory of microevolution in metacommunities (Urban et al. 2008, Pontarp et al. 2012). The lability of ecological trait evolution due to biogeographic variation may thus be a key evo-ecological process determining the structure of metacommunities.

Pillar and Duarte (2010) suggested that, in plant communities, evolutionary responses to disturbance may be particularly related to the existence of labile habitat use traits. Our study suggests that this may also apply to butterflies where responses to disturbance also involve some degree of evolutionary lability in traits that are consequently only partially phylogenetically conserved. An important conclusion from our findings is that phylogeny may not always provide useful direct insights into metacommunity organization as labile functional traits or functional traits with different evolutionary relationships might obscure the association between phylogenetic diversity and environmental variables (Anderson et al. 2011, Carboni et al. 2013, Liu et al. 2013, Purschke et al. 2013). This suggests, therefore, that phylogeny may not often be a reliable surrogate for traits involved in environmental filtering. More specific attention to trait evolution is clearly warranted to disentangle how species are distributed across different environments.

Most studies of community assembly suggest a dichotomy between cases where strong convergence of traits leads to similarity in species from different ancestries and cases where traits have a strong phylogenetic signal and common recent ancestry. Phylogenetic patterns in the distribution of species across communities are then interpreted as a function of whether the traits are convergent or conserved (e.g., Webb et al. 2002). Our results show that, phylogenetic signal might often be present but moderated across different parts of the evolutionary tree. In the Calestienne landscape, although a phylogenetic signal indicates that some closely related butterfly species have similar traits, there is stronger evidence for convergence among species that are much more distantly related but co-occur in similar habitats. A significant phylogenetic signal is therefore neither sufficient to demonstrate a lack of trait convergence nor to determine whether communities are likely to be phylogenetically structured. The model in which environment and phylogeny are independent, and independently shape species traits ($E \rightarrow T \leftarrow P$) was supported by the butterfly metacommunity in the Calestienne. The effect of the habitats (*Mesobrometum*, *Xerobrometum*, edge, and forest) and disturbance on species trait distribution is thus not fully captured by evolutionary history. Yang et al. (2012) applied the framework developed by Pillar and Duarte (2010) to plant communities affected by fertilization and found similar patterns (i.e., independent effects of environment and phylogeny) on two functional traits. As Yang et al. (2012) illustrated, phylogenetic conservatism in traits at the metacommunity level can also translate into correlations among traits and phylogeny at the community level, but these correlations are often independent of the (measured) environmental variables.

In the Calestienne butterfly communities, as both phylogeny and environment are independently correlated with species traits, both are therefore necessary to explain species trait states and patterns of coexistence. More generally, partial phylogenetic signals are more likely to be the rule in real communities as some lineages might be more labile with higher rates of evolution than others (Ackerly 2009). In order to understand local species assembly patterns and processes, we advocate that, instead of using phylogenies as proxies for traits, using evolutionary history in addition to life history traits is likely to provide much stronger insights (Pavoine and Bonsall 2011). By doing this, it is possible to distinguish the effects of ecological (e.g., environmental filtering) and evolutionary (e.g., trait-based convergence, lineage-dependent rates of diversification, speciation, and/or extinction associated with habitats) mechanisms on the distribution of functional groups. The crucial step of thoroughly identifying key life history traits (rather than, for instance, relying on simple phylogenetic surrogates) is critical to moving our understanding of (meta)community assembly beyond the classification of simple patterns towards the identification of the underpinning evolutionary and ecological processes.

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SUPPLEMENTAL MATERIAL

Ecological Archives

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