

LETTER

Tell me what you eat and I'll tell you when you fly: diet can predict phenological changes in response to climate change

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Abstract

Changes in phenology are correlated with climate change. However, we still struggle to understand the traits making species susceptible to climate change, and the implications of species' reactions for communities and food webs. Butterflies and moths are an ecologically important group that have shown pronounced phenological changes over the last decades. Tests using a > 150-year dataset from 566 European butterfly and moth species demonstrated that variation in phenological change was strongly related to traits describing plant–herbivore interactions (larval diet breadth, diet composition), and the life cycle. The results indicate that climate change related shifts in phenology are correlated with the seasonal availability and palatability of food plants. Lepidopterans feeding on herbaceous plants showed smaller shifts in flight periods but larger increases in voltinism than lepidopterans feeding on woody plants. Consequently, the effect of herbivorous lepidopterans may increase in herb-rich grassland ecosystems under warmer conditions, and not in forest ecosystems.

Keywords

Butterfly, climate change, flight period, generation, Lepidoptera, moth, phenology, species traits, voltinism.

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INTRODUCTION

Global climate change is altering the distribution, abundance and phenotypes of species, worldwide (Walther *et al.* 2002; Parmesan & Yohe 2003; IPCC 2007). Phenological changes are among the best-studied warming-related changes in life-history traits, because they are relatively easy to track, and a direct causality is well-accepted (Walther *et al.* 2002). They have been reported from many different taxonomic groups. For example, plants shortened life cycles, flowering and seed set have advanced (Fitter & Fitter 2002; Steltzer & Post 2009) and birds and other vertebrates have advanced their breeding season (Walther *et al.* 2002). Some of the most drastic phenological changes have been reported for insects (Parmesan & Yohe 2003; Menéndez 2007): since the late 1970s on various continents, seasonal appearance of many butterflies and other insects have advanced by up to several weeks (Roy & Sparks 2000; Walther *et al.* 2002; Forister & Shapiro 2003); multibrooded species have prolonged their flight period (Roy & Sparks 2000), and bark beetles,

butterflies and moths have shifted from univoltinism towards bi- or multi-voltinism (Jönsson *et al.* 2009; Altermatt 2010).

Many of these phenological changes are likely to have large consequences for local populations and interactions with other species. For example, the onset of flowering in plants and first appearance dates of pollinators is evolutionarily well-synchronized, but temporal mismatches among mutualistic partners have occurred during warming (Hegland *et al.* 2009). Also, earlier onset of development and increased voltinism may promote faster population growth (Steinbauer *et al.* 2004), making outbreaks of pest species more likely (Steinbauer *et al.* 2004; van Asch & Visser 2007). For herbivores, phenological shifts have negative consequences when they do not match host–plant phenology, or when phenological mismatches result in the production of an inappropriate diapausing stage, as found in the true bug *Nezara viridula*: the species occurs nowadays out of its historic range, yet females still lay eggs late in autumn even though their offspring have no chance of

attaining adulthood or surviving the winter (Musolin 2007). Many of these observed phenological changes are due to phenotypic plasticity, but evolutionary changes are likely, and may increase in importance (Bradshaw & Holzapfel 2006).

Phenology in insects is closely related to environmental variables, and differs between species and populations. For instance, Lepidoptera using larval food plants of poorly defended plants tend to be bi- or multi-voltine (Hunter & McNeil 1997), whereas Lepidoptera using a restricted set of strongly defended food plants tend to be univoltine (Shreeve *et al.* 2001; Cizek *et al.* 2006). Even within a species, such as the cabbage white butterfly, *Pieris rapae*, the speed of development depends on an intimate interaction between environmental temperature and larval food type (Kingsolver *et al.* 2006). There is a large body of research showing both a high interspecific and intraspecific variability in phenological traits, such as development rates, number of instars or diapause induction and a dependence of phenological trait expression on ambient temperature (Gotthard *et al.* 2000; Kingsolver 2007; Musolin 2007).

While changes in phenology along with increases in ambient temperature are widely documented, the relationship between phenological changes in the context of climate change and species traits seems to be largely unexplored in natural systems. However, to generalize and eventually mitigate effects of climate change, we must understand species-specific variation in the reaction norm to climate change. Three aspects are important: (1) comparing effects of climate change on a large number of species in natural communities, (2) attributing changes in phenology in the context of climate change to species traits and species ecology and (3) evaluating the evolutionary consequences (or potential) of climate change in whole communities.

I used extensive long-term data (> 150 years) on 566 butterfly and moth species from Central Europe for which I have documented changes in phenology and voltinism in an earlier study (Altermatt 2010). Here, I take an entirely new approach by studying if species traits can explain variation in different phenological changes. Thereby, I relate biological changes in the context of climate change to functional traits. I gathered species traits falling into four categories of species' life histories and ecology (Stearns 1992), and which describe: (1) characteristics of the life cycle, (2) the larval diet spectrum, (3) geographical range and abundance and (4) phylogenetic relationships among the Lepidoptera species. The choice of these categories was motivated because they match a set of hypotheses describing species-specific changes in phenology: (1) changes in phenology are constrained by aspects of a species' life cycle, such as the identity of the life stage that over-winters (Tauber *et al.* 1986). (2) For herbivores, different functional groups of plants may inherently differ in their availability as

a food resource. A difference in the diet spectrum of the herbivore can thus affect the ability for phenological changes. For example, plants may flush their leaves simultaneously (such as many trees) or sequentially (such as many herbaceous plants). Only in the latter case, fresh and potentially less defended leaves are available over most of the season, while the leaves of most trees and shrubs are only palatable over a short time-window in spring (Feeny 1970). I therefore hypothesized that species feeding on woody plants will shift their flight period to match the flushing of leaves, but may not be able to have a further generation (i.e., a change in voltinism), because the simultaneously flushed leaves will be less palatable for a second generation. Also, plants with year-round foliage or evergreen plants may be a more reliable food source for herbivores, but the leaves may be more defended and less palatable compared to plants with short-lived leaves (Feeny 1976; Rhoades & Cates 1976). Finally, I hypothesized that species with a more flexible larval diet (i.e., oligo- or polyphagous species) would show stronger changes in phenology than species with a very restricted larval diet, as the latter are constrained to the phenology of their single host-plant. (3) Populations of species that occur over a wide geographic range are adapted or plastic to match a wide range of climates, and dispersal may introduce genetic variability that is favourable in altered local conditions (Bradshaw & Holzapfel 2006), whereas species with a narrow geographic range have less inherent variation to deal with altered local conditions. I therefore hypothesized that species occurring over a wide geographic range would show a stronger change in phenology compared to species which are either rare or have a narrow geographic range. (4) Finally, I hypothesized that more closely related species would show more similar changes in phenology than species belonging to different phylogenetic clades.

There are good reasons to use Lepidoptera as a model system to study the interaction of species traits and climate change on phenology. First, Lepidoptera are one of the largest insect orders and their physiological ecology with respect to phenology is reasonably well understood (Scoble 1995). Second, they have a high interspecific and intra-specific variation in phenological traits, which are both under genetic and environmental control (Shapiro 1977; Tauber *et al.* 1986; Välimäki *et al.* 2008). Third, many species showed pronounced phenological changes in parallel with climate change (Roy & Sparks 2000; Forister & Shapiro 2003; Altermatt 2010). Finally, Lepidoptera are a globally important component of primary consumers in terrestrial ecosystems (Scoble 1995). Understanding the effects of environmental factors and species traits on phenological changes is thus essential to predict effects of Lepidoptera on important ecosystems, such as forests or grasslands.

MATERIAL AND METHODS

Study area

The study area in Central Europe consisted of a 30-km radius circle around the city of Basel, Switzerland (47°33′ N, 7°36′ E) and incorporates parts of Switzerland, France and Germany in about equal proportions (Altermatt *et al.* 2006; Altermatt 2010). This defined 3725 km² area has been used by Lepidopterists for more than a century (Altermatt *et al.* 2006). Precise long-term temperature data are available back to 1864 (Begert *et al.* 2005), showing an especially strong and unprecedented warming since the early 1980s (Paul *et al.* 2004; Begert *et al.* 2005; Rebetz & Reinhard 2008). Mean summer temperature during 1980–2008 was 1.2 °C higher than in the period of 1864–1979 (for a figure of annual summer temperatures in the study area, see Altermatt 2010). I therefore compared phenological responses of butterflies and moths before and after 1980 (year < 1980 and ≥ 1980, see also Altermatt 2010).

Data on Macrolepidoptera

I considered all species traditionally classified as Macrolepidoptera (Ebert 1991–2005) ever recorded in the study area (for details, see Altermatt *et al.* 2006). In total, the dataset consisted of 182 665 records of 1117 butterfly and moth species and covers the time period from 1850s to 2007. Butterflies were almost exclusively recorded during the day, whereas most species of the other families were recorded at light traps. There was no systematic difference in recording methods, data quality or investment efforts before or after 1980. The species identification within the dataset is of high quality, and identification of all museum records was verified and standardized to current taxonomic knowledge (Karsholt & Razowski 1996). Each record consisted of a species name, a location (minimally to within a 1 × 1 km tetrad) and a date. Only outdoor records of adults were included in the dataset. Because information on the number of individuals per record was deficient especially for museum records, I did not incorporate it. Thus, each record gave the occurrence of a species at a specific location and date.

For all analyses, to ensure a certain minimum accuracy of estimation of seasonality, I excluded all 506 species with fewer than 10 records before 1980 or 10 records after 1980. Furthermore, I excluded all 12 remaining migratory species. These species originate from distant places (in this case usually Northern Africa or Southern Europe). As their larval development was somewhere else, it does not make sense to use local variables to explain their phenology. Finally, I also excluded all remaining species in which the adults diapause in winter (26 species) or summer (7 species); for species with diapausing adults, phenology is hard to estimate as records

may be absent for a long period of the year, even though the population is in its adult stage. In total, 566 species were included in the analysis. In Central Europe, 303 of these species are univoltine and 263 are bi- or multi-voltine (Ebert 1991–2005). The larvae of 98.6% of these species are leaf chewers. To make sure that the outcome of the analyses was not strongly affected by species with few records, I repeated all analyses and included only species for which I had at least 20 records both before and after 1980 (447 species). The results were consistent with the main analyses and are given in the Appendix S1 in Supporting information.

Three different phenological response variables were calculated, one describing a phenological state (*flight-period length*), and two describing phenological changes (*flight-period shift* and *change in voltinism*). *Flight-period length* was calculated for each species as the range (in days) of the 95th percentile of all records (in Julian dates). Essentially, it is the average time period within a season used by adults. For the *flight-period shift*, I compared the flight period of univoltine species before and after 1980 (see also Altermatt 2010); specifically, I calculated the Julian date of the first 25% of individuals (25th percentile) observed during the entire flight period for each species, separately before and after 1980, and compared the difference of the date of the 25th percentile after 1980 and before 1980 (value after 1980 minus value before 1980, in days). The 25th percentile was used instead of the date of the first appearance, because the latter is sensitive to variation in sampling effort or population abundance (van Strien *et al.* 2008). To analyse species-specific variation in the advancement of the flight period, I only considered species that have a median flight period before August 1, as later-flying species postponed their flight period (Fig. 1). Finally, I calculated the *change*

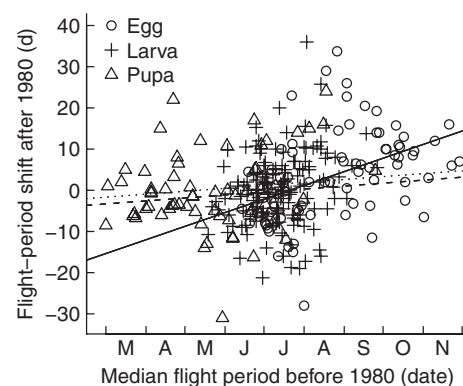


Figure 1 Flight-period shift after 1980 relative to before 1980 of univoltine Central European butterfly and moth species in relation to a species' median flight period before 1980 (date; March–November) and overwintering stage. The predicted correlation between the median flight period and the flight-period shift is given separately for species that overwinter as eggs (circles; solid line), larva (crosses; dashed line) or pupa (triangles; dotted line).

in voltinism of all bi- or multi-voltine species using kernel density estimates of the dates of records with the default function in R 2.10.1 (R Development Core Team 2009). The size of distinct modes gives the relative significance of each generation (for details, see Altermatt 2010). I expressed the change in voltinism as the relative frequency of the second generation after 1980 compared to before 1980. This measure indicates if a (facultative) second generation was more or less often expressed in those two time periods. I have previously shown that the *flight period* and *voltinism* of many butterflies and moths in the study area have significantly shifted over the last decades (Altermatt *et al.* 2006; Altermatt 2010).

I analysed if *flight-period shifts* depend on the time of the year at which a species flew. For plants, it was shown that warming advanced flowering and fruiting phenology for species that began to flower before the peak of summer heat but delayed reproduction in species that started flowering after the peak temperature (Sherry *et al.* 2007). It is unclear if a similar shift happens in butterflies and moths, as their phenology is not only influenced by temperature but also photoperiod.

I then analysed the phenological response variables *flight-period length*, *flight-period shift* and *change in voltinism* with generalized linear models (GLM), using 10 different explanatory variables to explain species-specific differences: (1) number of generations per year (after Ebert 1991–2005), describing for each species if it was uni- or bi-voltine. Less than 4% of all species considered have more than two generations within a season, and I pooled them with the bi-voltine species. This explanatory variable was not considered when the response variable was *change in voltinism*, which only considered bi-voltine species (see above). (2) Overwintering stage (egg, larva, pupa, after Koch & Heinicke 1991). (3) Diet breadth of the larval stages based on 5549 field-observed interactions between food plant species and Lepidoptera (data from Ebert 1991–2005). Diet breadth of the larval stages was classified as monophagous (only one food plant species), strongly oligophagous (> 1 food plant species, but only one food plant genus), oligophagous (> 1 genus but only one food plant family), or polyphagous (> 1 food plant family). (4) Whether diet of larval stages contained woody plants (trees or shrubs) or only herbaceous plants. Larval food plant data from Ebert (1991–2005) were classified as woody plants (including trees, shrubs and vines) or herbaceous plants (after Bundesamt für Naturschutz 2010). Lepidoptera species that have been reported to feed on at least one tree or shrub species were classified as woody-plant feeders, all other species have only been reported to feed on herbs and grasses, and were classified as herbaceous-plant feeders. (5) Whether diet of larval stages contained plants with year-round foliage or only containing plants with seasonal foliage. The larval food plant

data from Ebert (1991–2005) were classified into plants with year-round foliage (including evergreen trees, and herbaceous plants and grasses that have green leaves at all times of the year, such as ferns or perennial grasses) or only seasonal foliage (including deciduous trees, geophytes or annual plants) (Bundesamt für Naturschutz 2010). Lepidoptera species that have been reported to feed on at least one plant with year-round foliage were classified as having year-round foliage larval food plants, all other species were classified as having seasonal foliage food plants. (6) A coarse measure of the European distribution was obtained by using the number of European countries in which each species has been recorded (after Karsholt & Razowski 1996). (7) Local distribution was measured using the number of 5 × 5 km tetrads ever occupied within the study region (after Altermatt *et al.* 2006). (8) Local abundance was quantified as the total number of records within the study region (after Altermatt *et al.* 2006). (9) The distribution of the larval food plant was used as a measure of the rarity of the habitat; the specific metric was the median number of grid cells of all larval food plants in Southwest Germany (Baden-Württemberg Bundesamt für Naturschutz 2010) that were used by a species. The study area overlaps broadly with Southwest Germany, and the occurrence of plants and habitats is representative. (10) To measure phylogenetic relationships, Lepidoptera were grouped into seven superfamilies, based on a molecular phylogeny (Regier *et al.* 2009), and superfamily was used as a factor in the GLM. The seven clades were Bombycoidea, Drepanoidea, Geometroidea, Lasiocampoidea, Noctuoidea, Papilionoidea (including Hesperioidea) and Zygaenoidea.

In summary, these explanatory variables described the species' life cycle (variables 1–2), larval diet spectrum (variables 3–5), range and abundance (variables 6–9) and phylogeny (variable 10).

Statistical analyses

All analyses were conducted with R 2.10.1 (R Development Core Team 2009). Residual deviances of models were used as the goodness-of-fit criterion in the evaluation of the models. I compared the ability of different GLMs to independently explain the three phenological response variables, which can have a negative or positive value. Therefore, I used a Gaussian error distribution. The link function was identity. In the first phase of the model selection procedure, a model with all main effects and all two-way interactions and was fitted to the data. Then, the model was hierarchically simplified, using the Akaike Information Criteria (AIC) as the selection criterion in a stepwise algorithm (step, R Development Core Team 2009). I investigated the correlation matrix of the simplified model, and removed variables that were highly correlated ($r > 0.9$)

to get the final model. I individually removed correlated factors and visually compared the validity of the model assumptions, retaining the better model as the final model.

RESULTS

I found a significant relationship between the flight-period shift after 1980 and the median flight period before 1980 in univoltine species (Fig. 1; Table 1). Species that had a median flight period in the first half of the summer (i.e., before August) shifted their flight period to an earlier date after 1980 compared to before 1980, whereas species that had had a median flight period in the second half of the summer (i.e., from about August onwards) shifted their flight period to a later date. In other words, early season flyers became earlier, while late season flyers became later. The flight-period shift was significantly different for species with different overwintering stages, and there was a significant effect of the median flight period in explaining the flight-period shift. There was no significant difference between the seven different superfamilies. Based on the AIC, however, phylogenetic relationship was retained in the model.

The combination of variables explaining the observed phenological variance of the 566 butterfly and moth species was different for the three phenological response variables (*flight-period length*, *flight-period shift* and *change in voltinism*; Figs 2–4; Table 2). The presence of woody plants in the

Table 1 Influence of median flight period before 1980 and overwintering stage on flight-period shifts

| Covariate | Estimate | Std | | <i>P</i> -value |
|---|----------|-------|-----------------|-----------------|
| | | error | <i>t</i> -Value | |
| Intercept | −25.19 | 9.16 | −2.75 | 0.006 |
| Median flight period | 0.11 | 0.03 | 4.14 | < 0.0001 |
| Overwintering stage pupa | 18.70 | 7.37 | 2.54 | 0.012 |
| Overwintering stage larva | 17.04 | 9.00 | 1.89 | 0.059 |
| Drepanoidea | −2.01 | 8.48 | −0.24 | 0.813 |
| Geometroidea | 2.92 | 6.69 | 0.44 | 0.663 |
| Lasiocampoidea | −0.89 | 7.69 | −0.12 | 0.908 |
| Noctuoidea | 2.49 | 6.69 | 0.37 | 0.710 |
| Papilionoidea | 8.19 | 6.84 | 1.20 | 0.232 |
| Zygaenoidea | 3.50 | 7.10 | 0.49 | 0.623 |
| Median flight period × overwintering stage pupa | −0.08 | 0.04 | −2.31 | 0.022 |
| Median flight period × overwintering stage larva | −0.08 | 0.04 | −1.99 | 0.048 |

The 25th percentile of flight period after 1980 was compared with before 1980. A GLM was estimated, including both main effects and two-way interactions. Covariate = species' trait predictors, estimate = estimated effects, std error = standard error for the estimates effects.

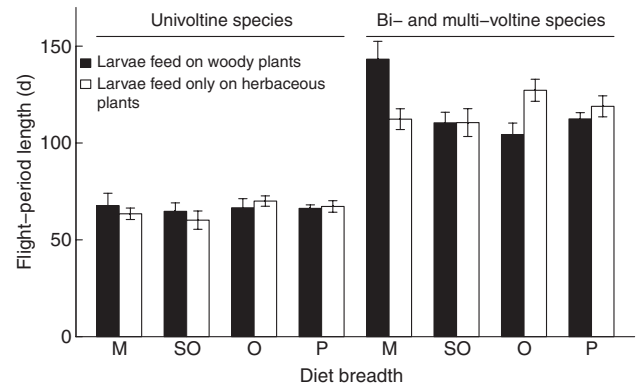


Figure 2 Flight-period length (95th percentile; mean \pm SE) of 566 Central European butterfly and moth species in relation to a species' larval diet breadth and diet spectrum, separately given for univoltine and bi- and multi-voltine species. The different diet breadth classes are monophagous (M), strictly oligophagous (SO), oligophagous (O) and polyphagous (P). Black bars show species that include woody plants in their larval diet, while white bars show species that strictly feed on herbaceous plants.

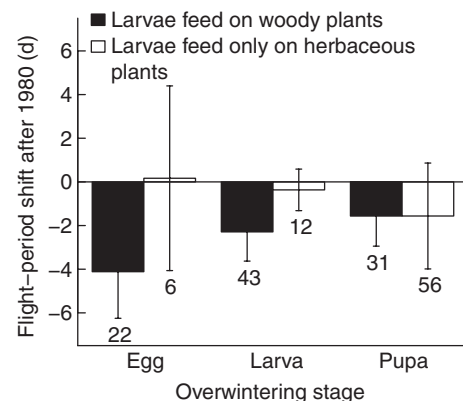


Figure 3 Flight-period shift after 1980 relative to before 1980 (mean \pm SE) of Central European butterfly and moth species in relation to a species' overwintering stage and larval diet spectrum. A negative value is a shift towards an earlier date after 1980 compared to before 1980. Black bars show species that include woody plants in their larval diet, while white bars show species that strictly feed on herbaceous plants. The number of species within a group is given below each bar.

larval diet was the only variable that was retained in the final model of every phenological response variable. Depending on the phenological response variable, further explanatory variables describing the species' life cycle (number of generations and overwintering stage), and larval diet (diet breadth and inclusion of plants with leaves all-year round) were retained in the model. Except for the European distribution, variables describing the distribution, abundance or rarity of the habitat (variables 7–9) or phylogeny (variable

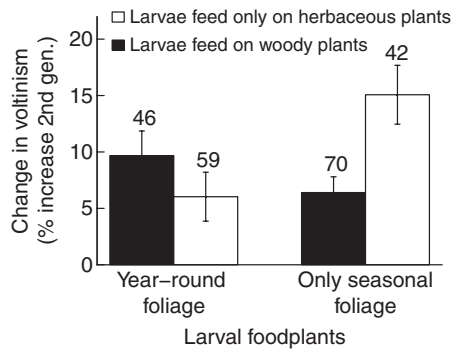


Figure 4 Relative increase of the second generation after 1980 compared to before 1980 (mean \pm SE) of Central European butterfly and moth species in relation to a species' larval diet. Larval diet of a species either included food plants with year-round foliage or was totally restricted to plants with seasonal foliage. Black bars show species that include woody plants in their larval diet, while white bars show species that strictly feed on herbaceous plants. The number of species within a group is given above each bar.

10) were not retained in the models, as they did not significantly contribute to explain phenological responses of the lepidopteran species.

The variance in *flight-period length* of butterfly and moth species was explained best by the number of generations, the larval diet breadth and presence of woody plants in the larval diet (Fig. 2; Table 2). There was a significant interaction between diet breadth and the inclusion of woody vs. herbaceous plants in the larval diet. Specifically, the flight period of monophagous species was longer when the larval food plant contained woody plants compared to herbaceous larval food plants. For oligophagous and polyphagous species, however, the flight period was shorter when the larvae feed on woody plants compared to herbaceous plants.

The *flight-period shift* was explained best by the identity of the overwintering stage, larval diet spectrum and the European range of the Lepidoptera species (Fig. 3; Table 2). Lepidoptera species whose larvae feed on woody plants shifted their flight period significantly more to an earlier date than species feeding only on herbaceous plants. The *flight-period shift* to an earlier date was most pronounced for species overwintering as eggs, and significantly different from species that overwinter either as larvae or pupae.

The *shift in voltinism* was explained best by two interacting variables describing the species' larval diet spectrum (Fig. 4;

Table 2 Influence of species traits on flight-period length, flight-period shift after 1980 and change in voltinism after 1980

| Covariate | Estimate | Std error | t-Value | P-value |
|--|----------|-----------|---------|----------|
| Flight-period length | | | | |
| Intercept | 78.8 | 5.14 | 15.3 | < 2e-16 |
| Two generations | 49.5 | 2.21 | 22.4 | < 2e-16 |
| Oligophagous | -18.9 | 6.28 | -3.0 | 0.0028 |
| Polyphagous | -14.1 | 5.36 | -2.6 | 0.009 |
| Strict oligophagous | -15.7 | 6.80 | -2.3 | 0.021 |
| Does not feed on woody plants | -15.8 | 6.09 | -2.5 | 0.0099 |
| Oligophagous \times does not feed on woody plants | 29.3 | 7.75 | 3.8 | 0.0002 |
| Polyphagous \times does not feed on woody plants | 19.4 | 7.02 | 2.8 | 0.006 |
| Strict oligophagous \times does not feed on woody plants | 13.3 | 8.77 | 1.5 | 0.13 |
| Flight-period shift (shift of the 25% percentile flight period) | | | | |
| Intercept | -24.3 | 11.4 | -2.1 | 0.03 |
| Overwintering stage pupa | 26.3 | 13.4 | 1.9 | 0.05 |
| Overwintering stage larva | 37.5 | 12.7 | 2.9 | 0.004 |
| Does not feed on woody plants | -15.1 | 8.43 | -1.9 | 0.05 |
| European distribution (# countries) | 0.756 | 0.41 | 1.8 | 0.07 |
| Overwintering stage pupa \times European distribution (# countries) | -0.899 | 0.48 | -1.9 | 0.06 |
| Overwintering stage larva \times European distribution (# countries) | -1.3 | 0.46 | -2.9 | 0.005 |
| Does not feed on woody plants \times European distribution (# countries) | 0.612 | 0.30 | 2.1 | 0.04 |
| Change in voltinism (relative increase of the second generation) | | | | |
| Intercept | 0.097 | 0.022 | 4.41 | 0.000017 |
| Does not feed on woody plants | -0.036 | 0.029 | -1.24 | 0.22 |
| Does not feed on plants with year-round foliage | -0.033 | 0.028 | -1.16 | 0.25 |
| Does not feed on woody plants \times does not feed on plants with year-round foliage | 0.123 | 0.041 | 2.99 | 0.0032 |

A GLM was fitted for each explanatory variable, including both main effects and two-way interactions. Covariate = species' trait predictors, estimate = estimated effects, std error = standard error for the estimates effects.

Table 2). Species with seasonal foliage, herbaceous larval food plants, showed the strongest shift towards a more expressed second generation, while species feeding on woody plants and herbaceous plants with year-round foliage showed the weakest shift in voltinism.

DISCUSSION

A large number of studies have supported the basic prediction that ecological changes, and especially phenological changes, correlate with climate change (Walther *et al.* 2002; Parmesan & Yohe 2003; Parmesan 2006; Menéndez 2007). However, the perception that each climate change response results from a single process misses critically important interactions and neglects ecological and evolutionary constraints. In accordance with my hypotheses, I found that recent phenological changes in 566 butterfly and moth species are correlated to species' life cycles and larval diet spectrum. Changes in the flight period of Lepidoptera flying at different times of the year (Fig. 1) were also in accordance with phenological changes observed in plants (Sherry *et al.* 2007).

Many plants, and especially trees, have advanced their leaf flushing and flowering over the last decades (Fitter & Fitter 2002; Walther *et al.* 2002). Experimental warming, however, showed that phenology only advanced for plant species flowering before the peak of summer heat but was delayed in plant species flowering after the peak temperature (Sherry *et al.* 2007). The warming-induced divergence towards the two ends of the growing season and the resulting gap in the plant community during the middle of the season are likely suboptimal for herbivores. Here, I showed that recent *flight-period shifts* of butterflies and moths (Fig. 1) are qualitatively similar to the changes in plant phenology: butterflies and moths shifted their flight period to either the beginning or the end of the season, depending if they were flying before or after mid-summer. An advancement of the flight period of univoltine butterflies and skippers has been reported for several places, such as Great Britain and California (Roy & Sparks 2000; Forister & Shapiro 2003). However, the species considered in these studies mostly flew in late spring and early summer. Late season species were not well-covered, and the shift of autumn-flying species to later dates was thus not strongly supported. In my dataset, I also analysed Lepidoptera from six other superfamilies, including moths that fly up to 3 months earlier or later in the year than butterflies. As there was no significant difference between the superfamilies (Table 1), the flight-period shift to either the beginning or the end of the season seems to be a general phenomenon within the order Lepidoptera. In the context of climate change, in temperate latitudes more butterflies and moths are thus expected to fly either in spring or autumn. Consequently, fewer butterflies and

moths are on their wings in the middle of the summer, which may be detrimental for insectivores such as bats that depend on moths as prey during that time (Scoble 1995).

While shifts in phenology were significant for all superfamilies (see also Altermatt 2010), the magnitude of the phenological change depended on various species traits, especially on those describing larval diet spectrum and diet breadth. Several hypotheses support the idea of a relationship between larval diet spectrum and herbivore phenology (Feeny 1976; Rhoades & Cates 1976), and voltinism of Lepidoptera may depend on the herbivore-defence of their larval host-plants (Hunter & McNeil 1997; Shreeve *et al.* 2001; Cizek *et al.* 2006). Typically, insects exploit plants within the time period shortly after the flushing of new leaves, when the leaves are chemically least defended (Feeny 1970). Functionally different plants (woody vs. herbaceous) differ in their pattern of leaf flushing, which could differently constrain the flight period of herbivores. Woody plants usually flush their leaves simultaneously and fresh, chemically least defended leaves are only available for a short time of the year (Feeny 1976; Rhoades & Cates 1976). Herbivorous insects feeding on woody plants are thus expected to be under strong selection to closely match the phenology to the flushing of leaves. Many herbaceous plants, however, produce leaves throughout the growing season. Consequently, constitutive defences of herbaceous food plants are expected to be weaker and the selective pressure to match the phenology of the food plant may be weaker for herbivores feeding on herbaceous plants.

In accordance to the apparency hypothesis (Feeny 1976; Rhoades & Cates 1976), the flight period of Lepidoptera depended on the inclusion of woody plants in the larval diet as well as on the number of plants used by the larvae (Fig. 2), and species using woody larval food plants had the most pronounced shift to an earlier flight period (Fig. 3). This is not only one of the first documentations that species-specific traits explain the effect of climate change on phenology, but has also large ecological implications, as butterflies and moths have an important role in terrestrial food webs. Their larvae are important herbivores and a key food resource for birds and other insectivores, and the adults are important pollinators (Scoble 1995). The finding that larval diet explains variation and changes in phenology (Figs 2 and 3) may thus have large consequences for other community members. A tighter relationship between phenology and environmental variables for woody-plant feeders than herbaceous-plant feeders, however, may not be universal in insects. In aphids, phenology and environmental variables are notably less correlated for species living all year on trees compared to species feeding on herbaceous plants (Harrington *et al.* 2007). Some species may also compensate for phenological shifts in other ways, such as shifting their diet, maturing at smaller sizes or adjusting reproduction

(Ayres & Scriber 1994; Scriber *et al.* 2008). The herein documented correlation between phenological changes and diet is based on data from a fairly narrow geographic range of most species, which is for most species more in the centre than at the edge of their range. At the edge of a species' range different shifts may be possible, as the set of usable food plants tends to decrease at the range margins (Scoble 1995). The ecological impact of the observed shifts may be especially hard to predict when multiple changes occur at a time, such as a species increasing its voltinism, but becoming rare because of a temporal mismatch with its host-plant. Because I used a correlative approach, I cannot infer a direct causality. Nevertheless, the findings are meaningful, because they support existing hypotheses, and may also be the starting point for studies which experimentally test the interaction between diet and temperature changes on phenological variables and development of insects. There are already experimental studies that addressed such aspects for individual species (Bradshaw & Holzapfel 2006; Kingsolver *et al.* 2006), but now need to be extended to a large number of species.

In an ecological and evolutionary context, the number of generations is the other important phenological variable. Changes in voltinism can drastically change the outcome of plant-herbivore interactions, by changing population growth and speeding up adaptation. A series of theoretical and empirical studies found changes in voltinism of insects due to climate change (Steinbauer *et al.* 2004; Braune *et al.* 2008; Jönsson *et al.* 2009; Altermatt 2010). Here, I showed that variables describing larval diet spectrum explained most of the observed variation in changes in voltinism (Table 2). Species feeding on herbaceous plants with seasonal foliage had a much larger shift towards a second generation than species feeding either on woody food plants or on herbaceous food plants with year-round foliage (Fig. 4). As a predominance of woody or herbaceous plants defines whole ecosystems like forests or grasslands, such differences could have consequences on a landscape level. Butterflies and moths living in grassland habitats may have had climatically restricted voltinism. At warmer temperatures and longer seasons, they may fit in another generation (Tobin *et al.* 2008), which may increase herbivory in grassland ecosystems and in agricultural crops consisting predominantly of herbaceous plants with seasonal foliage. In forests, however, the voltinism of butterflies and moths species may be mostly restricted by the temporal suitability of strongly defended food plants (Shreeve *et al.* 2001; Cizek *et al.* 2006). For these species, changes in voltinism may be detrimental, as a second generation would likely not match the seasonal palatability pattern of the foliage. While the guild of phloem-feeding bark beetles puts forests at a higher risk of herbivory in warmer years because of increased

voltinism (Jönsson *et al.* 2009), similar outbreaks of foliage-feeding Lepidoptera may be less likely.

Surprisingly, and contrary to further hypotheses, the number of larval food plants did not explain variation in phenological changes. Oligophagous or polyphagous species can switch from one herbaceous species to another either within the larval development or between different generations. Monophagous species, however, cannot change their food plant. One would thus expect that oligo- or polyphagous species are more flexible in changing their phenology, which was, however, not supported by my analysis. I also did not find a difference in phenological changes between common, ubiquitous species with a wide distribution and more narrowly distributed species. Perhaps, local populations of species which occur over a large range do not have more genetic or phenotypic flexibility to adjust to a warmer climate than species with a very local occurrence. The former, however, may still profit from immigration from populations that are adapted to different climatic conditions. Finally, phylogenetic relationship between the Lepidoptera only poorly described variation in phenological change. The lack of a correlation could also be because I used a molecular phylogeny of superfamilies and information on lower phylogenetic levels is missing.

In summary, different phenological changes were best explained by a different set of species-specific traits, which complicates predictions of the effects of climate change. However, changes in phenology were consistently related to traits describing larval diet spectrum, suggesting that climate change indirectly affects trophic relationships. As butterfly and moths feeding as larvae on woody plants reacted differently than species feeding only on herbaceous plants, climate change related phenology shifts in herbivore communities may be different for woodlands compared to grasslands or herbaceous agricultural systems. Consequently, these various ecosystems may experience different changes in herbivore pressure in response to climate change.

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Appendix S1 Analyses with restricted dataset.

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