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A unified framework for diversity gradients: the adaptive trait continuum

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ABSTRACT

Aim Adaptive trait continua are axes of covariation observed in multivariate trait data for a given taxonomic group. These continua quantify and summarize life-history variation at the inter-specific level in multi-specific assemblages. Here we examine whether trait continua can provide a useful framework to link life-history variation with demographic and evolutionary processes in species richness gradients. Taking an altitudinal species richness gradient for Mediterranean butterflies as a study case, we examined a suite of traits (larval diet breadth, adult phenology, dispersal capacity and wing length) and species-specific habitat measures (temperature and aridity breadth). We tested whether traits and species-specific habitat measures tend to co-vary, whether they are phylogenetically conserved, and whether they are able to explain species distributions and spatial genetic variation in a large number of butterfly assemblages.

Location Catalonia, Spain.

Methods We formulated predictions associated with species richness gradients and adaptive trait continua. We applied principal components analyses (PCAs), structural equation modelling and phylogenetic generalized least squares models.

Results We found that traits and species-specific habitat measures covaried along a main PCA axis, ranging from multivoltine trophic generalists with high dispersal capacity to univoltine (i.e. one generation per year), trophic specialist species with low dispersal capacity. This trait continuum was closely associated with the observed distributions along the altitudinal gradient and predicted inter-specific differences in patterns of spatial genetic variability (F_{ST} and genetic distances), population responses to the impacts of global change and local turnover dynamics.

Main conclusions The adaptive trait continuum of Mediterranean butterflies provides an integrative and mechanistic framework to: (1) analyse geographical gradients in species richness, (2) explain inter-specific differences in population abundances, spatial distributions and demographic trends, (3) explain inter-specific differences in patterns of genetic variation (F_{ST} and genetic distances), and (4) study specialist–generalist life-history transitions frequently involved in butterfly diversification processes.

Keywords

Adaptive/functional trait, butterflies, diet breadth, dispersal, diversification, F_{ST} , generalist–specialist, phenology, species richness gradients, thermal biology.

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INTRODUCTION

Species richness gradients emerge as a result of the combined outcomes of evolutionary and ecological processes. In evolutionary terms, the balance of speciation and extinction pro-

cesses is the ultimate origin of diversity and varies along latitudinal and altitudinal gradients (Mittelbach *et al.*, 2007). In addition, it has recently been stressed that clade diversification dynamics usually involve an initial phase of more rapid diversification (Rabosky, 2009) and alternate with secondary

diversification pulses frequently associated with climatic changes and biome shifts, the uplifts of mountain chains or shifts to new host-plant groups in the case of phytophagous insects (Janz & Nylin, 2008; Leneveu *et al.*, 2009; Winkler *et al.*, 2009), and more stable phases in which ecological processes or boundaries seem to regulate and limit diversity (Rabosky, 2009). The ecological processes that actively limit the geographical variation of diversity should arguably be related to the interaction of local environmental conditions with a variety of adaptive traits (Hodkinson, 2005; Carnicer *et al.*, 2011; Stefanescu *et al.*, 2011a).

At the inter-specific level, several studies report multivariate adaptive trait continua in a variety of taxa (i.e. an inter-specific axis of covariation between diverse traits, which can be used as a quantitative synthetic measure of life-history variation for a given taxon). For instance, trait continua have been described in plants (Wright *et al.*, 2004; Chave *et al.*, 2009), mammals (Bielby *et al.*, 2007), birds (Jeschke & Kokko, 2009; Sæther *et al.*, 2011), fishes (Jeschke & Kokko, 2009), phytoplankton (Litchman & Klausmeier, 2008) and marine bacteria (Lauro *et al.*, 2009). The mechanistic origin of these taxon-specific trait continua relies on the evolutionary emergence of contrasting life-history strategies that, in particular ecological contexts, maximize fitness by acquiring a different set of traits allowing for sustained population performance. In other words, trait continua describe and summarize the phenotypic space produced by evolutionary processes (Donovan *et al.*, 2011), highlighting trait combinations and the different ecological strategies that allow demographic performance. These continua often range from specialized to more generalist species and/or from slow to fast life-styles (Wright *et al.*, 2004; Bielby *et al.*, 2007; Sæther *et al.*, 2011). However, to our limited knowledge, the relationships between adaptive trait continua and demographic, distributional and genetic variables remain poorly assessed. Here we examine a general framework that inter-relates adaptive trait continua with population demography, diversification dynamics and spatial distributions. We use species richness gradients of Mediterranean butterflies as a model system to empirically test the proposed framework.

In the case of butterflies and other insect groups a number of apparently conflicting hypotheses have been proposed to explain the role of key adaptive traits in shaping present-day diversity gradients. For instance, some authors have stressed the importance of adaptive traits linked to thermal physiology and desiccation resistance in limiting either global distributions at the species level (Kellermann *et al.*, 2009; Stefanescu *et al.*, 2011a) or the geographical variation of phylogenetic diversity (Hawkins, 2010), while others point to the increase in insect host specificity at low latitudes or mid-altitudes (Scriber, 1973; Dyer *et al.*, 2007; Stefanescu *et al.*, 2011a), the associated increase of diversity of plant resources at lower latitudes and the evolutionary occurrence of host-plant shifts (Janz & Nylin, 2008; Janz, 2011). Likewise, a number of authors have recently stressed the importance of adaptive dispersal traits in actively shaping species-richness gradients (Carnicer *et al.*, 2008a; Craft *et al.*, 2010; Jocque *et al.*, 2010),

while others highlight the critical importance of phenological adaptations across latitudinal gradients (Pratt, 1994; Chuine, 2010).

Reconciling all of these hypotheses about species-richness gradients into one unified framework may be possible if species could be ordered along a continuum of variation in several inter-specifically correlated life-history traits, including host-plant range, phenology and dispersal capacity (the adaptive trait continuum framework; Table 1a). Under this scenario, these correlated traits would then jointly contribute to explaining both the evolutionary and ecological dynamics that generate and maintain diversity (Table 1b,c), the inter-specific differences in abundance and distribution, and the geographical structure of species-richness gradients (Table 1d). In line with these arguments, in the case of butterflies a diverse suite of traits has been proposed as critical in determining speciation (Janz & Nylin, 2008; McBride & Singer, 2010), extinction (Krauss *et al.*, 2003; Koh *et al.*, 2004; Kotiaho *et al.*, 2005) and ecological dynamics (Dennis *et al.*, 2005; Hodkinson, 2005; Menéndez *et al.*, 2007; García Barros & Romo Benito, 2010; Stefanescu *et al.*, 2011a,b), suggesting the possible existence of an inter-specific adaptive trait continuum.

To assess the reliability and usefulness of the adaptive trait continuum framework, our main aims were: (1) to investigate whether species may be ordered along a main axis of covariation given a suite of life-history traits (i.e. to examine the existence of an inter-specific adaptive trait continuum; Table 1, prediction A1); (2) to analyse the existence of significant phylogenetic signal in this set of variables (prediction A2); (3) to assess whether species spatial distributions may be influenced by a set of correlated adaptive traits (prediction A3); (4) to assess whether patterns of genetic variation consistently differ between species located at different extremes of the continuum (prediction B1); and (5) to examine environmental and resource variables to see whether they regulate species richness differently along the continuum (prediction D1).

METHODS

Data on butterfly assemblages

The Catalan Butterfly Monitoring Scheme (CBMS; <http://www.catalanbms.org/>) and the Andorran Butterfly Monitoring Scheme (BMSAnd; <http://www.bmsand.ad/>) consist of a network of 100 recording sites in the north-east of the Iberian Peninsula that are monitored on a weekly basis from March to September (30 sampling weeks per year) by means of visual counts of butterflies along fixed routes (for further details see Stefanescu *et al.*, 2011a). For the present study, we used data from 84 transect routes (mean length 1785 m, SD = 821 m, range: 565–4909 m) monitored between 1994 and 2007. A total of 169 butterfly species were recorded and considered in the analyses (Appendices S1 & S2 in Supporting Information).

Table 1 A list of the predictions of the adaptive trait continuum framework.

The adaptive trait continuum framework	General statements and predictions	References	Specific predictions for butterflies (case study)	Empirical tests
(a) Inter-specific continuum	Significant main axes of covariation will be observed in multivariate trait datasets at the inter-specific level, which can be used as a quantitative synthetic measure of life-history variation for a taxonomic group. Significant heritabilities and selection differentials will be observed for these traits	Wright <i>et al.</i> (2004), Bielby <i>et al.</i> (2007), Chave <i>et al.</i> (2009), Jeschke and Kokko (2009), Lauro <i>et al.</i> (2009), Donovan <i>et al.</i> (2011)	A1: Species can be ordered along an inter-specific continuum of adaptive life-history traits (diet breadth, phenology and dispersal capacity, wing length) and species-specific measures of thermal habitat (i.e. habitat thermal and aridity breadth). PCA analyses will show a consistent axis for these variables	This study
(b) Evolutionary and diversification dynamics	The phylogenetic signal of traits of the continuum will be significant, ranging from mid/low phylogenetic signals (for physiological, behavioural, life-history and phenology traits) to high phylogenetic signals (for morphological traits) •Diverse traits will significantly contribute to explain inter-specific differences in patterns of geographical distribution, demography and genetic variation. For these traits, significant interactions with environmental and habitat variables will be frequently observed	Blomberg <i>et al.</i> (2003), Carnicer <i>et al.</i> (2009) Stefanescu <i>et al.</i> (2011a), Carnicer <i>et al.</i> (2011)	A2: Phenological and behavioural traits (dispersal capacity, diet breadth) will be characterized by similar and significant phylogenetic signals. Comparatively higher phylogenetic signals will be observed in morphological traits (wing length) A3: Adaptive traits of the continuum interact and significantly contribute to explaining the distribution range of species in SEMs and phylogenetically corrected GLS models. SEM models incorporating correlations between life-history traits will obtain a significantly better fit	This study
(b) Evolutionary and diversification dynamics	Measures of geographical genetic differentiation (F_{ST} , genetic distance) will be significantly associated with quantitative measures of adaptive trait continuum (e.g. PCA axis values or other ordination measures) and inter-specific variation in dispersal capacity and trophic generalism	This study, Carnicer <i>et al.</i> (2011)	B1: Populations located at one extreme of the inter-specific continuum (diet specialists, short flight period length and less mobile species) will show significantly higher geographical genetic differentiation (F_{ST} , genetic distance)	This study
(b) Evolutionary and diversification dynamics	Species characterized by high dispersal capacity and trophic generalism will be significantly associated with the emergence of adaptive radiations and range expansion processes. Transitions between periods of range expansion and the radiation of generalist and highly dispersive forms and subsequent periods of regional trophic or habitat specialization, dispersal-capacity reduction and speciation will be documented in phylogenetic studies. Phenotypically plastic responses can mediate these evolutionary transitions	Janz and Nylin (2008), Hoberg and Brooks (2008), Van Bocxlaer <i>et al.</i> (2010), Pfennig <i>et al.</i> (2010), Janz (2011), Carnicer <i>et al.</i> (2011)	B2: Butterfly species characterized by a set of adaptive traits (high dispersal capacity, trophic generalism) are more prone to experience range expansion processes and initiate adaptive radiations. Transitions occur along the phylogeny between periods of range expansion and the radiation of highly dispersive and trophic generalist forms and subsequent periods of regional trophic specialization, dispersal-capacity reduction and speciation	Not tested in butterflies. Van Bocxlaer <i>et al.</i> (2010), Janz (2011)

(c)	Ecological dynamics	Multivariate adaptive trait continua will be significantly correlated with demographic variables	This study, Carnicer <i>et al.</i> (2011)	C1: Temporal population trends will be significantly associated with the inter-specific continuum	This study, Stefanescu <i>et al.</i> (2011b), Carnicer <i>et al.</i> (2011)
		Habitat generalist and trophic generalist life-styles will present a characteristic set of traits, being frequently significantly associated with wider geographical distributions and higher population densities. More specialized life-styles will be located at opposite extremes of the	Sæther <i>et al.</i> (2011), Janz (2011)	C2: Diet generalists will present wider distributions and will have higher population densities. Specialists will have more restricted and nested distributions, and smaller densities	This study, Stefanescu <i>et al.</i> (2011a)
		multivariate trait continuum relative to generalists, usually having more restricted and nested geographical distributions, smaller population densities and experiencing higher population extinction rates and spatially asynchronous dynamics		C3: Diet specialists will have increased temporal turnover and extinction rates, and generalists will have higher immigration rates	This study, Krauss <i>et al.</i> (2003)
(d)	Geographical patterns of species richness	Functional groups will be distributed along the observed multivariate trait continuum. Groups will be significantly associated with ordination measures (PCA/ordination values will differ between groups). Species richness patterns of functional groups will be differentially associated with resource and environmental variables	This study, Carnicer <i>et al.</i> (2011), Carnicer and Diaz-Delgado (2008)	D1: Species richness patterns of functional groups defined along the adaptive continuum (e.g. diet specialists versus generalists) will be differentially associated with resource distribution and environmental variables in structural equation models	This study, Menéndez <i>et al.</i> (2007)
		Qualitatively different latitudinal and altitudinal richness patterns will be observed for different functional groups distributed along the trait continuum	This study, Stefanescu <i>et al.</i> (2011a)	D2: Altitudinal patterns of species richness and host-plant richness distribution will consistently differ between functional groups located at different extremes of the continuum (e.g. diet specialists versus generalists)	This study, Stefanescu <i>et al.</i> (2011a)
				D3: Latitudinal richness patterns of diet specialists and generalists will differ qualitatively.	Scriber 1973, Dyer <i>et al.</i> 2007.

PCA, principal components analysis; SEM, structural equation model; GLS, generalized least squares.

Mitochondrial DNA data

Mitochondrial DNA data (cytochrome *c* oxidase subunit I, COI) were used to calculate average genetic distances among conspecific butterfly samples from Catalonia and Romania.

COI is a widely used mitochondrial DNA marker that provides sufficient variation for a general study of intra-specific genetic structure, as well as a study of inter-specific relationships between closely related taxa (Craft *et al.*, 2010). Besides geographical distance, the specific landscape barriers and types of habitat that separate two sampling locations have a serious impact on genetic distance. Thus, genetic distances normalized by geographical distance are not readily comparable. To overcome this problem, we used only original data from two selected regions so as to ensure a meaningful comparison between taxa. Catalonia and Romania were chosen because they are separated by an adequate geographical distance (*c.* 1900 km), share a reasonable number of common species and are representative of the Mediterranean and temperate areas, respectively (see Appendix S3 for further details on genetic analyses).

Environmental and host-plant data

For each sampling transect, we extracted from the Digital Climatic Atlas of Catalonia (http://www.opengis.uab.cat/acdc/english/en_model.htm) the mean annual temperature, the mean winter temperature (using January data) and the mean annual rainfall, and derived an aridity index (the modified Gausson aridity index; see Stefanescu *et al.*, 2011a). Altitudes were taken from a digital elevation model with a spatial resolution of 30 m (Stefanescu *et al.*, 2011a).

For each locality, we estimated the number of host plants available for monophagous, oligophagous and polyphagous species by filtering information from the Plant Biodiversity Data Bank of Catalonia (<http://biodiver.bio.ub.es/biocat/>), a database of the geographical distribution of all plants in Catalonia (see Appendix S3 for further details).

Butterfly and habitat measures

At each locality, we estimated butterfly species richness and community size, i.e. the total number of individuals recorded. For each butterfly species, we recorded the mean abundance (i.e. abundance per km averaged across transects), species' distribution range, i.e. the number of transect routes on which it was detected, and its altitudinal distribution (minimum altitude, maximum altitude and altitudinal range). Following Swanson and Garland (2009), we estimated the mean temperature along the transect routes where a species was found (habitat mean temperature) and calculated the range in °C between the maximum and minimum habitat mean temperature values reported (hereafter, 'habitat temperature breadth'). These calculations were carried out for mean winter temperature, mean annual temperature and the Gausson aridity index (hereafter, 'habitat mean aridity' and 'habitat aridity breadth'). Flight period length, i.e. the duration of the flight period in Catalonia

(number of months with flight activity) for each species was obtained from independent collections in the study area with precise sampling dates. In addition, species were classified according to the trophic specialization of their larvae. We distinguished between monophagous (butterflies feeding on plants of a single genus), oligophagous (butterflies feeding on plants of various genera from the same family) and polyphagous species (butterflies feeding on a diversity of plants belonging to various families) (Appendix S1). We also recorded the number of host-plant families, genera and species used by each butterfly species. Species were also classified according to their dispersal capacity (following Stefanescu *et al.*, 2011a). Each butterfly species was assigned an index of increasing mobility (hereafter, 'dispersal capacity') ranging from 1 to 4, according to the following criteria: 1, species living in metapopulations with very little dispersal between populations; 2, species living in metapopulations with a lot of dispersal between populations; 3, species living in patchy populations with non-seasonal migration; 4, species living in patchy populations with seasonal migration (see Appendix S3 for further details).

Hypothesis testing

To assess the adaptive trait continuum framework we designed a series of diagnostic predictions that are listed in Table 1. We were able to empirically test 9 out of the 11 predictions. For the two remaining predictions (B2 and D3) the data needed for a proper test were not available and here we only assess and discuss the existing empirical support in the literature. Below we provide a detailed explanation of the tests applied.

Description of the inter-specific continuum (predictions A1–A3)

Principal components analyses (PCAs) were applied to assess whether species could be ordered along a main axis characterized by a set of correlated adaptive traits and species-specific habitat variables (prediction A1). We performed a set of exploratory PCAs combining host-plant range, flight period length, wing length, dispersal capacity, habitat temperature breadth and habitat aridity breadth.

Wing length was not significantly correlated with the bulk of variables (with the exception of the dispersal capacity index; $R^2 = 0.17$, $P < 0.001$) and therefore was excluded from the final PCAs. Results including either habitat mean annual temperature breadth or habitat winter temperature breadth, or both variables, were qualitatively similar.

To explore whether the set of variables examined effectively presented a significant and similar phylogenetic signal (prediction A2), we first compiled a cladogram for the 169 species observed in Catalonia from available published sources (Appendix S2). Unresolved nodes in the phylogeny were included as soft polytomies (Appendix S2). The PDAP package was used to transform the phylogenetic tree into a matrix of phylogenetic distances. Subsequently, the Physig module was applied to assess

the phylogenetic signal by estimating the K statistic for each trait (Blomberg *et al.*, 2003; see Appendix S3 for all the methodological details).

To test whether the examined adaptive traits of the inter-specific continuum contributed significantly to explaining the observed variation in species distribution ranges (prediction A3), we applied structural equation models (SEMs) using the *sem* package in R (Fox *et al.*, 2010; R Development Core Team, 2011). A scheme of the examined causal paths and tested SEMs is presented in Appendix S4. These models were selected after comparing several alternative models, using model fit parameters as selective criteria [chi square and significance, goodness of fit, root mean square error of approximation index (RMSEA) and Akaike's Bayesian information criterion (BIC)]. The SEMs tested the influence of diet breadth (number of host-plant species used), flight period length (number of months in which the species flies), dispersal capacity and wing length. In addition, they also allowed us to assess the reliability of indirect effects of body size (measured as wing length) on diet breadth, flight period length and dispersal capacity. Complementary SEM analyses were also applied combining trait and habitat climatic variables (Appendix S4). According to the adaptive trait continuum hypothesis, we expected that several adaptive traits would robustly show significant direct and indirect effects in explaining range variation between species in the SEM analyses (prediction A3). Specifically, we tested whether SEM models that explicitly incorporate inter-specific correlations among life-history traits (dispersal capacity, flight period length and diet breadth) obtained a significantly better fit, as expected (prediction A3). We complemented SEMs with phylogenetic generalized least squares (PGLS) models, to ensure that results are robust to the effect phylogenetic autocorrelation.

Evolutionary dynamics (predictions B1 and B2)

Reduced dispersal capacity and increased host specificity in the adaptive trait continuum are expected to be associated with increased genetic differentiation (Nève, 2009; Craft *et al.*, 2010). To assess this prediction we evaluated whether available estimates of the fixation index F_{ST} and Kimura two-parameter genetic distances varied consistently along the inter-specific continuum and whether they were significantly correlated with the PCA scores of the multivariate analysis (prediction B1). F_{ST} describes the proportion of the genetic variance contained in a subpopulation (the subscript S) relative to the total genetic variance (the subscript T), and ranges from 0 (no spatial genetic structure) to 1 (all genetic variation is due to differences among subpopulations). F_{ST} values were extracted from a review of the studies conducted in Europe (Appendix S5). Following Nève (2009), we first regressed F_{ST} against the maximum geographical distance between populations in each study and extracted the residual values. To assess prediction B1, residuals were then plotted against the PCA axis (first axis of the PCA of host-plant range, flight period length, dispersal capacity, habitat winter temperature breadth and habitat aridity breadth). Data for the Kimura two-parameter genetic distance were obtained from

COI sequences from 256 specimens representing 18 different species (Appendix S6). Based on the PCA values, we selected the seven most specialized and the seven most generalist species that occur in both regions and of which at least four specimens per region were available. The same criteria were employed to select four species close to the average PCA value (Appendix S6).

Janz and Nylin (2008) recently hypothesized that butterfly diversification dynamics may be marked by evolutionary transitions between host-plant generalist and specialist forms (the so-called 'oscillation hypothesis' of host-plant range and speciation). These studies and similar approaches (Hoberg & Brooks, 2008; Jahner *et al.*, 2011; Janz, 2011) suggest that diversification processes of species located at the opposite extremes of the inter-specific continuum evaluated here may be qualitatively different, with different diversification processes and/or extinction rates occurring in generalists and specialists (prediction B2).

Ecological dynamics (predictions C1–C3)

Several studies have previously suggested that highly mobile species and diet generalist species are usually locally more abundant and have broader distribution ranges than sedentary species having narrow diets (Cowley *et al.*, 2001; Dennis *et al.*, 2005; Janz, 2011), and also that they differ significantly in their demographic responses to the impacts of global change (Kotiaho *et al.*, 2005; Stefanescu *et al.*, 2011b). We examined whether butterfly population trends in Catalonia could be explained within the adaptive trait continuum framework by regressing species PCA scores against published estimates of butterfly population trends in Catalonia (prediction C1). Population trends were estimated as the slope of log-linear regressions of abundances from the period 1994–2008 using TRIM software and were available for 78 species (see Stefanescu *et al.*, 2011b, for methodological details; a list of the evaluated species is given in Appendix S1). We also assessed whether diet generalists are usually more widespread and have higher population densities (prediction C2) by means of a Tukey–Kramer test of mean abundances, ranges and PCA scores for specialists (monophagous butterflies) and generalists (polyphagous and oligophagous butterflies). Similarly, we assessed differences in species turnover (measured as the temporal coefficient of yearly variation of species richness in transects with five or more years of data) between these three groups (prediction C3).

Geographical patterns of species richness (predictions D1–D3)

If specialists and generalists can be ordered along an axis of correlated adaptive traits (predictions A1–A3), we may then expect that these two groups will interact with local environmental conditions in different ways. This will in turn translate into group-specific differences in species-richness patterns. We performed a SEM analysis to assess whether species-richness patterns of specialist (S; monophagous butterflies) and generalist groups (G; oligophagous and polyphagous) located at oppo-

site extremes of the inter-specific adaptive trait continuum were differentially associated with resource distribution and environmental variables (prediction D1). In addition, we analysed whether these differences translated into geographical differences in the structure of altitudinal patterns of species richness (prediction D2). Finally, we reviewed the available evidence in the literature regarding qualitatively different latitudinal patterns of butterfly species richness in diet specialists and generalists (prediction D3).

RESULTS

Inter-specific adaptive trait continuum (predictions A1–A3)

The PCAs (Table 2, Appendices S7 & S8) indicated that the bulk of the variance between the examined variables was concentrated along a main orthogonal axis, as expected (prediction A1; Table 1). Along this axis, observed variation in life-history traits and habitat use ranged from long flight periods, strong dispersal capacity, broad host-plant range and broad thermal and aridity tolerance to the opposite extremes. Tests for phylogenetic signal (Table 3) confirmed the existence of significant and similar values in the examined variables (prediction A2). Only wing length had a significantly higher phylogenetic signal than the rest of the variables (Table 3; Tukey–Kramer test for grouped traits, $P < 0.001$; Appendix S9).

The SEM analyses (Fig. 1a) indicated that interactions between the traits made a significant contribution to explaining the differences in the distribution ranges between species (prediction A3). The indirect effects of wing length were only significant in dispersal capacity. PGLS models indicated that the tested effects on species range were robust to phylogenetic autocorrelation (Table 4). Interestingly, SEM models that did not incorporate correlations between life-history traits (i.e. the internal arrows interconnecting dispersal capacity, diet breadth and flight period length in Fig. 1a) obtained a non-significant fit [$\chi^2 = 101.51$, $\text{Pr} > \text{ChiSq} = 0$; goodness of fit 0.79, $\text{BIC} = 70.73$], providing empirical support for the adaptive trait continuum framework (prediction A3). A supplementary SEM model com-

Table 2 Summary of the principal components analysis (PCA) between habitat aridity breadth, habitat winter temperature breadth, number of host-plants, dispersal capacity and flight period length (prediction A1).

	PCA 1	PCA 2	PCA 3
Eigenvalue	2.97	0.78	0.59
Explained variance	59.49	15.94	11.83
Habitat aridity breadth	0.50	−0.40	0.21
Habitat winter temperature breadth	0.48	−0.48	0.22
Number of host plants	0.37	0.66	0.62
Dispersal capacity	0.42	0.42	−0.51
Flight-period length	0.45	0.02	−0.51

paring species-specific habitat climatic variables and traits is shown in Fig. 1b. This model reports significant direct and indirect effects of habitat climatic variables on spatial range distributions.

Evolutionary and diversification dynamics (predictions B1 and B2)

The first PCA axis was significantly correlated with residual F_{ST} values ($R^2 = 0.292$, $P = 0.009$; Fig. 2a) and with average Kimura two-parameter genetic distances ($R^2 = 0.262$, $P = 0.03$; Fig. 2b) as expected (prediction B1), thereby revealing a significant relationship between the reported inter-specific continuum and both gene flow and spatial genetic patterns (see Appendix S7 for additional results). Prediction B2 was not empirically tested but the available evidence in the literature is debated below in the discussion.

Ecological dynamics (predictions C1–C3)

PCA scores on the first axis (PCA 1) were significantly correlated with population trends from 1994 to 2008 (Fig. 2c). The best fit was obtained by a second-order polynomial function. Significant negative trends (light grey dots in Fig. 2c) were more abun-

Table 3 Observed phylogenetic signal for the suite of variables examined (prediction A2).

Variable	Phylogenetic signal (K)	P -value
Morphological traits		
Wing length	0.68	< 0.001
Dispersal capacity	0.29	< 0.001
Life-history phenology		
First month of flight	0.27	< 0.001
Last month of flight	0.25	< 0.001
Flight period length	0.26	< 0.001
Thermal tolerance variables		
Mean habitat temperature	0.28	< 0.001
Mean habitat winter temperature	0.28	< 0.001
Mean habitat water deficit	0.25	< 0.001
Habitat temperature breadth	0.19	0.015
Habitat winter temperature breadth	0.22	0.002
Habitat water deficit breadth	0.23	0.001
Diet breadth		
Number of host-plant families	0.21	0.006
Number of host-plant genera	0.18	0.016
Number of host-plant species	0.17	0.065
Distribution		
Minimum altitude	0.24	< 0.001
Maximum altitude	0.20	0.025
Mean altitude	0.23	< 0.001
Altitudinal range	0.17	0.027
Number of localities (range)	0.20	0.001
Abundance		
Mean local abundance	0.20	0.008

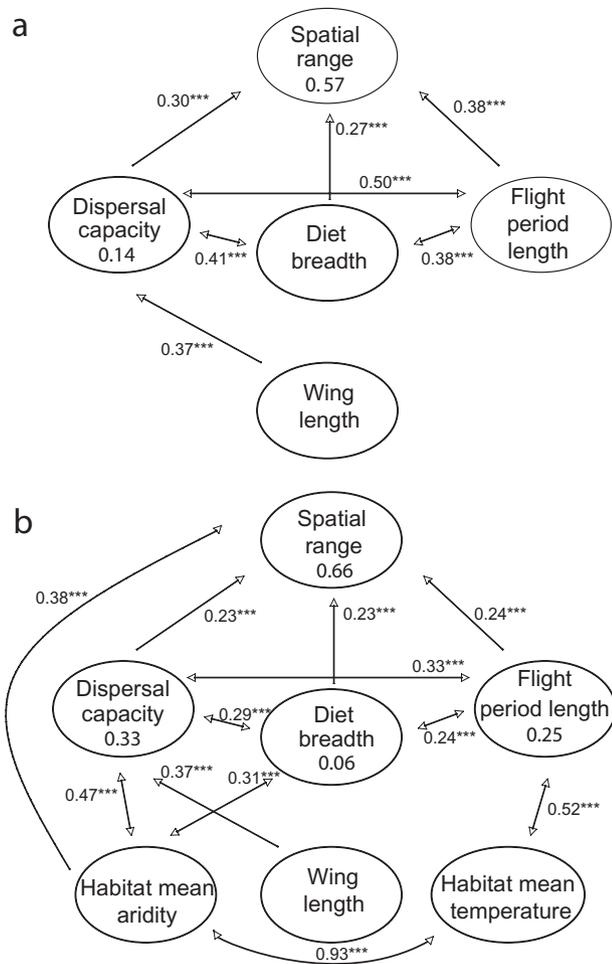


Figure 1 Structural equation model (SEM) obtained for species spatial distribution ranges. Standardized coefficients are provided for each path. The significance is also indicated (*** $P < 0.001$). Numbers inside the circles indicate the proportion of explained variance of endogenous variables. (a) SEM for species spatial range using trait variables (dispersal capacity, diet breadth, flight period length and wing length) as independent predictor variables. Model fit summary: model $\chi^2 = 2.69$; d.f. = 3; $\text{Pr}(>\text{ChiSq}) = 0.44$; root mean square error of approximation (RMSEA) = 0; goodness of fit index 0.99; adjusted goodness of fit index = 0.97; Akaike's Bayesian information criterion (BIC) = -12.70. (b) SEM for species spatial range using trait variables and species-specific habitat variables (habitat mean aridity and winter temperature) as independent factors. Model fit summary: model $\chi^2 = 11.66$; d.f. = 9; $\text{Pr}(>\text{ChiSq}) = 0.23$; RMSEA = 0.04; goodness of fit index: 0.98; adjusted goodness of fit index = 0.94; BIC = -34.35.

dant than positive ones and were distributed across all PCA 1 values, despite being more frequent in species characterized by low PCA 1 values. Tukey–Kramer tests indicated that diet specialists (i.e. butterflies with monophagous larvae) effectively had significantly smaller ranges, lower mean densities and lower PCA scores than generalists ($P < 0.001$; Appendix S10), as expected (prediction C2). Diet specialists also sustained higher

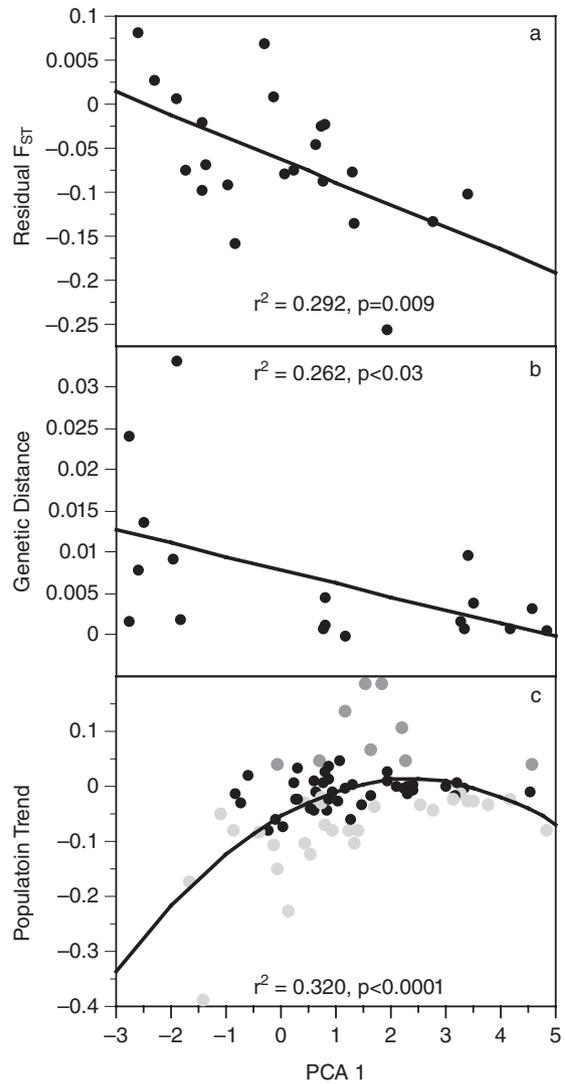


Figure 2 Observed relationships between principal components analysis axis 1 (PCA 1) and: (a) residual F_{ST} values for European butterfly populations; (b) average Kimura two-parameter genetic distances between Catalan and Romanian populations of 18 butterfly species; (c) population trends in Catalonia. Light grey dots indicate declining population trends; black dots stable population trends; dark grey dots increasing population trends (Appendix S1). A list of the butterfly species and reference sources for F_{ST} and genetic distance are provided in Appendices S5 & S6. Plotted F_{ST} values are residual values obtained after regressing F_{ST} against the maximum geographical distance between populations. PCA 1 accounts for the covariation between flight-period length, diet breadth, dispersal capacity, habitat temperature and aridity breadth. PCA 1 scores are highest for trophic generalists with high dispersal capacity and extended flight period length.

turnover rates (temporal coefficient of variation of species richness) than oligophagous species, but did not have significantly higher turnover rates than polyphagous species, thus providing only partial support for prediction C3.

Table 4 Results obtained in the phylogenetically corrected generalized least squares (PGLS) model. A comparison of the estimates obtained by an ordinary least squares (OLS) model is provided. Results are robust after correcting for phylogenetic independence. Neither wing length nor the interaction term wing length \times dispersal capacity showed significant effects in the multiple regression models. All estimates significant at $P < 0.0001$.

Dependent variable	Independent variables	OLS estimates	PGLS estimates	d.f.	Model fit
Range	Number of host-plant species	1.61 \pm 0.35	1.71 \pm 0.34	165	OLS: $R^2 = 0.57$ AIC _c = 1447 PGLS: $R^2 = 0.51$ AIC _c = 1498
	Dispersal capacity	8.61 \pm 1.79	10.27 \pm 2.08		
	Flight-period length	4.74 \pm 0.75	4.94 \pm 0.82		

Geographical patterns of species richness (predictions D1–D3)

According to prediction D1, SEM models demonstrated a qualitatively different association of species-richness patterns in specialists (monophagous) and generalists (oligophagous, polyphagous) with resource and environmental variables (Fig. 3). Monophagous species richness differed from generalist groups in being negatively affected by the direct effects of temperature. Similarly, a strong positive effect of host-plant species richness was only observed in diet specialists. In contrast, generalist species-richness trends were associated with the direct negative effects of habitat aridity, and no direct effects of temperature were observed (Fig. 3). Consistent with these differences, altitudinal patterns of both butterfly species richness and host-plant richness differed qualitatively between diet specialists and generalists (prediction D2; Fig. 4). Notably, parallel patterns in the altitudinal distribution of host-plant richness and butterfly richness were only observed in specialists (monophagous) (Fig. 4a), which is consistent with the results from the SEM models. The altitudinal peaks in host-plant richness and total butterfly abundance (community size) differed between the three groups (Fig. 4). Interestingly enough, these altitudinal trends are in line with the evidence for latitudinal clines in butterfly specialization that are documented in the literature (Scriber, 1973; Fiedler, 1998; Dyer *et al.*, 2007; prediction D3).

DISCUSSION

Our results document the existence of a set of adaptive traits and species-specific thermal habitat variables that consistently covary at the inter-specific level along a butterfly life-history continuum. This continuum seems to be closely associated with demographic and evolutionary dynamics of butterfly communities and the geographical structure of species-richness gradients. Indeed, we have shown that this continuum is associated with local population abundances, temporal population trends and turnover dynamics. Moreover, available measurements of spatial genetic variation (F_{ST}) for European populations were also correlated with the position of species along the continuum and a significant association was also observed with a measurement of genetic distance. Our results support the view that

specialist and generalist butterflies have repeatedly evolved through qualitatively different combinations of life-history traits (see Appendix S11 for an extended and in-depth discussion).

A variety of theoretical models have discussed the different roles played by trophic generalists and specialists in community function (reviewed in Richmond *et al.*, 2005), and the role of adaptive traits in the evolutionary emergence of resource specialists and generalists (reviewed in Carnicer *et al.*, 2008b). These studies suggest that generalists are favoured in fluctuating or more human-disturbed environments. In line with these theoretical assertions, our results and previous empirical studies have found a relatively low but stable number of widespread trophic generalists across altitudinal or latitudinal gradients (Scriber, 1973; Stefanescu *et al.*, 2011a), with more abundant populations usually found in local environments subject to human disturbance or fluctuations (Stefanescu *et al.*, 2011a; Fig. 4). By contrast, sharp increases in species richness are mainly accounted for by trophic specialists and species with low dispersal capacity that concentrate in less fluctuating or disturbed environments, as well as in mountain ranges, and therefore tend to have geographically nested and more restricted ranges (Scriber, 1973; Carnicer *et al.*, 2008a, 2011; Janz, 2011; Stefanescu *et al.*, 2011a). Our results agree with these previous observations and highlight the fact that the differences in the correlated life-history traits between trophic generalists and specialists are crucial for understanding the geographical structure of species-richness gradients, the relative importance of both kinds of organisms in different geographical areas and inter-specific differences in species abundances and ranges.

McGill (2010) has recently pointed out that all current unified mathematical theories of diversity (continuum, neutral, metapopulation, fractal, Poisson and MaxEnt models) assume that species are characterized by spatially nested ranges or clustered distributions. These theories also produce or require significant differences in abundance between species at meta-community or regional scales (Hanski & Gyllenberg, 1997; McGill, 2010). In the case of butterflies the adaptive trait continuum framework helps to explain why species show spatially nested range distributions and have inter-specific differences in abundance at regional level. In sum, we provide a framework

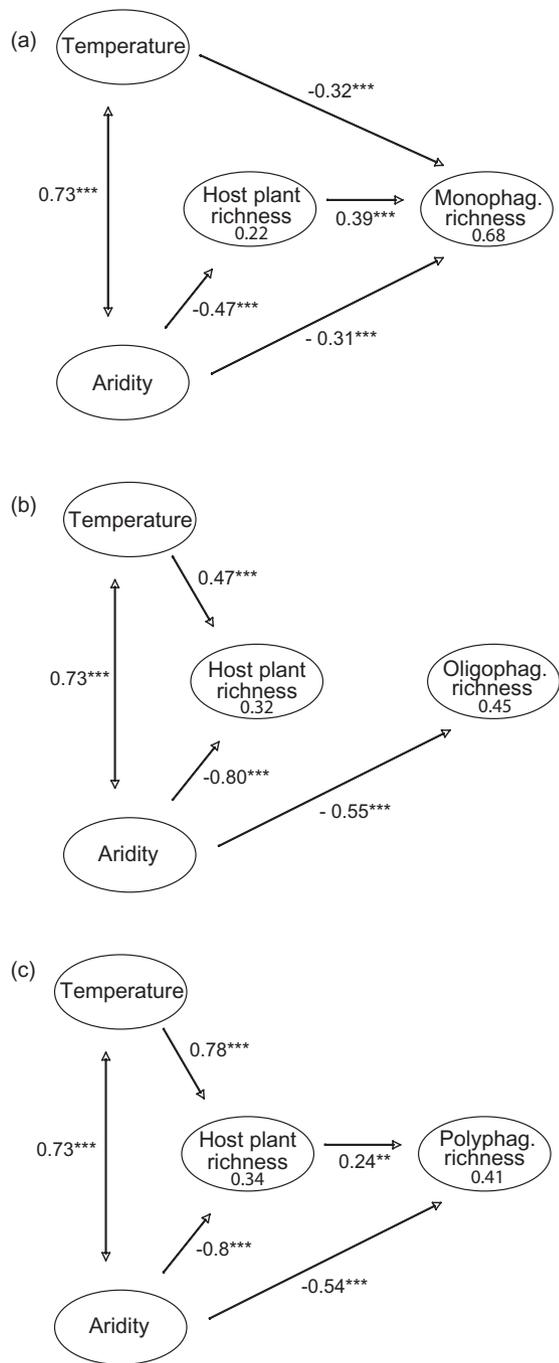


Figure 3 Structural equation model (SEM) obtained for (a) specialist species richness (monophagous) and generalist species richness (oligophagous (b) and polyphagous (c)). Standardized coefficients are provided for each path. The significance of coefficients is also indicated (***) $P < 0.001$). Numbers inside the circles indicate the proportion of explained variance of endogenous variables. Model fit summary: (a) model $\chi^2 = 0.086$; d.f. = 1; $\text{Pr}(> \text{ChiSq}) = 0.76$; root mean square error of approximation (RMSEA) = 0; goodness of fit index 0.99; Akaike's Bayesian information criterion (BIC) = -4.34. (b) Model $\chi^2 = 3.36$; $\text{Pr}(> \text{ChiSq}) = 0.07$; d.f. = 1; goodness of fit index = 0.98; RMSEA index = 0.17; BIC = -1.07; (c) $\chi^2 = 0.02$; $\text{Pr}(> \text{ChiSq}) = 0.88$; d.f. = 1; goodness of fit index = 0.99; RMSEA index = 0; BIC = -4.41.

that links species life histories with some basic assertions shared by all these mathematical theories of biodiversity.

Critically, we still need to explore empirically whether speciation dynamics in butterflies differs qualitatively between species located at opposite extremes of the specialist–generalist continuum, as per the predictions of the oscillation hypothesis of host-plant range and speciation (Janz & Nylin, 2008; Table 1). Our results and previous analyses reveal that population extinction rates differ between butterflies with specialist and generalist diets, being higher in the former group and clearly associated with a set of adaptive traits (Krauss *et al.*, 2003; Kotiaho *et al.*, 2005; Appendix S10). Moreover, in terms of diversification dynamics, recent empirical studies in other taxonomic groups effectively give support to the existence of oscillatory dynamics between contrasting life-history forms, with rapid evolutionary shifts in dispersal capacity and changes in multiple adaptive traits such as diet breadth and other lineage-specific life-history traits (Hoberg & Brooks, 2008; Janz & Nylin, 2008; Van Bocxlaer *et al.*, 2010; Jahner *et al.*, 2011; Janz, 2011). In addition, available empirical and theoretical evidence suggests that phenotypically plastic responses, environment-specific gene expression and modularity in regulatory and developmental networks may play a key role in specialist–generalist evolutionary transitions and associated diversification processes (Janz & Nylin, 2008; Pfennig *et al.*, 2010; Carnicer *et al.*, 2011; see Appendix S11 for an extended discussion and complementary references). Overall we conclude that the explicit consideration of multiple adaptive traits along inter-specific continua provides an integrative framework linking life-history variation and genetic variation, population trends and spatial distributions of butterfly populations.

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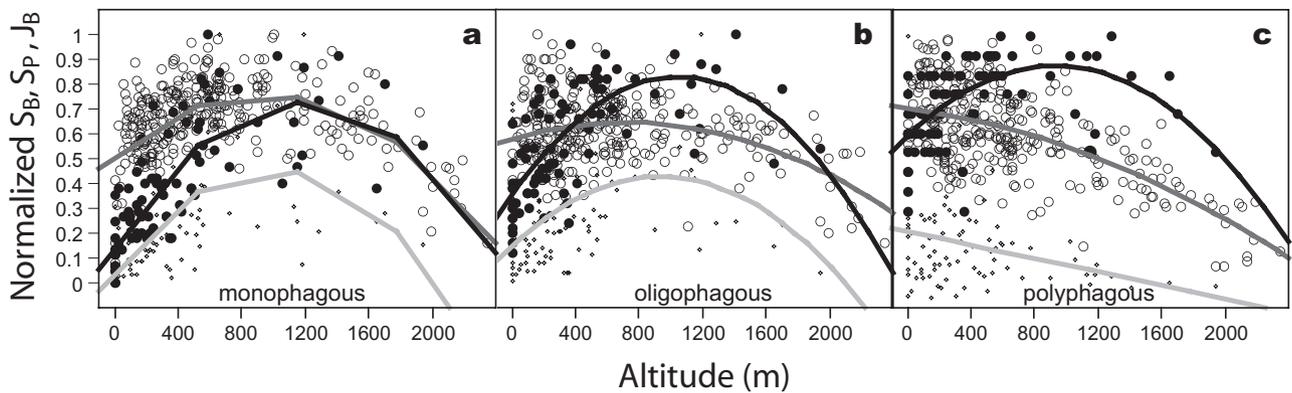


Figure 4 Altitudinal variation of host-plant species richness (dark grey line, white dots); butterfly species richness (black line, black dots) and the total number of individuals at each locality (also termed community size, light grey line, black crosses) for (a) monophagous, (b) oligophagous and (c) polyphagous butterfly species. Altitudinal tendencies were fitted using quadratic polynomial regression (JMP package; version 7).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

- Appendix S1** Butterfly species recorded in the study, host-plant trophic group and TRIM population trends.
- Appendix S2** Phylogenetic relationships between the butterfly species present in Catalonia.
- Appendix S3** Supplementary methods.
- Appendix S4** A scheme of the structural equation models (SEMs) for species spatial distribution ranges.
- Appendix S5** List of species, F_{ST} values and sources from which data were extracted.
- Appendix S6** List of species and specimen data that were sequenced to obtain the average Kimura two-parameter genetic distances between Catalonia and Romania.

Appendix S7 Extended results of the principal component analyses (PCAs) of the adaptive trait continuum.

Appendix S8 Standardized major axis regressions between phenology, dispersal capacity, diet breadth and habitat aridity breadth.

Appendix S9 Phylogenetic signal observed in several butterfly traits and species-specific habitat variables.

Appendix S10 Comparison of the means of range, density, coefficient of variation of species richness and first axis PCA scores among trophic groups.

Appendix S11 Supplementary discussion.

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BIOSKETCHES

Jofre Carnicer is interested in species richness gradients, evolutionary ecology, plant–animal networks, global change biology and sustainability science.

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