



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, among 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.

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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 (C.D. Thomas et al. 2004; 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

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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; J.A. Thomas et al. 2004; 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),

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