Temperature-related shifts in butterfly phenology depend on the habitat

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Abstract

Many species are becoming active earlier in the season as the climate becomes warmer. In parallel to phenological responses to climate change, many species have also been affected by habitat changes due to anthropogenic land use. As habitat type can directly affect microclimatic conditions, concurrent changes in climate and habitat could have interacting effects on the phenology of species. Temperature-related shifts in phenology, however, have mostly been studied independent of habitat types. Here, I used long-term data from a highly standardized monitoring program with 519 transects to study how phenology of butterflies is affected by ambient temperature and habitat type. I compared forests, agricultural areas and settlements, reflecting three major land use forms, and considered butterfly species that were observed in all three of these habitats. Seasonal appearance of the butterflies was affected both by the ambient temperature and the habitat type. As expected, warmer temperatures led to an overall advancement of the appearance and flight period of most species. Surprisingly, however, phenology of species was delayed in settlement habitats, even though this habitat type is generally associated with higher temperatures. A possible explanation is dispersal among habitat types, such that source–sink effects affect local phenology. When there is little productivity in settlement areas, observed butterflies may have immigrated from forest or agricultural habitats and thus appear later in settlements. My findings suggest that a spillover of individuals among habitats may affect phenology trends and indicate that phenological studies need to be interpreted in the context of habitat types. This becomes especially important when defining strategies to prevent or mitigate effects of climate and land-use changes on phenology and abundance of species.

Keywords: biodiversity monitoring, flight period, Lepidoptera, metacommunity, seasonal appearance, source–sink, temperature change, urban ecology

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Introduction

Global climate change and habitat changes are altering the occurrence and abundance of species worldwide (Walther *et al.*, 2002; Parmesan & Yohe, 2003; Travis, 2003; Thomas *et al.*, 2004; IPCC, 2007; Altermatt *et al.*, 2008). Over the last decades, many habitats and continents have been strongly affected by a changing climate (Walther *et al.*, 2002). Over the same time, many landscapes have also changed due to intensification of agriculture, deforestation or urbanization (Warren *et al.*, 2001; Thomas *et al.*, 2004). While climate and habitat change may go hand-in-hand, the consequences for local communities are not necessarily the same, and can either add up or diverge (Dale, 1997; Warren *et al.*, 2001; Travis, 2003; Franco *et al.*, 2006). Consequently, a comprehensive understanding of the individual and combined consequences of these two processes on

communities is necessary to prevent or mitigate their negative effects.

Temperature increases over time are one of the most commonly studied aspects of global climate change, and subsequent phenological changes are reported for many organisms. Phenology often directly depends on temperature (Walther *et al.*, 2002; Helmuth *et al.*, 2005). For example, plants advanced flowering and seed-set in warmer years (Fitter & Fitter, 2002; Steltzer & Post, 2009), birds and other vertebrates have advanced their breeding season (Dunn & Winkler, 1999; Walther *et al.*, 2002), and seasonal appearance of many butterflies and other insects have advanced by up to several weeks on various continents in a period of pronounced warming since the late 1970s (Roy & Sparks, 2000; Walther *et al.*, 2002; Forister & Shapiro, 2003; Musolin, 2007; Altermatt, 2010b).

In parallel, many habitats have been changing drastically, mostly due to anthropogenic influence (Fischer & Lindenmayer, 2007). Globally, the transition of forests into agricultural lands and the development

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of grassland habitats into villages, towns and road infrastructure are some of the most common habitat transformations (Tilman *et al.*, 2001; Foley *et al.*, 2005). These habitat transformations have large consequences for local organisms, as they affect the occurrence of resources, competitors or other key aspects of a species' life cycle (Warren *et al.*, 2001; Fischer & Lindenmayer, 2007). Consequently, the species communities in agricultural or urbanized habitats are often different and depleted compared to those of forested and other natural habitats. Habitat transformations can also modify the microclimate. Heat emission caused by domestic heating during winter and a reduced ambient cooling during the night due to temperature storage in concrete and asphalt warms up towns and urbanized areas (Oke, 1982; Fischer *et al.*, 2012). Middle-sized and large cities form heat islands with higher average temperatures than their surroundings, which can directly affect the phenology of species (Defila & Clot, 2001; Neil & Wu, 2006).

Few studies addressed whether warming and habitat type or habitat change have combined effects on phenology and population dynamics (Defila & Clot, 2001; Warren *et al.*, 2001). A limitation of these studies was that they only focused on one habitat or included different sets of species for different habitat types. For example, flowering period of the Horse Chestnut (*Aesculus hippocastaneum*) in the city of Geneva has advanced due to a combined effect of warming due to climate change and urbanization (Defila & Clot, 2001). However, Horse Chestnut is not native to Central Europe and is only planted in urbanized and developed areas and does not occur in other habitat types. Thus, phenological changes related to climate change or habitat type are hard to disentangle. In well-studied butterfly communities in Great Britain, population trends of different butterfly species were positively affected by warming but negatively affected by habitat change or habitat loss (Warren *et al.*, 2001). However, habitat changes mostly affected the abundance and distribution of habitat specialists, restricted to specific habitats such as heathlands, whereas mobile habitat generalists profited from the warming.

From a conservation perspective, it is important to know if and how habitat type and climate change-related temperature changes affect phenologies of species (O'Connor *et al.*, 2012). Phenological changes can have large consequences for ecosystems. The life cycle of many insects depends on a close matching with the phenology of their host plant, and mismatches, especially changes in voltinism (Altermatt, 2010a), may result in disruption of plant–insect interactions or host –parasite interactions (Memmott *et al.*, 2007; Jönsson *et al.*, 2009).
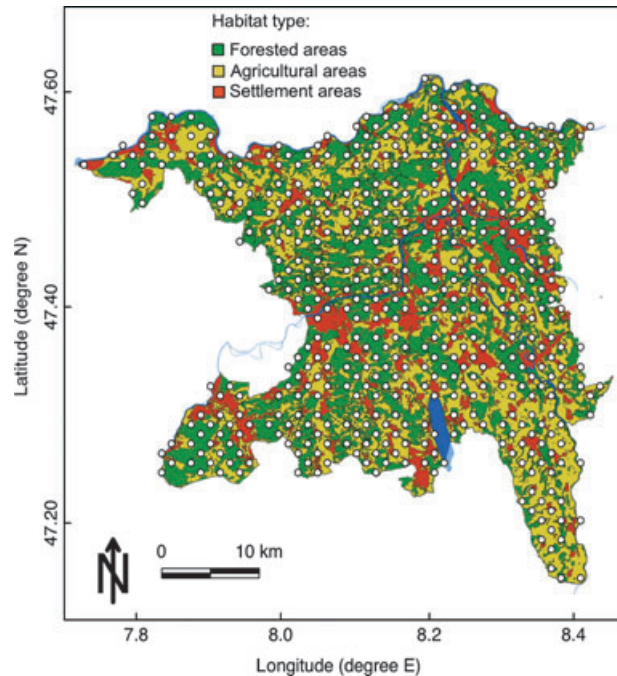

Fig. 1 Map of the canton of Aargau (Switzerland) showing the 519 transect localities (white dots) used in this study. The different habitat types are given in colour: forested (green), agricultural (yellow) and settlement areas (red); lakes and large rivers are in blue.

Here, I used long-term data from a randomized monitoring program conducted in parts of Switzerland to study how phenology of butterflies is affected by ambient temperature and habitat type. I compared forests, agricultural areas and settlements, reflecting three major land use forms in Central Europe (Fig. 1), and only considered butterfly species that were observed in all three of these habitat types. The three habitat types remained constant during the whole study period, and also have been relatively unchanged for the preceding decades, excluding transitory effects that may occur during the transformation of one habitat type into another.

Material and methods

Study area

The study area is the Swiss canton of Aargau (centre coordinates: 47°22′31″ N/8°05′03″ E). It is located in the northern part of Switzerland, and belongs geologically to the Jura mountains and the Central Plateau of Switzerland. The canton of Aargau has an area of 1404 km². The vertical extension ranges from 260 m above sea level to 908 m above sea level. About 490 km² (35%; Fig. 1) of its area are forested, 618 km² (44%) are used for agriculture, and 217 km² (15%) are developed and consist of road and railway infrastructure, villages

and towns (land cover values from 2005, Statistik Aargau, 2010). The remaining area is mostly open waters (ponds and streams) and marginal habitat types.

Biodiversity monitoring project

In the whole canton of Aargau, biodiversity is monitored in a long-term research project (Stapfer, 1996; Roth *et al.*, 2008). The diversity of butterflies has been measured since 1998 on a randomly placed, regular grid that covers the entire canton (Fig. 1). In total, 519 grid sites are included, about 20% of which are monitored annually. The 519 grids are representatively covering the main habitat types in the study area (34% of the transects are in forests, 45% in agricultural areas and 20% in settlement areas; see previous paragraph on land cover estimates). This study focuses on all butterflies and burnet moths (Lepidoptera: Papilionoidea: Papilionidae, Pieridae, Nymphalidae, Lycaenidae and Zygaenoidea: Zygaeninae; in the following all are referred to as "butterflies") recorded in that monitoring program from 1998 to 2010.

Butterflies were recorded using standardized transect counts (method after Pollard *et al.*, 1995) along transects of 250 m length. Butterflies were recorded within 5 m to each side of the transect line, and each site was visited 11 times per sampling year in regular time intervals from April 21 to September 21. Transect samplings were only conducted when meteorological conditions were favourable for butterflies to fly. All observed individuals were identified to the species level. Some species were only recorded as species complex. This refers to *Leptidea sinapis* and *L. reali* (here called *Leptidea sinapis* complex and treated as one species), *Colias hyale* and *C. alfacariensis* (here called *Colias hyale* complex and treated as one species) and *Pieris brassicae*, *P. rapae* and *P. napi* (here called *Pieris* sp. and treated as one species). In total, 55 250 individuals of 50 butterfly species were recorded. About 28% of the records are from forest habitats, 60% from agricultural habitats and 12% from settlement habitats. These numbers are closely reflecting the coverage of the study area by the three habitat types (see above), thus giving on average comparable butterfly densities in these habitats. The higher number of individuals in the agricultural habitat is mostly driven by the most common species, *Pieris* sp. Here, I restrict myself to the 28 species that have been recorded in all three main types of habitats in the canton of Aargau (see next paragraph).

The habitat directly surrounding each transect (0.25 ha) was classified using the European CORINE Land Cover typology (CEC, 1994). I used level one of these categories to characterize the habitat surrounding the transect, distinguishing agricultural habitats (arable land, permanent crops and pastures; Fig. 1), forested habitats (forests and woodland shrub vegetation), artificial surfaces (in the following called "settlement habitat," including urban fabric, roads and railways and construction sites) and other classes (wetlands; <2% of the sites and thus excluded from further analyses). Each transect was assigned to one of these three classes, based on the land cover class that covered >50% of the transect. A few transects were excluded from the following analyses because they could not be unambiguously assigned to one land class (i.e., when all three major habitat types were present and none of them covered >50% of the transect). I analysed how the habitat surrounding the transects affected phenology of the butterfly species. I conducted all comparisons on the level of the whole study area, and not on the scale of individual transects. As transects were randomly placed across the landscape, and the amount of observational efforts (i.e., number of transects) was constant across the different years, I could use the data on the butterfly fauna and phenology to be representative of the landscape level.

The fieldwork of the monitoring program was conducted by men doing their civilian service. Each of them was carefully selected to maintain high quality standards. The civilian servants received intensive training, and their field method and identification skills were controlled continuously. They worked in the program fulltime and generally for multiple seasons. The program was quality certified, following detailed procedures (Weber, 2008). This included the collection of certain difficult-to-identify taxa to be double-checked by a butterfly expert. The collection of specimens specifically targeted "difficult" groups (e.g., checkerspots, burnet moths or Lycaeniinae). Furthermore, 10% of all transects were monitored by two independent people using a blinded approach, meaning that the fieldworkers did not know which transects were being double-monitored. This allowed disentangling the (undirected) sampling error from possible individual bias. When an individual bias occurred, all data of that particular observer were discarded, and the transects were monitored again the following year. Altogether, these measures and the quality tests (Weber, 2008) assured that the data fulfilled highest quality standards.

Temperature data

Three official weather stations of the Federal Office of Meteorology and Climatology (MeteoSwiss) are located in close vicinity of the canton of Aargau. They are located North-westwards, Eastwards and South-westwards of the canton of Aargau (weather station "Basel/Binningen," 47°32′ N/07°35′ E, 316 m a.s.l.; "Bern/Zollikofen," 46°594′ N/7°27.8′ E, 553 m a. s.l., and "Zürich/Fluntern," 47°22.7′ N/8°33.9′ E, 556 m a.s.l.). I used monthly mean values of homogenized air-temperature data (Begert *et al.*, 2005) averaged over the three weather stations and calculated annual *mean spring temperature* (March to May) and *mean summer temperature* (June to August) for the years 1998–2010. I decided *a priori* on the meteorological definition of spring and summer, as many insect species can be grouped in to "spring" or "summer" species. This coarse classification may not capture all phenological details. To compare how the flight period of individual species matches with the spring and summer period, respectively, I refer to the detailed phenograms of all butterfly species, published in Altermatt *et al.* (2006).

Statistical analyses

Two different phenological response variables were calculated, one describing the phenological timing of the flight

period (*appearance*), and one describing a phenological state (*flight-period length*). *Appearance* is the date of the first 25% of the individuals for each species observed during the entire flight period per year. The use of this 25th percentile instead of the date of the first appearance or other phenological measures describing the onset of flight periods is recommended because it is not biased by variation in sampling effort or population abundance (Van Strien *et al.*, 2008). *Flight-period length* was calculated for each species as the range (in days) of all records (in Julian dates). Essentially, it is the maximum time period within a season used by adults. Contrary to *appearance*, *flight-period length* is sensitive to population size and sampling efforts, and is thus more difficult to interpret.

I used paired Wilcoxon signed-rank tests to compare the appearance and flight-period length of species across the three different habitat types. With this test, I compared the overall mean value of the phenological response variables for each butterfly species in each habitat, to test if phenology differed between the habitats. As a nonparametric test, it makes few assumptions and serves my main purpose, namely comparing if habitat type affects phenology.

I then ran linear models (ANCOVAs) to predict how annual appearance of each species (at the landscape level and not at the transect level) is affected by habitat type (agriculture, forest and settlement), annual mean spring or mean summer temperature and the interaction between habitat type and temperature. I was mostly interested in species-specific parameters on the slope and intercept of the predicted date of appearance relative to either spring or summer temperature, and less in the *P*-values for different species (Crawley, 2002). A positive or negative slope indicated if a species postponed or advanced its seasonal appearance with increasing temperature and if and how this depended on habitat type. The intercept-comparison across different habitat types (to test on the effect of habitat type) was coerced to the mean temperature across all years (for an evaluation and justification of this method see Schielzeth, 2010). Thereby, the intercept comparison was done at a biologically meaningful temperature (which it would not be at an intercept comparison at 0, meaning at 0 °C). Parameter values of all models are given for all species.

In addition, I analysed the data using a mixed-effect model approach. Detailed justification, description and results of the mixed model approach are given in the supporting information file (Fig. S2, section "b) Extended analysis using mixed-effect models"). The results and conclusions of the mixed-effect model approach were quantitatively and qualitatively highly similar to the main analyses. All analyses were conducted in R 2.12.1 (R Development Core Team, 2010).

Results

Mean temperature in the study area ranged from 8.64 °C to 11.43 °C (spring) and from 17.57 °C to 21.73 °C (summer) over the years 1998–2010 (Fig. 2). There was no significant change in temperature over time (spring: $F_{1,11} = 0.05$, $R^2 = 0.001$, $P = 0.82$; summer: $F_{1,11} = 0.13$, $R^2 = 0.01$, $P = 0.73$). Coinciding with an exceptional heat wave in Europe (Schar *et al.*, 2004), mean summer
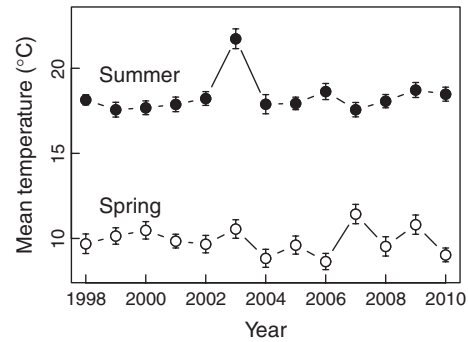
Fig. 2 Annual spring (March to May, white dots) and summer (June to August, black dots) air-temperature for the canton of Aargau. Mean ± se value of three different weather stations. There was no significant change in mean temperature over the study period from 1998 to 2010, but there was considerable inter-annual variation, especially in spring.

temperature in 2003 was much higher than in all other years.

The date of appearance of many butterfly species significantly correlated with annual mean spring temperature (Table 1a) or summer temperature (Table 1b) and habitat type. The interaction of temperature and habitat type on date of appearance was significant for four species (Table 1). Slope and intercept estimates of the ANCOVA models are given for each species and habitat type (Table 1). The appearance of 14 of the 28 butterfly species significantly or marginally significantly advanced to an earlier date when the spring or summer temperature was warmer (Table 1), and only two species significantly postponed their appearance to a later date. Furthermore, there was also an overall significant trend in advancing the flight period over time. The slope of a linear regression between year and annual 25% appearance was negative for 24 of the 28 species, showing that the advancement in appearance over time was significant across all species (sign test, $P = 0.0002$).

Using the mean across all years, appearance of the 28 butterfly species was significantly later in the season in settlement habitats compared to forested and agricultural habitats (Bonferroni-corrected paired Wilcoxon signed-rank tests between the habitat types: settlement vs. agriculture, mean difference = 9.7 days, $V = 324$, $P = 0.01$; settlement vs. forest, mean difference = 11.8 days, $V = 67$, $P = 0.004$; forest vs. agriculture, mean difference = 2.1 days, $V = 189$, $P = 0.76$; Fig. 3). The later appearance of species in settlement habitat compared to either forested or agricultural areas remained significant when conducting the same analysis on a subset of 14 species that were found on at least 25 transects in each habitat type (Wilcoxon signed-rank tests between the habitat types: settlement vs. agriculture, $V = 20$, $P = 0.04$; settlement vs. forest, $V = 98$, $P = 0.002$; Fig. S1).

Table 1 Species-specific parameter estimates from the ANCOVA models on the annual date of appearance relative to spring (a) and summer (b) temperature T, habitat type (agricultural, forested and settlement habitats) as well as the interaction between T and habitat type. The intercept is the Julian date of appearance (i.e., the Julian date of the first 25% of butterflies' appearance) at the mean temperature across all years. Significant and marginally significant p-values (≤ 0.1) are given in bold numbers. Species that start their flight period in summer (June to August) are marked with a §-symbol. All other species start their flight period in spring (mid-April to May)

Butterfly species	Slope			Intercept			P-value		
	Agricultural habitat	Forested habitat	Settlement habitat	Agricultural habitat	Forested habitat	Settlement habitat	T	Habitat	Interaction T × habitat
a) Spring									
Aglais urticae	7.02	1.36	−13.37	143.4	147.7	162.3	0.66	**0.03**	**0.10**
Anthocharis cardamines	−1.35	−2.75	−2.82	122.0	120.1	121.8	**0.10**	0.71	0.89
Aphantopus hyperantus	−4.11	−5.15	−4.43	191.8	189.6	191.7	**<0.01**	0.69	0.96
Araschnia levana	5.36	−2.97	−17.31	177.9	180.6	172.1	0.74	0.90	0.58
Argynnis paphia §	−7.19	−7.43	13.46	210.3	199.7	214.8	0.24	0.12	**0.10**
Celastrina argiolus	−11.93	−2.86	−40.11	167.0	184.7	170.8	**0.09**	0.29	0.38
Coenonympha pamphilus	−10.48	−5.01	−12.71	155.7	143.6	161.2	**0.09**	0.22	0.83
Colias crocea §	3.92	3.70	10.84	208.4	250.9	232.2	0.19	**0.10**	0.93
Colias hyale complex	−5.53	−6.16	−11.33	194.6	213.1	197.4	0.27	0.47	0.92
Cyaniris semiargus	−11.76	−1.20	−26.36	163.3	168.8	179.6	**0.08**	0.32	0.32
Cynthia cardui	4.24	−7.83	−15.63	167.3	160.8	178.9	0.28	0.22	0.18
Gonepteryx rhamni	5.96	3.97	12.04	141.8	137.4	168.8	0.24	**0.05**	0.87
Inachis io	8.74	21.50	23.38	139.7	151.4	172.6	**0.03**	0.12	0.73
Lasiommata megera	−12.56	3.50	12.17	167.5	185.4	218.5	0.67	**0.02**	0.46
Leptidea sinapis complex	−4.50	−9.61	−11.39	161.1	160.0	157.4	0.25	0.94	0.91
Limenitis camilla §	−8.41	−9.37	18.11	188.7	179.7	167.0	0.16	**0.01**	**<0.01**
Lycaena tityrus	−27.52	−15.32	4.11	173.8	175.8	211.4	**0.08**	0.53	0.77
Lysandra bellargus	−21.51	−31.80	4.03	200.8	188.6	229.0	**0.02**	0.55	0.67
Maniola jurtina §	−6.58	−7.56	1.97	185.6	184.3	187.5	**<0.01**	0.52	**0.02**
Melanargia galathea §	−5.60	−5.97	−5.56	184.2	181.2	180.1	**<0.001**	0.21	0.99
Mellicta parthenoides	−34.46	−15.98	−22.50	176.7	192.0	180.3	**0.02**	0.57	0.75
Papilio machaon	−10.52	−14.06	−3.37	156.3	177.8	177.4	0.32	0.35	0.88
Pararge aegeria	−3.46	−1.63	−16.08	154.7	150.1	152.4	0.24	0.91	0.55
Pieris sp.	−6.85	−5.68	−8.12	177.5	166.8	182.7	0.12	0.15	0.97
Polygonia c-album	−3.50	1.22	−1.83	184.0	170.1	206.2	0.76	**0.03**	0.94
Polyommatus icarus	−12.83	−6.70	−15.61	175.0	164.7	185.0	**0.06**	0.21	0.82
Vanessa atalanta	−3.79	−15.53	−4.35	197.0	193.5	214.1	0.11	**0.05**	0.49
Zygaena filipendulae §	11.91	19.70	10.05	199.9	198.7	211.8	0.11	0.63	0.88
b) Summer									
Aglais urticae	−0.48	−1.22	0.34	143.4	147.6	163.4	0.89	**0.05**	0.98
Anthocharis cardamines	−0.99	−1.32	−1.68	122.0	120.1	121.9	0.20	0.70	0.96
Aphantopus hyperantus	−2.71	−4.35	2.00	191.8	189.6	191.7	0.15	0.70	**0.08**

Table 1 (continued)

a) Spring

| Butterfly species	Slope			Intercept			P-value		
	Agricultural habitat	Forested habitat	Settlement habitat	Agricultural habitat	Forested habitat	Settlement habitat	T	Habitat	Interaction T × habitat
Araschnia levana	6.66	−9.64	63.86	178.1	180.6	184.6	0.80	0.89	**0.03**
Argynnis paphia §	−2.10	−6.15	−23.94	211.4	199.7	209.7	**0.09**	**0.10**	0.35
Celastrina argiolus	−4.83	21.45	−1.24	167.7	190.1	190.9	0.49	0.27	0.60
Coenonympha pamphilus	0.62	3.92	21.10	155.8	143.6	161.3	**0.02**	**0.15**	**0.05**
Colias crocea §	11.44	−9.59	−31.26	206.2	252.1	220.8	0.60	**0.03**	0.38
Colias hyale complex	−0.10	28.01	2.06	194.6	217.9	196.6	0.85	0.50	0.70
Cyaniris semiargus	−1.72	−4.36	−7.28	163.3	168.8	178.3	0.43	0.41	0.95
Cynthia cardui	−8.02	−3.60	−4.25	167.3	163.5	178.1	**0.10**	0.33	0.84
Gonepteryx rhamni	9.70	4.64	−1.33	139.8	137.4	169.6	0.25	**0.05**	0.64
Inachis io	3.79	−14.89	2.58	139.7	151.3	172.9	0.68	0.14	0.42
Lasiommata megera	−6.77	−0.66	−28.85	169.5	185.4	218.5	0.30	**0.03**	0.71
Leptidea sinapis complex	3.61	−8.27	2.07	161.1	158.1	154.9	0.74	0.85	0.53
Limenitis camilla §	−3.09	−2.60	1.82	186.9	179.8	160.6	0.20	**0.10**	0.70
Lycaena tityrus	14.10	−6.36	−19.41	173.6	180.7	206.3	0.33	0.34	0.86
Lysandra bellargus	−26.08	23.82	−2.19	192.5	193.9	226.6	0.74	0.46	0.64
Maniola jurtina §	−2.22	−3.89	−0.15	185.6	184.3	187.5	**0.10**	0.61	0.47
Melanargia galathea §	−2.62	−2.15	−0.41	184.2	181.2	180.2	0.13	0.35	0.70
Mellicta parthenoides	27.14	76.91	−29.53	184.3	197.8	157.5	0.33	0.91	0.19
Papilio machaon	2.37	32.46	14.00	156.3	183.8	180.9	0.71	0.33	0.68
Pararge aegeria	−6.71	−5.99	14.46	154.6	150.1	152.5	0.88	0.92	**0.07**
Pieris sp.	−2.19	2.15	0.17	177.5	166.8	182.8	0.99	0.17	0.87
Polygonia c-album	−6.62	0.41	−15.60	184.5	170.1	211.6	0.15	**<0.01**	0.22
Polyommatus icarus	10.09	7.56	7.15	175.0	164.7	185.1	**0.08**	0.22	0.96
Vanessa atalanta	−2.44	−5.44	−5.44	197.0	193.5	213.8	0.20	**0.07**	0.92
Zygaena filipendulae §	−12.82	−30.79	4.84	199.4	188.4	213.7	**0.08**	0.82	0.76
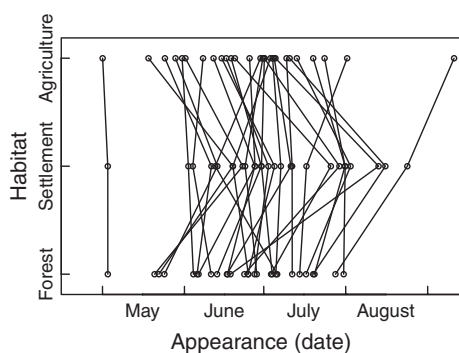
Fig. 3 Appearance (date of 25% of all individuals of a species observed, mean across all years) of 28 butterfly species across the three habitat types. For each species, the values across different habitats are connected with a line.

Across all years, length of flight period of the 28 butterfly species was significantly shorter in settlement habitats compared to agricultural habitats (Bonferroni-corrected paired Wilcoxon signed-rank test: settlement vs. agriculture, $V = 385.5$, $P < 0.001$; Fig. 4), but not significantly different in settlement habitats compared to forested habitats ($V = 98.5$, $P = 0.1$) and forested habitats compared to agricultural habitats ($V = 296$, $P = 0.1$).

In the last step, I used the estimates of the regression models (Table 1) to predict the expected changes in appearance with a 1 °C warming of the annual spring or summer temperature and the habitat type. The model predictions suggest a mean shift of the date of appearance to a date earlier by 5 days when spring temperature increases by 1 °C (Fig. 5a), but no such shift is predicted with increasing summer temperature (Fig. 5b). The shift in appearance is predicted to be equal among the three habitat types.

Discussion

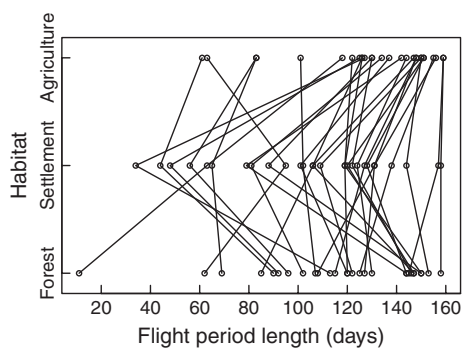Until now, little has been known about how habitat type and climate change interact to affect phenology.

Fig. 4 Flight-period length of 28 butterfly species across the three habitat types. For each species, the values across different habitats are connected with a line.
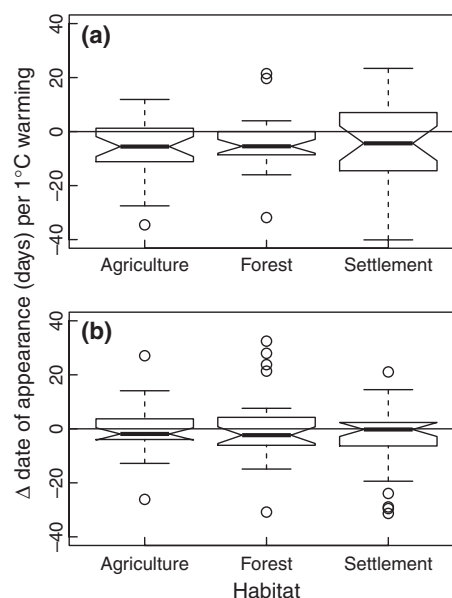
Fig. 5 Predicted shift (in days) of the date of appearance of all 28 butterfly species in the different habitat types per 1 °C of warming in spring (a) and summer (b). The predictions are taken from the parameter values of the ANCOVA models (Table 1). The thick line in the boxplots gives the median, the box is the interquartile range, and whiskers extend to the most extreme data point that is no more than 1.5 times the interquartile range.

Without taking into account different responses among habitats, managing and mitigating the effects of climate change on phenology may be biased towards particular ecosystems. Using a long-term data set from a standardized monitoring program (Fig. 1), I found that seasonal appearance of butterflies was significantly correlated with mean ambient seasonal temperature, habitat type, as well as an interaction of temperature and habitat type (Table. 1). As expected, warmer temperatures lead to an advancement of the appearance for most species, and the effect of warming on appearance was most pronounced for spring temperatures (Table. 1). However, appearance of butterfly species was not shifted earlier in the settlement habitats than in other habitats (Fig. 3), despite the higher temperatures associated with this habitat type (Oke, 1982; Neil & Wu, 2006). In fact, butterflies of the same species started flying significantly later in settlement habitats compared to agricultural and forest habitats (Fig. 3).

Local population dynamics could explain species' later appearance in settlement than agricultural or forest areas. The influence of population effects on phenology has been recently documented for birds and insects, where overall regional declines in abundances masked phenological responses to climate change (Miller-Rushing *et al.*, 2008; Ellwood *et al.*, 2012). Here, I suggest that the dispersal of butterflies may result in

their later appearance in settlement habitats. Butterfly individuals from agricultural and forested habitats could immigrate into (suboptimal) settlement habitats. With a temporal delay associated with such dispersal, the observed phenological variables would be postponed in settlement habitats, thereby causing an interaction of warming and habitat type on the observation of individuals. Thus, in mobile animals effects consistent with source–sink dynamics may affect observed phenological trends. Such an effect is not expected for immobile plant individuals, where warming and urbanization are both consistently advancing phenology (Defila & Clot, 2001).

The three habitat types considered here are not equally suitable for all butterfly species, and some habitats provide better resources than others. In particular, the settlement habitat is suboptimal for many species (Schweizerischer Bund Für Naturschutz, 1987). The reduced suitability of settlement habitats is supported by a shorter total flight period therein (Fig. 4). A shorter flight period could indicate a smaller population size or a shorter lifespan, but can also be an artefact of reduced sampling effort. Although it is not possible to disentangle these three mutually nonexclusive explanations, I suggest that at least part of the shorter flight-period length is due to a smaller population size of butterflies in settlement habitats. In a recent article, Forister et al. (2011) observed that declines in population size of many butterfly species result in shorter flight-period lengths. Thus, the shorter flight-period lengths observed here in settlement habitats are consistent with smaller populations, as observed in another butterfly system. An inequality in habitats can create source–sink population dynamics (Brown & Kodrick-Brown, 1977; Pulliam, 1988). In such a scenario, large population sizes in one habitat and subsequent dispersal due to random or density-dependent dispersal may lead to a migrant driven increase in population size in another locality at a later time point (Brown & Kodrick-Brown, 1977). It is well known that many butterflies live in patchy habitats, and dispersal among patches creates metacommunity dynamics (Ehrlich & Hanski, 2004; Hanski & Gaggiotti, 2004). Also, source–sink dynamics have been documented for butterflies (Harrison et al., 1988; Boughton, 1999), yet the consequences for phenology have not been examined. I cannot directly show the occurrence of source–sink dynamics. However, with source–sink dynamics, possibly coupled with age-dependent dispersal, we expect to see a shift in seasonal appearance of butterflies across different habitats driven by seasonal movement patterns and not by developmentally constrained phenology per se. Agricultural or forested areas may act as source populations, from which individuals of the same species relocate into settlement areas at a later stage of their adult lives. The settlement areas are generally less suitable for butterflies (Warren et al., 2001), and may be analogous to an ecological trap as observed in other species (Boal & Mannan, 1999; Battin, 2004). Furthermore, differences in the observation of organisms between different habitats may not only be interpreted as phenological differences, but could also indicate sink–source dynamics.

Although I did not have data on local dispersal of these butterflies, females of some of these species are known to shift from local dispersal during early adulthood to longer-distance dispersal in later life to lay remaining eggs at more distant localities (Schweizerischer Bund Für Naturschutz, 1987). Also, settlement areas are known to provide important nectar sources during the second half of the summer, when agricultural crops and pastures are harvested and cease to function as nectar sources. This could directly induce shifts in habitats and act as an evolutionary strategy to colonize new areas.

I could exclude that species-specific restrictions to one habitat type are causing the observed pattern, by comparing the same 28 butterfly species across all three habitats. All species were observed in all habitat types, and as mostly generalist species can reproduce in a variety of habitats. By using a phenological variable that does not appear to be biased by population size (Van Strien et al., 2008), I ensured that the difference in seasonal appearance among the habitats is not an artefact of different population sizes. However, my study indicates that phenological studies based on observations of mobile adults may not be able to account for dispersal among localities, and individuals observed locally may not necessarily reflect local phenologies.

Although appearance between the three habitat types was significantly different for many butterfly species (Fig. 3), flight period length was only significantly different among settlement and agricultural habitats (Fig. 4). However, and contrary to appearance, flight period lengths may be affected by population sizes, which could interfere with phenological habitat effects.

The predicted magnitude of shifts in flight period (Fig. 5) was consistent with other studies that related onset of flight periods with temperature (Roy & Sparks, 2000; Forister & Shapiro, 2003; Altermatt, 2010b). The herein observed higher number of significant relationships between appearance and spring temperature vs. appearance and summer temperature is in accordance with these previous findings that spring temperature has a larger influence on flight period than summer temperature. I also found an overall significant temporal change in appearance, with 24 of 28 species advancing their seasonal appearance over the 13 years. The advancement of individual species was not always

significant, probably due to the relatively short time period over which the monitoring program was conducted (1998–2010). During the same time period, no significant temporal trend in mean spring and summer temperature was observed (Fig. 2). This trend does not suggest that temperature in Central Europe did not increase since 1998, but the high interannual variance in mean temperature and some extreme hot years (e.g., 2003) may have masked long-term trends. Many studies have shown that temperature in Central Europe increased significantly, especially since the 1980's, and the years from 1998 onwards were among the warmest ever measured (Schar *et al.*, 2004; CH2011, 2011).

As changes in phenology are often compared over several decades during which concurrent habitat changes are likely or even documented (Warren *et al.*, 2001; Altermatt, 2010b), the conclusions of such studies could be affected by a dependence of phenology on habitat type. My findings indicate that phenological studies need to be interpreted in the context of the habitat type, as conversions of habitats may interact with temperature-related shifts in flight period. For example, habitat changes such as urbanization may not only reinforce (Defila & Clot, 2001) but also mask phenological changes due to climate change. The consideration of habitat type when looking at changes in phenology is especially important when defining strategies to prevent or mitigate effects of climate and land-use changes on phenology and abundance of species.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Figure S1. Appearance (date of 25% percentile of all individuals of a species observed, mean across all years) of 14 butterfly species across the three habitat types. The analysis was restricted (compared to Fig. 3) to the 14 species that were found on at least 25 transects in each habitat type. For each species, the values across different habitats are connected with a line. The later appearance of species in settlement habitat compared to either forested or agricultural areas was consistent and remained significant compared to the analyses performed on the whole dataset with all 28 species (Wilcoxon signed-rank tests between the habitat types: settlement vs. agriculture, mean difference = 10.2 days, $V = 20$, $P = 0.04$; settlement vs. forest, mean difference = 7.6 days, $V = 98$, $P = 0.002$).

Figure S2. Boxplots on Julian date of 25% appearance of all species in the different habitat types.

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