

Relative importance of density-dependent regulation and environmental stochasticity for butterfly population dynamics

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Abstract The relative contribution of density-dependent regulation and environmental stochasticity to the temporal dynamics of animal populations is one of the central issues of ecology. In insects, the primary role of the latter factor, typically represented by weather patterns, is widely accepted. We have evaluated the impact of density dependence as well as density-independent factors, including weather and mowing regime, on annual fluctuations of butterfly populations. As model species, we used *Maculinea alcon* and *M. teleius* living in sympatry and, consequently, we also analysed the effect of their potential competition. Density dependence alone explained 62 and 42% of the variation in the year-to-year trends of *M. alcon* and *M. teleius*, respectively. The cumulative Akaike weight of models with density dependence, which can be interpreted as the probability that this factor should be contained in the most appropriate population dynamics model, exceeded 0.97 for both species. In contrast, the impacts of inter-specific competition, mowing regime and weather were much weaker, with their cumulative weights being in the range of 0.08–0.21; in addition, each of these factors explained only 2–5% of additional variation in *Maculinea*

population trends. Our results provide strong evidence for density-dependent regulation in *Maculinea*, while the influence of environmental stochasticity is rather minor. In the light of several recent studies on other butterflies that detected significant density-dependent effects, it would appear that density-dependent regulation may be more widespread in this group than previously thought, while the role of environmental stochasticity has probably been overestimated. We suggest that this misconception is the result of deficiencies in the design of most butterfly population studies in the past, including (1) a strong focus on adults and a neglect of the larval stage in which density-dependent effects are most likely to occur; (2) an almost exclusive reliance on transect count results that may confound the impact of environmental stochasticity on butterfly numbers with its impact on adult longevity.

Keywords Inter-specific competition · *Maculinea* · Mark-recapture · Mowing regime · Weather

Introduction

Understanding factors that shape population trends is a key issue in both theoretical and applied ecology. In classic early papers (e.g. Nicholson 1933; Andrewartha and Birch 1954) the authors often saw the problem in ‘black-and-white’, advocating the decisive role of either intrinsic regulation or external environmental drivers in population dynamics. Nowadays, it is generally agreed that both groups of factors act jointly, and the debate is about their relative impact (Sinclair and Pech 1996; Stenseth et al. 1998; Ranta et al. 2000; Benton et al. 2006). A strong effect of density-dependent regulation is widely accepted in vertebrate research (Fromentin et al. 2001; McKilligan

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2001; Patterson and Power 2002; Williams et al. 2003; Chase et al. 2005; Salvidio 2007). In contrast, population dynamics of invertebrates are believed to be influenced predominantly by environmental stochasticity (Hawkins and Holyoak 1998; Watt and Woiwod 1999; Larsson et al. 2000). In practice, the above statement refers to insects since few studies in other invertebrate taxa have managed to obtain time series that were long enough to allow a thorough analysis (Sibly et al. 2005). Based on long-term surveys of butterflies, which are the most frequently monitored insect group (Thomas 2005), it has been suggested that weather patterns are the crucial component of this environmental stochasticity (Ehrlich et al. 1972; Dempster 1983; Pollard 1988; Roy et al. 2001).

A major drawback of population dynamics studies carried out in the past is that few of them made an effort to quantify the impact of both density-dependent regulation and environmental stochasticity (Lewellen and Vessey 1998). Many focused on just a single factor, while typically stating or implying that other significant effects are likely, although these were not assessed (e.g. Lima et al. 1998; Williams and Liebhold 2000). Only recently, with the development of relevant methodological frameworks (Sinclair and Pech 1996; Rothery et al. 1997; Zeng et al. 1998; Chan et al. 2004) has there been progress in designing comparative studies that simultaneously evaluate the effects of density-dependent regulation and environmental stochasticity.

The aim of the study reported here was to assess the relative importance of density dependence versus density-independent factors, including weather and habitat management, for butterfly population dynamics. As model species, we used two specialist *Maculinea* butterflies occurring sympatrically at a site in northern Italy, which were surveyed with the mark-release-recapture technique. *Maculinea* species have been among the most intensively investigated butterfly species during the past two decades. As a result, many aspects of their biology are well known (Thomas and Settele 2004; Settele et al. 2005), which facilitates the interpretation of the factors affecting their year-to-year population changes.

Materials and methods

Study species

Butterflies of the genus *Maculinea* have highly specialised myrmecophilous life-styles. They are univoltine, with adults flying in summer months. Eggs are laid on specific foodplants, which typically also serve as primary nectar sources for the adults (Elmes and Thomas 1992; Thomas 1995). Larvae feed on the foodplants for approximately the

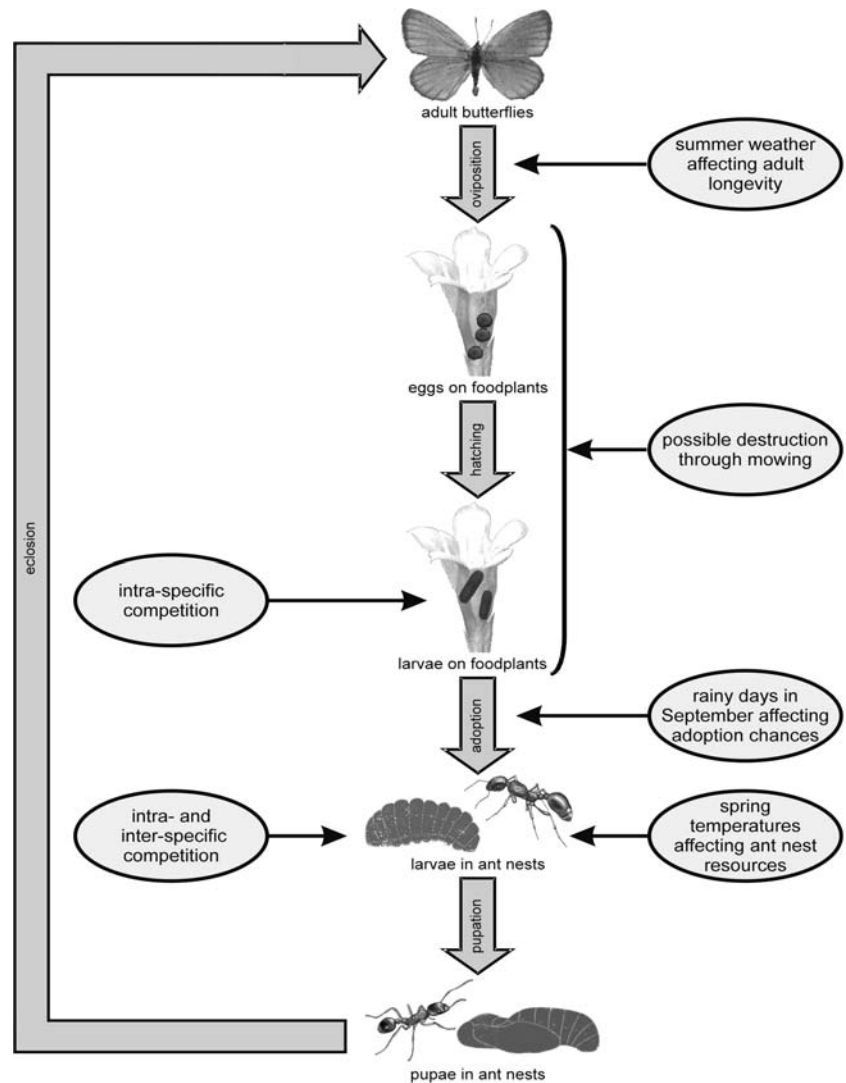
first 3 weeks, then spend the rest of their life as parasites in *Myrmica* ant nests, either preying on the ant brood ('predatory strategy') or being fed by nurse ants ('cuckoo strategy') (Elmes et al. 1991; Thomas and Wardlaw 1992; Thomas 1995). The species that were the subject of our study were *M. teleius*, with the predatory strategy, and *M. alcon*, with the cuckoo strategy. As specific foodplants and specific *Myrmica* ant hosts are the two crucial resources for *Maculinea*, density-dependent as well as density-independent mortalities experienced during larval development in foodplants and ant nests are critical parameters for year-to-year population growth (Hochberg et al. 1992, 1994; Fig. 1).

The population dynamics of *Maculinea* may be complicated by larval polymorphism, i.e. the co-occurrence of 1- and 2-year developing larvae, which has been reported for several species in this genus (Thomas et al. 1998b; Schönrogge et al. 2000; Witek et al. 2006). The possible implication of this phenomenon is that the population size in a given year would be a function of not only that of the previous year, but also of that 2 years before. However, larval polymorphism is apparently restricted to northern and mountain localities (Scandinavia, The Netherlands, Poland, the Alps, the Pyrenees), and it has not been observed in the central and southern parts of the distribution range of *Maculinea* butterflies in Eurasia (France, Italy, Hungary, southern Russia, central Asia) (P. Nowicki et al., unpublished data). In the populations investigated in our study, we always found only a single cohort of *Maculinea* larvae when examining ant nests. In addition, the assertion of the absence of larval polymorphism in these populations is well supported by unimodal patterns (within each sex) of adult recruitment during the flight period; for polymorphic populations, bimodal patterns should be expected (compare Nowicki et al. 2005c). Consequently, we did not consider larval polymorphism in our population dynamics models.

Study area

The field study was conducted at the Caselette site near Turin, northern Italy (45°07'N; 07°29'E; 360 m a.s.l.), which is a 2.9-ha wet meadow dominated by *Molinia caerulea* and constitutes a part of the NATURA-2000 site 'Monte Musine—Laghi di Caselette' (IT1110081). Despite its status, however, it must be stressed that the site has not been the focus of management specifically aimed at conservation. Certain parts of the site are mown for hay by local landowners. The mowing pattern remains spatially consistent, with exactly the same meadow fragments, just slightly smaller or larger, being mown each year. The proportion of mown area ranged between 55 and 69% during the duration of the study. Mowing is carried out

Fig. 1 Schematic representation of the life-cycle of *Maculinea* butterflies and major potential drivers shaping their population dynamics. Note: intra-specific larval competition on foodplants is unlikely to occur at the investigated Caselette site due to foodplant overabundance



mostly from July to early September, which is an unfavourable period for *Maculinea* because their eggs and larvae developing on foodplants are then destroyed.

The Caselette site is characterised by very high densities of *Gentiana pneumonanthe* (1.55 m^{-2}) and *Sanguisorba officinalis* (1.62 m^{-2}), which are the foodplants of *M. alcon* and *M. teleius*, respectively. Since both plants have, on average, approximately 12 flowers per plant (authors' unpublished data), and female fecundity can be safely assumed as 150 eggs in the case of *M. alcon* and twofold lower, i.e. 75 eggs, in the case of predatory *M. teleius* (Hochberg et al. 1992; Thomas et al. 1998a; note that other authors, such as Maes et al. 2004 and Meyer-Hozak 2000, consider even lower estimates more realistic), a substantial overabundance of foodplant flowers is assumed to be available for oviposition. The estimated number of flowers per single *Maculinea* egg was approximately 5 in 2002, when both species reached their highest numbers, and up to 43–63 (*M. alcon*–*M. teleius*) in other years. The above 2002

estimate for *M. alcon* is in good agreement with the number of eggs actually recorded on a random sample of 416 *G. pneumonanthe* plants (0.16 per flower). For *M. teleius* eggs, counting eggs is not feasible because this species lays its eggs deep within the inflorescences of *S. officinalis* flowers (Thomas et al. 1991). Certain plants may be preferred for oviposition over others due to their location, appearance or phenological differences (Figurny and Woyciechowski 1998; Bonelli et al. 2005; Nowicki et al. 2005d; Musche et al. 2006; Arnyas et al. 2006, 2009). However, even if the majority of eggs are concentrated on 30–60% of the foodplants, as found in our and other studies (Figurny and Woyciechowski 1998; Wynhoff 2001; Nowicki et al. 2005d, 2007; Arnyas et al. 2009), it still seems justified to conclude that the probability of larval competition on foodplants is negligible at the population scale, even though more than one egg may occasionally be laid on a single flower (as we sometimes observed for *M. alcon*). The above conclusion is concordant with the

findings of Elmes et al. (1996), who proved that for *M. rebeli*, the abundance of its *G. cruciata* foodplants becomes a limiting factor only below 1500 per hectare, i.e. at more than a tenfold lower density than recorded in Caselette.

The local host ant species of both *M.alcon* and *M.teleius* is *Myrmica scabrinodis*, which is, in fact, the only *Myrmica* species present at the Caselette site. The density of its nests can be estimated at about 0.55 m^{-2} —i.e. it is relatively high, but within the range found in similar studies (compare Wynhoff 2001; Griebeler and Seitz 2002; Maes et al. 2003; Glinka and Settele 2005). However, it has to be considered that only those nests that are large enough may support *Maculinea*: at least 350 ant workers are necessary to allow the development of a single *M.teleius* larva (Thomas and Elmes 1998). At the investigated meadow we roughly assessed the proportion of suitable ant nests at 20–40%, based on nest diameter as a proxy for the number of workers (G. Elmes, personal communication). Consequently, the effective density of ant nests constituting a resource for *Maculinea* is 2.5- to fivefold lower than the recorded density. The situation in which ant abundance is a limiting factor for *Maculinea* populations while foodplant abundance is not is the most typical for these butterflies (Wynhoff 2001; Nowicki et al. 2007; Anton et al. 2008; Batáry et al. 2009).

The *Maculinea* populations in Caselette are well isolated. The site is surrounded by woodlands and residential areas, and the distance to the nearest other site with (much smaller) populations of the two focal species is over 2 km. Taking into consideration the relatively low mobility of *Maculinea* butterflies (see review in Nowicki et al. 2005b), a significant impact of dispersal on the dynamics of the investigated populations is unlikely, although the occasional exchange of single individuals every few years cannot be excluded. It is worth noting that in Poland local populations have been shown to function as independent demographic units despite distances of only several 100 m separating them (Nowicki et al. 2007).

Mark-release-recapture survey

Populations of both species in Caselette were surveyed with mark-release-recapture (MRR) for 12 years between 1997 and 2008. Each year, the sampling was conducted with uniform intensity and covered the entire flight period, which lasted from mid-July to late August. Butterflies were captured on a regular basis by a single person between 1000 and 1600 hours on every second day (with very few exceptions caused by unfavourable weather). The data collected were analysed with the Cormack-Jolly-Seber type constrained models (Schwarz and Arnason 1996; Schwarz and Seber 1999) using the MARK 4.3 program (White and Burnham 1999). The fit of the Cormack-Jolly-Seber type

models was assessed separately for each species and year with the Akaike Information Criterion corrected for small sample size (AIC_c) (Akaike 1973; Hurvich and Tsai 1989). As recommended by Burnham and Anderson (2001), we subsequently selected the model with the smallest number of parameters from among the supported ones, i.e. those with AIC_c differing from the minimal one by less than 2. The outcome of the above routine was straightforward, and the model $\phi(.)p(.)$ (i.e. the model with survival and capture probability equal for both sexes and constant over time) was selected in all cases. Equal survival is typical for adult butterflies, but equal capture probability is not necessarily so, because males are often captured more effectively than females (e.g. Watt et al. 1977; Sutcliffe et al. 1997; Kuras et al. 2000; Nowicki et al. 2005a). However, the strong performance of the model $\phi(.)p(.)$ in our study does not imply the lack of inter-sexual differences in capture probabilities but merely reflects the fact that these differences were negligible for the analysis of MRR data. Each year, males of both species were captured in slightly higher proportions than females; nevertheless, inter-sexual differences remained insignificant as capture probabilities of both sexes were relatively low. Using the model $\phi(.)p(.)$, we derived the seasonal population sizes of *M.alcon* and *M.teleius* over the investigated period according to the procedure described by Nowicki et al. (2005a).

Time-series analysis

The time-series obtained were analysed with two types of models: Gompertz type (Gompertz 1825), as applied by Rothery et al. (1997):

$$\ln(N_{t+1}/N_t) = \alpha + \beta N_t \quad (1)$$

and the Hassell type (Hassell 1975) in the simplified form of:

$$N_{t+1}/N_t = xr/(x + rN_t) \quad (2)$$

where N_t is the population size in a given year, while $r = \exp(\alpha)$ represents basic reproductive rate. Carrying capacity (K) for the above models can be estimated as $-\alpha/\beta$ and $x(r-1)/r$, respectively. To facilitate model fitting, which otherwise might lead to unrealistic parameter estimates, for r we assumed maximum year-to-year population growth rates to be those recorded, i.e. 3.29 for *M.alcon* and 4.16 for *M.teleius*. These figures were very similar to those obtained in an extensive study in Poland (3.0 and 4.3, respectively; Nowicki et al. 2007).

The reason for testing both types of models was that the Gompertz-type model is easier to interpret and thus more popular in population ecology, while the Hassell-type model seems to be more suitable for species with discrete non-overlapping generations (Hassell et al. 1976; Bellows

1981), such as most butterflies. For the Hassel-type model, we assumed only a single phase of density dependence, namely larval competition in ant nests (as in Nowicki et al. 2007), rather than the two phases adopted by Hochberg et al. (1992) in their HTE Hassel-type model. Our choice was based on the assessment that in the populations investigated, competition on foodplants is unlikely due to foodplant overabundance (see **Study Area** section for explanation).

The aforementioned basic models, which account only for density dependence, were subsequently made more complex through the inclusion of additional factors: (1) inter-specific competition defined as the density-dependent negative effect of the population size of the co-occurring *Maculinea* species (C_t); (2) mowing regime represented by the proportion of meadow area mown in a given year (M_t); (3) weather (W_t). The full models, with all of the factors included, reached the form of:

$$\ln(N_{t+1}/N_t) = \alpha + \beta N_t + \gamma C_t + \delta M_t + \varepsilon W_t \quad (3)$$

and

$$N_{t+1}/N_t = xr/(x + rN_t + yC_t) + aM_t + bW_t \quad (4)$$

Weather data were obtained from the Regional Agency for Environmental Protection in Piedmont (ARPA Piemonte). From among a wide range of possible weather parameters, we focused on those that appear potentially important for *Maculinea* butterflies, i.e. the number of hours of sunshine in July and August (W_{1t}), the number of rainy days in September (W_{2t}) and the number of days in spring (March–June) on which the average temperature exceeds 8°C (W_{3t}). The number of hours of sunshine in summer months was used as a measure of weather favourability during *Maculinea* flight period, which should affect adult oviposition performance. However, the effect of summer weather favourability is difficult to define with weather parameters, since both too cold and too hot weather as well as too wet and too dry conditions may be considered to be unfavourable for butterflies. Hence, in an alternative approach, we also applied adult longevity, calculated on the basis of MRR survival estimates as $\hat{e} = (1 - \hat{\phi})^{-1} - 0.5$, as a surrogate for summer weather favourability (W'_{1t}). Adult longevity is known to directly influence female fecundity in butterflies (Kemp and Rutowski 2004; Bauerfeind and Fischer 2008). Increasing number of rainy days in September is likely to negatively affect the chances of *Maculinea* larvae to be adopted by *Myrmica* ants, which typically do not forage on rainy days. Similarly, the average springtime temperature of 8°C is a proxy for the threshold at which *Myrmica* ants start to forage (G. Elmes, personal communication). Consequently, the number of warmer days is positively correlated with the resources of ant nests

and thus, indirectly, also with *Maculinea* larvae survival inside of them (Fig. 1).

The aforementioned weather factors were tested separately in the population dynamics models. In addition, two composite indices of overall weather suitability (W_t and W'_t , depending on which summer weather parameter was used), were also tested. These were calculated as the sum of the three weather factors standardised against their mean values across all years analysed:

$$W_t^{[1]} = W_{1t}^{[1]}/\text{avg}(W_1^{[1]}) - W_{2t}/\text{avg}(W_2) + W_{3t}/\text{avg}(W_3) \quad (5)$$

It should be noted that the number of rainy days in September is included as a negative value in the above equation because we assumed that its effect on *Maculinea* would be negative.

All of the factors used as model predictors (thus excluding the pairs of weather parameters that were never included together in models) were only moderately correlated with one another (Pearson's $r < 0.45$, thus within the range in which variables in multivariate analyses may be regarded as fairly independent; Legendre and Legendre 1998), with the exception of density dependence and competition ($r = 0.587$). Consequently, the effect of competition is partially 'masked' by the predominant effect of density dependence, and its strength may be underestimated. Nevertheless, we decided to keep the competition as a predictor in our analysis because it anyway performed at least as well as weather or mowing.

The performance of the population models designed, i.e. basic and full models as well as all possible intermediate models, was assessed separately for the Gompertz-type and Hassel-type models using their AIC_c and Akaike weights (Burnham and Anderson 2001). Akaike weight can be interpreted as the probability of a model being the most appropriate one. We subsequently evaluated the relative importance of density-dependent regulation, inter-specific competition, mowing regime and weather patterns on the basis of the cumulative weight of models including a particular factor. The above procedure closely follows the approach suggested by Johnson and Omland (2004) (see this reference for its full rationale). Finally, we compared the fractions of additional variation in year-to-year trends of *Maculinea* populations explained by different factors.

While evaluating the relative importance of the factors we only considered their main effects. The interactions, although tested as well, never introduced significant improvements to the models. For each model, the inclusion of any interaction, either of the factors already contained in the model or of the others, was rejected by the likelihood ratio test (P always above 0.2). Furthermore, as revealed by the AIC_c values, the models with interactions invariably

performed worse than those with main effects only because they suffered from over-parameterisation. Note that with four main effects, there may be up to 11 different interactions; thus, total number of combinations is greater than the length of our time series.

Results

Mark-release-recapture estimates

Capture probabilities of both species were positively correlated with year (Pearson's $r = 0.848$ and 0.724 for *M. alcon* and *M. teleius*, respectively), which probably reflects the increasing experience of people participating in sampling during the course of the study. Increasing experience in this respect can be taken to mean a better ability to detect butterflies rather than an improved efficiency in netting them: from the very beginning of the survey, virtually all butterflies observed were successfully captured. For this reason, an alternative explanation for the negative correlation between year and capture probabilities involving changes in butterfly mobility (cf. Dempster 1991) does not seem plausible.

Capture probabilities were also negatively correlated with seasonal population size (Pearson's $r = -0.489$ and -0.483 for *M. alcon* and *M. teleius*, respectively), which is also an intuitive result, since we did not increase sampling intensity with increasing population size. Year and population size together explained a substantial proportion of variation in capture probabilities (*M. alcon*: $R^2 = 0.772$, $P = 0.0013$; *M. teleius*: $R^2 = 0.572$, $P = 0.0219$). In contrast, they had no apparent effect on survival estimates

(*M. alcon*: $R^2 = 0.068$, $P = 0.7279$; *M. teleius*: $R^2 = 0.076$, $P = 0.7011$). Instead, survival was strongly influenced by average temperatures in July–August (*M. alcon*: $R^2 = 0.502$, $P = 0.0462$; *M. teleius*: $R^2 = 0.586$, $P = 0.0293$). The relationship was unimodal (*M. alcon*: $\hat{\phi} = -0.55 + 0.13\text{temp} - 0.0033\text{temp}^2$; *M. teleius*: $\hat{\phi} = -2.97 + 0.35\text{temp} - 0.0084\text{temp}^2$), indicating that moderate temperatures in the range of 19.5–21°C are optimal for the adult survival of both species. The survival rates recorded (Table 1) corresponded with the average life span of 2.0–2.7 days for *M. alcon* and 2.3–3.8 days for *M. teleius*.

During study period the population of *M. alcon* fluctuated between approximately 150 and 1600 butterflies. The range was considerably wider for *M. teleius*: approximately 200–2,800 butterflies (Fig. 2). The greater stability of the *M. alcon* population was also confirmed by the lower coefficient of variation (CV) of population size estimates [0.48 vs. 0.70 for *M. teleius*]. Population size fluctuations in both species were well synchronised with each other (Pearson's $r = 0.656$; $P = 0.0282$).

Factors affecting population dynamics

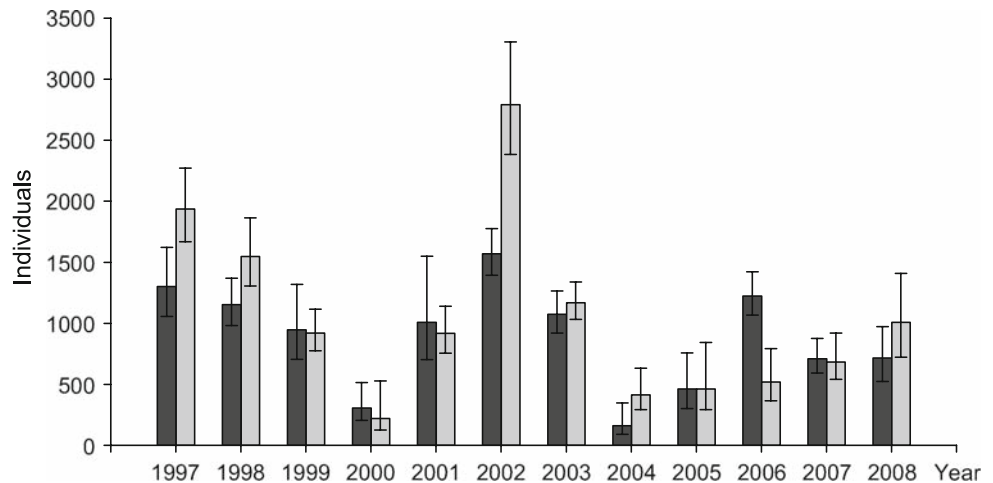
In the analysis of population time-series, Hassel-type models performed consistently better than Gompertz-type models for both species (Table 2). Consequently, in the subsequent consideration of factors influencing the population dynamics of *Maculinea* butterflies, we predominantly rely on the results of Hassel-type models. Year-to-year changes in both species were clearly density dependent (Fig. 3). The results of the test for density dependence of Pollard et al. (1987) were significant for both species (*M. alcon*: $r = -0.699$, $P = 0.0209$; *M. teleius*: $r = -0.643$, $P = 0.0349$).

Table 1 Basic parameters of the Cormack-Jolly-Seber mark-release-recapture models applied for estimating sizes of the investigated *Maculinea* populations

Year	<i>M. alcon</i>			<i>M. teleius</i>		
	<i>n</i>	$\hat{p} \pm \text{SE}$	$\hat{\phi} \pm \text{SE}$	<i>n</i>	$\hat{p} \pm \text{SE}$	$\hat{\phi} \pm \text{SE}$
1997	284	0.18 ± 0.04	0.66 ± 0.04	614	0.22 ± 0.02	0.77 ± 0.01
1998	305	0.22 ± 0.06	0.67 ± 0.04	546	0.30 ± 0.04	0.68 ± 0.03
1999	267	0.24 ± 0.06	0.66 ± 0.05	346	0.28 ± 0.06	0.72 ± 0.04
2000	111	0.33 ± 0.19	0.68 ± 0.13	83	0.34 ± 0.28	0.71 ± 0.21
2001	298	0.28 ± 0.07	0.63 ± 0.05	311	0.29 ± 0.06	0.70 ± 0.04
2002	404	0.23 ± 0.04	0.69 ± 0.03	861	0.25 ± 0.02	0.72 ± 0.01
2003	344	0.32 ± 0.06	0.59 ± 0.04	420	0.33 ± 0.05	0.64 ± 0.03
2004	49	0.31 ± 0.22	0.61 ± 0.14	135	0.34 ± 0.06	0.72 ± 0.03
2005	110	0.29 ± 0.07	0.66 ± 0.03	153	0.33 ± 0.07	0.74 ± 0.03
2006	435	0.34 ± 0.06	0.63 ± 0.03	165	0.28 ± 0.06	0.73 ± 0.03
2007	333	0.42 ± 0.05	0.66 ± 0.03	346	0.47 ± 0.05	0.75 ± 0.02
2008	300	0.38 ± 0.06	0.66 ± 0.03	549	0.44 ± 0.03	0.76 ± 0.01

n Number of individuals captured in season; \hat{p} average daily capture probability; $\hat{\phi}$ average daily survival rate

Fig. 2 Twelve-year population size dynamics (\hat{N} with 95% confidence intervals) of *Maculinea alcon* (dark bars) and *M. teleius* (light bars) occurring sympatrically at the Caselette site



As indicated by the AIC_c values, the models containing only density-dependent regulation performed by far the best (Table 2), explaining approximately 62 and 42% of the variation in the population dynamics of *M. alcon* and *M. teleius*, respectively. It should also be stressed that the cumulative weight of models with density dependence, i.e. the probability that this factor should be included in the most appropriate model, was very high, exceeding 0.97 for both species (Table 3). The influence of the three other factors analysed, i.e. inter-specific competition, mowing regime and weather patterns, cannot be excluded as the cumulative weights of these factors were above 0.05 (Table 3). However, their effects were rather weak, at least in comparison with those of density-dependent regulation, with each of them explaining an additional 2–4% and 3–5% of the variation in the population dynamics of *M. alcon* and *M. teleius*, respectively. Thus, the total fraction of variation explained by full models increased to approximately 74 and 54%, respectively (Table 2). The aforementioned effects were always in the expected direction—i.e. weather suitability positively influenced year-to-year trends of both *Maculinea* species investigated, while the proportion of mown area and inter-specific competition had negative impacts.

With respect to all of the weather parameters tested, the models with a composite weather index using adult longevity as a surrogate of summer weather favourability performed the best, followed by those with the composite index using the number of sunshine hours in summer (Table S1 in the [ESM](#)). The outcome of the models with the three weather parameters analysed separately revealed that the effect of weather suitability was dominated by the variation in the number of rainy days in September. The models with this parameter performed only slightly worse than those with the composite indices of weather suitability, whereas the effects of the number of warm spring days as well as summer weather suitability were marginal (Table S1 in the [ESM](#)).

Carrying capacity estimates remained fairly insensitive to the specific model, at least among Hassel-type models. The approximately 3-ha Caselette site was found to be capable of supporting approximately 800–900 *M. alcon* adults and 900–1200 *M. teleius* adults (Table 2).

Discussion

Our results provide evidence for density-dependent regulation in *Maculinea* butterflies, which had been postulated earlier by theoretical simulation models (Hochberg et al. 1992, 1994; Mouquet et al. 2005a, b). The cumulative Akaike weight of models with density dependence reached almost 1, indicating that it is virtually impossible to model *Maculinea* population dynamics without using this factor. Moreover, density dependence alone explained a predominant fraction (>60%) of variation in the year-to-year trends of *M. alcon* and a substantial proportion (>40%) in the case of *M. teleius*. In contrast, all other factors analysed, namely inter-specific competition, mowing regime, and weather, had much lower cumulative weights and explained only a few percent of variation each, in roughly equal proportions. Therefore, the influence of environmental stochasticity, as represented by weather and mowing, appears to be rather minor in our study.

The impact of mowing is obviously a case-specific phenomenon. The effect that we detected was marginal because the proportion of mown land in Caselette, although high, varied little between years. A more pronounced effect of mowing should be expected on meadows subjected to a more variable mowing regime. However, mowing patterns on *Maculinea* sites are usually highly consistent (Settele et al. 2005, Nowicki et al. 2007). The fact that the direction of the mowing effect in our study was negative should not be used as an argument against mowing applied as a meadow management tool in conservation programmes.

Table 2 Performance of population dynamics models tested for *Maculinea* butterflies as indicated by Akaike's information criterion corrected for small sample size (AIC_c), Akaike weight (w) and fraction of variance explained (R^2); carrying capacities (K) derived under the models with density dependence are presented as well

Model complexity	Hassel-type models				Gompertz-type models			
	AIC_c	w	R^2 (%)	K	AIC_c	w	R^2 (%)	K
<i>M. alcon</i>								
Density-dependence	20.90	0.693	61.78	873	29.84	0.267	43.87	857
Density-dependence*competition	24.54	0.112	67.79	907	30.30	0.212	49.77	1,023
Density-dependence*mowing	25.55	0.068	68.05	848	31.40	0.122	48.75	919
Density-dependence*competition*mowing	26.84	0.036	70.71	826	33.88	0.035	52.28	903
Density-dependence*weather	27.41	0.027	66.77	793	30.98	0.151	49.17	707
Density-dependence*competition*mowing*weather	27.80	0.022	73.52	919	39.81	0.002	54.84	856
Density-dependence*competition*weather	28.78	0.014	69.64	813	33.71	0.039	53.58	703
Density-dependence*mowing*weather	29.66	0.009	68.91	923	33.76	0.038	51.94	781
Competition	30.41	0.006	25.98	–	34.33	0.028	17.05	–
Competition*mowing	30.52	0.006	34.11	–	34.51	0.026	20.47	–
Competition*weather	30.79	0.005	33.28	–	34.48	0.026	20.14	–
Competition*mowing*weather	32.66	0.002	35.53	–	36.68	0.009	22.11	–
Weather	33.71	0.001	21.65	–	34.45	0.027	17.40	–
Mowing	34.49	0.001	20.78	–	35.33	0.017	14.13	–
Mowing*weather	35.84	0.000	27.43	–	39.89	0.002	18.69	–
<i>M. teleius</i>								
Density-dependence	28.70	0.524	41.98	1,124	32.83	0.325	28.82	1,015
Density-dependence*competition	31.20	0.150	48.02	877	34.94	0.113	30.05	1,299
Density-dependence*mowing	31.62	0.122	46.76	1,205	35.04	0.107	28.97	1,072
Density-dependence*weather	31.69	0.118	46.63	983	33.98	0.183	30.68	875
Density-dependence*competition*weather	34.34	0.031	50.80	1,010	37.07	0.039	33.45	1,099
Density-dependence*competition*mowing	35.35	0.019	50.63	1,109	37.82	0.027	32.10	1,239
Density-dependence*mowing*weather	35.48	0.018	49.83	880	37.22	0.036	32.77	830
Weather	37.81	0.006	15.42	–	36.68	0.047	12.22	–
Competition	38.41	0.004	14.11	–	36.89	0.043	12.30	–
Mowing	39.01	0.003	13.39	–	38.27	0.021	10.93	–
Density-dependence*competition*mowing*weather	39.96	0.002	53.60	911	44.04	0.001	33.66	972
Competition*weather	40.80	0.001	19.53	–	37.42	0.033	18.76	–
Mowing*weather	41.01	0.001	18.30	–	39.00	0.015	18.12	–
Competition*mowing	41.62	0.001	18.45	–	41.92	0.003	17.85	–
Competition*mowing*weather	45.05	0.000	21.37	–	40.93	0.006	20.47	–

In the case of models that also include inter-specific competition, in which K values also depend on the population size of the co-occurring *Maculinea* species (C_i), carrying capacities were calculated assuming mean C for the entire study period. The models are listed in an increasing AIC_c order of Hassel-type models, but the order for Gompertz-type models was fairly similar. The weather in the models is represented by the best-performing weather parameter, i.e. the composite index (W_i) using adult longevity. The performance of the models applying other weather parameters is presented in the Table S1 in the [Electronic Supplementary Material](#) (ESM)

We only tested its immediate effect on year-to-year population trends; over the long term mowing is likely to have a positive effect. Mowing is necessary to halt meadow succession, and in this way it enables *Maculinea* carrying capacities to stay at a high level (Mouquet et al. 2005a; Johst et al. 2006). Nevertheless, our findings imply that mowing should be better avoided during the *Maculinea* flight period and immediately thereafter, when larvae

develop on foodplants, i.e. from July to mid September (although the specific time may differ between locations). Optimally, mowing should be performed either early or late in the season in order to maintain its positive long-term effect while preventing the negative short-term one. Another option may be to apply a rotational scheme in which a small and different fragment of meadow is mown each year within a cycle of several years. Thorough

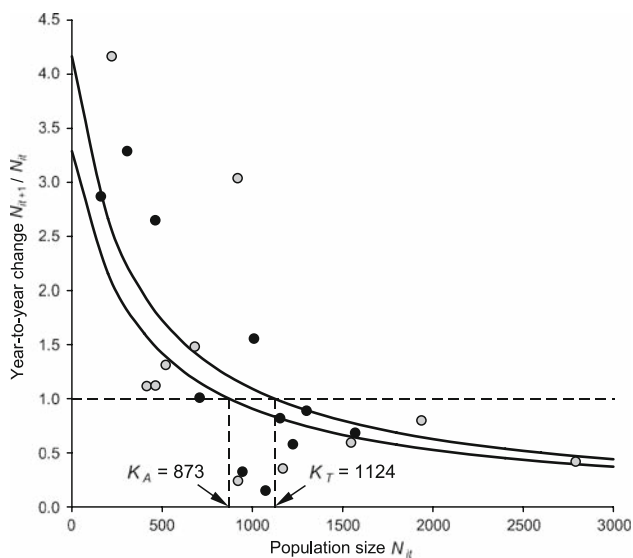


Fig. 3 Density dependence of year-to-year changes in the investigated populations of *M. alcon* (black dots; lower line) and *M. teleius* (grey dots; upper line). The fitted functions represent basic Hassel-type model $N_{t+1}/N_t = xr/(x + rN_t)$, with the parameters being $x_A = 1254$, $r_A = 3.29$ and $x_T = 1479$, $r_T = 4.16$, respectively for both species. The resulting carrying capacities (K) are indicated by arrows

Table 3 Relative importance of factors affecting the dynamics of the investigated populations of *Maculinea* butterflies as revealed by Hassel-type models

Predictor	<i>M. alcon</i>		<i>M. teleius</i>	
	Σw	ΔR^2 (%)	Σw	ΔR^2 (%)
Density dependence	0.979	61.78	0.984	41.98
Competition	0.202	4.04	0.209	4.46
Mowing	0.143	3.80	0.166	3.35
Weather	0.079	2.63	0.177	3.37

Σw , Cumulative Akaike weight of models containing a given factor; ΔR^2 , the additional variation explained by the factor. In the case of density dependence, which was clearly the predominant predictor, ΔR^2 simply represents R^2 explained by the basic models including only this factor. In contrast, for the three other factors, it was calculated as the mean difference in R^2 in the pairs of models (only those including density dependence were considered) with and without the factor concerned

analyses of the influence of various mowing schemes on *Maculinea* populations have been provided by Johst et al. (2006) and Grill et al. (2008).

The significant synchrony of *M. alcon* and *M. teleius* population trends may be used as an argument for a strong effect of environmental stochasticity. However, apart from being a result of environmental stochasticity, such a synchrony may be partly explained as a by-product of trophic interactions between species (Liebhold et al. 2004; Raimondo et al. 2004)—in our case, competition caused by using the same ant host. More importantly, it is sometimes

considered that all variation in population dynamics unaccounted for by density dependence and direct management should be viewed as a manifestation of environmental stochasticity (e.g. Kolzsch et al. 2007). Obviously, we cannot exclude that a significant fraction of variation in the dynamics of the investigated *Maculinea* populations should be attributed to some environmental drivers, especially weather parameters, that were beyond the scope of our research. In fact, this is a common problem of all population dynamics studies since weather parameters can be analysed in countless combinations. However, we argue that not all of the unexplained variation should be attributed to environmental noise. Instead, a substantial part may derive from the application of oversimplified density-dependence models. An argument along this line is the considerably better performance of Hassel-type models as compared with Gompertz-type models. It is easy to imagine that the effect of density dependence could be even more profound if more complex models based on a thorough biological knowledge of *Maculinea* were applied. The above seems particularly true for *M. teleius*. The fact that models fitted for this species performed poorer than those for *M. alcon* is likely to reflect the different larval strategy of both species in host ant nests. While cuckoo-feeding *M. alcon* larvae engage in contest competition, *M. teleius* larvae experience more acute scramble competition (Thomas and Wardlaw 1992; Thomas et al. 1993; Thomas 1995), the outcome of which is highly dependant on the numbers of larvae reaching particular ant nests. Consequently, to precisely model *M. teleius* dynamics, one should adopt spatially explicit models that would obviously require far more detailed data than we managed to gather.

With regard to the predominant effect of density-dependent regulation, and the only minor one of environmental stochasticity that we found in the present study, a key question is how far these findings can be generalised. As already indicated above as well as in the **Materials and methods** section, both the Caselette site and populations occurring there are typical of *Maculinea* butterflies in most aspects. The few peculiarities of the investigated populations include strong isolation, presence of only one *Myrmica* host species, location on the southern edge of species distribution and possibly, the lack of larval polymorphism, although we would argue that the last characteristics is at least as common among *Maculinea* as the presence of larval polymorphism (see **Materials and methods**). More importantly, larval polymorphism reduces the sensitivity of *Maculinea* populations to environmental stochasticity (Hovestadt et al. 2007). Therefore, the effect of environmental stochasticity in an average *Maculinea* population is predictably even weaker than we found. The same is true for the location because populations from the edges of species distribution (both northern and southern), as those

in Caselette, are likely to be more strongly affected by environmental stochasticity than those occurring in distribution centres (Curnutt et al. 1996; Brooks 2000; Williams et al. 2003). The presence of a single ant host and its use by two *Maculinea* species should not have any significant consequences for their population dynamics other than increased competition as compared with more typical sites, where the overlap in ant host use by different *Maculinea* species is far from complete (compare Witek et al. 2008). Finally, isolation should not change the relative strength of the effects of environmental stochasticity and density dependence, but it only makes their assessment much easier due to the absence of dispersal. When all of the above are taken into account, the domination of density dependence over environmental stochasticity detected in Caselette is probably even stronger in most other *Maculinea* populations.

Another issue is how representative *Maculinea* are for other butterflies. Admittedly, their highly specialised myrmecophilous life-styles and, in particular, the strong intra-specific larval competition in ant nests, make *Maculinea* butterflies very prone to experiencing density-dependent effects. We are not aware of any other butterfly population research that has quantitatively compared the relative role of density-dependent regulation and environmental stochasticity. However, there have been several studies in recent years that have revealed strong density-dependent effects, typically occurring in their larval stage, in several butterfly species of different taxonomic position (Schtickzelle and Baguette 2004; Schtickzelle et al. 2005; Baguette and Schtickzelle 2006; Pickens 2007).

The fact that the role of density-dependent regulation in butterflies may have been frequently underestimated in the past, especially in general reviews (e.g. Dempster 1983; Warren 1992; Parmesan and Matthews 2005; but see Wilson and Roy 2009), supposedly derives from two main reasons. The first is overlooking the importance of larval survival and instead paying too much attention to adult performance (e.g. mating success, oviposition, etc.). The other reason is that most butterfly population studies rely on relative abundance indices, based on observed adult numbers (Thomas 2005; Nowicki et al. 2008; van Swaay et al. 2008). In reality, such indices derive from a combination of adult population sizes and adult longevities (Zonneveld 1991; Nowicki et al. 2008). In other words, the numbers of butterflies observed, regardless of whether they refer to particular sampling days or are summed for entire seasons, depend not only on how many adults are produced within a single generation, but also on how long they live and thus on how well they accumulate from one day to the next. As a result, fluctuations in these abundance indices reflect not only the effect of environmental stochasticity on population size, but they are also amplified by the

simultaneous effect of environmental stochasticity on adult longevity. It is worth noting that the majority of the aforementioned studies, in which density-dependence rather than environmental stochasticity was found to be the primary factor affecting butterfly population dynamics, used MRR methods that explicitly account for variation in adult longevity.

Our results, together with those of a number of earlier studies, indicate that density-dependent regulation may be a more wide-spread phenomenon in butterflies than it has been previously thought. As such, this factor definitely deserves more attention in future research into population ecology of this taxon. In contrast, the importance of environmental stochasticity (especially if restricted to weather) for butterfly populations has probably been overemphasised to date. Furthermore, since butterflies are representative of terrestrial insects in many aspects of their ecology (Thomas 2005), there is good reason to expect a similar pattern within this most species-rich group of animals.

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