

Indications for rapid evolution of trait means and thermal plasticity in range-expanding populations of a butterfly

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Abstract

Currently, poleward range expansions are observed in many taxa, often in response to anthropogenic climate change. At the expanding front, populations likely face cooler and more variable temperature conditions, imposing thermal selection. This may result in changes in trait means or plasticity, the relative contribution of which is not well understood. We, here, investigate evolutionary change in range-expanding populations of the butterfly *Pieris mannii*, by comparing populations from the core and the newly established northern range under laboratory conditions. We observed both changes in trait means and in thermal reaction norms. Range-expanding populations showed a more rapid development, potentially indicative of counter-gradient variation and an increased cold tolerance compared with core populations. Genotype-environment interactions prevailed in all associated traits, such that the above differences were restricted to cooler environmental conditions. In range-expanding populations, plasticity was decreased in developmental traits enabling relatively rapid growth even under cooler conditions but increased in cold tolerance arguably promoting higher activity under thermally challenging conditions. Notably, these changes must have occurred within a time period of ca. 10 years only. Our results suggest, in line with contemporary theory, that the evolution of plasticity may play a hitherto underestimated role for adaptation to climatic variation. However, rather than generally increased or decreased levels of plasticity, our results indicate fine-tuned, trait-specific evolutionary responses to increase fitness in novel environments.

KEYWORDS

cold tolerance, counter-gradient variation, genotype-environment interaction, heat tolerance, local adaptation, phenotypic plasticity, *Pieris mannii*, range expansion

1 | INTRODUCTION

Elucidating the factors that shape species ranges is of central concern in both evolutionary biology and ecology (Hardie & Hutchings, 2010; Polechová, 2017). Recently, many taxa have been reported to

shift or expand their ranges in response to anthropogenic climate change (Chen et al., 2011; Pinsky et al., 2020). This is especially true for many insect taxa, including butterflies, as their ectothermic nature makes them highly sensitive to changes in temperature (Breed et al., 2013; Halsch et al., 2020). While range shifts often result from

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niche following in response to climate change, evolutionary adaptation at expanding range margins can also play a crucial role and may slow down or increase the speed of range expansions (Chuang & Peterson, 2016).

Recent studies suggest that thermal sensitivity is an important trait affecting the success of poleward range expansions (Chuang & Peterson, 2016; Lancaster et al., 2015; Titelboim et al., 2019). This likely reflects the different climatic conditions in newly colonized regions at higher latitudes or altitudes compared to the core range, including lower temperatures and a higher climatic variability at daily and annual scales (Jones et al., 1999; Lancaster et al., 2015; Marshall & Sinclair, 2012). Given that environmental temperature is a key determinant of growth, activity and metabolic rate in ectothermic organisms (Angilletta, 2009), novel climatic conditions may thus exert strong selection pressures on expanding populations (Bridle & Vines, 2007; Lancaster et al., 2016; Therry et al., 2014), even if the new areas are in general thermally suitable for colonization (Chen et al., 2011).

Possible evolutionary responses to new climatic conditions include an increased constitutive (baseline) thermotolerance or a higher plasticity therein (Chevin & Hoffmann, 2017; Donelson et al., 2019; Merilä & Hendry, 2014). Both mechanisms may be important for local adaptation and depend on sufficient genetic variation within populations (Reger et al., 2017; Scheiner et al., 2020; Swaegers et al., 2015). When a species approaches its northern range limit, theory and metapopulation modelling predicts selection for phenotypic plasticity (Sultan & Spencer, 2002; Hardie & Hutchings, 2010; but see Hendry, 2016), but according empirical evidence is still scarce (Gerken et al., 2015). Indeed, the expression of baseline vs. induced thermal tolerance may strongly depend on the environmental context encountered and on associated costs (Marshall & Sinclair, 2010, 2012; Scheiner et al., 2020). While a high baseline thermal tolerance may be beneficial in both stable or unpredictable environments (Hallsson & Björklund, 2012; Teets et al., 2011), high plasticity may be especially beneficial in predictably (i.e. seasonally or daily) changing environments (Deere et al., 2006; Overgaard et al., 2011; but see Manenti et al., 2015). Thus, an important question is which of the mechanisms is most beneficial under the conditions experienced at expanding range margins (Merilä & Hendry, 2014).

In general, spatial patterns may differ between heat and cold tolerance (Gunderson & Stillman, 2015; Lancaster et al., 2015), following Brett's heat-invariant hypothesis (Brett, 1956). The latter predicts less variation in upper than in lower thermal limits due to a combination of intrinsic (e.g. limited evolutionary potential for heat tolerance) and extrinsic (e.g. greater thermoregulatory potential to counteract heat- compared to cold stress) mechanisms (Bozinovic et al., 2014; Pintanel et al., 2019). In addition, selection on heat tolerance is expected to be relaxed while selection on cold tolerance should be strong if ranges expand into cooler areas (Andersen et al., 2015; Lancaster et al., 2015; Sunday et al., 2012), implying that both traits appear to be physiologically and evolutionarily decoupled (Brett, 1956; Deere et al., 2006; Fischer & Karl, 2010; Gerken et al., 2016). In summary, populations having successfully

TABLE 1 Temperature data for representative locations within the newly colonized (Germany; Hannover-Langenhagen, 52.28°N 9.42°E) and the core range (France; Nice, 43.39°N 7.12°E) of *Pieris mannii* ssp. *alpigena*

Temperature [°C]	Germany	France
Mean daily mean	13.4	18.9
Mean daily minimum	8.4	15.4
Mean daily maximum	19.7	22.5
Absolute minimum	-7.9	2.9
Absolute maximum	38.1	35.8

Note: Given are mean daily mean temperatures, mean daily minimum and maximum temperatures, and absolute minimum and maximum temperatures during the vegetation period from April to October. Mean values are based on the years 1961–1990 and absolute extremes on the years 1946–1993 (France) or 1936–2001 (Germany) (<https://www.dwd.de>).

expanded their range into cooler environments may be characterized by an increased tolerance to cold temperatures and thermal fluctuations. While there is accumulating evidence for adjustments in thermal tolerance during range expansions (e.g. Batz et al., 2020; Titelboim et al., 2019), little is known about the relative contribution of increased baseline tolerance versus plasticity, and the few existing studies yielded mixed results (Lancaster et al., 2015; Leonard & Lancaster, 2020; Nguyen et al., 2019). Moreover, even fewer studies considered developmental plasticity (long-term acclimation to thermal conditions during the developmental period) as potential driver of ectotherm thermotolerance (Bowler & Terblanche, 2008; Diamond et al., 2017) and for increasing fitness-related traits in range-expanding species (Carbonell & Stoks, 2020).

Against the above background, we, here, assess developmental plasticity and genetic adaptation in life-history traits and thermal tolerance (here defined as the resistance to cold- and heat stress) in the Mediterranean butterfly species *Pieris mannii* (Mayer, 1851). This species has recently undergone a massive poleward-range expansion of ca. 1000 km within a period of 10 years (Reinhardt et al., 2020; Wiemers, 2016). The underlying mechanisms are not fully understood, but a recent study indicates a major role of genetic changes in host plant preference, while a direct role of anthropogenic climate change could be largely ruled out (Neu et al., 2021). Whether adaptation to the novel climatic conditions experienced within the newly colonized range may also have facilitated the ongoing range expansion is hitherto unknown. We, here, studied developmental traits and adult thermal tolerance in replicated populations from the species' core area and newly colonized range. We specifically aimed at unravelling the relative contribution of genetic adaptation and developmental plasticity (Merilä & Hendry, 2014). Temperatures are substantially cooler (Table 1) and more variable at the northern range margin compared with core area of the species due to more pronounced seasonality at higher latitudes (e.g. Shah et al., 2017). The higher variability is reflected by a larger standard deviation across monthly mean temperatures (from January to December) in the northern compared to the historic distribution range (Germany,

SD = 6.04 vs. France, SD = 5.28; data derived from <https://www.dwd.de>, as outlined in Table 1). We thus hypothesized that populations from the species' northern range margin show (i) increased cold but not heat tolerance, (ii) realized through increased plasticity rather than baseline thermal tolerance, (iii) and a more rapid development to compensate for the cooler ambient temperatures.

2 | MATERIALS AND METHODS

2.1 | Study species

Pieris mannii (Lepidoptera: Pieridae) is a widespread, Mediterranean butterfly species with a distribution ranging from Morocco across Mediterranean Europe to Turkey and Syria (Kudrna et al., 2011). With up to five partly overlapping generations a year, both in Mediterranean and Central Europe, the species is polyvoltine (Hensle & Seizmair, 2017; Pähler, 2016; Wiemers, 2016). Diapause takes place in the pupal stage (Settele et al., 2015). The species uses several plant species of the Brassicaceae family for oviposition (Geier, 2016; Lafranchis et al., 2015). Adults are nectar feeders, accepting a wide variety of species (Settele et al., 2015). Originating from south-east France, the subspecies *P. mannii alpigena* (Verity, 1911) has recently shown a spectacular poleward range expansions (Hensle & Seizmair, 2015, 2017; Kratochwill, 2011), which is characterized by its unparalleled speed. Starting in 2008, the species has already colonized large parts of Germany and is continuously spreading northwards (Reinhardt et al., 2020; Wiemers, 2016). While the species is restricted to xerothermic habitats and associated host plants in southern France (Lafranchis et al., 2015; Ziegler & Eitschberger, 1999), the expanding German populations appear to accept a much broader range of host plants (Neu et al., 2021; Geier, 2016), which may enable the use of novel habitats (Hensle, 2016; Hensle & Seizmair, 2015, 2017; Pähler, 2016). This is despite the cooler climate in Germany compared with France (Table 1).

2.2 | Population sampling and offspring rearing

In June and July 2018, fresh females were collected from three locations each in the species' core distribution area (southern France: Valbonne 43.63°N 7.02°E, $n = 16$; Saorge 43.98°N 7.55°E, $n = 11$; Roquefort-la-Bédoule 43.26°N 5.65°E, $n = 14$) and the newly colonized range (Germany: Verl 51.87°N 8.52°E, $n = 19$; Bad Kreuznach 49.84°N 7.87°E, $n = 12$; Habitzheim 49.85°N 8.88°E, $n = 11$). All sampled individuals belong to the range-expanding subspecies *P. mannii alpigena*, which is abbreviated to *P. mannii* henceforth. The minimum straight distance between the sampling sites was 80 km (Figure 1). Caught females were transferred to a climate chamber at University of Greifswald for egg-laying under controlled conditions (temperature: 25°C, relative humidity: 60%, photoperiod: L18:D6). Females were kept individually in translucent boxes (30 × 20 × 21 cm), each equipped with a leaf of greenhouse-grown wild rocket (*Diplotaxis*

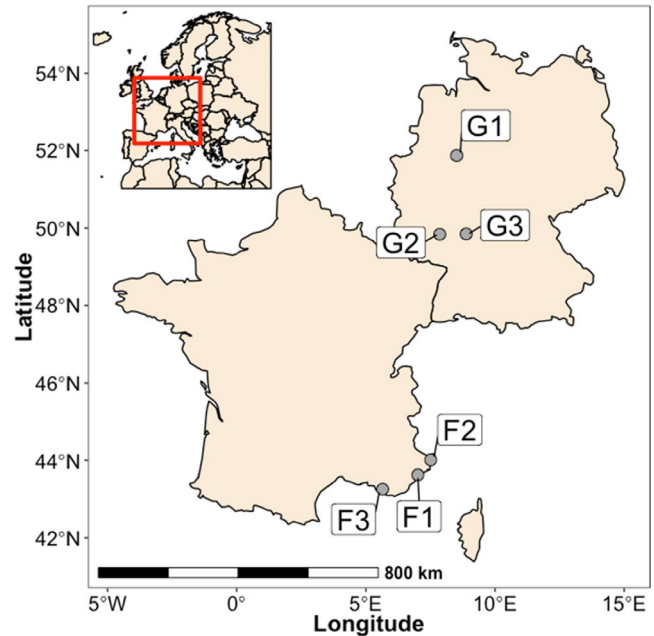


FIGURE 1 Sampling sites of replicated *Pieris mannii* populations in Germany (G1–3) and southern France (F1–3). Top left: Geographical location of the sampling sites within Europe (axes are not to scale)

tenuifolia) as oviposition substrate, fresh flowers, 20 vol % sucrose solution, and water. On a daily basis, eggs were collected and the leaf was replaced. Every other day, flowers and sugar solutions were renewed. Hatched larvae were reared individually in translucent plastic boxes (10.5 × 8 × 4.5 cm) lined with moistened filter paper and *ad libitum* access to leaves of *D. tenuifolia* for feeding. The leaves were renewed every day. After adult eclosion, butterflies were allowed to mate randomly within populations, but excluding full-sib matings. The above procedure was repeated to produce an F2 generation, which was used for subsequent experiments.

2.3 | Experimental design

We used a full-factorial split-brood design with two temperature regimes for larval rearing, mimicking the average summer temperatures in the core (T_C , mean: 22°C) and newly colonized range (T_N , mean: 18°C; Table 2). F2 generation hatchlings were randomly assigned to one or the other treatment. Larvae were reared in climate cabinets (Sanyo MLR-351H, Japan) as outlined above, using ecologically realistic diurnal temperature cycles, which are more relevant for understanding thermal adaptation to natural conditions than constant temperatures (e.g. Kingsolver & Gomulkiewicz, 2003; Petavy et al., 2001). We derived our average experimental temperatures from weather station data representing ambient data, even though microhabitat temperatures admittedly are a more relevant predictor of butterfly body temperature than ambient temperature (Buckley & Kingsolver, 2012; Kleckova et al., 2014). Relative humidity was set to 60% and photoperiod to L18:D6 throughout.

TABLE 2 Diurnal temperature cycles (°C), representative for the core (T_C) and the newly colonized northern (T_N) range, used to rear *Pieris mannii*

Time of day (h)	T_C	T_N
24–4	18	12
4–8	20	16
8–12	23	21
12–16	26	24
16–20	24	20
20–24	21	15
Daily mean [°C]	22	18
Δ min–max temperature [°C]	8	12

To exclude potential site-effects, we randomly rearranged the box positions within the cabinets on a daily basis. We scored larval time (from hatching to pupation), pupal time (from pupation to adult eclosion), pupal mass (scale: Kern 410), and larval growth rate (pupal mass (mg)/larval time (days)) for all individuals.

After adult eclosion, butterflies were sexed based on their discal wing spots (Ziegler & Eitschberger, 1999), individually marked and separated by sex. Subsequently, they were transferred to cages (30 × 20 × 21 cm) equipped with 20 vol% sucrose solution, fresh flowers and water, and kept at their respective larval temperature regime. A maximum of eight butterflies was kept per cage. We measured two well-established proxies of cold- and heat stress resistance in insects, namely 'chill-coma recovery time' (CCRT) and 'heat knock-down time' (HKDT) (e.g. Bauerfeind & Fischer, 2014; Fischer et al., 2010; Stazione et al., 2020; Tonione et al., 2020). All individuals were tested for CCRT on day 2 of adult life and for HKDT the day after.

For scoring CCRT, butterflies were placed individually into translucent plastic boxes (10.5 × 8 × 4.5 cm) and exposed for 20 h to −5°C (Panasonic MIR-554-PE, Japan). Subsequently, individuals were allowed to recover at room temperature (20°C), and the time until they were able to stand on their legs was scored. Afterwards, they were moved back to their cages and allowed to recover for 24 h. Then, individuals were transferred to small, translucent plastic boxes (\varnothing : 5 cm, height: 4.2 cm) and exposed to 43°C (Sanyo MIR-553, Japan). The small size of the boxes was chosen to prevent the animals from spending excessive amounts of energy for flight. Using digital cameras (RS Pro, 776-9387, Germany) placed inside the climate cabinets, we scored the time until individuals were physically knocked down (lying on the bottom of the box for at least 20 s) as HKDT. The temperatures and exposure times used were based on previous studies with a closely related species (*Pieris napi*; Bauerfeind & Fischer, 2014) and pilot tests with *P. mannii*.

2.4 | Statistical analyses

All traits were analysed with generalized linear mixed models (GLMMs) with a gamma distribution and a log-link function. We

included temperature treatment, origin (i.e. country of population sampling), sex and all interactions as fixed factors in all models. Furthermore, population nested within origin, and family (i.e. the offspring of an individual female) nested within origin and population were included as random effects. Non-significant interactions were removed using stepwise backward elimination. Best distribution fit of GLMMs was evaluated based on visual inspection and lowest AIC values. Test statistics for fixed effects and interactions were obtained by ANOVA 'type-III' analyses and for random effects by pairwise model comparison via likelihood ratio tests (Bolker et al., 2009). Between-group comparisons were performed by Tukey HSD tests. All data were analysed using R. 3.6.2 with the packages 'lme4' to compute generalized mixed models, 'car' to perform ANOVA analyses, 'multcomp' to perform post hoc tests, and 'fitdistrplus' to evaluate model distribution fit. Throughout, all means are given ± 1 SE.

3 | RESULTS

3.1 | Developmental traits

Temperature regime affected all four measured traits significantly (Table 3). Individuals reared at warmer temperatures (T_C) developed faster (larval time: 16.7 ± 0.1 days; pupal time: 8.4 ± 0.1 days) than those reared at cooler temperatures (T_N , larval time: 24.9 ± 0.1 days; pupal time: 14.1 ± 0.1 days; Figure 2). Concomitantly, larval growth rate was significantly higher at T_C than at T_N (T_C : 7.1 ± 0.1 mg/day; T_N : 5.5 ± 0.1 mg/day) while pupal mass was lower (T_C : 116 ± 0.6 mg; T_N : 134 ± 0.6 mg). Origin significantly affected larval time and growth rate, and tended to affect pupal time but not pupal mass. As indicated by significant temperature by origin interactions for the above traits except pupal mass, significant differences were restricted to T_N , at which German individuals developed significantly faster than those from France (Figure 2). Sex-differences were significant for all traits measured. Larval (females: 21.7 ± 0.3 days > males: 20.9 ± 0.3 days) and pupal times (11.9 ± 0.2 days > 11.2 ± 0.2 days) were longer for females than males. Males showed higher pupal masses (131 ± 0.8 mg > 121 ± 0.8 mg) and growth rates than females (6.51 ± 0.07 mg/day > 5.80 ± 0.09 mg/day). Replicate population was only significant for larval time, and family was non-significant throughout.

3.2 | Thermal tolerance

Chill-coma recovery time was significantly shorter in individuals kept at T_N (283 ± 13 s) than at T_C (520 ± 17 ; Table 3). The significant temperature by origin interaction indicates that German individuals recovered quicker from chill coma than French ones when kept at T_N (Figure 3). Heat knock-down time was not significantly affected by any of the fixed factors. However, it differed among

TABLE 3 Results of generalized linear mixed models for the effects of temperature, population origin, sex, their interactions (all fixed), population (random, nested within origin) and family (random, nested within population and origin) on offspring life-history and thermal tolerance traits (chill-coma recovery time, CCRT; heat knock-down time, HKDT) in *Pieris mannii*

Trait/source	d.f.	χ^2	<i>p</i>
Larval time			
Temperature	1	1333.8	<0.001
Origin	1	4.5	0.034
Sex	1	49.3	<0.001
Temperature*Origin	1	47.6	<0.001
Population [Origin]	2	7.3	0.025
Family [Origin*Population]	3	7.3	0.062
Residual deviance	7.45 with 656 d.f.		
Pupal time			
Temperature	1	1485.6	<0.001
Origin	1	3.7	0.053
Sex	1	92.1	<0.001
Temperature*Origin	1	36.6	<0.001
Population [Origin]	2	4.0	0.134
Family [Origin*Population]	3	4.0	0.260
Residual deviance	11.12 with 655 d.f.		
Pupal mass			
Temperature	1	439.0	<0.001
Origin	1	0.1	0.766
Sex	1	114.7	<0.001
Population [Origin]	2	0.5	0.781
Family [Origin*Population]	3	0.5	0.920
Residual deviance	4.62 with 657 d.f.		
Growth rate			
Temperature	1	445.2	< 0.001
Origin	1	4.4	0.036
Sex	1	165.4	< 0.001
Temperature*Origin	1	31.3	< 0.001
Population [Origin]	2	4.0	0.136
Family [Origin*Population]	3	4.0	0.263
Residual deviance	11.22 with 656 d.f.		
CCRT			
Temperature	1	20.4	< 0.001
Origin	1	< 0.001	0.984
Sex	1	0.4	0.508
Temperature*Origin	1	6.0	0.014
Population [Origin]	2	5.5	0.062
Family [Origin*Population]	3	8.1	0.044
Residual deviance	446.26 with 589 d.f.		
HKDT			
Temperature	1	2.0	0.153
Origin	1	0.6	0.447

(Continues)

TABLE 3 (Continued)

Trait/source	d.f.	χ^2	<i>p</i>
Sex	1	0.2	0.656
Population [Origin]	2	6.3	0.043
Family [Origin*Population]	3	8.7	0.034
Residual deviance	3.07 with 517 d.f.		

Note: Non-significant interactions were removed using stepwise backward elimination. Significant *p*-values are shown in bold.

replicate populations, and effects of family were significant for both proxies of thermal tolerance. There was no significant correlation between CCRT and HKDT (Pearson: $t_{521} = 1.53$, $r = 0.07$, $p = 0.13$).

4 | DISCUSSION

We found pronounced developmental plasticity to temperature in all traits measured except in adult heat tolerance. Main effects of origin were found for development time and growth rates, indicating more rapid development in the newly colonized range as expected (hypothesis iii). Genotype-environment interactions were present for offspring development times and adult cold tolerance. The latter indicates that, indeed, the populations from the newly established range showed greater plasticity in cold tolerance (hypothesis ii), such that it was only increased at cooler temperatures (hypothesis i).

Many butterfly species and other insects are known for their ability to respond plastically to short- and long-term temperature variation (e.g. Fischer & Karl, 2010; Franke et al., 2019). The patterns found here, more rapid development but reduced body size at higher temperatures, echo the strong dependence of developmental rates on ambient temperature and the temperature-size rule, as found in nearly all ectotherms (Atkinson, 1994; Verberk et al., 2021). An increased cold tolerance at lower temperatures has also been repeatedly shown (Clark & Worland, 2008; de Jong & Saastamoinen, 2018), likely reflecting adaptive phenotypic plasticity (Sgrò et al., 2016). Likewise, local adaptation is typically found in species with large ranges (Angilletta et al., 2003; Yampolsky et al., 2013). Here, we show a genetically based more rapid development in individuals from the newly colonized, cooler range, thus documenting counter-gradient selection (Hodgson & Schwanz, 2019; Nürnberger, 2013). More rapid development will likely enable more generations when facing reduced season length in combination with lower temperatures and greater seasonal variation, thereby promoting population growth and spread (Phillips et al., 2010). Interestingly though, the differences documented here, indicative of local adaptation, must have evolved within a very short time period of ca. 10 years only.

Baseline cold tolerance was partly higher (at lower temperatures) in the range-expanding populations, again indicating surprisingly rapid local adaptation. Evolutionary changes in baseline thermal tolerance have been also shown in some other studies (e.g. Carbonell & Stoks, 2020; Preisser et al., 2008; Swaegers

FIGURE 2 Developmental traits of *Pieris mannii* from France or Germany in relation to temperature regime (ø 22°C: core temperature regime T_C ; ø 18°C: newly established northern range temperature regime T_N). (a) Larval developmental time, (b) pupal developmental time, (c) pupal mass, (d) larval growth rate. Letters above bars indicate significant differences among treatment groups. Group sample sizes range between 146–245 individuals

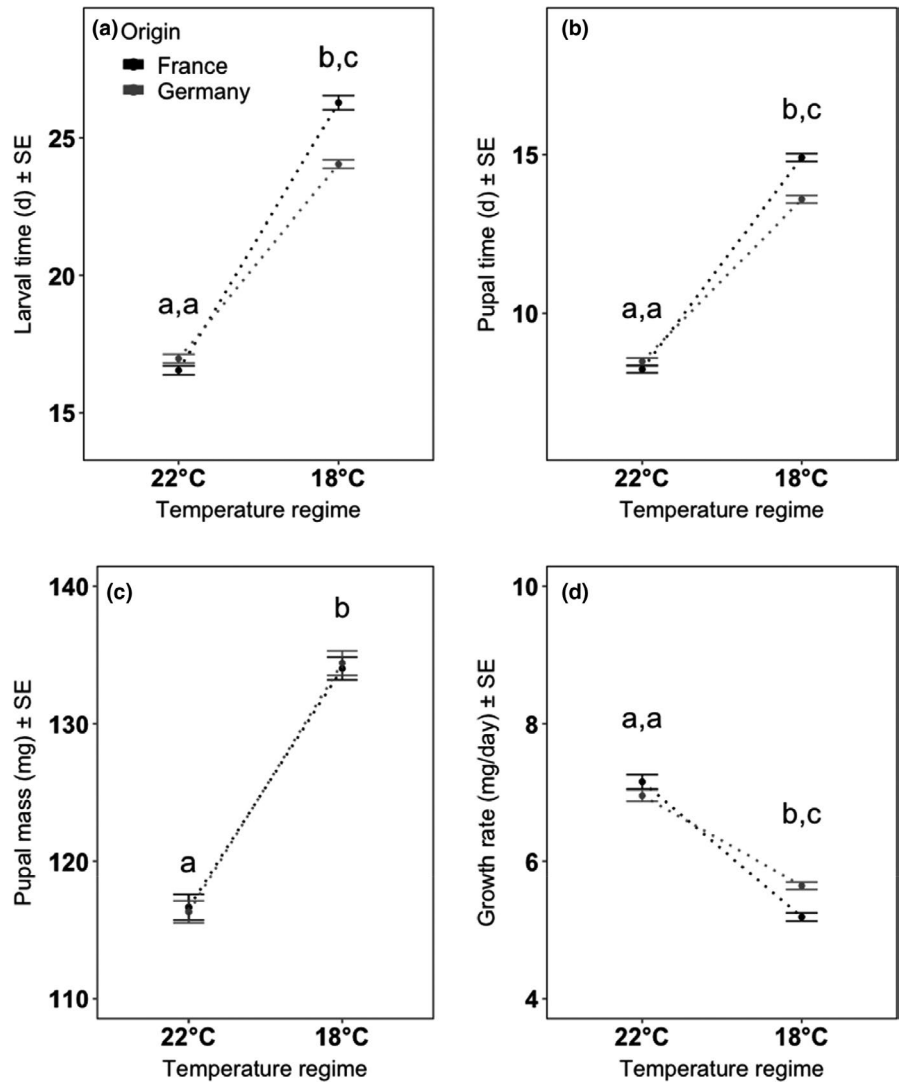
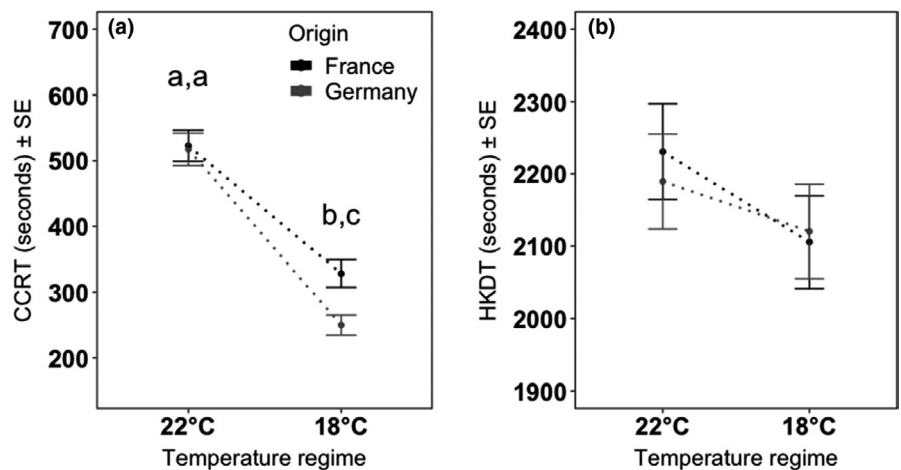


FIGURE 3 (a) Chill-come recovery time (CCRT) and (b) heat knock-down time (HKDT) of adult *Pieris mannii* from France or Germany in relation to developmental temperature regime (ø 22°C: core temperature regime T_C ; ø 18°C: newly established northern range temperature regime T_N). Letters above bars indicate significant differences among treatment groups. Group sample sizes range between 108–182 individuals



et al., 2015). However, the difference in our study was only found at cooler temperatures, pointing towards an evolved increase in temperature-induced plasticity within the expanding populations. This finding is consistent with contemporary theory, suggesting that rapid evolution of plasticity is an important response

to environmental variation (Kelly, 2019; Levis & Pfennig, 2016; Sommer, 2020), in particular, during the colonization of new habitats (Chevin & Lande, 2011; Lande, 2015). Accordingly, individual-based simulations showed that plasticity in environmental tolerance tends to increase at the front edge of the distribution

when species enter a novel habitat (Schmid et al., 2019). Empirical evidence supporting such predictions is slowly accumulating. For instance, spatially varying selection on plasticity was found in functional, morphological and tolerance traits when comparing introduced and native populations of invasive plant species (Matesanz et al., 2012; Nicotra et al., 2015; Turner et al., 2015). Moreover, Rohner and Moczek (2020) found increased temperature-induced plasticity in morphological and life-history traits in expanding populations of an invasive horned beetle.

Note that in our study plasticity was increased in thermal tolerance only, while it was reduced in developmental traits. The reduced plasticity in the latter ensures relatively rapid development in expanding populations even at lower temperatures and may, therefore, be adaptive. Similarly, the increased plasticity in cold tolerance may enable higher levels of activity under suboptimal thermal conditions. Our results thus question the notion of general reductions or increases in plastic responses. Instead, they suggest fine-tuned, trait-specific adjustments increasing fitness.

If evolution of increased plasticity in thermal tolerance took place, an important promoting factor may have been the enormous pace of the species' range expansion. This suggests high dispersal rates in this species, which are predicted to facilitate the evolution of plasticity (Eierman & Hare, 2016; Hendry, 2016; Scheiner & Holt, 2012). Another factor affecting genetic variation and plasticity in thermal tolerance is the level of thermal stress (Fischer et al., 2020; Hendry, 2016). Often, low levels of thermal stress favour selection on plasticity, whereas high levels favour increased baseline tolerance due to costs associated with plastic responses (Hendry, 2016; Van Buskirk & Steiner, 2009). The presence (and absence; e.g. Murren et al. (2015)) of plasticity costs may be, however, highly context dependent. While mainly large plastic responses under particularly stressful environmental conditions tend to impose costs, small plastic responses and less stressful environmental conditions do not (Hendry, 2016 and references therein). At the time of sampling, the northernmost populations of *P. mannii* were still within the predicted climate niche of the species (Neu et al., 2021), suggesting that the overall thermal stress level is relatively low, thus favouring plasticity.

As expected, the expanding populations showed no change in heat tolerance. Thus, they may show an increased thermal niche breadth, as previously observed in invasive species (Davidson et al., 2011; Richards et al., 2006) across urban-rural temperature clines (Diamond et al., 2017) and in other range-expanding species (e.g. Lancaster et al., 2015). Yet, data on the critical thermal maximum (CT_{max}) and minimum (CT_{min}) of the species will be needed to obtain reliable information on thermal tolerance niche breadth (Sinclair et al., 2016).

It is noteworthy mentioning that we only tested the mobile, adult life stages for thermal stress tolerance within the scope of this study. There is, however, accumulating evidence about the role of other insect life stages for the adaptation to novel thermal conditions encountered during range shifts (e.g. in eggs of *Colias* butterflies (MacLean et al., 2016) and larvae of the damselfly *Ischnura elegans* (Carbonell & Stoks, 2020)). Due to the rather low mobility of the

immature life stages in many butterfly species and, resulting from that, limited options to buffer heat—or cold stress by microhabitat choice, selection may act even stronger on the internal thermal stress resistance of those life stages. Future studies should, therefore aim at targeting the thermal tolerance of immature life stages of *P. mannii* individuals from range-expanding population. Moreover, we merely used two developmental temperature treatments for our common garden design. Given the typically non-linear nature of thermal reaction norms (e.g. von Schmalensee et al. (2021)), two temperatures do not permit conclusions regarding the evolution of entire thermal performance curves. Thus, future studies will greatly benefit from adding more temperature treatments to the study design.

In summary, our results indicate rapid local adaptation in trait means as well as in plastic responses to thermal variation. Our findings suggest that the evolution of plasticity may play a hitherto underestimated role for species' adaptation to climatic gradients and change (Kelly, 2019). Notably, changes in thermal reaction norms are likely to have caused increased or decreased levels of plasticity in range-expanding as compared with core populations, depending on the trait considered. In all cases changes in thermal reaction norms seemed to enhance the fitness of range-expanding populations in their newly colonized range. Although evidently more data are needed to settle this issue, we question the notion of generally increased or decreased plasticity in range-expanding populations, and advocate a trait-specific consideration based on adaptive hypotheses.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

AN and KF devised the experiments; AN collected and analysed the data; both authors wrote the paper.

PEER REVIEW

The peer review history for this article is available at <https://publons.com/publon/10.1111/jeb.13969>.

DATA AVAILABILITY STATEMENT

Data are deposited at Mendeley Data (<https://doi.org/10.17632/zxtx4dt6y9.1>).

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