

Resource specialists lead local insect community turnover associated with temperature – analysis of an 18-year full-seasonal record of moths and beetles

Philip Francis Thomsen^{1†}, Peter Søgaaard Jørgensen^{2*†}, Hans Henrik Bruun², Jan Pedersen³, Torben Riis-Nielsen⁴, Krzysztof Jonko⁵, Iwona Słowińska⁶, Carsten Rahbek³ and Ole Karsholt⁷

¹Centre for GeoGenetics, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark;

²Center for Macroecology, Evolution and Climate, Department of Biology, University of Copenhagen, Copenhagen, Denmark;

³Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark;

⁴Department of Geosciences and Natural Resource Management, University of Copenhagen, Copenhagen, Denmark;

⁵Okopowa 113/37, 91-849 Łódź, Poland;

⁶Department of Invertebrate Zoology and Hydrobiology, University of Łódź, Banacha 12/16, 90-237 Łódź, Poland; and

⁷Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark

Summary

1. Insect responses to recent climate change are well documented, but the role of resource specialization in determining species vulnerability remains poorly understood. Uncovering local ecological effects of temperature change with high-quality, standardized data provides an important first opportunity for predictions about responses of resource specialists, and long-term time series are essential in revealing these responses.

2. Here, we investigate temperature-related changes in local insect communities, using a sampling site with more than a quarter-million records from two decades (1992–2009) of full-season, quantitative light trapping of 1543 species of moths and beetles.

3. We investigated annual as well as long-term changes in fauna composition, abundance and phenology in a climate-related context using species temperature affinities and local temperature data. Finally, we explored these local changes in the context of dietary specialization.

4. Across both moths and beetles, temperature affinity of specialists increased through net gain of hot-dwelling species and net loss of cold-dwelling species. The climate-related composition of generalists remained constant over time. We observed an increase in species richness of both groups. Furthermore, we observed divergent phenological responses between cold- and hot-dwelling species, advancing and delaying their relative abundance, respectively. Phenological advances were particularly pronounced in cold-adapted specialists.

5. Our results suggest an important role of resource specialization in explaining the compositional and phenological responses of insect communities to local temperature increases. We propose that resource specialists in particular are affected by local temperature increase, leading to the distinct temperature-mediated turnover seen for this group. We suggest that the observed increase in species number could have been facilitated by dissimilar utilization of an expanded growing season by cold- and hot-adapted species, as indicated by their oppositely directed phenological responses. An especially pronounced advancement of cold-adapted specialists suggests that such phenological advances might help minimize further temperature-induced loss of resource specialists.

6. Although limited to a single study site, our results suggest several local changes in the insect fauna in concordance with expected change of larger-scale temperature increases.

Key-words: climate change, community temperature index, community turnover, diet specialists, ecological specialization, light trap, phenology shift

*Correspondence author. E-mail: PSJorgensen@bio.ku.dk

†These authors contributed equally to this work.

Introduction

Natural experiments observed in long-term time series are essential for uncovering how species respond to ongoing environmental change (Magurran *et al.* 2010; Dornelas *et al.* 2013). For instance, the UK breeding bird survey (BBS) and UK butterfly monitoring scheme (UKBMS) are examples of long-term monitoring (*c.* 20 and 40 years, respectively), which have yielded valuable insights to bird and insect populations in a changing world (e.g. Warren *et al.* 2001; Diamond *et al.* 2011; Devictor *et al.* 2012). Additionally, the Rothamsted Insect Survey has been running for 50 years and is the most comprehensive local long-term multispecies data set on insects in the world (Shortall *et al.* 2009; Mutshinda, O'Hara & Woiwod 2011). Such data sets are not common (Magurran *et al.* 2010), and they rarely include standardized full-seasonal sampling, since this task is highly labour-intensive. Insect sampling in light traps can be replicated spatially to make inferences on general regional patterns reflecting environmental change, but is often limited by local variation in personal skills and sampling intensity (Gimesi *et al.* 2012). Local sampling, on the other hand, cannot generalize on regional or global patterns, but standardization and intensification of sampling is easier. A highly standardized data set is important for uncovering authentic local patterns (Shortall *et al.* 2009), which can be further investigated in spatially replicated data. Hence, uncovering local ecological effects of climate change with high-quality data is an important first step in making predictions on regional or global patterns. Biological responses to recent climate change have been established across various taxonomic groups and geographical regions, and insects are sentinels for some of the strongest reported responses (Roy & Sparks 2000; Walther *et al.* 2002; Forister & Shapiro 2003; Parmesan & Yohe 2003).

Here, we use extensive and standardized light-trapping data from Copenhagen, Denmark, spanning almost two decades (1992–2009) of full-seasonal individual-based recordings of moths and beetles. The sampling represents a single site located in a stable urban habitat with minimal variation in the near surroundings over the study period. The light trap was operated by the same three persons throughout the study period, who also identified and counted all individuals. A single study site facilitated standardized weekly sampling throughout the entire season in two decades.

We analysed the data for signals indicative of local effects from climate change. Specifically, we investigated annual as well as long-term changes in fauna composition, abundance and phenology across both taxa in a climate-related context using species temperature affinities and temperature data from local weather stations within few kilometres from the sampling site. Furthermore, we explored these local changes in the context of resource specialization.

Ecological specialization is a central concept in ecology and generally describes the trade-off between the capacity to exploit a range of environmental conditions and the ability to use each one (Futuyma & Moreno 1988; Devictor *et al.* 2010; Poisot *et al.* 2011). The evolutionary success of this overall strategy has resulted in approximately 70% of all herbivorous insects being specialists (Price *et al.* 2011). However, specialists are increasingly shown to be declining and experiencing higher past (McKinney 1997) and present (Warren *et al.* 2001; Kotiaho *et al.* 2005; Devictor *et al.* 2008; Stefanescu *et al.* 2011) extinction risk during periods of environmental change. This can lead to loss of specialized species and thus functional homogenization of ecosystems (Devictor *et al.* 2008; Colles, Liow & Prinzing 2009; Clavel, Julliard & Devictor 2011). For example, a recent Danish study on butterflies using a century of occurrence records showed that the most severe local-scale declines occurred among sedentary host plant specialists (Eskildsen *et al.* 2015). One general hypothesis accounting for these observations is that stable environmental conditions have favoured the evolution of specialist species, whereas fluctuating conditions have favoured generalists, and that these divergent evolutionary roots cause generalist species to better cope with global environmental change (Futuyma & Moreno 1988; Kassen 2002).

Materials and methods

STUDY SITE AND DATA COLLECTION

A modified Robinson light trap was installed 17.5 m above ground at the roof of the Zoological Museum in Copenhagen, Denmark (N 55.702512°, E 12.558956°). A 250 W mercury vapour bulb was used as light source. In the trap, 1,1,2,2-tetrachlorethane was used as killing agent. The trap was emptied on an approximately weekly basis and was active from April–November 1992–2009. All individual records of Lepidoptera and Coleoptera were collected, identified to species level and counted yielding qualitative (species) and quantitative (number of individuals within each species) data for the entire study period. All handling and identification of material was carried out consistently throughout the entire period by the same three persons: for Lepidoptera (OK) and Coleoptera (initiated by the late Dr. Michael Hansen and completed by JP). The final data set was subjected to a thorough quality check, and the few records (<20 individual records) that could not be accounted for by comparison of collection periods were discarded. We excluded the first (1992) and the last year (2009) of the data set to minimize start-up effects (operating the trap in a standardized manner comparable to the remainder of the study period) and influence from alteration of the local habitat in 2009. Furthermore, in 1992 and 2009 the trap was not active in the entire season. To account for variation in sampling intervals, we grouped the data set into standardized 10-day periods the first starting on 1st of January (Julian Day 1) and the last period ending on December 26 (Julian Day 360). The 10-day interval is slightly longer than the mean sampling interval of 7 days.

SPECIES TRAITS

We used the data base from the European Butterflies and Moths website based on extensive literature surveys, to identify moth resource specialists and generalists (www.lepidoptera.eu). Specialists were defined as species feeding on only one host plant species or, when species-level data was not available, one host plant genus (monophagous species). These two definitions of specialists (broad and strict monophagous) yielded consistent results. Generalists are defined as any species that feeds on two or more host plant species or genera. This grouping method catches the highest number of true monophagous species. We categorized beetles as generalist carnivorous and omnivorous species (Cantharidae, Carabidae, Coccinellidae, Dytiscidae, Hydrophilidae, Melyridae, Staphylinidae, Silphidae, Elateridae, Scirtidae) or specialist phytophagous species (Chrysomelidae, Curculionidae, Attelabidae, Brentidae). We define the latter category as resource specialists since they are, to a much higher degree, depending on a seasonally restricted food source in both the larval and adult stage. To validate this family-level approach, we further classified beetles on larval diet at the species level into herbivorous (algophagous, depositophagous, detritivores, mycetophagous, phytophagous, pollenophagous, rhizophagous), carnivorous (incl. necrophagous and coprophagous) and omnivorous (species belonging to two or more broad diet categories). Herbivorous species were then further classified as mono-, oligo or polyphagous species. Specialists were then defined as mono- and oligophagous herbivorous species, while generalists were defined as carnivorous, omnivorous and polyphagous herbivorous species (Hansen 1964; Böhme 2005). Xylophagous and saprophagous species dependent on the complex resource of dead wood were omitted.

We obtained an index of species' biogeographical temperature affinity by calculating the mean annual temperature across all countries where a species occurs. For this species temperature index (STI), temperature data was obtained from WorldClim (Hijmans *et al.* 2005), and occurrence data was obtained from Fauna Europaea (Karsholt & van Nieukerken 2011; Alonso-Zarazaga, Audisio & de Jong 2013) (www.fauna-eu.org). Based on STI, we calculated a community presence temperature index (CTI). The CTI averages STI across all species present in a given sample, without attempting to account for species abundances. Based on STI, we divided moths and beetles into two quantiles. Due to the larger data set of moths, we further analysed this group divided into four STI quartiles, in order to get a picture of more gradual temperature-related changes in the fauna. The quantiles represent species that can be characterized as cold-dwelling (1st quantile, 1st and 2nd quartile) or hot-dwelling (2nd quantile, 3rd and 4th quartile), based on the geography of their European distribution.

We use a presence-based STI since this index is less vulnerable to intrinsic and stochastic fluctuations in local numbers. We use mean temperature for calculating the index since this is likely most robust considering uncertainty in species occurrence data.

ENVIRONMENTAL DATA

Mean daily temperature was retrieved from two Danish weather stations closest to the study locality: Landbohøjskolen (N 55-679835°, E 12-540634°) and Sjølsmark (N 55-876506°, E 12-430277°). The data was made available by the Danish Meteorological Institute. From the daily data, we calculated growing degree

days (GDD) using a threshold of 10°C with a 30-day sliding window for 1992–2009. Since initial analysis done on data from both stations yielded consistent results, we report results from the closest weather station, Landbohøjskolen, in the final analysis. We further include a satellite-derived measure of vegetation greenness, the Normalized Difference Vegetation Index (NDVI) (Tucker *et al.* 2005) in order to complement the GDD with an index showing biotic effects of temperature – in this case on plants.

STATISTICAL ANALYSIS

A number of regression techniques were applied to investigate trends in the data set. We used GDD as explanatory variable for the analysis of seasonal temperature's general influence in the data set. For every 10-day period, we performed linear regression with species' first and last occurrence, richness and abundance as response variable. Regressions on first and last occurrence were performed on the cumulative proportion of annual first and last occurrences in each 10-day period. Predicted values of the response variable in the 10% and 90% GDD quantiles were used to characterize the influence of temperature between a cold and hot year. Linear regression methods were also used to detect directional change in community composition using the qualitative (occurrence-based) Whittaker dissimilarity index (Whittaker 1972) and CTI, in both cases using year as explanatory variable. In the analysis of community turnover, we used the last year as reference year for all other yearly indices. We used ANOVA and chi-square tests to investigate trends in species abundance and number of species lost and gained between the first (1992–2000) and second (2001–2009) half of the study period, respectively. In the analysis of species abundance trends, we included all species with more than three records in both the first and second half of the study period. We used quantile regression methods on all 254 080 records to investigate changes in the relative abundance distribution as well as first and last occurrences over time. Using the R-package *quantreg*, we quantified temporal change in the 5%, 10%, 25%, 50%, 75%, 90%, 95% quantiles. Initial sorting of data was performed in Microsoft Excel (Redmond, WA, USA) and SAS v. 9.2 (Cary, NC, USA). All subsequent statistical analyses were performed in R v. 2.15.3 (Vienna, Austria).

Results

CATCHMENT AREA OF THE LIGHT TRAP

In total, the trap caught 254 080 individuals and 1543 species of moths and beetles, representing *c.* 42% and 12% of the moth and beetle species found in Denmark, respectively (Table 1). The species composition indicated that the majority of species in the light trap were caught from the nearest surroundings in and around Copenhagen, but also included a number of species living in habitats at least 10 km away and most likely further. Thus, the trap caught several species of Lepidoptera whose larvae are monophagous on plants not growing in the near vicinity, for example *Monochroa tetragonella* (on *Glaux maritima*), *Scrobipalpa stangei* and *Gynnidomorpha vectisana* (on *Triglochin maritimum*), *Phiaris metallicana* (on *Vaccinium uliginosum*) and *Lycophotia porphyrea* (on

Calluna vulgaris). Also the ground beetles *Harpalus gri-seus*, *Harpalus calceatus* and *Dolichus halensis* caught in the trap are expected to originate from sun-exposed sandy

Table 1. Overview of moth and beetle species, families, superfamilies and individuals recovered in the light trap throughout the 18-year study period

	Species	Families	Individuals
LEPIDOPTERA	1076	52	220 341
COLEOPTERA	467	52	33 739
Total	1543	104	254 080

Superfamily	Species	Superfamily	Species
LEPIDOPTERA		COLEOPTERA	
Eriocranioidea	2	Caraboidea	92
Hepialoidea	2	Staphylinioidea	111
Nepticuloidea	30	Scarabaeoidea	8
Adeloidea	5	Hydrophiloidea	42
Tischerioidea	1	Histeroidea	1
Tineoidea	18	Scirtoidae	12
Gracillarioidea	59	Byrrhoidea	8
Yponomeutoidea	60	Elateroidea	25
Douglasioidea	1	Bostrichoidea	24
Gelechioidea	187	Clerioidea	7
Alucitoidea	1	Cucujoidea	59
Pterophoroidea	6	Tenebrionidea	26
Epermenioidea	2	Chrysomeloidea	12
Choreutoidea	2	Curculionoidea	40
Tortricoidea	183		
Cossoidea	1		
Zygaenoidea	1		
Papilionoidea	3		
Pyraloidea	105		
Drepanoidea	12		
Lasiocampoidea	3		
Bombycoidea	9		
Geometroidea	137		
Noctuoidea	246		

or gravel habitats at least 10 km away. Besides these more or less local migrants, the trap also captured several species of so-called migrating Lepidoptera, which are species that cannot survive the winter in Denmark, and must have arrived from more southern countries. These include *Etiella zinckenella*, *Palpita vitrealis*, *Euchromius ocella*, *Agrius convolvuli* and *Protoschinia scutosa*.

Among the total catch of the light trap, seven species of Lepidoptera (*Stigmella stettinensis*, *Phyllonorycter robi-niella*, *Oegoconia novimundi*, *Gelechia sestertiella*, *Scrobipalpula tussilaginis*, *Aglossa caprealis* and *Diplopseustis perieresalis*) and two species of Coleoptera (*Harmonia axyridis* and *Rushia parreyssii*) were recorded for the first time in Denmark during this study. Established Danish populations of *O. novimundi*, *G. sestertiella*, *S. tussilaginis* and *H. axyridis* have later been confirmed.

SUMMARY STATISTICS

Species richness and abundance showed a unimodal peak in the month of July and 90% of a year's species had occurred at least once by August (Julian day 212) (Fig. 1). The overall data set showed a high degree of sensitivity to temperature (monthly GDD) such that a clear advancement of first occurrences (Fig. 1a, e) and increase in richness (Fig. 1b, f) and abundance (Fig. 1c, g) could be observed between a cold and hot year for most 10-day periods (10% vs. 90% GDD quantile, Table S1, Supporting information). Thus, GDD explained on average 34%, 15%, 16% and 14% and at maximum 89% (day 151), 78% (day 151), 60% (day 151) and 70% (day 131) of yearly variation in moth first occurrence, species richness, abundance and last occurrence across all 10-day periods, respectively (Fig. 1, Table S1, Supporting information). For beetles, average explained variation was 26%, 16%,

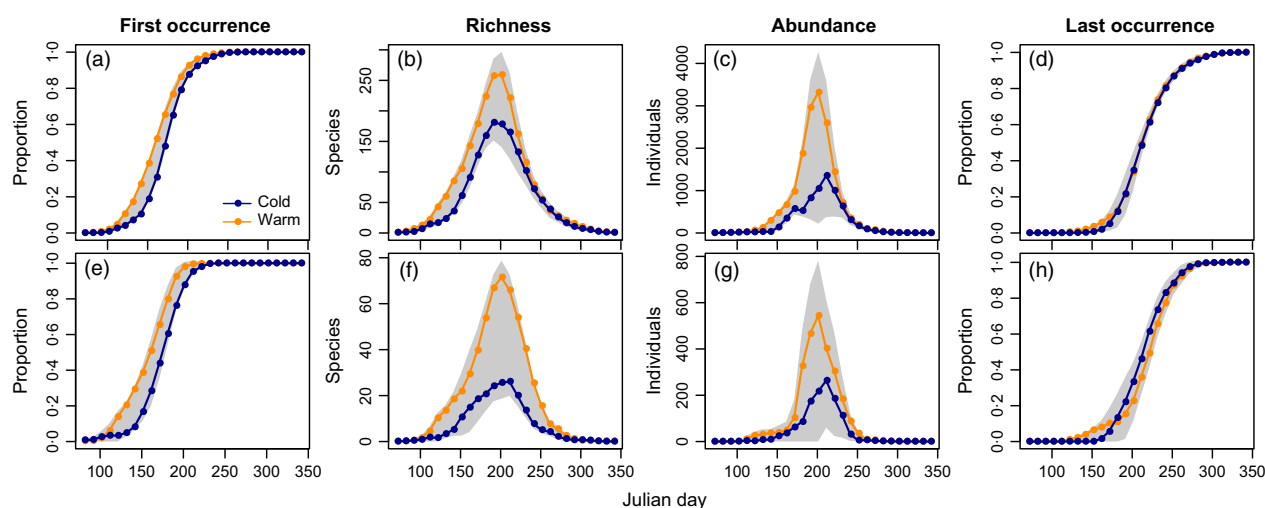


Fig. 1. Influence of temperature on the periodical community dynamics of moths (a-d) and beetles (e-h). The figure shows the influence of monthly growing degree day (GDD) sum on first (a,e) and last species occurrences (d,h), species richness (b,f) and abundance (c,g) per 10-day period. Blue (orange) lines indicate regression predictions using the 10% (90%) periodical GDD quantile. During warm periods, first occurrences are at an advanced stage and species richness and abundance are at an elevated level. Last occurrences are less influenced by GDD, but are delayed in beetles during warm periods. Grey areas indicate \pm standard error around the grand mean for the 16-year period.

8% and 13% and maximums 68% (day 131), 54% (day 241), 56% (day 241) and 50% (day 161), respectively. For both taxa, last occurrences tended to advance with increasing temperatures early in the year, whereas last beetle occurrences were delayed and moth occurrences showed little temperature sensitivity later in the year (Fig. 1 d, h, Table S1, Supporting information). There was an overall tendency for annual species richness (moths: $P = 0.01$, adjusted $R^2 = 0.33$; beetles: $P = 0.001$, adjusted $R^2 = 0.69$) and abundance (moths: $P = 0.12$, adjusted $R^2 = 0.10$; beetles: $P = 0.03$, adjusted $R^2 = 0.36$) to increase with summer temperature.

COMMUNITY TURNOVER

We observed a steady decrease in community dissimilarity over the 16 years, using the last year as reference (Whittaker presence/absence index, moths: $P < 0.01$, $b = -0.004$, $t = -3.2$, $R^2 = 0.44$, df.res = 13, beetles: $P < 0.01$, $b = -0.008$, $t = -3.3$, $R^2 = 0.41$, df.res = 13; Fig. 2). During the study period (1992–2009), GDD increased between the first (1992–2000) and the second half (2001–2009) in all 36 10-day periods (mean change per 10-day period = 0.39°C between the two nine-year periods, SE = 0.04, $t_{1,35} = 8.9$, $P < 0.001$). Community temperature index (CTI) steadily increased during the study period for moths ($P < 0.05$, $t_{1,14} = 2.7$, $b = 0.03$, $R^2 = 0.34$, Fig. 3a) but remained stable for beetles ($P > 0.05$, $t_{1,14} = -0.5$, $b = -0.01$, $R^2 = 0.02$, Fig. 3b). CTI did not change over time for generalist groups of polyphagous moths ($P > 0.05$, $t_{1,14} = 0.7$, $b = 0.01$, $R^2 = 0.03$, Fig. 3c) and carnivorous and omnivorous beetles ($P > 0.05$, $t_{1,14} = 0.9$, $b = 0.03$, $R^2 = 0.05$, Fig. 3d), but increased markedly for specialized groups of monophagous moths (*strict monophagous*: $P < 0.001$, $t_{1,14} = 5$, $b = 0.09$, $R^2 = 0.64$, Fig. 3e, *broad monophagous*: $P < 0.01$, $t_{1,14} = 3.7$, $b = 0.07$, $R^2 = 0.49$) and herbivore beetles ($P < 0.01$, $t_{1,10} = 3.9$, $b = 0.34$, $R^2 = 0.60$, Fig. 3f). Further subclassification of beetles validated that CTI remained stable for generalist polyphagous herbivores ($P > 0.05$, $b = -0.1$, $R^2 = 0.1$) and carnivorous and omnivorous species ($P > 0.05$, $b = -0.01$, $R^2 < 0.1$), but increased during the study period for specialized mono- and oligophagous herbivores ($P < 0.05$, $b = 0.3$, $R^2 = 0.4$) (Fig. S1, Supporting information).

In order to assess the reductive or expansive nature of the temperature driven community turnover, we measured change in species abundance (Fig. 4a,b) and the number of species gained and lost from the first (1993–2000) to the second half (2001–2008) of the study period (Fig. 4c–h). Mean species abundance increased for beetles ($t_{1,46} = 2.3$, $P < 0.05$, 10% mean increase) and increased insignificantly for moths (6.5% mean increase, $t_{1,240} = 1.3$, $P = 0.19$). Abundance change was significantly different between moth species temperature quantiles ($F_{2,239} = 4.8$, $P < 0.05$) such that the cold quantile had the lowest mean growth rate (-41% , $t_{1,120} = 2.5$, $P = 0.54$) and the hot quantile increased (18% increase, $t_{1,119} = 2.5$, $P < 0.05$). Mean abundance increased insignificantly for both beetle temperature quantiles ($P > 0.05$, 1st quantile $t_{1,23} = 2.1$ and mean = 12%, 2nd quantile $t_{1,22} = 1.2$ and mean = 8%).

For both moths and beetles, significantly more species were gained in the second period of the study than were lost (moths: $\chi^2_{1,1} = 5.5$, $P < 0.05$ and beetles: $\chi^2_{1,1} = 7.2$, $P < 0.01$, respectively, Fig. 4c,d). While change in cold-dwelling species quartiles and quantiles were insignificant, significantly more new hot-dwelling species were observed in the second period than were lost (moths: $\chi^2_{1,1} = 17.5$, $P < 0.001$ and beetles: $\chi^2_{1,1} = 6.4$, $P < 0.05$, Fig. 4c,d). For generalist moths and beetles, we either observed stable or small increases in the number of cold-dwelling species as well as increases or insignificant increases among hot-dwelling species (Fig. 4e,f). Among resource specialists, we observed a net gain of hot-dwelling species (moths: $\chi^2_{1,1} = 12.1$, $P < 0.001$ and beetles: $\chi^2_{1,1} = 8.3$, $P < 0.05$) and non-significant declines among cold-dwelling species (moths: $\chi^2_{1,1} = 2.0$ and beetles: $\chi^2_{1,1} = 1.3$, $P > 0.05$, Fig. 4g,h). Resource specialists was the only group that showed significant differences in the number of gains and losses between cold and hot species (moths: $\chi^2_{2,1} = 10.8$, $P < 0.001$ and beetles: $\chi^2_{2,1} = 6.4$, $P < 0.05$) (Fig. 4), also when beetles were further subclassified into diet groups ($\chi^2_1 = 5.7$, $P < 0.05$; Fig. S2, Supporting information).

The proportion of specialist to generalist species did not change over the study period (moths: $P = 0.65$, $\chi^2_{1,7} = 0.5$, SE = 0.03, specialists per year = 29.4%, specialists in total = 31.5%, and beetles: $P = 0.52$, $\chi^2_{2,6} = 0.6$, SE = 0.1, specialists per year = 22.9%, specialists in total = 30.5%).

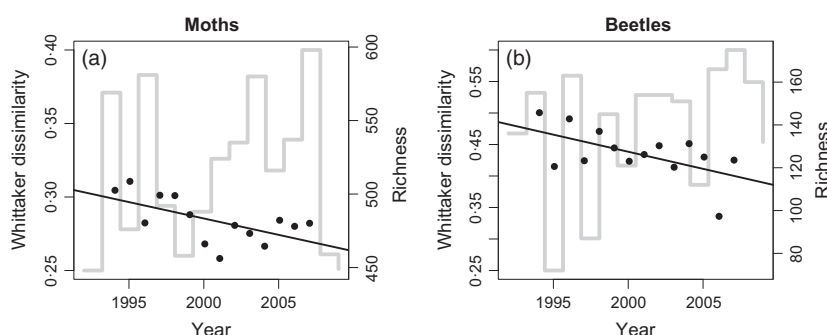


Fig. 2. Long-term community turnover in moths (a) and beetles (b). Qualitative community dissimilarity declines over the 18-year period in both moths and beetles (black points and regression lines). Whittaker dissimilarity is measured using 2008 as a reference year and grey bars indicate annual species richness.

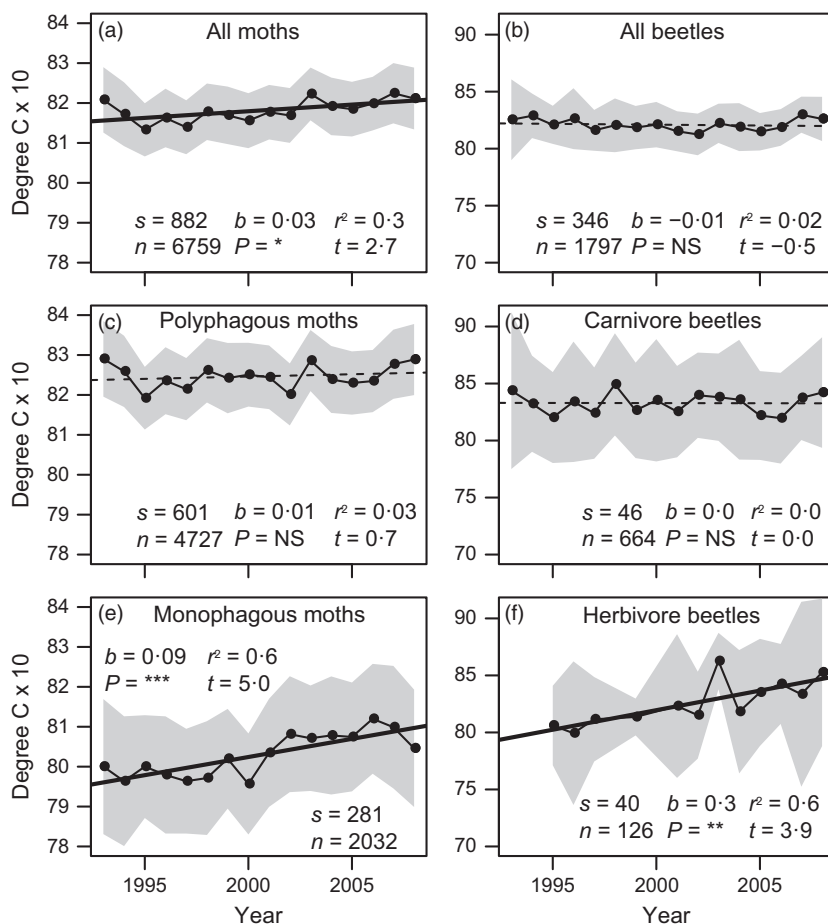


Fig. 3. Long-term development in climatic community composition of moths (a, c, e) and beetles (b, d, f). An increase in community temperature index (CTI) indicates that the community holds more species with a more southerly distribution (higher species temperature index). While CTI increases in more specialized consumers – monophagous moths (e) and herbivore beetles (f) – CTI remains stable in the more generalized consumers – polyphagous moths (c) and carni- and omnivorous beetles (d). Moths overall shows an increasing CTI (a), while CTI remains stable across all beetles (b). s : number of species, n : number of individuals. Significance levels: ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

PHENOLOGY OF RELATIVE ABUNDANCE

We performed quantile regression utilizing all 254 080 records to compare phenological change in relative abundance between hot- and cold-dwelling species. Phenological responses varied markedly between STI groupings (Figs S3–S4, Supporting information, Fig. 5). For moths, the first STI quantile as well as the first two STI quartiles all advanced their relative abundance (Fig. 5c, Figs S3, S5–S7, Supporting information), while the second STI quantile and the third and fourth STI quartiles delayed them (Fig. 5d, Figs S3, S5–S7, Supporting information). In addition, neighbouring STI quartiles (1st vs. 2nd, 3rd vs. 4th) advanced or delayed different parts of the relative abundance distribution (Figs S3–S4, Supporting information). While the 1st STI quantile of moth species advanced their 10%, 25% and 50% quantile with 16 ($P < 0.001$, Table S2, Supporting information), 22.8 ($P < 0.001$, Table S2, Supporting information) and 14.5 days ($P < 0.001$, Table S2, Supporting information) during the 16-year period, respectively, the 2nd STI quantile advanced their 50% quantile with 16 days ($P < 0.001$, Table S2, Supporting information) and 95% quantile with 17.8 days ($P < 0.001$, Table S2, Supporting information). In comparison, the 3rd STI quantile delayed their 5%, 10%, 25% and 75% quantile with 11.4 (Table S2, Supporting information), 16 ($P < 0.001$, Table S2, Supporting

information), 22.9 ($P < 0.001$, Table S2, Supporting information) and 14.5 days ($P < 0.001$, Table S2, Supporting information) during the 16-year period, respectively, while the 4th STI quantile delayed both their 90% and 95% quantile with 12.3 days ($P < 0.001$, Table S2, Supporting information). For beetles, the 2nd STI quantile advanced their 5% and 95% quantile with 13.3 ($P < 0.001$, Table S2, Supporting information) and 11.4 days ($P < 0.001$, Table S2, Supporting information), respectively, while all other phenological changes were on the order of less than a tenth of day (Fig. S4, Supporting information).

Moths and beetles generally advanced their first occurrence over the study period (Fig. 1, Table S1, Supporting information). Using quantile regression, we found that this trend was driven by similar trends in the first, second and third quartile of first occurring species ($P < 0.05$). Over the period, the mean change corresponded to a 2-week advance in arrival date (i.e. first occurrence date). In contrast, last occurrences of moths and beetles remained unchanged ($P > 0.05$).

Discussion

In this study, we present the analysis of an 18-year data set of two diverse insect taxa with full-season individual-based recordings of 254 080 individuals and 1543 species

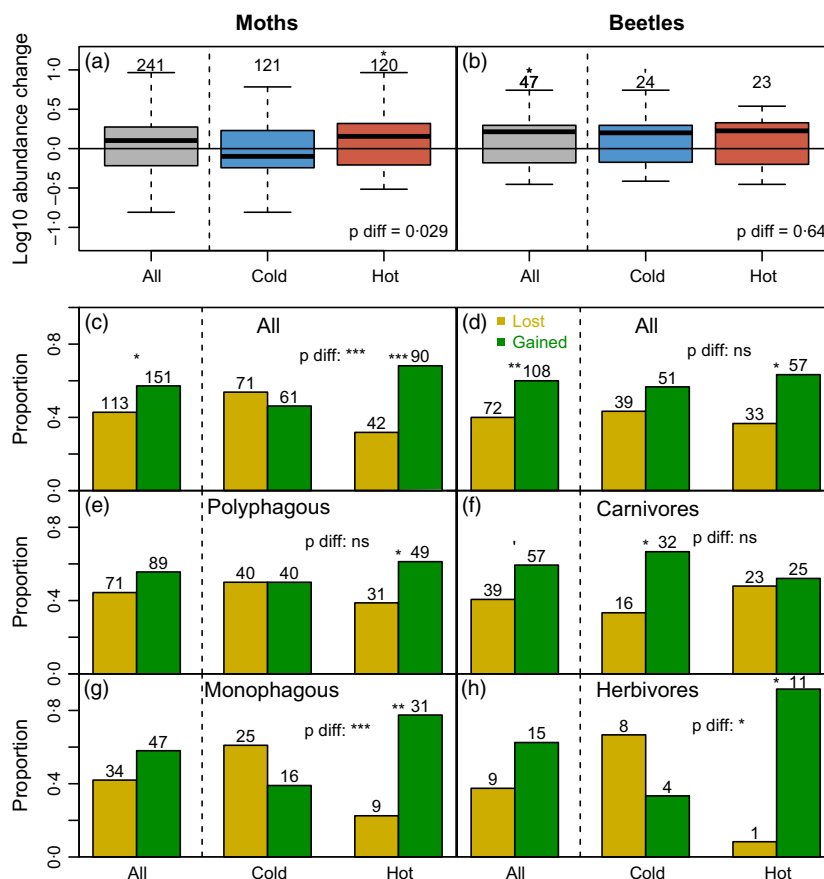


Fig. 4. Temperature-related trends in abundance (a–b) and net species gain (c–h) between the 1990s and 2000s. p diff. indicates whether there is a difference in the trend between cold and hot species. Hot-dwelling moths increase in abundance (a), while beetle abundance increases for both quantiles (b). Both moths (c) and beetles (d) and their generalist (e–f) and specialist (g–h) consumers show a net gain of species from the first to the second period (left columns). Overall, net gains are strongest among hot-dwelling species (c–d), while net gains of hot-dwelling species are the strongest among specialized consumers (g–h). Specialist moths and beetles also show (insignificant) net losses among cold-dwelling species (g–h). Only moths and specialist consumers of moths and beetles showed significant differences in the number of gains and losses between cold and hot species. Significance levels: ns, $P > 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$.

of moths and beetles. Although our findings are limited to a single study site, the analysis indicates the ability of this detailed and extensive monitoring scheme to characterize multiple ongoing local changes during a period of global and local warming. We detected a 0.14 and 0.48°C increase in CTI between 1993 and 2008 for specialist groups of monophagous moths and herbivore beetles (Fig. 3), respectively. This corresponds to rates of 0.009 (moths) and 0.03°C year⁻¹ (beetles). Cold- and hot-dwelling generalists both increased or remained stable in species richness over time, while for specialists there was only a net increase of hot-dwelling species (Fig. 4). We further demonstrate a diverging phenological response of cold- and hot-dwelling species, where cold-dwelling species advanced their relative abundance, while hot-dwelling species delayed their relative abundance (Fig. 5). Our results are indicative of a local temperature-related turnover of the insect fauna driven by resource specialists.

LIMITATIONS OF LOCAL SAMPLING

Temperature represents the main abiotic factor directly affecting the biology of herbivorous insects and positively influences development, survival, range and abundance – in temperate regions mainly by increasing winter survival (Bale *et al.* 2002; Forister & Shapiro 2003). While climate change seems an obvious cause for the observed increase in temperature affinity of the local fauna, other potential

drivers can account for these patterns. These factors include local habitat and land-use change, changes in plant species composition, precipitation patterns and city development – several of which have previously been shown to affect arthropod community composition (Schaffers *et al.* 2008; Lizée *et al.* 2011; Eglington & Pearce-Higgins 2012; Kampichler *et al.* 2012). Notably, for birds it has been demonstrated that habitat and climate signals can be difficult to separate and that the interaction of the two differs between habitats (Clavero, Villero & Brotons 2011; Barnagaud *et al.* 2012; Kampichler *et al.* 2012). For example, bird communities in forest habitats have colder-dwelling species with more northern distributions than communities in open areas (Clavero, Villero & Brotons 2011). Our study site is situated within a large city and might therefore not represent changes in other rural sites or larger areas of natural habitats. Importantly, however, the management of the sampling site and its near surrounding urban park habitat have remained stable in the study period, so we do not expect a major change in the insect community caused by habitat affinity. Likewise, the development and increase of the Copenhagen city area during the study period are of such limited extent that it is expected not to have influenced or altered local temperature patterns. Finally, while a regional community already dominated by hot-dwelling species could lead to a turnover primarily to be observed in this group, the division of our data into quartiles and

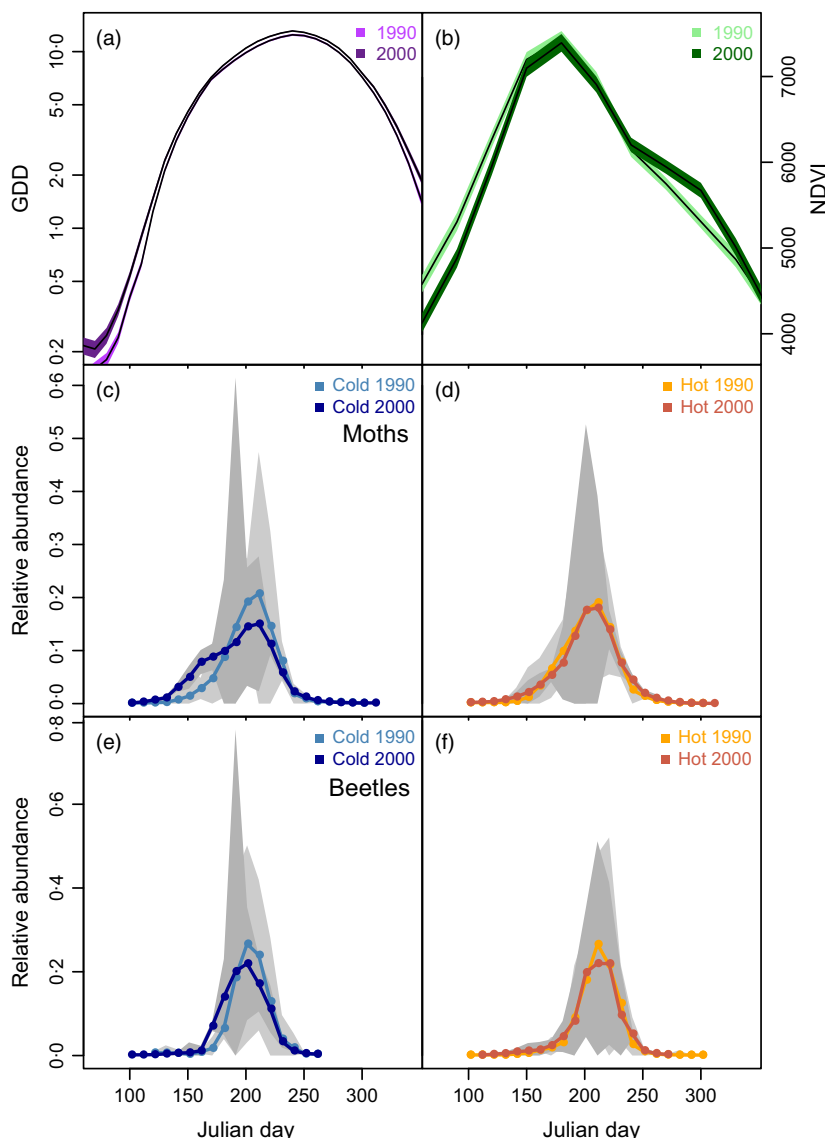


Fig. 5. Temperature-related change in relative abundance between the 1990s (light colours) and 2000s (darker colours). Growing degree day (GDD) sums were higher throughout the year of the second period (a). In contrast, vegetation greenness (NDVI) decreased in spring and increased in late autumn (b). Relative abundance of cold-dwelling moths (c) increased in spring and decreased or remained stable later in the year. In contrast, relative abundance of hot-dwelling moths (d) exhibited less pronounced spring increases and also increased in the autumn. Beetles generally mimicked the pattern of moths with spring increases of cold dwellers (e) and less pronounced change among hot dwellers (f).

quantiles based on temperature affinity within the data itself accounts for this unlikely bias. We therefore propose that the observed local changes could be interpreted in the context of ongoing temperature changes at a larger scale.

COMMUNITY TURNOVER

Community turnover as a consequence of temperature change has recently been studied for, for example butterflies (Dennis *et al.* 2010), dragonflies (Flenner & Sahlén 2008), bugs (Southwood, Henderson & Woiwod 2003), lake invertebrates (Angeler & Johnson 2012), plants (Cleland *et al.* 2013) and marine macro-invertebrates (Sagarin *et al.* 1999). However, the local pattern observed from our data of gains in many southern species and loss of a few northern was especially strong when diet specialists were considered separately (Fig. 4, Fig. S2, Supporting information). This indicates that a

change towards a more hot-dwelling local fauna was driven particularly by specialists, and we thus observe a differential turnover among dietary groups. In fact, the pattern was nearly reversed among non-herbivore (i.e. generalist) beetles (Fig. 4). Furthermore, resource specialists within both taxa showed significant differences in the number of gains and losses between cold- and hot-dwelling species (Fig. 4, Fig. S2, Supporting information). A change towards more hot-dwelling communities using CTI (Fig. 3, Fig. S1, Supporting information) has been studied previously to demonstrate northwards shifts in birds and butterfly communities (Devictor *et al.* 2012). The version of CTI used in this study is based on presence/absence and ignores abundance. We believe that it is therefore more robust in recovering temperature-mediated turnover, since insect abundance is more prone to annual fluctuations also caused by other factors such as intrinsic population dynamics and trophic interactions (Wallner 1987).

Speculating on a mechanism for differential turnover

Our local observations seem to support the hypothesis that temperature-mediated responses, as predicted by increasing temperatures, are stronger among diet specialists (Diamond *et al.* 2011). It has previously been suggested that diet specificity of insect herbivores is also associated with narrow environmental tolerances (Forister *et al.* 2012). For example, species richness of monophagous butterflies at a Mediterranean study site differed from oligo- and polyphagous groups in being directly affected by temperature (Carnicer *et al.* 2013). Also, from the classic study on richness patterns of phytophagous insects on various host plants (Southwood 1961; Kennedy & Southwood 1984; Brändle & Brandl 2001), it is found that host plants with larger distribution ranges harbour more insect species, but this species-area-like relationship is only strong for polyphagous insects and weaker to absent for oligophagous and monophagous species (Tahvanainen & Niemela 1987). This implies that polyphagous species generally have a higher range filling capacity than do specialists, with range defined as host plant range. In contrast, monophagous insects on a single host plants often decrease or even disappear towards the host range margin of the plant, suggesting some other limiting factor than resource quantity such as temperature or dispersal ability (Southwood 1961). Assuming that inferences from these range filling patterns transfer to the local scale, where dispersal limitation is less likely to be a factor, we speculate that temperature is the main driver explaining the observed differential turnover. We suggest that specialists will be relatively more limited by temperature. Generalists, on the other hand, would be more limited by antagonistic biotic interactions (Fig. S8, Supporting information), which implies fewer available niches for generalist species changing their phenology or entering the community as a result of warmer temperatures (Fig. S9, Supporting information). We hypothesize that resource specialists in particular are affected by local temperature increase seen throughout the study period, leading to the distinct local temperature-mediated turnover seen for this group.

DIVERGING PHENOLOGY OF COLD- AND HOT-DWELLING SPECIES

Due to the fine-grained resolution and full-season extent, our data set allows comparison of community turnover patterns with changes in phenology of the relative abundance among species with varying temperature affinity. Exploring the opportunity provided by the fine-scale data set, we observed some of the largest phenological shifts recorded (up to 1.4 days year⁻¹, Fig. S3, Supporting information) (Roy & Sparks 2000; Walther *et al.* 2002; Forister & Shapiro 2003). Intriguingly, these phenological changes varied systematically with temperature affinity such that cold-dwelling species advanced their relative abundance, while hot-dwelling species delayed their rela-

tive abundance (Fig. 5, Figs S3–S4, Supporting information). Such a diverging phenological response could have several important implications for the seasonality of ecosystem functioning and we next assess the potential explanations for this observed pattern.

Speculating on a mechanism for diverging phenology

Overall, the observed phenological response could indicate that cold- and hot-dwelling species exploit different resources that differ in phenology and that they track the temperature-induced phenological response of their resources. Many plants have advanced their leaf flushing and flowering over the last decades (Walther *et al.* 2002), and length of the growing season has increased (Menzel & Fabian 1999). An experimental set-up showed that warming advanced the phenology for plant species flowering before the peak of summer heat but delayed the phenology for plant species flowering after the peak temperature (Sherry *et al.* 2007), and another study suggests that spring phenophases of early-season plants will probably continue to diverge from late-season plants with temperatures warming in the future (Wang *et al.* 2015). This warming-induced divergence towards the two ends of the growing season will likely result in subsequent divergent phenological responses of the herbivore communities. Shifts from univoltinism towards bi- or multivoltinism may also partially explain the delayed phenology of hot-dwelling species. Such shifts are widely demonstrated for butterflies and moths as a response to climate change (Altermatt 2009; Pöry *et al.* 2011). Generally, our results support the previous evidence that diet indeed influences phenological changes of insects in response to climate change (Altermatt 2010).

Advanced relative abundance was particularly evident for cold-dwelling specialists (Fig. S6, Supporting information) and less pronounced for generalists (Fig. S7, Supporting information). Given that specialists show the strongest temperature-mediated turnover (Fig. 4, Fig. S2, Supporting information), we speculate that the phenological responses of the cold-dwelling specialists could play an important role in minimizing further local loss of specialists under climate change (Fig. S9, Supporting information). If replicated in other long-term data sets, our findings could thus suggest divergent phenological responses as one of the mechanisms facilitating community expansions in response to global warming.

IMPLICATIONS FOR LONG-TERM LOCAL STUDIES

Using an 18-year time series of moths and beetles, we observe several local changes that are in concordance with changes expected from large-scale temperature increases. In an age of environmental change, we see the role of long-term, fine-scale monitoring not merely to describe changes in fauna compositions. It can also detect the impact of specific drivers of faunal change. Here, we have

found an important role of resource specialization to explain the multifaceted compositional and phenological response of insect communities to temperature increases. In order to validate the generality of these patterns, we encourage that our findings are replicated by other standardized, long-term full-season monitoring studies.

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Data accessibility

Raw data are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.s4945> (Thomsen et al. 2015).

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Supporting Information

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

Fig. S1. Long-term development in climatic community composition of beetles further sub-classified into generalists: carni- and omnivorous species (a) and polyphagous herbivores (b), and specialists: mono- and oligophagous herbivores (c).

Fig. S2. Temperature related trends in net species gain between the 1990's and 2000's of beetles further sub-classified into generalists: carni- and omnivorous species (a) and polyphagous herbivores (b), and specialists: mono- and oligophagous herbivores (c).

Fig. S3. Quantile regression of all individual moth records showing phenological change in abundance distributions through the entire study period, and shown for individual species temperature quantiles.

Fig. S4. Quantile regression of all individual beetle records showing phenological change in abundance distributions through the entire study period, and shown for individual species temperature quantiles.

Fig. S5. Temperature related change in relative abundance of all species between the 1990's (light colours) and 2000's (darker colours).

Fig. S6. Temperature related change in relative abundance of resource specialists between the 1990's (light colours) and 2000's (darker colours).

Fig. S7. Temperature related change in relative abundance of resource generalists between the 1990's (light colours) and 2000's (darker colours).

Fig. S8. Conceptual model of biotic and abiotic factors limiting insect herbivores, shown for trophic generalist and specialist as well as hot- and cold-dwelling species.

Fig. S9. Conceptual model of explaining the relatively larger phenological responses to climate warming in trophic specialists compared to trophic generalists.

Table S1. Test statistics underlying Figure 1.

Table S2. Test statistics supporting Figure S3–S4 (Supporting information).