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General declines in Mediterranean butterflies over the last two decades are modulated by species traits

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Abstract

Species' responses to environmental changes are highly idiosyncratic and context-dependent. Although intrinsic traits (i.e. those that define species niches) may play a key role, little empirical evidence exists regarding their relationship to demographic responses. We used data for 66 butterfly species representing five ecological and two life-history traits to study the effect these factors have on population growth rates and variations in populations. Using a novel methodological approach, we provide here improved estimates of population change. Our results reveal declines in 70% and increases in 23% of the studied species, clear evidence of more serious population declines in Catalan butterflies than those that have previously been reported. Declines were associated with species' degree of habitat specialisation and the number of generations. For all species, fluctuations were greater within than between years and, on average, the latter was 1.5 times greater. Our results indicated that habitat specialists and multivoltine species are more likely to suffer severe annual fluctuations in population abundance; and that multivoltine species and extreme larval specialists had the most marked fluctuations within seasons. We also found higher resilience to environmental changes in generalist species, which is concordant with biotic homogenisation in disturbed communities. However, amongst the declining species there were also many generalists, which indicates a potential general reduction in this group that goes beyond faunal homogenisation. Given butterflies are biodiversity indicators, these patterns are a possible reflection of an overall impoverishment in biodiversity.

Keywords

Population trends, specialization, voltinism, species traits, butterflies, Bayesian hierarchical modeling

1. Introduction

Understanding the pressures affecting species population dynamics is a central issue in ecology and management, especially when the aim is to safeguard biodiversity (Sutherland et al. 2013). Pressures provoked by global change have accelerated the decline of many species (Vitousek 1997, Chapin et al. 2000, Vitousek et al. 2008), with some facing or undergoing extinction (Butchart et al. 2010, Pimm et al. 2014). In particular, climate change and habitat transformation (i.e. habitat loss and fragmentation) are among the main pressures exerted by global change that species are having to confront (Thomas et al. 2004a, Visconti et al. 2015).

Several studies have suggested that certain intrinsic ecological (i.e. those that define species ecological niches) and life-history traits predispose a species to respond distinctly to specific environmental pressures (Krauss et al. 2010, Murray et al. 2011, González-Suárez and Revilla 2013). For instance, species with better dispersal ability can shift their ranges faster than those with less capacity to disperse. This is an advantage in areas in which climate change is provoking asynchronies between the species niche and the environment (e.g. Croxall et al. 2002, Butchart et al. 2010, Chen et al. 2011). Species whose traits enable them to cope well with current pressures are expected to persist while the others might face declines and, eventually, local extinction. It is therefore not surprising that an increasing number of studies have evaluated the relationship between species traits and their responses to environmental pressures.

Previous studies have quantified these responses as changes in species richness and distributions for a wide range of taxa (e.g. Thuiller et al. 2008, Stefanescu et al. 2011a, Eskildsen et al. 2015), or have evaluated extinction probabilities or vulnerability (e.g. González-Suárez and Revilla 2013; Fernández-Chacón et al. 2014). However, few empirical studies have actually addressed demographic trends (Dapporto and Dennis 2013, Curtis et al. 2015), in part because of the difficulty in gathering high-quality data at relevant spatial and temporal scales. The recent upsurge in citizen-science projects has provided a useful way of obtaining the data needed for this kind of analysis (Schmeller et al. 2009, Devictor et al. 2010).

In this paper we examine the relationship between ecological and life-history traits, and demographic trends in a set of butterfly species. To do so, we used empirical count data gathered by a volunteer-based project, the Catalan Butterfly Monitoring Scheme, over 20 years in the Mediterranean region of north-eastern Spain. Butterflies are good indicators of biodiversity (Thomas 2005) and respond quickly to climate change and habitat transformation (Stefanescu et al. 2003, Thomas et al. 2004b, Krauss et al. 2010), thereby minimising – in comparison, for example, to plants and birds – the demographic time lag inherent in extinction debts (Krauss et al. 2010, Devictor et al. 2012, but see Sang et al. 2010). Therefore, butterfly demographic patterns in relation to species intrinsic traits can contribute to a better understanding of how a wide range of organisms (e.g. insects and other short-lived organisms) respond under such pressures.

To gather species demographic patterns we estimated (i) their population growth rate, i.e. the direction of the population trend (positive, stable or negative) and its strength, and (ii) the population variation, i.e. the dispersion of temporal changes in population numbers due to intrinsic (density-dependence processes) and external (cyclic or stochastic) factors.

We hypothesised that habitat specialisation will decrease population growth rate but increase population variability (hypothesis 1), an idea that is based on previous studies suggesting the existence of a relationship between this trait and population trends in butterflies (e.g. Stefanescu et al. 2011a; see Dapporto and Dennis 2013 for a comprehensive discussion). Nevertheless, other traits besides habitat specialisation could also influence demographic trends as the species respond to global change. For instance, dispersal ability in fragmented landscapes is directly related to colonisation and the persistence of butterfly populations (Fernández-Chacón et al. 2014). Therefore, we predicted that better dispersal ability will increase growth rate and reduce population variability (hypothesis 2). Furthermore, during a period of climate warming, we would expect thermophilous species to have more positive population trends and less population variability than those adapted to colder climates (as seen in birds; e.g. Stephens et al. 2016) (hypothesis 3). In addition, traits influencing butterflies' responses to increasing temperatures may also be important for explaining population trends (e.g. Diamond et al. 2011). A series of studies have suggested that an increase in the number of generations per reproductive season (i.e. the production of extra generations) occurs under climate warming, although its effect on populations remains unclear (e.g. Altermatt 2010, Van Dyck et al. 2015). Intuitively, a positive effect is expected since a larger proportion of adults will develop and reproduce during the season and so we hypothesised that there will be a higher growth rate in multivoltine than in univoltine species (hypothesis 4). Finally, we also predicted more positive trends and less variation in species overwintering in mature (pupa and adult) than in immature stages (egg and larva; hypothesis 5) given previous findings that suggest that species overwintering in the egg stage or as unfed neonate larva are currently undergoing the most serious declines (Breed et al. 2012).

2. Material and Methods

2.1. Study area and data collection

The study area was the Mediterranean region of Catalonia, Menorca (north-east Spain) and Andorra. This area is a biodiversity hotspot in which butterfly species are threatened by climate warming (e.g. increasing aridity; Stefanescu et al. 2011a) and habitat transformation (e.g. the abandonment of traditional land use and increasing urbanisation; Herrando et al. 2015).

Data were obtained from monitoring surveys carried out in 1994–2014 as part of the Catalan Butterfly Monitoring Scheme (CBMS; see: www.cbms.org) and the Andorran Butterfly Monitoring Scheme (BMSAnd; see www.iea.ad/bmsand). Both schemes consist of a network of sites in which visual counts of adult butterflies along transects are undertaken by volunteers every week between March and September (i.e. the whole flight period of most species). Transects are fixed routes of about 2 km in length and 5 m in width, which are divided into shorter sections corresponding to homogeneous habitat types (average section length: 186 m, median: 162 m, range: 20–871 m). The transects used in our study (n = 116) are located at 0–1650 m a.s.l. and cover a comprehensive range of environmental conditions (Fig. A.1). Although the number of surveyed transects varied between years, an important fraction remained stable throughout the whole recording period (for further details, visit www.catalanbms.org). Nevertheless, our modeling approach allowed us to assess species abundance at sites in years in which surveys were not performed via updating with the Markov Chain Monte Carlo (see next section).

2.2. Species selection and modeling approach

A total 183 species were sampled, of which we selected 82 species representative of a diverse range of ecological and life-history traits (Table A.1) and regularly recorded across all years and sites.

To test our hypotheses, we applied an open-population binomial mixture Bayesian hierarchical model (Kéry et al. 2009). This model estimates abundance over time using count data from open populations corrected by the imperfect detection inherent to observational error (see full model description in Appendix B and R code in Appendix C). In previous studies (e.g. Stefanescu et al. 2011b; Herrando et al. 2015), population trends were calculated via the widely used TRIM software (Pannekoek and Strien 2005). Nevertheless, this methodological approach does not take into account the detection probability that observational counts are subject to or its variation over time. This could mask real abundances and temporal trends in populations and their drivers (Kéry 2004, Kéry and Plattner 2007, Kéry et al. 2009).

For each species, abundance was set as time and section specific, and its estimation was extended to include the relationship with the population growth rate (r_{sp}) and the seven major habitat types in the area (meadows, forests, arable crops, woody crops, gardens, ruderal vegetation, and non-suitable habitat). Habitat types were not significantly correlated and were expressed as a percentage of habitat per section (Table A.2). The detection probability – with which species abundance was corrected – was set as time-specific.

The time step was set as intervals of two weeks to account for seasonality in both the abundance and the detection probability, and to include a closure period for the repeated counts used to analyse detectability. Two-week intervals have been postulated as an acceptable closure period for butterfly species richness (Kéry and Plattner 2007). Although slight changes in butterfly abundance may occur at this resolution level, we consider that they are small enough to ensure that our model remains valid.

2.3. Temporal population variability of species abundance

Population variability was assessed using the coefficient of variation (i.e. the dispersion around the mean), a relative measure of variation that is independent of the population size and so can be used to compare species. We used two temporal windows: seasonal (i.e. within years; CV_W) to include the seasonality (excluding the seasonality related to non-surveyed months: October-February), and inter-annual variation (i.e. between years; CV_B). Seasonal variation was defined as the ratio of the standard deviation to the mean of the time series of abundance within each year, which gave a total of 20 values per species (one for each of the 20 years recorded). To obtain the inter-annual variation without including the seasonal variation in the calculation, we calculated the standard deviation and mean abundance per year and defined CV_B as their ratio, which generated a single value for each species.

2.4. Species ecological and life-history traits

For each species, we used a total of seven intrinsic traits divided into five ecological (i-v) and two life-history (vi-vii) traits: (i) adult habitat specialisation measured using the Species Specialisation Index (SSI), quantified as the coefficient of the variations in the average density in the available habitat, as defined by Julliard et al. (2006); (ii) larval trophic specialisation, ranging from 1 (extreme specialists) to 3 (extreme generalists), following Stefanescu et al. (2011a) and Fernández-Chacón et al. (2014); (iii) the degree of preference for forests versus open areas, as evaluated by Herrando et al. (2015); (iv) average forewing length (measured in mm), which has been shown to act as a satisfactory proxy for dispersal ability in butterflies (Kuussaari et al. 2014; but see Sekar 2012); for this measurement, data were extracted from García-Barros et al. (2013) with sexes pooled given their close correlation (Fig. A.2); (v) the Species Temperature Index (STI), as defined in Schweiger et al. (2014); (vi) voltinism, categorised as uni-, bi- or multivoltine (≥ 3 generations/year), according to Stefanescu et al. (2011a) and Fernández-Chacón et al. (2014); and (vii) overwintering stage, either immature (i.e. egg or larva) or mature (i.e. pupa or adult), with a third category for migratory species (i.e. not overwintering in the region), as per García-Barros et al. (2013).

2.5. Statistical analyses

The effects of the seven species traits on the growth rate estimates were tested using linear regressions (i.e. the growth rate fitted to a Gaussian distribution).

Both seasonal and inter-annual population variability were analysed in terms of the described traits using a Generalised Linear Mixed Model (GLMM) and a Generalised Linear Model (GLM), respectively. These two models were fitted to a Gamma distribution given that the coefficients of variation were positive, continuous, skewed and of increasing variance; species identity was set as a random effect.

For each analysis, a global model was first defined containing all the above mentioned covariates and potential interactions. Model selection was carried out by discarding terms sequentially. In the case of the linear regression analysis model, selection was based on the adjusted r-squared to take into account the number of observations and of model parameters. Model selection for the generalised models was based on AICc selecting those models differing from Δ AICc< 2. Model averaging and estimates weighting for the most likely models were obtained via R package MuMIn (Bartoń 2014). Analyses were performed in R using package lme4 (Bates et al. 2014).

Temporal changes in the detection probability were tested in relation to species voltinism. We used a Generalised Additive Mixed Model (GAMM), with two-week intervals throughout the year (1–15) set as the non-lineal term and species as a random effect, to account for the inherent specific variability. The detection probability was fitted to a Gamma distribution with an inverse link. Analyses were performed in R using package gamm4 (Wood 2014).

3. Results

Sixteen of the 82 regularly recorded species failed to converge in our modeling approach (Table A.3). The remaining 66 species were all present in more than 10 transects, which conferred inferential strength on the analysis (e.g. Oliver et al. 2010). Annual population growth rates ranged between -0.11 and 0.04 ($r_{average}$ = -0.02); 15 species (22.7%) had a significantly positive rate, five (7.6%) were stable and 46 (69.7%) had a negative rate. Significance was based on the exclusion of zero values in the Bayesian Credible Interval values at 95% (Appendix D). When testing for significance using a conventional Poisson regression, only one species (*Euphydryas aurinia*) was considered as stable (r = 0.00035, z = 0.92, p = 0.36; Appendix D).

3.1. Population growth rate and species traits

The best models for the estimated population growth rates included habitat specialisation, the degree of preference for forests versus open areas, wing length and voltinism (Table A.4).

Population growth rates decreased with the increase in habitat specialisation, thereby indicating lower population growth rate in habitat specialists (p = 0.021, Table 1a, Fig. 1b). Nevertheless, several generalist species did also show declines (e.g. 71% of those species with SSI <1.5, for range, median and average values of 0.62–2.18, 1.23 and 1.24, respectively). Multivoltine species had a steeper negative rate than both uni- and bivoltine species (Table 1a, Fig. 1b). Results also suggested steeper negative rates in forest species; however, this effect was not significant. The effect of wing length – similarly not significant – was nearly negligible despite being included in the best models (Table 1a).

3.2. Temporal variation of abundance and species traits

Seasonal variation was greater than inter-annual variation in species abundance (range = 0.004–1.54 and 0.05–0.72, respectively), although the mean value of the inter-annual variation was 1.5 times higher (average = 0.14 and 0.22 for seasonal and inter-annual variation, respectively; Fig. A.3).

Although 38% of the seasonal variation was species-specific, voltinism was the main factor involved, as variation increased from uni- to multivoltine species (all $p < 0.0001$; Table 1b, Fig. 2a). Seasonal variation was lesser in larval trophic generalists (i.e. larval specialisation 3, $p = 0.006$) and species overwintering in an immature stage ($p = 0.003$; Table 1b, Fig. A4). Habitat specialisation and the degree of preference for forests versus open areas were also included in the best models but without any significant relationship (Tables 1b and A.5a).
Voltinism and habitat specialisation were the main factors defining inter-annual variation, both leading to increased values ($p < 0.04$; Table 1c, Fig. 2b). The degree of preference for forests versus open areas was included in the best models (Table A.5b), increasing the inter-annual variation non-significantly (Table 1c). No other traits were included in the best models (Table A.5).

3.3. Temporal changes in detection probability

The detection probability increased linearly over the years (Estimate = -0.006) for all uni-, bi- and multivoltine species. Although there were no differences between these species ($p_{interactions} > 0.11$), the detection probability was constantly lower for univoltine species (Q1 = 0.01; Estimate = 1.12, $p < 0.001$; Fig. 1a).

4. Discussion

This study reveals negative trends in 70% of the studied species, indicating a severe decline among Mediterranean butterflies. Population trends are partly predicted by the ecological and life-history traits of the species. In particular habitat specialisation and voltinism have the highest influence, whilst other traits have a marginal or null effect.

4.1. Population trends and species traits

Population growth rates decreased with increasing habitat specialisation. This finding agrees with the steeper declines detected in populations of butterfly specialists (compared to habitat generalists) in the same region (Stefanescu et al. 2011b; Carnicer et al. 2013) and in other European countries (van Swaay et al. 2006, Eskildsen et al. 2015, Curtis et al. 2015). Habitat generalists have a wider range of available resources that can fulfil their needs, which give them an advantage in environments that are being transformed. Under a context of global change, this may in turn lead to a biotic homogenisation of natural communities, i.e. the substitution of many specialists by a few generalist species, a process that is one of the main drivers of declines in biodiversity worldwide (McKinney and Lockwood, 1999). This effect has been noted to occur in the butterfly fauna in several European countries (e.g. Ekroos et al. 2010, Ockinger et al. 2010).

Despite the negative relationship between habitat specialisation and population rates, many generalist species were also found to be in decline. This situation is comparable to some extent to other areas affected by severe anthropic pressure (Leon-Cortes et al. 1999, 2000, Van Dyck et al. 2009). Further investigation is needed to evaluate whether or not these general negative trends can be explained by the interaction of environmental pressures such as climate change and habitat transformation, and by ecological traits. For example, Stefanescu et al. (2011a) suggested that habitat generalist species are most affected by the increase of aridity and landscape intensification in lowlands, while specialists are more affected by land abandonment and climate warming in mountain areas.

In contrast to our intuitive expectation, uni- and bivoltine species registered similar trends, while multivoltine species had significantly steeper declines. For example, in Germany multivoltine species dominate butterfly communities when land use intensification is severe (Börschig et al. 2013). However, multivoltine species may be the most negatively affected by climate change in the Mediterranean when their last summer generations have to confront the most rigorous conditions and extreme drought events. To a degree, this situation is comparable with the recent decline of the generalist multivoltine butterfly *Lasiommata megera* in central Europe, where the addition of an extra generation represents a developmental trap resulting in high larval mortality (Van Dyck et al. 2015). Likewise, multivoltinism could expose a species to detrimental events several times in the same season and thus lead to a severe decline, a scenario that could become more relevant given longer and more frequent extreme climatic events, as predicted by Giorgi and Lionello (2008) for the Mediterranean region.

Strikingly, the degree of preference for forests versus open areas was not significant for either population growth rate or variation, which may indicate that we failed to capture this effect properly for the set of studied species. In a recent study this preference was found to be advantageous both for butterflies and birds, as woodland species had more positive population trends (Herrando et al. 2015). Nevertheless, in this study trends were evaluated in a subset of transects covered by natural vegetation affected by land abandonment (n = 74) rather than in all available transects, as was the case in our study (n = 116). The addition of other types of habitat transformations such as increasing urbanisation probably diluted the positive trend of forests in natural areas at a regional scale.

Wing length, which we considered as a proxy for dispersal, had nearly no effect in our models. However, some authors have questioned its relationship with dispersal ability (see Sekar 2012). In addition, the fact that the Species Temperature Index did not predict population trends may initially be surprising given the prediction of general declines in cold-adapted species and the opposite trends in warm-adapted species in the current context of climate warming (e.g. Devictor et al. 2012). However, our results confirm some previous analyses at site level that show that population trends are in fact independent of the thermal niche of the species (Stefanescu et al. 2011b). Indeed, our findings suggest that interactions with other climatic and non-climatic factors may be more important for explaining population trends (Oliver et al. 2015, Settele and Wiemers 2015).

4.2.Temporal population variation and species traits

Although seasonal variation was greater than inter-annual variation, average values showed the opposite pattern. Both measures were positively affected by voltinism, that is, population variation at differing time scales was higher in multivoltine species, which suggests that there was a higher risk of strong fluctuations.

To a lesser degree, seasonal variation was affected by extreme larval trophic generalism and the overwintering stage. The lower variability in larval trophic generalism supports the hypothesis of specialisation traits relating to higher sensitivity to environmental changes. Likewise, fewer seasonal variations were found in species overwintering in immature stages (egg or pupa), which could indicate a major buffering capacity in immature stages against extreme climatic events, a result that contrasts with the findings of Breed et al. (2012). Indeed, species overwintering in mature stages will emerge earlier in the spring, thereby exposing themselves to extreme climatic events at the beginning of the season that could provoke fluctuations in populations.

In addition to voltinism, inter-annual variation was also affected by habitat specialisation, with habitat specialists showing consistently greater variation than habitat generalists. This interesting finding – that we interpret to be a reflection of the greater sensitivity of habitat specialists to environmental perturbations – highlights how difficult it is for these species to adapt to the ongoing environmental transformations (in both climate and landscape) in the region. This agrees with the differences in the relative impact of environmental perturbations on specialist and generalist species richness (Stefanescu et al. 2011a).

4.3. Modeling approach: open-population Binomial Hierarchical Bayesian

The percentage of declining species obtained with our approach was almost two times higher than previously obtained with TRIM for the region (Fig. A.5; Stefanescu et al. 2011b; Carnicer et al. 2013).

Different estimates of abundance between models are to be expected whenever trends in detection probability occurred, as our model accounted for the error in the observational process while TRIM does not. In the later model type, abundances are likely to be underestimated when the detection probability is low. The increasing probability of detection over time in our data (Fig. 1A) means that population trends will be underestimated when the population trend is negative because there will be fewer differences between the (under)estimates of abundances during the first years of surveys and the estimates during the latter years. However, they will be overestimated when the population trend is positive since there will be greater differences between the (under)estimates of abundances during the first years of surveys and the estimates during the latter years. In our case, the detection probability increased over time, probably due to the lower amount of experience of the volunteers at the start of the project. Thus, our estimations gained in accuracy by adding the detection probability. The benefit of accounting for the detection probability has been demonstrated by Dail and Madsen (2011) and Pellet et al. (2012).

The differences in the results obtained using our approach and TRIM could also be explained by the different parameterisation of the time scale of the models (every two weeks versus annual) and the model structure (lineal versus non-lineal). Therefore, although we recommend the use of models that take into account the detection probability to reduce uncertainty caused by observational error, we are unable to endorse any particular approach until further comparisons between these two methodologies using equal parameterisations have been conducted.

5. Conclusions

Our results indicate a very serious general decline of the butterfly fauna in the western Mediterranean, affecting 70% of the studied species. Although this decline also covers many generalist species, overall the highest vulnerability in terms of population trends was found for specialist and multivoltine species. Taken together with previous work, our analysis suggests that global change – including land abandonment and intensification and climate change – is behind the observed negative trends (Stefanescu et al. 2003, 2011a,b; Herrando et al. 2015). Moreover, changes in land cover and more extreme climatic events are expected to exacerbate these serious declines in the future. Furthermore, given that butterflies are also regarded as good indicators for other terrestrial insects (Thomas 2005; but see Musters et al. 2013), the observed patterns may also be indicative of global biological impoverishment. Under this scenario, local habitat management (i.e. conservation aimed at increasing habitat availability and connectivity) focused on the requirements of declining species might help mitigate these negative trends (Curtis et al. 2015) or even potentially revert population declines (e.g. Dapporto and Dennis 2013).

Finally, this study also highlights the potential of models that take into account detection probability and provides empirical evidence for their robustness and usefulness with volunteer-based projects and monitoring programs. Therefore, we recommend their use if temporal or spatial variation in the observational error is suspected to occur.

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Fig 1. Observed (dots) and model derived predictions (lines) for (a) the detection probability in relation to years; (b) population growth rates (*r*) in relation to the Species Specialisation Index (SSI) for univoltine (black), bivoltine (yellow) and multivoltine species (blue). In both figures, $n_{univoltine}$ = 30, $n_{bivoltine}$ = 11 and $n_{multivoltine}$ = 25. Parameters were estimated using weighted estimates of the best models. Continuous lines relate to the estimated fit that sets all the other covariates as constant at their median value; dashed lines denote the 95% confidence intervals.

Fig 2. (a) Violin plots for the seasonal coefficient of variation in the abundance of the butterfly species (CV_W) in relation to their voltinism, grey shapes show the density distribution of the y-axis covariate, grey circles stand for the median, black bars for the quartiles Q1 and Q3; (b) observed data (dots) and model-derived predictions (lines) for the inter-annual variation (CV_B) in relation to the Species Specialisation Index (SSI) for univoltine (black squares), bivoltine (yellow circles) and multivoltine species (blue triangles). In both figures, $n_{univoltine}$ = 30, $n_{bivoltine}$ = 11 and $n_{multivoltine}$ = 25. Parameters were estimated using weighted estimates of the best models. Continuous lines relate to the transformed estimated fit setting all the other covariates as constant at their median value; dashed lines denote the 95% confidence intervals.

Table 1. Weighted parameter estimates of the effect sizes and the associated standard errors of the species traits retained in the best models for (a) population growth rates, (b) the seasonal (CV_W) and (c) inter-annual (CV_B) coefficients of variation in the abundance of the butterfly species. Models for CV were fitted to a Gamma distribution with an inverse link (i.e. estimates are produced with an inverted sign); estimates are expressed within this distribution. Significant p values are marked in italics.

Parameter	Estimate	Std. Error	t or z value	p value (H_0 = Estimate = 0)
(a)				
Intercept: vol-univoltine	8e-4	9e-4	0.837	0.403
vol-bivoltine	1e-4	6e-4	0.170	0.865
vol-multivoltine	-0.001	4e-4	2.163	*0.031*
SSI	-0.001	6e-4	2.304	*0.021*
of-e	-0.007	0.012	0.558	0.577
wl	4e-4	1e-5	0.274	0.784
(b)				
(Intercept): ls-1, ow-immature, vol-univoltine	6.003	0.457	13.127	*<2e-16*
vol-bivoltine	-1.585	0.399	-3.970	*7e-5*
vol-multivoltine	-1.769	0.325	-5.444	*1e-7*
SSI	-0.200	0.388	0.515	0.607
ls-2	0.554	0.325	1.702	0.088
ls-3	1.099	0.403	2.724	*0.006*

of-e	12.025	8.475	1.419	0.156
ow-mature	-0.957	0.326	2.934	0.003
ow-migratory	0.113	0.683	0.165	0.869
random effect	Variance	Std.Dev.	Residual	Std.Dev.
Species	0.380	0.617	0.436	0.660
(c)				
Intercept: vol-univoltine	8.686	1.169	7.285	*<2e-16*
vol-bivoltine	-1.764	0.842	2.057	*0.039*
vol-multivoltine	-2.423	0.715	3.325	*8e-4*
SSI	-2.231	0.722	3.031	0.002
of-e	-16.843	17.755	0.939	0.348

SSI: Species Specialisation Index; ls: larval trophic specialisation; of-e: open-forest estimate; wl: wing length; STI: Species Temperature Index; vol: voltinism; ow: overwintering stage