Climate warming affects the rate and timing of the development in ectothermic organisms. Short-living, ectothermic organisms (including many insects) showing thermal plasticity in life-cycle regulation could, for example, increase the number of generations per year under warmer conditions. However, changed phenology may challenge the way organisms in temperate climates deal with the available thermal time window at the end of summer. Although adaptive plasticity is widely assumed in multivoltine organisms, rapid environmental change could distort the quality of information given by environmental cues that organisms use to make developmental decisions. Developmental traps are scenarios in which rapid environmental change triggers organisms to pursue maladaptive developmental pathways. This occurs because organisms must rely upon current environmental cues to predict future environmental conditions and corresponds to a novel case of ecological or evolutionary traps. Examples of introduced, invasive species are congruent with this hypothesis. Based on preliminary experiments, we argue that the dramatic declines of the wall brown \( \textit{Lasiommata megera} \) in northwestern Europe may be an example of a developmental trap. This formerly widespread, bivoltine (or even multivoltine) butterfly has become a conundrum to conservationist biologists. A split-brood field experiment with \( \textit{L. megera} \) indeed suggests issues with life-cycle regulation decisions at the end of summer. In areas where the species went extinct recently, 100% of the individuals developed directly into a third generation without larval diapause, whereas only 42.5% did so in the areas where the species still occurs. Under unfavourable autumn conditions, the attempted third generation will result in high mortality and eventually a lost or ‘suicidal’ third generation in this insect with non-overlapping, discrete generations. We discuss the idea of a developmental trap within an integrated framework for assessing the vulnerability of species to climate change.

**Climate change and phenology**

For a wide range of taxonomic groups, there is ample evidence of the impacts of global warming on their occurrence in both space and time (Parmesan 2007). The most widely documented responses since the early days of climate change research involve phenological shifts (Angilletta 2009). Phenology is the temporal dimension of an organism’s natural history as it captures the timing of the life cycle over the year (i.e. when it will develop, reproduce and enter dormancy). As a result, phenology is a major structuring element of an organism’s ecology and evolution (Forrest and Miller-Rushing 2010). In temperate and boreo-artic regions, the timing of particular life cycle stages and phenomena is essential for an organism’s fitness.

The observed phenological patterns in plants and animals in response to global warming are generally congruent with an earlier spring and a prolongation of the favourable period of the year for growth and reproduction (Parmesan and Yohe 2003, Menzel et al. 2006). In principle, this can be the result of genetic changes by natural selection (G), plastic responses (E) or genetic changes in reaction norms (GxE). In some cases, there is evidence of additive genetic variation for phenology-related traits (Van Asch et al. 2007). Thermally-sensitive traits that affect phenology, including for example growth rate and development time, may also be influenced by interaction effects between genes and the environment (Barton et al. 2014). So far, the majority of documented responses to climate change appear to be examples of phenotypic plasticity (Gienapp et al. 2008, Valtonen et al. 2011, Schilthuizen and Kellermann 2013). Plastic responses require, however, reliable environmental cues to provoke a phenotypic response (Reed et al. 2010).

Changes in phenology can be either adaptive or maladaptive. Evolutionary biologists are usually not very excited about maladaptive plasticity as selection will wipe it out, but from a population dynamics viewpoint, maladaptive phenology may have significant short-term consequences for population abundance under novel conditions. Hence, it can be a factor of significance for conservation under climate change in addition to other factors including: 1) the shrinking of populations of cold-adapted species (Turlure et al. 2010), 2) local extinctions due to extreme weather conditions (McLaughlin et al. 2002), and 3) phenological...
mismatches between resources and consumer (Saino et al. 2011, Nakazawa and Doi 2012). Adaptive responses to seasonal environments have received much attention and stimulated the construction of several life history models of optimal growth and development (Gotthard 2008), but the potential of maladaptive temporal responses should not be ignored under altered organism–environment interactions under climate change.

Short-living, ectothermic organisms, such as many insects, are of particular interest in this context. Both their larval development and adult activities are strongly sensitive to climatic conditions. Moreover, as they are short-lived with often one or more generations per year, changing climatic conditions may have considerable impact on their life-cycle regulation. Insects can take advantage of an early start in spring, as they may experience an extended time horizon for development and reproduction under changed thermal conditions (Végvári et al. 2014). This, in turn, may provide opportunities for an increase in the number of generations per year (i.e. voltinism; Altermatt 2010). This issue has particularly attracted attention in applied entomology as several pest species of crops and tree stands can have pronounced negative impacts if they occur with multiple generations per year and grow above economically significant thresholds (Ge et al. 2005, Tobin et al. 2008). Although patterns of earlier appearances and an increase in voltinism have been documented in a number of species, there is still much to learn about the mechanisms causing adaptive responses, but also about those cases where there is a lack of adaptive response.

Changed phenology is typically expressed in a human-biased way using calendar date. However, what really matters for the development and life cycle regulation of ectothermic organisms is how calendar date relates to ‘thermal time windows’ or degree-days. Degree-days provide an accumulated energetic measure relevant for the development and growth of the focal species based on the sum of mean daily temperatures above a given threshold from a meaningful starting date till the phenological event of interest (Trudgill et al. 2005). As phenology determines the set of environmental conditions experienced at a particular stage of the life cycle (e.g. specific degree-days thresholds), it may in turn affect decision making by organisms as they rely upon environmental cues and internal response systems that were functional in their evolutionary history.

The field of cue-response systems and maladaptive behaviour that leads to ecological and evolutionary traps under human-induced rapid environmental change has attracted much attention the last decade (Robertson et al. 2013). So far, most studies in this field have dealt with maladaptive habitat and resource use in anthropogenic environments, although the significance of ecological novelty and the potential emergence of traps in a context of climate change and shifts in timing have been acknowledged in the recent literature (Sih et al. 2011). To the best of our knowledge, we are not aware of studies dealing explicitly with developmental traps under climate change that fool organisms to make erroneous decisions during development because of altered cue accuracy. For example, a developmental trap could occur when a larval insect, which relies upon environmental cues for winter diapause induction, interprets novel climatic conditions as suitable for direct development. However, if the season ends before development is completed, the insect risks losing this generation (Fig. 1). In many (potentially) multivoltine insects, life-cycle regulation is mainly based on the photoperiod experienced during key phases of the development (Friberg et al. 2011). We may expect that the information on seasonal change – conveyed by the photoperiod – is blurred by rapid warming. Some studies presented in different frameworks (e.g. invasive species) are highly relevant to this issue, as we will discuss below.

In this paper, we outline the potential significance of the developmental trap concept for short-living ectothermic organisms. We focus on diapause induction at the end of the season under temperate-zone conditions when such organisms have to decide on adding another generation within the same growing season, or alternatively, entering a developmental pathway of arrested development. So far, most phenology-related work has focused on early-season phenology, but there is a need for late-season studies to better understand population consequences (Karlsson 2014). Whilst the dominant diapause-inducing cue (photoperiod) will be unaffected by global climate change, higher temperatures may modify rates of development, leading to a decoupling of synchrony between diapause-sensitive life-cycle stages and critical photoperiods for diapause induction (Bale and Hayward 2010). We were particularly inspired by the case of the wall brown butterfly Lasiommata megera. This butterfly used to be widespread, but over the last few decades it has shown a dramatic decline in northwestern Europe (Van Dyck et al. 2009). Based on the literature and on results from an exploratory translocation experiment, we infer the possibility of a developmental trap in L. megera as an explanation of its regional population decline and we discuss the broader relevance of such a phenomenon for species showing developmental plasticity and multivoltinism in combination with altered phenology under changing environmental conditions.

Range dynamics, climate change and maladaptive decisions

One convincingly demonstrated consequence of climate change is range shift and pole ward expansion (Parmesan and Yohe 2003, Hickling et al. 2006). However, it is also expected that there will be interactions between climate change and latitudinal clines in phenology and life-cycle regulation (Bradshaw and Holzapfel 2001, Välimäki et al. 2012). Southern genotypes that disperse northwards could be considered as being pre-adapted to ‘northern’ conditions under climate change. However, these southern types could in principle have their range expansion restricted by developmental traps. For example, in laboratory and field experiments, Dalin et al. (2010) demonstrated latitudinal variation in how the chrysomelid beetle Diorhabda carinulata responded to day length for diapause induction and how the responses affected insect voltinism across the introduced range. This beetle, which was introduced for biocontrol, failed to establish south of 38 N latitude because of a mismatched critical daylength response for diapause induction. Likewise, developmental mismatches may have the potential to restrict range-expansion in response to climate change.
Phenological adaptations in insects have led to well-developed theoretical perspectives on optimizing development time and body size in a seasonal environment along latitudinal clines (e.g., clinal ‘saw-tooth’ pattern; Roff 1980, Nylin and Svärd 1991). Theory predicts different patterns for univoltine and bivoltine life cycles and season length, which may result in complex latitudinal patterns for life history traits and size. However, latitude is not always a good predictor. In recent work on the voltinism, body size and temperature in North American Papilio butterflies, it was shown that latitude is not always a good predictor of population responses due to the existence of local ‘climatic cold pockets’. Temperatures in northern Michigan and Wisconsin appeared to have historically induced strong constraints on body size, but this has rapidly changed during the recent decade with local summer warming (Scriber et al. 2014). According to the authors, the effects on body size are most likely a result of phenotypic plasticity. Climate change is likely to induce altered eco-evolutionary dynamics across the range of many insects. Southern genotypes that disperse northwards could be considered as being pre-adapted to ‘northern’ conditions under climate change, but these southern types could in principle face problems with interpreting local environmental cues (e.g. photoperiod) to make appropriate decisions on life-cycle regulation including late summer diapause induction.

The question of how range shift and developmental traps may interact is further confounded by the fact that a species may have populations that differ in phenology and voltinism within the same region (Krumm et al. 2008). For example, in those areas where the butterfly Pieris napi has a second and third brood, a significant part of the pupae derived from the spring generation are diapause pupae and do not develop into butterflies until the following year (Lees and Archer 1980). Such a pattern could be the result of multiple colonization events from different source regions with different phenological profiles, or of phenologically aberrant sub-populations with unusual local topographies and hence microclimates (Shapiro 1975). Another reason for the co-existence of different developmental profiles and phenologies could be bet-hedging (Danforth 1999). Hence, the picture of one species-specific phenological type in one particular area may hardly do justice to the complex situation which prevails for several multivoltine species.

The first step towards predicting voltinism changes and the potential for developmental traps in response to climate change is to understand the evolution of these characteristics. Insects indeed show great diversity in their life styles, including diapause induction, and similar responses among species or populations might be the result of convergent evolution but through different mechanisms (Masaki 1999). Therefore, more case studies are needed to better understand the processes that lead to specific phenological responses and their consequences for life-cycle regulation (e.g., diapause induction) under climate change. In this case, zones of transition between different levels of voltinism are of particular interest (Nylin and Svärd 1991). Although adaptive plasticity is widely assumed in multivoltine organisms, human-induced rapid environmental change could blur the relationship between the environmental cues organisms use to make developmental decisions on the one hand and the anticipated state of the environment on the other. This, in turn, opens the possibility of a developmental trap making organisms opt for a low fitness developmental pathway relative to the prevailing environmental conditions. The key point is that changed phenology may challenge the way ectotherms deal with the available time horizon for development and reproduction at the end of the summer season, which in turn may result in high mortality.

Parallels with invasive, introduced species

Both climate change and biological invasions involve the ability of organisms to deal with new environmental conditions outside the range experienced in the population of origin. While the fields of climate change and biological invasions have largely developed independently (Ward and Masters 2007), researchers interested in climate change effects are likely to get insights and ideas from studies on introduced pest species.

An analogue to the climate change induced ‘developmental trap’ is the situation in which an invading species produces a mismatched number of generations due to cue responses evolved under the selection regime of the area of origin (the ghost of selection past). For example, during the early stages of range expansion in Japan, the green stink bug Nezara viridula induced diapause much later than local native species, resulting in significant reproductive losses (Musolin 2007). As another example, the weevil species Hyperodes bonariensis native to South America was introduced in New Zealand where it continued to show a ‘relic diapause’, which was maladaptive under the new environmental conditions (Goldson and Emberson 1980).

Developmental traps may also occur in conjunction with more complicated interactions with the biotic environment. For example, the cotton bollworm Helicoverpa armigera, a major pest species, has been shown to produce a fifth generation in northern China that ultimately resulted in a suicidal generation. In this case however, the proportion that did so varied with host crop (Ge et al. 2005).

Changes in voltinism may also interact with other life-history traits of the organism. For example, the introduction of the fall webworm Hyphantria cunea in Japan resulted in a part of the colonized range into a shift to a trivoltine life style. Voltinism in the webworm, however, is related to the number of instar-stages during development, which is in turn correlated with developmental period, pupal weight and forewing length (Gomi et al. 2003).

Developmental trap hypothesis and a butterfly under dramatic decline

Butterflies are popular study organisms for ecology, evolution and conservation (Watt and Boggs 2003). Also in the context of responses to weather and climate change, they attracted much attention over the last decades (Dennis and Shreeve 1991, Roy and Sparks 2000). Butterflies are also the subject of well-established recording schemes providing useful spatial and temporal datasets on change in abundance and occurrence (Forister and Shapiro 2003, Van Swaay et al. 2008). Moreover, their life styles strongly relate to the thermal dimension of the environment in time and space as they are flying, sun-basking organisms in the adult
stage and usually less mobile ectotherms in the larval stages (Clench 1966, Dennis 1993, Kingsolver 1989, Bryant et al. 2000). Several butterfly studies addressed phenological shifts (Stefanescu et al. 2003, Diamond et al. 2011), but whether the concept of a developmental trap is applicable remains to be analyzed.

In this context, we are particularly interested by the case of the wall brown butterfly *Lasiommata megera*. This widespread grassland butterfly has become a conundrum to conservation biologists. Although the species used to be abundant and widespread across its European range, it has declined dramatically over the last few decades both in distribution and abundance in northwestern Europe, even reaching levels of conservation concern in some areas (Van Dyck et al. 2009, Maes et al. 2012). Populations of *L. megera* in northern and southern Europe are, however, stable and sometimes even expanding (Van Swaay et al. 2013). The population decline in northwestern Europe (i.e. Belgium, the Netherlands and UK) appears to show a typical spatial pattern; inland populations showed the strongest declines (resulting in several currently *L. megera* free areas, whereas it used to be one of the most widespread and stable species until the early 1990s), but populations close to the seaside are still surviving. Although *L. megera* has experienced habitat loss and wild flower declines in different types of grassland in landscapes under intense human use (WallisDeVries et al. 2012), the dramatic decline and the typical spatial pattern of the response is not, or far less, reflected in other butterflies susceptible to similar habitat and resource issues (e.g. small heath *Coenonympha pamphilus*; Maes et al. 2012). Therefore, conservation biologists are in search of a sound explanation for its strong and rapid decline.

We argue that *L. megera* has the biological profile of a candidate species for experiencing a developmental trap. The species overwinters as a half-grown caterpillar (3rd instar), and the decision to develop directly into a third generation, or alternatively to diapause, is made as a young larva (before the 3rd instar, although the exact time window of sensitivity is not yet known). In the northern part of its range, the species is bivoltine and to the south and southeast of Europe it occurs in three or four overlapping generations even in intensively farmed areas (e.g. Slovenia; Verovnik et al. 2012; Fig. 1). Intriguingly and opposite to related satyrine butterflies (e.g. *Pararge aegeria*, Nylin et al. 1989), univoltine populations are not known in *L. megera*. Hence, in northern Europe it only occurs in areas where it is able to complete two generations (Nylin and Svärd 1991). This suggests that it has lost the (genetic) ability of a univoltine life cycle that would require inducing larval diapause even if environmental conditions still remain suitable for a certain time period. This implies a major difference in life history with the very closely related species *L. maera*, which is univoltine in Sweden, but bivoltine further south (Gotthard et al. 1999). Developmental decisions in response to day length depend in this species on the seasonal state of the larvae. The relationship between growth rate and temperature of *L. maera* was found to be highly dependent on the level of time-stress resulting from the day-length regime (Gotthard et al. 2000).

We will focus on three lines of circumstantial evidence that regional warming may affect late summer diapause induction in *L. megera* in northwestern Europe. In this region, *L. megera* always occurs in two generations per year, but in warm summers a partial third generation may occur. Comparing the phenology patterns of the period 1981–2000 and 2001–2010 in Belgium indicated an overall increased occurrence of the third generation (Maes et al. 2013). However, the pattern differs between the inland area, where *L. megera* has disappeared, and the coastal area, where it still occurs (Fig. 2). In the coastal populations, the third generation has become relatively more abundant in the period 2001–2010 than in the period 1980–2000. In the inland populations this generation has become much longer in the recent period, but the phenology figure is ‘blurred’ in this case by the gradual extinctions in the local inland populations.

In a split-brood breeding experiment in the field, we tested whether developmental decisions are different in the areas where populations have disappeared (i.e. inland area) and in areas where populations still occur (i.e. coastal area). At the time of the second generation (i.e. summer generation), we introduced a total of 253 young caterpillars of *L. megera* into four different Belgian sites (two inland sites and two coastal sites) where they could grow and develop on potted host grass (greenhouse-reared *Pestaca rubra*) in individual enclosures. The sites were at similar latitude (between 51°07′ and 51°21′), but the two inland sites were located ca 140 km to the east compared to the coastal sites. Interestingly, 100% of the caterpillars in the inland sites developed directly to the adult stage (i.e. a third generation), whereas only 42.5% of the conspecifics in the coastal sites did so.

In order to explore potential cues for developmental decisions in *L. megera*, we analyzed ambient temperatures during the period in which the second generation offspring are still small caterpillars in both regions (i.e. August–September). Photoperiod was obviously not different between the areas, but temperature clearly was. During the experiment, ambient temperature was on average 0.5°C warmer on the inland sites compared to the coastal sites. However, this difference was much stronger at the level of the caterpillars on the host plants (i.e. 5 cm above ground-level the inland sites were on average 1.2°C warmer than the coastal sites; data logger measurements i-buttons). Over the last 30 years, daily temperature during the period of the second (and third) generation increased and has been significantly warmer in the inland sites than in the coastal sites (Maes and Van Dyck unpubl. data based on meteorological records). Most climate change studies rely on general ambient temperature data, but these do not necessarily reflect operational temperatures in relevant microhabitats and climates of insects (Bennie et al. 2014).

Although these observations do not provide a ‘smoking gun’ for a developmental trap in *L. megera*, they are congruent with the hypothesis. Our split-brood field experiment suggests problems with life cycle regulation decisions at the end of summer in areas where the species went extinct, but much less so in areas where populations still occur. In the former areas, all individuals developed directly without going into larval diapause. If direct development in autumn is a bad option – at least in some years – such a developmental trap may lead to a ‘suicidal’ third generation. This, in turn, will have strong population consequences affecting the abundance of the species in the next spring generation as we are in a scenario of non-overlapping, discrete
generations. In such cases, the long-term population growth rate is determined by its geometric mean and unusual low values will have a strong impact on persistence. In some insects, there is a developmental buffer against seasonal variability caused by within-population variation in diapause induction. Our working hypothesis for *L. megera* in northwestern Europe states that changed thermal conditions in the inland populations have created a mismatch between the seasonal cue and the diapause induction response, whereas this effect is less severe in the populations closer to the seaside which were less exposed to warming effects. Given the magnitude of the effect, as suggested by our field experiment, inland populations can be rescued by recolonisation by pre-adapted genotypes, or types on which natural selection can adjust the reaction norms of the developmental response, rather than by selection from standing genetic variation. Given the highly fragmented nature of remaining populations and the absence of substantial standing genetic variation, a fast rescue is thus not likely. Interestingly, northern genotypes would be the best to rescue these *L. megera* populations as they have adapted to enter diapause at longer day lengths. It is now warranted to start a detailed research program on the environmental cues (combinations of photoperiod and temperature) and responses of different populations of *L. megera*, including transplant experiment, to test these ideas. Of course, the idea of developmental trap does not exclude the additional or synergistic role of other environmental factors to explain the dramatic decline of *L. megera* in northwest-Europe.

**Conclusion and perspectives**

Several studies on the ecological responses of climate change have addressed patterns of phenological change. Although there is clear evidence for some general patterns, including earlier first appearance and increased voltinism, in short-living ectothermic organisms such as insects, there is still much to learn about the diversity of mechanisms or processes that cause (mal)adaptive responses. If the relationship between environmental cues and the developmental response is blurred under ‘novel’ seasonal conditions, it opens the possibility of a developmental trap. We argue that this field needs more attention and studies on phenology and development of species that have been introduced outside their range and climatic space help developing ideas.

In lowland areas, the requirement to move larger distances to track climate, especially if combined with dispersal limitation due to habitat fragmentation, can cause a lag in
Figure 2. Phenological pattern of *L. megera* in inland populations (a) and coastal populations (b) in Flanders (north Belgium) in recent years (2001–2010) and in the previous period (1981–2000). Data are based on an extensive butterfly recording scheme (for details we refer to Maes et al. 2012, 2013). To visualize the phenology patterns in the two periods (n = 1064 and n = 922 recordings, respectively), we fitted a smoother through the relative number of observations per day using the geom_density function in the ggplot2 package (Wickham 2009) in R ver. 3.1.1.

the response to new climatic conditions (Moritz and Agudo 2013). The phenomenon of a developmental trap may also open a new perspective on climate debt effects (i.e. limited ability of organisms to track rapid climate change; Travis et al. 2013) within the core of the distribution range of certain species. Climate debt has been shown in, for example birds and butterflies, at the northern edge of their range (Devictor et al. 2012). If populations in transition zones between different degrees of voltinism are trapped, then it could create – at least temporarily – holes in the distribution of such a species.

At this stage, it is difficult to make sound predictions on the general significance of developmental traps across species and climate zones. Under variable conditions the co-occurrence of different developmental patterns within a generation may provide resilience at the population level (Pavan et al. 2013). We argue that the profile of species particularly susceptible to developmental trapping are multivoltine species that show strong thermal plasticity of development and use photoperiod as an important cue for life-cycle regulation. Of course, the vulnerability of species to this process is always determined by a combination of exposure and intrinsic sensitivity (Williams et al. 2008).

More generally, our forum paper calls for putting more emphasis on sensory ecology (cue–response system) in the field of the ecology and evolution of phenology. Integrating life-history theory, developmental biology, biogeography and climate research by focusing on developmental traps provides an exciting scope for integrative biology that will help to better understand the mechanisms of the
diverse temporal and ultimately population impacts of climate change.

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