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Climatic warming increases voltinism in European butterflies and moths

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Climate change is altering geographical ranges, population dynamics and phenologies of many organisms. For ectotherms, increased ambient temperatures frequently have direct consequences for metabolic rates, activity patterns and developmental rates. Consequently, in many insect species both an earlier beginning and prolongation of seasonal duration occurred in parallel with recent global warming. However, from an ecological and evolutionary perspective, the number of generations (voltinism) and investment into each generation may be even more important than seasonality, since an additional generation per unit time may accelerate population growth or adaptation. Using a dataset extending back to the mid-nineteenth century, I report changes in the voltinism of butterfly and moth species of Central Europe. A significant proportion of 263 multi-voltine species showed augmented frequency of second and subsequent generations relative to the first generation in a warm period since 1980, and 44 species even increased the number of generations after 1980. Expected ecological consequences are diverse. Since multi-voltinism has been linked to insect outbreaks they include an increase in the abundance of herbivorous pests of agriculture and forestry. However, disruption of the developmental synchrony associated with multi-voltinism and host plant phenology may also reduce fitness, potentially having unexpected consequences for species of conservation concern. The ability of species to adapt evolutionarily to a changing environment may be facilitated by increased voltinism.

Keywords: climate change; phenology; lepidoptera; generation

1. INTRODUCTION

For survival, development and reproduction have to be synchronized with favourable seasons, and diapause with unfavourable periods (Roff 1983; Stearns 1992). In temperate regions, ectotherms, such as insects, have a characteristic regular summer–winter cycle with some interyear variation in the length of the breeding period. The length of the favourable season also influences the number of generations per year (Roff 1983; Stearns 1992). The production of multiple generations a year involves a choice between alternative developmental pathways, direct development and diapause. If the dormant stage cannot be reached in time, or if environmental conditions become adverse as the season proceeds, individuals may not survive. Crucial aspects are whether there is sufficient time for entire new generations to complete development, and whether conditions for juvenile development are sufficiently stable throughout the season (van Asch & Visser 2007).

Lepidoptera are one of the largest insect orders. Their life cycles vary from uni- (annual) to bi- (two generations per year) and multi-voltine (more than two generations per year) among species and populations (Scoble 1995). Voltinism is under genetic and environmental control (Scoble 1995). In species with wide geographical ranges, threshold values of diapause-inducing cues vary among populations so that individuals enter the developmental pathway resulting in diapause at a locally

appropriate time (Tauber *et al.* 1986). Many species and populations are bi- or multi-voltine at lower latitudes, and become univoltine at higher latitudes (Tauber *et al.* 1986; Välimäki *et al.* 2008). Often, a transition region occurs, where the second or third generation is irregular and scarce, and even within populations a polymorphism in voltinism may be maintained (Shapiro 1977; Van Dyck & Wiklund 2002; Välimäki *et al.* 2008). In species with such partial summer generations, only a fraction of larval stages produced in spring will develop into adults without diapause, while the rest will hibernate and be effectively univoltine. The expression of voltinism and other life-history traits mostly depends on the photoperiod and on the local climatic conditions (Scoble 1995). Several theoretical studies predict a change in voltinism due to climate change (Porter *et al.* 1991; Yamamura & Kiritani 1998). Empirical data supporting these ideas, however, are scarce, and mostly based on short-term observations and extrapolations for single species (Bale *et al.* 2002; Tobin *et al.* 2008).

Facing a period of global climate change (IPCC 2007), a series of concurrent biological phenomena are commonly reported, including altered geographical ranges, colonization dynamics, abundances and phenologies of many organisms (Hill *et al.* 1999; Parmesan *et al.* 1999; Walther *et al.* 2002; Parmesan & Yohe 2003; IPCC 2007; Altermatt *et al.* 2008). Phenological changes such as earlier flowering or earlier start of reproduction 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 (Roy & Sparks 2000; Walther *et al.* 2002). For some plants, a shortening of life-cycles has been found (Steltzer & Post 2009). For butterflies and other insects, an earlier onset of the

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flight period and, for multi-voltine species, a longer flight period has been found at various places (Roy & Sparks 2000; Forister & Shapiro 2003; Harrington et al. 2007). Also, an interaction between voltinism and the extension of a species' range-limits are predicted (Crozier & Dwyer 2006). A longer flight period caused by warmer temperatures may induce changes in phenology (Braune et al. 2008) and allow production of an increased number of generations per season (Roff 1980; Yamamura & Kiritani 1998; Braune et al. 2008). In partially bi- or multi-voltine species an increase in individuals belonging to the second or subsequent generations is expected (Roff 1980; Stearns 1992), since a larger proportion of the first generation's offspring will directly develop and reproduce within the same season, rather than diapause. Ultimately, the tendency to undergo direct development rather than diapause may manifest in the occurrence of generations previously not known, which has already been suggested by Yamamura & Kiritani (1998). Recent mathematical models predict such temperature-related production of additional generations in different pest-species, such as the spruce bark beetle *Ips typographus* (Jönsson et al. 2009) or the grape berry moth *Paralobesia viteana* (Tobin et al. 2008). Likewise, bi-voltinism of the Australian geometrid moth *Mnesampela privata* is predicted in warm years when development commences early in the season (Steinbauer et al. 2004). One can thus hypothesize that a pronounced warming may increase voltinism and investment into subsequent generations in a lepidopteran community. However, there is a surprising lack of empirical data on a relationship between climate change and voltinism for a larger number of species covering a long period of time. It is especially unknown if such changes have already taken place, and how many species they might affect. The lack of empirical long-term data is somewhat intriguing, especially given the magnitude of warming during recent decades and the evolutionary and ecological significance of voltinism.

On a global scale, air temperatures have increased since the mid-nineteenth century, and most of this warming occurred during 1920–1944 and after 1975–1980 (Jones & Moberg 2003; Luterbacher et al. 2004). In Central Europe, an unprecedented warming has been observed especially since the early 1980s (Walther et al. 2002; Paul et al. 2004; Rebetez & Reinhard 2008). Long-term data show that the increasing annual temperature trends from Central Europe were twice as large as mean trends for the Northern Hemisphere (Jones & Moberg 2003; Rebetez & Reinhard 2008), and most of the warming occurred in spring and summer (Rebetez & Reinhard 2008). Because this exceptional warming may foreshadow a global process (IPCC 2007), I used a dataset on Central European butterflies and moths extending back to the mid-nineteenth century to analyse concomitant life-history changes. I analysed if the pronounced warming since 1980 was correlated with changes of the voltinism and investment into different generations in 263 multi-voltine butterfly and moth species.

2. MATERIAL AND METHODS

(a) *Study area*

The study area in Central Europe (see the electronic supplementary material, figure S1) considers a circular area with a radius of 30 km around the city of Basel (47°33′ N, 7°36′ E) and incorporates parts of Switzerland, France and Germany in about equal proportions (Altermatt et al. 2006). The definition of this 3725 km^2 area has been used by lepidopterists for more than a century (Altermatt et al. 2006). Therefore, extensive long-term records for butterflies and moths are available since the mid-nineteenth century (Altermatt et al. 2006). Furthermore, precise long-term temperature data are available back to 1864 (Begert et al. 2005).

(b) *Weather data*

The official weather station 'Basel/Binningen' of the federal office of meteorology and climatology is almost precisely located in the centre of the study area (47°32′ N / 07°35′ E; 316 m a.s.l). I used monthly mean values of homogenized air-temperature data (Begert et al. 2005). In a first step I calculated the annual *mean summer temperature* for the half-year of April to September between 1864 and 2008. To allow for temporal autocorrelation, I used time-series bootstrap values of Mann−Kendall's rank correlation to test for a monotonic trend in the summer temperature time series. I then calculated the deviation of the annual mean summer temperature from the long-term average temperature. For the long-term average temperature, I used the 1961–1990 WMO standard normal period (WMO 1959; Scherrer et al. 2006), which is an often-used reference to depict temperature anomalies from long-term values. For the same data I also calculated discrete symmetric normalized smoothing (Daniell) kernels with a moving average of 10 years (R Development Core Team 2008). Finally, I compared the mean summer temperatures before 1980 with those at or after 1980 with a Wilcoxon signed-rank test.

(c) *Data on Macrolepidoptera*

I considered all species that are traditionally classified as Macrolepidoptera (Ebert 1991–2005) and were ever recorded in the study area (Altermatt et al. 2006). In total, the dataset consisted of 182 665 records of 1117 butterfly and moth species. The dataset is based on extensive historic museum records, on practically all faunistic publications from that region (Altermatt et al. 2006) as well as my own field data. Because of the large number of species considered, the long period of time and the large area covered, the data are of heterogeneous origin (Altermatt et al. 2006). Data from almost 200 different collectors have been considered from the 1850s to 2004 (Altermatt et al. 2006). I added unpublished recent records from 2005 on and historic data that were previously unavailable (Altermatt et al. 2006). Butterflies were almost exclusively recorded during the day, while most species of the other families were recorded at light traps. Methods of data collecting may have been different in the nineteenth century and early twentieth century. However, there is no indication of a systematic difference in recording methods, data quality or investment efforts regarding the different generations before or after 1980 (Altermatt et al. 2006). Species identification was verified at all museum records and standardized according to current taxonomic knowledge (Karsholt & Razowski 1996). The species identification within the dataset is of high quality (for details see Altermatt et al. 2006).

Each record consisted of a species name, a location (minimally to within a 1 × 1 km monad, but mostly to within 50 × 50 m) and a date (transformed into an ordinal date). Only

outdoor records of adults were used. Because information on the number of individuals per record was deficient especially for museum records, I did not incorporate it. Thus, each record gave only the occurrence of a species at a specific location and date.

The following species were excluded from the analysis: all migratory species (34 species), all species in which the adults diapause in summer (seven species) or winter (38 species), and all species for which only records of larval stages are known (13 species). This resulted in 1025 species, from which I selected all 355 species that are reported in literature (Ebert 1991–2005) to be at least partially bi- or multi-voltine in Central Europe. The remaining 670 species are univoltine (636 species), or their voltinism is debated (34 species). From these 355 bi- or multi-voltine species I further excluded all species that occurred only before or after 1980, because no temporal comparison can be made. I then calculated the voltinism, using kernel density estimates of the dates of record with the default function in R 2.8.0 statistical software (R Development Core Team 2008). Kernel density estimation is a non-parametric way of estimating the probability density function of a random variable, in my case occurrence of butterflies and moths over time. Kernel density estimates can be seen as a 'smoothed' version of a histogram, with the advantage that no artificial end points of bins have to be defined. The size of distinct modes gives the relative significance of each generation. I used the default kernel-bandwidth, which is estimated from the data and which is scale invariant (R Development Core Team 2008). I used that method to exclude an influence of potentially different sampling efforts, which could have occurred when using individual records directly. Given a sample of individual flight records of a species, kernel density estimation extrapolate the individual data and predict the flight period and relative occurrence of individuals of the entire population over the summer. Univoltine species will have unimodal kernel density distribution, while bi-voltine species will have a bimodal distribution, etc. I calculated species-specific kernel density estimates for the flight data before 1980 and after 1980. To compute reasonable kernel density estimates, a minimal number of records is necessary. I arbitrarily decided to include only species for which at least 10 records both before and after 1980 were available. I deliberately chose the low number of at least 10 records both before and after 1980, because I did not want to exclude many species just because of their rarity. However, to exclude the possibility that the species with few records might bias the analysis, I repeated the same analysis and included only species for which I had at least 20 and 30 records, respectively, both before and after 1980. This resulted in 263 species (minimal number of records before and after 1980 more than 9), 226 species (minimal number of records before and after 1980 more than 19) and 191 species (minimal number of records before and after 1980 more than 29) that were used in the analysis. It should be noted that the species excluded in the first of these three cases were mostly very rare species that are often restricted to one or two localities in the whole study area.

I determined the frequency of the second and subsequent generations relative to the first generation. From the multi-voltine species, less than 7 per cent were known to have regularly more than two generations per year (Ebert 1991–2005), while the others were predominantly bi-voltine. I thus pooled the second and eventual subsequent generations

for the analysis. I defined the change between the first and the second and subsequent generation as the date at which the slope between the peaks of the kernel density curve (representing the flight period) was minimal. For each species, the area under the curve before and after that date was used as the relative proportion of the first generation and the subsequent generations, respectively. I compared the relative proportion of the generations for all species before and after 1980 with a paired Wilcoxon signed-rank test. I also tested for shifts in the phenology of these 263 species, using the Julian date of the first 25 per cent of the individuals of each species observed before and after 1980, done for the first and second generation, respectively (van Strien *et al.* 2008). This method is better than the often-used date of the first appearance, as the latter is sensitive to different sampling efforts or different population abundances (van Strien *et al.* 2008).

Finally, I analysed potential changes in the number of generations, looking for the occurrence of an additional, previously unknown generation. For that analysis, I included also all univoltine species. From all 1025 species for which I had at least 10 records both before and after 1980, I determined the number of generations observed before and after 1980, both using kernel density curves and information on single outlying flight-dates and compared them with published data on the number of generations (Ebert 1991–2005). I also considered individuals that were reported out-of-date, and interpreted them as erratic generations, even though they might not reproduce successfully (Roff 1980). I then compared this observed number of generation found in the study area both before and after 1980 with an exact binomial test with the usual number of generation that is reported for these species in literature (Ebert 1991–2005) for these species in Central Europe.

3. RESULTS

In my study area in Central Europe, mean summer temperatures increased significantly between when records began in 1864 and 2008 (Mann–Kendall $\tau = 0.33$, time series bootstrap to deal with temporal autocorrelation, N bootstrap = 50 000, $p = 0.006$, figure 1). Summer temperatures exceeded the long-term average in almost every year since the beginning of the 1980s (figure 1) and mean summer temperature was significantly higher during 1980–2008 than 1864–1979 (15.8°C versus 14.6°C, Wilcoxon signed-rank test, $W = 439$, $p < 0.00001$).

Considering in total 263 bi- and multi-voltine butterfly and moth species, I found a highly significant proportional increase to second and subsequent generations after 1980 compared with before 1980 (figure 2; paired Wilcoxon signed-rank test, $n = 263$ species, $V = 26\,121$, $p < 0.00001$). The second or subsequent generations of 190 of the 263 species (=72%) became more pronounced after 1980 compared with before 1980. The proportional increase to second and subsequent generations after 1980 compared with before 1980 was also significant and consistent when analysing the different species-rich taxonomic groups individually (Rhopalocera, Geometroidea and Noctuoidea, table 1, figure 3). Also, the shift was found and highly significant when only including species for which at least 20 records exist both before and after 1980 (paired Wilcoxon signed-rank test, $n = 226$ species, $V = 19\,453.5$, $p < 0.00001$), or for which at least 30
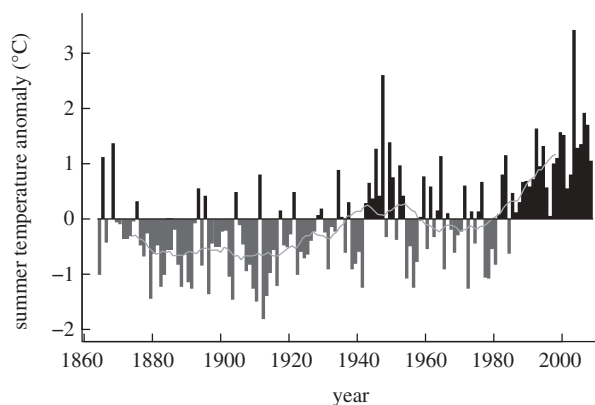
Figure 1. Mean summer temperature anomalies in the study region in Central Europe. Annual summer temperature anomalies above the long-term average are given in black, while anomalies below the long-term average are given in dark grey. The light grey line is the symmetric normalized smoothing kernel with a moving average of 10 years.

records exist both before and after 1980 (paired Wilcoxon signed-rank test, $n = 191$ species, $V = 13\,905$, $p < 0.00001$). However, by excluding species for which fewer records exist one might induce a bias and exclude rare species. I thus refer in the following to the analysis that included the most species (e.g. all 263 species for which at least 10 records exist both before and after 1980).

In parallel to the changes in voltinism, the species shifted their flight period to an earlier date. I found a significant shift of the Julian date of the first 25 per cent of the individuals of each species observed during the first and second generation, respectively. On average, the Julian date of the first 25 per cent of all individuals of a species observed was 2.1 days earlier after 1980 compared with before 1980 for the first generation (*t*-test, $t_{262} = 3.1$, $p = 0.002$), and 4.3 days earlier for the second generation (*t*-test, $t_{225} = 4.9$, $p < 0.0001$). The results are quantitatively the same and the significance levels even higher when including only species for which a larger number of records exist (data not shown, explanation see above).

In some species not only the relative frequency of generations, but also the number of generations changed. A change in the number of generations may transform a locally univoltine into a bi-voltine species or a bi-voltine into a multi-voltine, or vice versa. Such additional 'generations' may not be well-expressed and consist of few erratic adults, which hatched much beyond the known flight period (Ebert 1991–2005). From the whole dataset (1025 species) I compared all species reported to be uni- or bi-voltine (Ebert 1991–2005) with my data (please note that unlike all previous analyses, this analysis included also univoltine species). In 44 species known to be either univoltine or bi-voltine in Central Europe (Ebert 1991–2005), I found an additional second or third generation after 1980, which was unknown in the study area before 1980. In contrary, in only 19 species such out-of-date records were known before 1980 but not after 1980. Thus, there were significantly more species having either an additional generation or at least sporadic individuals beyond their usual reported voltinism after 1980 compared with before 1980 (exact binomial test, $p = 0.002$).
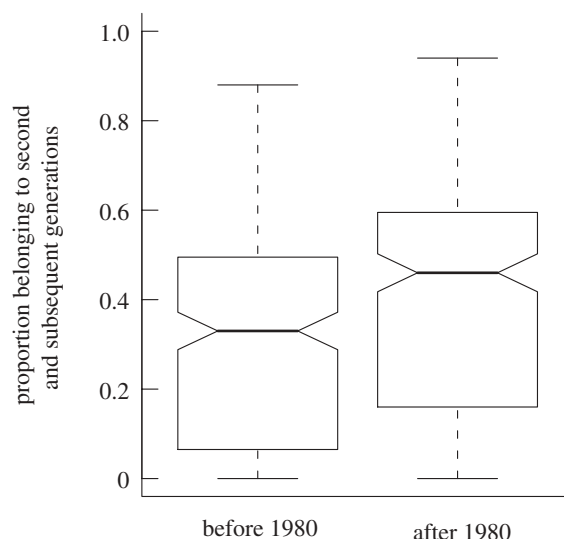
Figure 2. Species-specific proportion of records belonging to the second or subsequent generations before and after 1980. Boxplots depict the median and the range of the relative proportion of the second and subsequent generations for in total 263 bi- and multi-voltine butterfly and moth species from Central Europe. On average, there was a highly significant shift in the voltinism in favour of the second and subsequent generations after 1980 (paired Wilcoxon signed-rank test, $n = 263$ species, $V = 26\,121$, $p < 0.00001$).

4. DISCUSSION

Climatic warming since the late 1970s and early 1980s (Walther *et al.* 2002; Paul *et al.* 2004; Rebetez & Reinhard 2008) has been linked to a series of concurrent biological phenomena including altered geographical ranges, community dynamics, abundances, and phenologies of many organisms (Walther *et al.* 2002; Parmesan & Yohe 2003; IPCC 2007; Altermatt *et al.* 2008). Phenological changes such as earlier flowering, earlier start of reproduction, or a prolongation of seasonal duration are among the best-studied warming-related changes in life-history traits (Roy & Sparks 2000; Walther *et al.* 2002; Parmesan 2006). However, from an ecological and evolutionary perspective, the number of generations (voltinism) and investment into each generation may be even more important than seasonality. The potential of changes in the number of generations is large (Porter *et al.* 1991), since many insect species exhibit variation in the number of generations and may have a facultative second or third generation in favourable years (Van Dyck & Wiklund 2002).

A series of theoretical studies suggest changes in voltinism of insects due to climate change (Yamamura & Kiritani 1998; Steinbauer *et al.* 2004; Braune *et al.* 2008; Tobin *et al.* 2008; Jönsson *et al.* 2009). These studies are based on the well-known fact that temperature (Annila 1969; Van Dyck & Wiklund 2002)—besides day length—is an important factor determining generation time in insects. These mathematical models predict a temperature-related production of a second generation in the future based on current knowledge on developmental time at different temperature regimes, mostly focussing on single species. However, empirical data on current changes in voltinism for a whole community have been previously lacking.
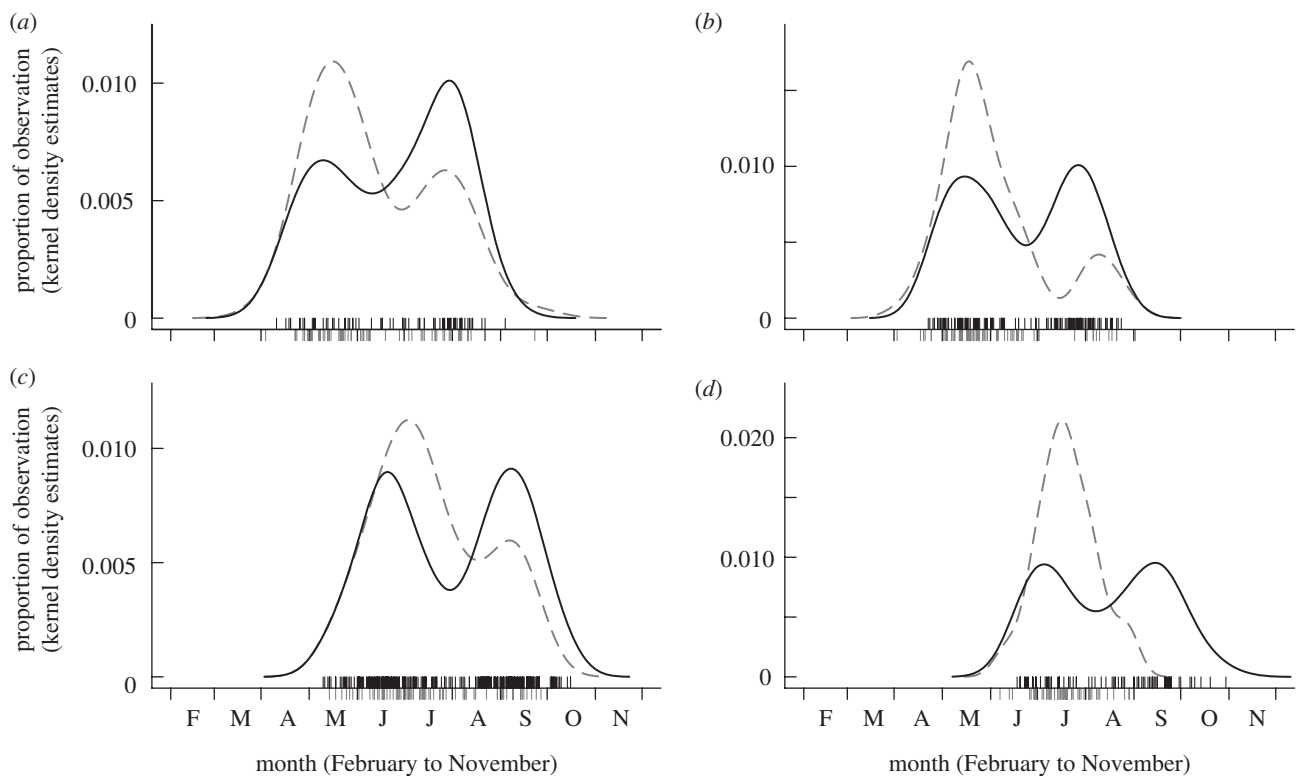
Figure 3. Four examples of species that showed a pronounced change in favour of the second generation after 1980 compared with before 1980. The species belong to four different families of butterflies and moths: (*a*) *Leptidea sinapis* (Pieridae), (*b*) *Plagodis dolabraria* (Geometridae), (*c*) *Hypena proboscidalis* (Noctuidae) and (*d*) *Lithosia quadra* (Arctiidae). All species are known to be at least partially bi-voltine. The second generation, however, was more expressed after 1980 compared with before 1980. The frequency distribution and rugs (depicting individual records with tick marks) are shown in dashed grey for records before 1980 and in solid black for records after 1980.

Table 1. Test on the relative occurrence of the second and subsequent generations relative to the first generation in all large taxonomic groups after 1980 compared with before 1980. The Wilcoxon signed-rank test was done separately for all large taxonomic groups (butterflies and five moth superfamilies; only species for which at least 10 records before and after 1980 exist were included). Data as in figure 2, but split into the six taxonomic groups. In all species-rich groups, there was a highly significant shift in the voltinism in favour of the second and subsequent generations after 1980 compared with before 1980, also remaining significant when correcting for multiple testing (*p*-value Bonferroni-corrected).

taxonomic group	relative occurrence after 1980 (%)	*n* species	*V*	*p*	*p*-Bonferroni
Zygaenoidea (burnet moths)	+36	2	3	0.5	n.s.
Sphingoidea (hawk moths)	+10	8	27	0.035	n.s.
Rhopalocera (butterflies and skippers)	+11	43	745	0.00025	0.0015
Drepanoidea (hook tip moths)	+7	9	33	0.24	n.s.
Geometroidea (geometrid moths)	+10	110	5124	<0.000001	<0.000001
Noctuoidea (noctuid moths)	+6	91	2617	0.00054	0.0032

In my study area in Central Europe, temperatures increased significantly over the last decades, and the increase was especially pronounced since about 1980 (figure 1). This change is consistent with the absolute strongest temperature increase in many other places in Central Europe, indicating a large-scale rather than local phenomenon (Scherrer *et al.* 2006; Rebetez & Reinhard 2008). I thus compared the voltinism of each species separately before and after 1980 as a breakpoint, because the changes in temperature in Central Europe were most pronounced since 1980 (Walther *et al.* 2002; Paul *et al.* 2004; Rebetez & Reinhard 2008), which is also evident from the local temperature data (figure 1). I found an increased investment into the second and

subsequent generations relative to the first generation for 263 multi-voltine species after 1980 (figure 2). To my knowledge, this is the first empirical demonstration of changes in the voltinism on a large temporal and taxonomic scale due to climate change. The observed phenomenon may be rather general, as I found a consistent change in voltinism within different species-rich taxonomic groups (table 1). Also, the analysis is robust with respect to the number of species considered. Significance levels were even higher when reducing the sample size by the exclusion of species for which fewer records were known (thus limiting the analyses for species with a minimal number of individuals recorded both before and after 1980 to either 20 or 30, compared with 10).

Finally, there was also no qualitative difference between the day-flying butterflies, most often recorded by traditional netting, and the nocturnal moths caught at light traps. I therefore conclude that the observed changes are not due to bias in how records were recorded.

A functional explanation for the changes in voltinism may be the earlier onset of the flight period, which prolongs the season and allows the production of an additional generation. Consistent with other studies (Roy & Sparks 2000; Forister & Shapiro 2003), I found on average a shift of the flight period of the 263 species to an earlier date. Because these species fly earlier in the summer season, individuals of the first generation may also reproduce earlier. A more rapid larval growth and development due to higher temperatures would be another explanation: as a consequence, more individuals of the subsequent generation develop when both day-length as well as temperature are less shifted to autumn-conditions, and they may directly develop with the same season rather than diapause in a larval stage. Finally, a mutually non-exclusive explanation is the replacement of uni- or bi-voltine populations in Central Europe by immigrants from Southern European populations, which may be bi- or polyvoltine.

Some species even increased the number of generations after 1980. Such a change transforms a locally univoltine into a bi-voltine species or a bi-voltine into a multi-voltine. Initially, such additional 'generations' may not be well-expressed and consist of just a few adults, which hatched much beyond the known flight period (Ebert 1991–2005). An increased number of generations may not only promote population growth (by having more generations per unit time), but also speed up evolutionary processes and adaptation. However, in some species these individuals of this additional generation might not successfully reproduce, since they are out of their natural life cycle—for instance, when the larval food plant is seasonally not available. For these species a change in voltinism may be detrimental.

The documented changes in voltinism confirm the flexibility and high adaptability of insects to environmental change. Insects are among the fastest recorded organisms reacting to global warming (Walther *et al.* 2002), and changes in voltinism have been predicted (Yamamura & Kiritani 1998; Steinbauer *et al.* 2004; Tobin *et al.* 2008; Jönsson *et al.* 2009). For a few Lepidoptera, an increase in the number of generations per time has occurred following invasion into another region (Gomi & Takeda 1996), eventually causing economic damage after large populations built up (Gomi & Takeda 1996). Generally, a faster generation time and more generations per year directly increase the fitness of an organism because the population growth rate increases (Roff 1980, 1983; Stearns 1992). Thus, changes in the voltinism towards more generation per unit time or a higher investment into progressing generations may promote the outbreak of pest species (Porter *et al.* 1991; Steinbauer *et al.* 2004).

All of the herein studied species are herbivores, and increases in voltinism may amplify their negative influence on plant communities (Porter *et al.* 1991), especially since many long-lived plants (e.g. bushes, trees) may be unable to speed up their life cycle. Most of the observed changes in voltinism were qualitative, and not yet quantitative,

meaning that species known to be partially multi-voltine invested more into progressing generations within a season. I predict, however, that the phenomenon may become more and more quantitative as well, generally increasing the number of generations per season. This, of course, will directly increase the evolutionary trajectory, and adaptation to a changing environment may become more feasible (Stearns 1992).

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Fig. S1. Study area (grey circle) in Central Europe.