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COMMUNITY ECOLOGY - ORIGINAL RESEARCH

Rising temperature reduces divergence in resource use strategies in coexisting parasitoid species

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Abstract Coexistence of species sharing the same resources is often possible if species are phylogenetically divergent in resource acquisition and allocation traits, decreasing competition between them. Developmental and life-history traits related to resource use are influenced by environmental conditions such as temperature, but thermal trait responses may differ among species. An increase in ambient temperature may, therefore, affect trait divergence within a community, and potentially species coexistence. Parasitoids are interesting models to test this hypothesis, because multiple species commonly attack the same host, and employ divergent larval and adult host use strategies. In particular, development mode (arrested or continued host growth following parasitism) has been recognized as a major organiser of parasitoid life histories. Here, we used a comparative trait-based approach to determine thermal responses of development time, body mass, egg load, metabolic rate and energy use of the coexisting *Drosophila* parasitoids *Asobara tabida*, *Leptopilina heterotoma*, *Trichopria drosophilae* and *Spalangia erythromera*. We compared trait values between species and development modes, and calculated trait divergence in response to temperature, using functional diversity indices. Parasitoids differed in their thermal response for dry mass, metabolic rate and lipid use throughout adult life, but only teneral lipid reserves and egg load were affected by developmental mode. Species-specific trait responses to temperature were probably determined by their adaptations in resource use (e.g. lipogenesis or ectoparasitism). Overall, trait values of parasitoid species converged at the higher temperature. Our results suggest that local effects of warming could affect host resource partitioning by reducing trait diversity in communities.

Keywords Climate change · Community · Idiobiont · Insect · Koinobiont

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Introduction

Many mechanisms for stable coexistence of species rely on ecological and evolutionary differences that reduce competition through reduced niche overlap (Chase and Leibold 2003). For instance, coexisting species may possess divergent life-history trade-offs between main functions, such as development, reproduction and survival, reflecting differential acquisition and allocation of the shared resources (Pelosse et al. 2007; Harvey 2008; Jervis et al. 2008; Le Lann et al. 2012). Community assembly may favour phylogenetically distant species that possess dissimilar traits, leading to decreased competition within communities (MacArthur and Levins 1967; Tilman 1982). However, various developmental and life-history traits related to resource use show considerable phenotypic plasticity (Violle et al. 2012). The magnitude of intraspecific trait variation caused by phenotypic plasticity can be equally large in magnitude as interspecific trait variation (Canham et al. 1999; Valladares et al. 2000; Jervis et al. 2001), as was shown for physiological and morphological traits of related plant species in response to light conditions (Valladares et al. 2000). A change in environmental conditions can therefore cause a drastic change in the trait values, and phenotypic plasticity should be taken into account in trait-based comparisons aiming to explain species coexistence (Berg and Ellers 2010).

Due to global warming, average temperatures have risen by about 0.8 °C since the early twentieth century and a further increase of about 3 °C is predicted during the twenty-first century (IPCC 2007). These figures mask the fact that at local and regional scales warming effects can even be more intense, as is predicted for Western Europe (IPCC 2007). In ectotherms, ambient temperature is a major determinant of intraspecific trait variation throughout various life stages (Atkinson 1994; Angilletta et al. 2004). To persist, species thus need to be able to cope with challenging thermal changes (Hance et al. 2007; van Baaren et al. 2010). However, there are large interspecific differences in thermal responses among species within a community (Berg et al. 2010). As a consequence, the regional or local effects of global warming may alter trait divergence among co-occurring species sharing the same resources, and ultimately affect the ability of species to coexist.

Parasitoid insects are excellent model organisms to study questions concerned with the effect of temperature on trait divergence and species coexistence. Parasitoids develop in or on other arthropods, limiting larval resource acquisition to the quantity of resources that is contained within a single host. Numerous parasitoid species that commonly attack the same host species show divergent larval and adult host use strategies, such as host stage attacked (Price 1972, 1974; Askew and Shaw 1986), level of host specialisation (Harvey and Witjes 2005; Harvey et al. 2008), and life-history traits, such as rate of metabolic expenditure and lipid reserves (Pelosse et al. 2007; Le Lann et al. 2012), which are primarily used for life span and reproduction (Ellers and van Alphen 1997). The trait divergence within parasitoid communities is thought to facilitate coexistence among species.

Much of the divergence in traits relating to host use can be captured by the contrast between two larval development modes: idiobiosis and koinobiosis (Harvey et al. 2013). Idiobiont parasitoids fix the developmental stage of their host at the time of parasitism, which causes host resources to gradually decline in quality during development of the parasitoid. In contrast, koinobiont parasitoids allow hosts to develop after parasitism and can manipulate feeding behaviour and growth of their hosts to increase resources availability (Askew and Shaw 1986; Vinson 1988; Godfray 1994; Visser and Ellers 2008). Comparative analyses have shown that in general koinobionts attack early larval host instars, produce small yolk-poor (hydropic) eggs, have higher maximum egg loads, higher daily rates of oviposition, higher lifetime fecundities, and longer pre-adult but shorter adult life spans than idiobionts (Blackburn 1991a, b; Mayhew and Blackburn 1999; Harvey 2005; Traynor and Mayhew 2005; Jervis et al. 2008, 2012). While development mode is a fixed trait for species, many associated life-history traits are highly sensitive to temperature, and it is unknown if the dichotomy in trait values associated with development mode is sensitive to temperature.

In this study, we use a comparative approach to test if differential thermal responses to an increase in ambient temperature can lead to a reduction in trait divergence within a community of parasitoid species sharing similar host resources. For this purpose, we used a small community composed of two koinobiont and two idiobiont parasitoid species that all attack the fruit fly, *Drosophila melanogaster* (Diptera: Drosophilidae), during summer (Carton et al. 1986; Fleury et al. 2009). For each species, we assessed thermal responses of traits by measuring development time, body mass, teneral egg production and lipid reserves as well as their metabolic rate and lipid use during adult life at two temperatures. We tested for differences in traits and trait plasticity between species and between larval development modes. Finally, we examined overall trait divergence of species within this community at different temperatures, using classical functional trait diversity indices (Villéger et al. 2008; Pavoine and Bonsall 2011), to test if niche differentiation is maintained or if an increase in temperature leads to trait convergence.

Table 1 Biological and life-history traits of the four solitary *Drosophila* parasitoids

Family Species	Braconidae *Asobara tabida*	Eucoilidae *Leptopilina heterotoma*	Diapriidae *Trichopria drosophilae*	Pteromalidae *Spalangia erythromera*
Larval developmental mode				
Koinobiosis/idiobiosis	Koinobiont[a]	Koinobiont[a]	Idiobiont[a]	Idiobiont[a]
Host stage attacked	Larvae[a]	Larvae[a]	Pupae[a]	Pupae[a]
Ecto-/endoparasitism	Endoparasitoid[a]	Endoparasitoid[a]	Endoparasitoid[a]	Ectoparasitoid[a]
Adult resource strategies				
Lipogenesis	No[b]	Yes[b]	No[b]	No[b]
Host feeding	No[c]	No[c]	No[a]	No[f]
Adult resource allocation				
Egg type	Hydropic[a]	Hydropic[a]	Anhydropic[f]	Anhydropic[a]
Arrhenotoky/thelytoky	Arrhenotoky[a]	Arrhenotoky[a]	Arrhenotoky[a]	Thelytoky[a]
Diapause	Yes[a]	No[a]	No[a]	No[a]
Host range (in Western Europe)	Mainly *D. melanogaster*, *D. subobscura* and *D. obscura*[a,d]	*Drosophila*, *Chymomyza* and *Scaptomyza* fly species[a,d]	*D. melanogaster*[a,d,e]	*D. melanogaster*, *D. subobscura*, *D. busckii*, *D. phalerata*, *D. kuntzei* and *Musca* fly species[a,d]

[a] Carton et al. (1986)

[b] Visser et al. (2010)

[c] Eijs et al. (1998)

[d] Fleury et al. (2009)

[e] Romani et al. (2002)

[f] Le Lann, unpublished data

Materials and methods

Study site and sampling

The host *D. melanogaster* originated from laboratory strains maintained at the Institute of Biology in Leiden since 1966. Parasitoid species were collected within two time periods: (1) from June to August 2008, and (2) from June to July 2011, in Vieux-Vy sur Couesnon in France (48°21′05″N, 1°29′16″W) using 30 open traps (i.e. a plastic container with a 3-cm-diameter aperture covered with a mesh with 2-mm openings) baited with bananas and yeast. Bananas were retrieved, replaced by new ones every 2 weeks and then placed at room temperature until parasitoid emergence. Each trap was colonised and species identity determined to start cultures with more than 10 individuals per species. In Western Europe, the parasitoids sampled are part of a natural small community composed mainly of the larval koinobionts: *Asobara tabida* (Hymenoptera: Braconidae) and *Leptopilina heterotoma* (Hymenoptera: Eucoilidae), and the pupal idiobionts: *Trichopria drosophilae* (Hymenoptera: Diapriidae) and *Spalangia erythromera* (Hymenoptera: Pteromalidae) (Carton et al. 1986; Fleury et al. 2009). Species-specific biological and life-history traits reported in the literature have been summarized in Table 1.

Rearing and experimental conditions

For rearing and experiments, hosts and parasitoids were kept at 20 and 23 ± 1 °C to mimic warmer predicted average summer temperatures (averages for sampling years 2008 and 2011 were between 16 and 17 °C at collection sites; Météo France, Vieux-Vy sur Couesnon) (IPCC 2007). Experimental temperatures were further chosen to ensure that all parasitoid species could develop, as higher average temperatures severely affect survival of immature parasitoids (van Strien-van Liempt 1983; Le Lann, unpublished data). For each temperature regime, other abiotic conditions remained similar: 70 ± 10 % RH and a 12:12 h light:dark regime, with the exception of *A. tabida* which was reared under a 16:8 h light:dark regime at 20 °C to prevent entry into diapause (Carton et al. 1986; Fleury et al. 2009). Hosts were reared under these conditions for at least two generations before use in experiments.

Drosophila melanogaster flies were allowed to lay eggs on standard *Drosophila* food medium (Visser et al. 2010) during 1 day, after which adults were removed. After *D. melanogaster* egg laying, second instar larvae and newly formed pupae (1 day old) were collected for larval and pupal parasitoid rearing, respectively. For all parasitoid species, females aged 6–10 days were provided with hosts in separate glass jars on an agar–Nipagine substrate. Only for larval parasitoids, the substrate was supplemented with a baker's yeast suspension to allow *Drosophila* larvae to feed.

To ensure a sufficient number of progeny for all experiments, 20–30 foundresses per parasitoid species and temperature were used. About 200 second instar *Drosophila* larvae were offered daily to each *L. heterotoma* and *A. tabida* female, whereas each *T. drosophilae* female was offered 60 pupae each day, during three consecutive days. Due to the slow oviposition rate of *S. erythromera* (with a maximum of 4 eggs laid per day; Carton et al. 1986), females were offered 20 hosts for oviposition, which were replaced the first day and then twice every 2 days during 6 days. Females were fed ad libitum with acacia honey. The ensuing progeny was then used for trait measurements.

Trait measurements

Development time

At each temperature, development time was recorded and vials were checked twice a day for newly emerged females ($n = 5$–89 females per species per temperature). These females were divided into three groups for further measurements. The first group was then used to measure egg load and lipid content at emergence, the second group at 1 day old to measure metabolic rate and the last group for measuring lipid content at 7 days old. Adult females of the first group were unfed and females of the second and third group were fed ad libitum with acacia honey. Females were frozen and stored at −20 °C until further analyses.

Teneral resource allocation

At emergence, egg load, lipid content and dry mass of each female ($n = 5$–46 females per species per temperature) were determined following the method of Ellers (1996). In short, a female was placed in a drop of distilled water on a small piece of cover slip of known weight and dissected under a binocular (940; Olympus SZX9) to extract the ovaries. Eggs were counted under a microscope (94; Olympus BH2). The piece of cover slip with the dissected body of the female was dried for 3 days at 80 °C and weighed (Metler-Toledo UMX2, micro-electrobalance, sensitivity: 0.1 µg). We obtained the dry weight of the female by subtracting the weight of the cover slip. Lipids were extracted by placing the cover slip in a vial containing 4 ml of ether. After 24 h, the cover slip was washed with fresh ether and re-dried for 3 days at 80 °C. The dry weight of the female was then determined and lipid content calculated as the difference in dry weight before and after ether extraction.

Resting metabolic rate

To measure the resting metabolic rate (RMR) of the wasps, flow-through respirometry (Sable Systems International) was used. Measurements were performed without light (from 10:30 am to 4:30 pm). Females were placed individually in small cylindrical chambers in a climate room regulated at 20 or 23 ± 1 °C. For each species at each temperature, the metabolic rate of 20 females, fed with honey and aged 12–24 h, was measured (except for *L. heterotoma* 20 °C: $n = 28$, and *T. drosophilae* 23 °C: $n = 17$). Their CO_2 production was measured with a CO_2 infrared analyser (CA-10A Carbon Dioxide Analyzer, Berlin, Germany). Temperature and flow rates were maintained with a temperature controller (Pelt-5) and a mass flow valve controller (MFC-2), respectively. Ambient air was drawn and CO_2 and water were scrubbed with a Drierite–Ascarite column. Four cycles of records of 85 min each, with a sample every second, were performed for each female and were automatically transformed from ppm to µL-CO_2 per hour by Expedia software (Sable Systems, Berlin, Germany), taking into account flow rate, temperature and barometric pressure. We considered the average of three mean recordings as a measure of the RMR for each individual. The first measurement was left out and taken as an acclimation period to allow the parasitoids to accustom to their new environment. The value of the blank tube was subtracted from each measured value. As fresh body mass is known to be highly positively correlated with metabolic rate in parasitoids (Le Lann et al. 2011b, 2012), females were frozen and stored at −20 °C at the end of the experiment and their fresh body mass determined using a micro-electrobalance (Mettler Toledo XP2U, precision: 0.1 µg). Mass-corrected RMR was calculated by dividing RMR by fresh body mass.

Lipid use during adult life

Temporal variation in lipid content between emergence and 7 days was compared between species at both temperatures. Lipid contents of newly emerged females were measured using the method of Ellers (1996) (i.e. the same females used to measure teneral resources: $n = 5$–46 females per species per temperature). Lipid content of non-dissected 7-day-old females were measured using the

Table 2 Linear mixed models analyses of resource acquisition, allocation and use in *Drosophila* parasitoids according to their temperature of exposure, developmental mode, species and time (i.e. age of the females: emergence and 7 days old)

Variables	Development time			Teneral dry mass			Teneral lipid reserves			Teneral egg load			Mass-corrected RMR			Lipid use over adult life		
	F	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*	*F*	*df*	*P*
Factors																		
Temperature	101.26	1	<0.001	11.26	1	<0.001	0.02	1	0.88	0.55	1	0.47	8.72	1	<0.01	1.91	1	0.17
Developmental strategy	30.07	1	<0.001	2.52	1	0.12	7.47	1	<0.01	317.19	1	<0.001	20.45	1	<0.001	15.87	1	<0.001
Species within strategy	47.97	2	<0.001	4.07	2	<0.05	4.35	2	<0.05	20.40	2	<0.001	55.99	2	<0.001	7.55	2	<0.001
Time	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.89	1	0.17
Covariate																		
Dry mass	–	–	–	–	–	–	532.19	1	<0.001	11.33	1	<0.001	–	–	–	953.41	1	<0.001
Interactions between factors																		
Developmental strategy × temperature	0.04	1	0.85	0.35	1	0.56	5.66	1	<0.05	4.06	1	0.05	3.33	1	0.075	0.03	1	0.86
Species within strategy × temperature	1.83	2	0.17	3.19	2	<0.05	0.55	2	0.58	0.88	2	0.36	8.46	2	<0.001	7.50	2	<0.001
Temperature × time	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.01	1	0.94
Developmental strategy × time	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	25.77	1	<0.001
Species within strategy × time	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	11.11	2	<0.001
Interactions between factor and covariate																		
Developmental strategy × dry mass	–	–	–	–	–	–	15.92	2	<0.001	–	–	–	–	–	–	19.78	1	<0.001
Species within strategy × dry mass	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7.83	2	<0.001
Time × dry mass	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	24.6	1	<0.001

F: *F* test values; df: degrees of freedom; P: *P* values; *dash signs* indicate when factors, covariates and their interactions were not included in the models method of Visser et al. (2010) ($n = 4$–62 females per species per temperature). This method is derived from Ellers (1996), but individuals are freeze-, rather than oven-dried, for 2 days before and after ether extraction.

Statistical analyses

To test for differences in thermal response of the traits described above, linear mixed models (LMMs) were performed using temperature, larval developmental mode, species within development mode, and their interactions as fixed factors with foundress female nested within species as a random factor.

Dry mass at emergence, development time and mass-corrected RMR were analysed including only the factors listed above. To analyse lipid content and egg load at emergence, dry mass was included as an additional covariate. Finally, temporal variation in lipid content during adult life was analysed using dry mass as a covariate and time (i.e. emergence or 7 days old) as an additional factor along with interactions between time and fixed factors described above.

Data were either cube root (lipid content) or log (metabolic rate) transformed to meet assumptions of residual normality and homoscedasticity. *P* values reported were those of the saturated models that contained all factors and their interactions. However, covariates and their interactions with the factors were removed from the models when they were not significant (dash signs; Table 2). All analyses were performed with IBM SPSS Statistics 20.0 (SPSS, 2012, Chicago, IL, USA www.spss.com).

Finally, to examine if trait divergence of species changed with temperature, we considered species exposed to the two different temperatures as two different communities, and calculated two indices of functional diversity for each community. First, the functional richness index (FRic) (Villéger et al. 2008) reflects the range of functional trait variability in a given species community. Second, Rao's quadratic entropy index of diversity (RaoQ) (Pavoine and Bonsall 2011) expresses the sum of dissimilarities in the trait space among all possible pairs of species weighted by the product of relative species abundance. Both indices vary between 0 and 1. The abundance of each species was fixed at 1 for each temperature, because quantifying changes in community structure or composition was not the purpose of our study. Functional diversity estimates were based on averaged values of the six traits measured in this study: development time, teneral dry mass, lipid content, egg load, mass-corrected RMR, and the amount of lipid used or produced between emergence and 7 days. We computed these indices using the standard FD package (Laliberté and Shipley 2011) in R 2.12.1 (R Development Core Team 2010).

Results

Thermal plasticity in development and teneral resource allocation

Dry mass and development time decreased with increasing temperature (Fig. 1a, b; Table 2). Dry mass responses to temperature differed between species within developmental mode but not between developmental modes (Fig. 1a; Table 2), indicating that temperature affected dry mass in a similar way in both koinobionts and idiobionts (Table 2). Idiobionts had a longer development time than koinobionts and species differed within development mode (Fig. 1b), but there was no significant interaction between temperature and development mode or species (Table 2).

Temperature differentially affected lipid content of koinobionts and idiobionts, with a stronger decrease in lipid content in koinobionts (Fig. 1c; Table 2). Lipid content at emergence increased with dry mass and was higher in koinobionts than idiobionts (Fig. 1c). Additionally, there was an interaction between development mode and dry mass, meaning that dry mass affected lipid content of koinobionts more than that of idiobionts (Fig. 1c). There was no significant interaction between temperature and species within development mode (Table 2).

There was a significant interaction between temperature and development mode: the number of eggs of koinobionts decreased with increasing temperature whereas the egg load of idiobionts was more or less constant across temperatures (Fig. 1d; Table 2). Egg load decreased with decreasing dry mass and differed between development modes, with koinobiont species having a higher number of eggs at emergence than idiobionts (Table 2). Species within development modes also differed in their number of eggs (Fig. 1d).

Thermal plasticity in energy use throughout adult life

In general, mass-corrected RMR increased at a higher temperature and idiobionts had a higher RMR than koinobionts (Table 2). This was mainly due to an effect of species within development modes with *S. erythromera* having a higher RMR than all species and differing from the others in its response to temperature by having a lower RMR at the highest temperature (Fig. 2a). There was no interaction between development modes and temperature (Table 2).

Between emergence and 7 days, lipid content co-varied positively with dry mass and differed between development modes and species. There was no effect of time or temperature as a main factor, but there were several significant interactions with dry mass and development modes indicating that these factors did have an effect on lipid

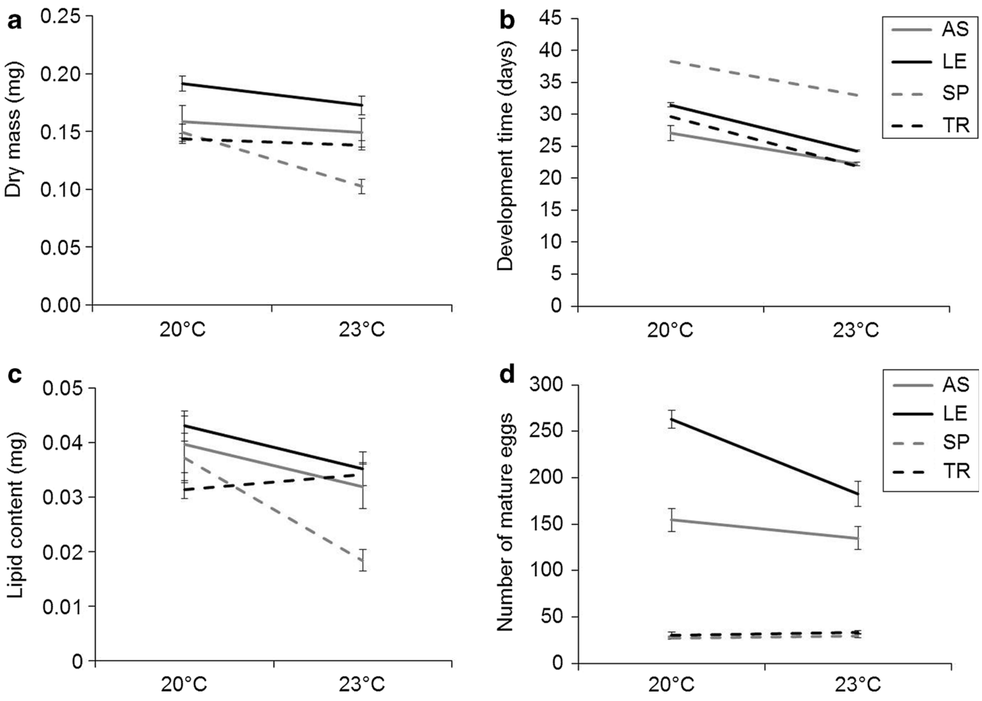

Fig. 1 Dry mass at emergence (mg) (mean ± SE, $n = 5$–46 per species per temperature) (**a**), development time (days) (mean ± SE, $n = 5$–89 per species per temperature) (**b**), lipid content at emergence (mg) (mean ± SE, $n = 5$–46 per species per temperature) (**c**) and egg load at emergence (number of mature eggs) (mean ± SE, $n = 5$–23 per species per temperature) (**d**) at two temperatures (20 and 23 °C) of the *Drosophila* parasitoids: *Asobara tabida* (*AS*), *Leptopilina heterotoma* (*LE*), *Spalangia erythromera* (*SP*) and *Trichopria drosophilae* (*TR*). *Solid* and *dashed lines* represent thermal reaction norms of larval koinobiont and pupal idiobiont species, respectively

content. The response of lipid content to temperature and time was largely species-specific, as indicated by the significant interactions between species within development modes and temperature or time (Table 2; Fig. 2b).

Effect of temperature on community trait diversity

Overall, species traits showed convergence at higher temperature, as both indices were lower at 23 °C than at 20 °C, indicating a reduction in divergence (Fig. 3).

Discussion

Temperature-induced plasticity affects resource use and life-history traits in various organisms, such as plants (Coleman and Bazzaz 1992), birds (Cavieres and Sabat 2008), mammals (Reale et al. 2003), and especially ectotherms such as Daphnia (Mitchell et al. 2004), insects (Bochdanovits and De Jong 2003; Colinet et al. 2007; Geister et al. 2009) and lizards (Luo et al. 2010). Here, we demonstrated that thermal plasticity in key resource acquisition and allocation traits causes a reduction in overall trait divergence within the community.

In ectotherms, the effect of temperature is best documented for body size, with about 80 % of the species following the temperature–size rule (TSR) (i.e. individuals have larger body sizes at lower temperatures through longer development times; Atkinson 1994, Angilletta et al. 2004). In parasitoids, the majority of species achieve a larger body size at low temperatures (Elliott et al. 1995; Bazzocchi et al. 2003; Li and Mills 2004; Colinet et al. 2007; Foray et al. 2011; Le Lann et al. 2011b; Wu et al. 2011; Baffoe et al. 2012; Dosdall et al. 2012), although some idiobionts do not follow the TSR when host resources are limiting (i.e. constraining the quantity of energy that can be acquired by the parasitoid larva; Boivin 2010; Nealis et al. 1984). In our study, all species responded classically to increased temperature, because they developed faster at the high temperature and reached a smaller adult body size.

Warmer developmental temperatures can also reduce *Drosophila* host size (Atkinson 1994; Bochdanovits and De Jong 2003) and thereby may affect parasitoid development and body size differently according to their development mode (Cohen et al. 2005; Harvey 2005). Here, we did not find differential thermal responses in growth and body size between koinobiont and idiobionts. Our results revealed a species-specific thermal response in body size, and the decrease in body size was most pronounced for *S. erythromera*, increasing divergence in body size of the community at the higher temperature. Body size divergence is frequently observed in coexisting species and may cause resource partitioning depending on the impact on foraging behaviours and prey size (Petchey et al. 2008). Parasitoid body size has been previously shown to be positively correlated with dispersal distance (Ellers et al. 1998), and a decrease in body size may therefore cause a more localised host searching behaviour, affecting the spatial distribution of parasitism risk of hosts. Increased body size divergence

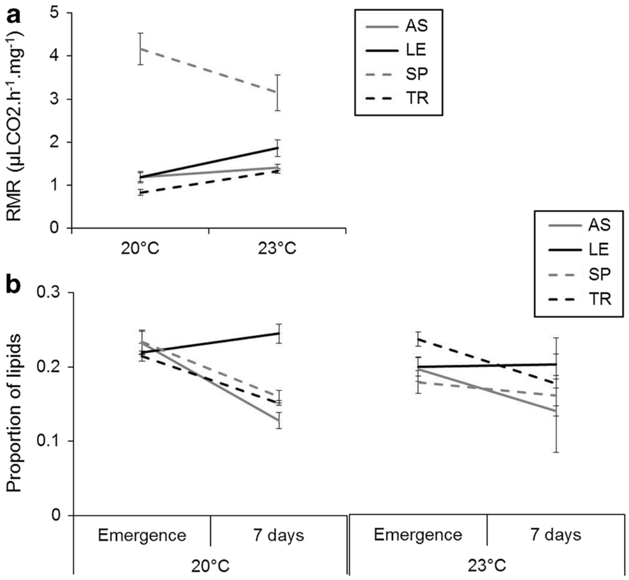

Fig. 2 Mass-corrected resting metabolic rate (RMR) (μL CO_2 h^{-1} mg^{-1}) (1 day old) (mean ± SE, $n = 17$–28 per species per temperature) (**a**) and proportion of lipids used over time (emergence and 7 days old) (mean ± SE, $n = 4$–46 per species per temperature) (**b**) at two temperatures (20 and 23 °C) of the *Drosophila* parasitoids: *Asobara tabida* (*AS*), *Leptopilina heterotoma* (*LE*), *Spalangia erythromera* (*SP*) and *Trichopria drosophilae* (*TR*). *Solid* and *dashed lines* represent thermal reaction norms of larval koinobiont and pupal idiobiont species, respectively

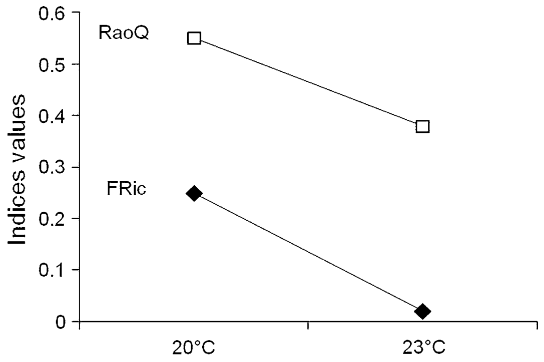

Fig. 3 Rao's quadratic entropy indices of diversity (RaoQ; *open square*) and Functional richness (FRic; *black diamond*) based on six species traits (development time, dry mass, lipid content and egg load at emergence, mass-corrected RMR and the amount of lipid used or produced between emergence and 7 days) in the community of *Drosophila* parasitoids exposed at two temperatures (20 and 23 °C) (RaoQ: 20 °C: 0.55; 23 °C: 0.38/FRic: 20 °C: 0.25; 23 °C: 0.02)

in the *Drosophila* parasitoid community may thus affect the structure of the food web through changes in host–parasitoid population dynamics (Cohen et al. 2005; Petchey et al. 2008).

Previous comparative work has identified development mode as a major organiser of parasitoid life histories (Mayhew and Blackburn 1999), and our results confirm the relevance of this dichotomy for understanding intraspecific trait variation in important host use traits. Despite much variation at the species level, our results indeed show that allocation of larval resources to adult lipid reserves and egg load, two niche-defining life-history traits among parasitoids (Ellers et al. 2000), differ between development modes. Overall, koinobionts had a higher number of eggs at emergence than idiobionts, confirming earlier differences in egg load found between development modes (Mayhew and Blackburn 1999). Higher fecundities are generally found in species attacking younger host stages (Price 1973; Blackburn 1991a, b; Jervis et al. 2012); and our results conform to this as our two koinobiont species attack young *Drosophila* larvae whereas the two idiobiont species attack older pupal hosts. In our study, koinobionts also had larger teneral lipid reserves than idiobionts. Larger lipid reserves are known to be associated with higher longevity in the koinobionts *A. tabida* and *L. heterotoma* (Ellers et al. 1998; Eijs and van Alphen 1999), suggesting that, in this specific community, these koinobionts may not have shorter lifespans than pupal idiobionts, as this pattern is observed for a broader range of species (Mayhew and Blackburn 1999).

In addition to the difference in trait values associated with development mode, we also found that differences in thermal responses of key traits were partly associated with development mode. Koinobiont parasitoids are expected to have stronger thermal responses, since they kill their hosts only when their development is completed. This thus incurs a double cost from elevated temperatures: through a reduced performance of their host as well as a reduction in their own performance (Hance et al. 2007). Indeed, only for egg load and lipid reserves at emergence is this pattern observed. At a higher temperature, we observe a decrease in egg load and lipid reserves of koinobionts at emergence, in contrast to idiobionts that show a constant egg load and no consistent change in lipid reserves across temperatures. Thermal conditions can therefore reduce divergence of life histories of koinobionts and idiobionts through differential plasticity of key traits, potentially altering their niche complementarity.

In fact, many parasitoid species are constrained by the quantity of teneral lipid reserves as they cannot accumulate additional lipids during adult life (Visser and Ellers 2008; Visser et al. 2010) due to their inability to synthesise lipids de novo from dietary sugars (Visser et al. 2012). Only the larval koinobiont parasitoid *L. heterotoma* is capable of lipogenesis (Visser et al. 2010), as it accumulates lipids between emergence and 7 days at the lower temperature, suggesting a different resource use strategy during adult life (Le Lann et al. 2012). However, at the higher temperature, no lipid accumulation was seen in *L. heterotoma* (nor in the other species). Under warm conditions, lipids are probably consumed at a higher rate because metabolic rate typically increases with temperature (Gillooly et al. 2001), resulting in constant lipid levels over time.

For the thermal response of metabolic rate, no effect of developmental mode is found. Nevertheless, divergent thermal responses of metabolic rate are found between species, with *S. erythromera* having a fourfold higher mass-corrected RMR than the other species and a decrease of its RMR with temperature. A possible explanation for the high RMR may be that *S. erythromera* is adapted to cooler temperatures, for instance because of activity earlier in the season (Le Lann et al. 2011a). To sustain physiological processes at lower temperatures, more mitochondria and enzymes are needed (Hochachka and Somero 2002), resulting in temperature compensation (Clarke 1993). Differential use of microhabitats with cooler temperatures may have promoted sympatry (Qu et al. 2011), as is found in other species; however, such thermal niches may be lost under climate warming. More studies are needed to describe temperature effects on *Drosophila* parasitoid communities and particularly the abundance and activity of idiobiont species over seasons (Fleury et al. 2009).

Niche complementarity has often been invoked as a mechanism for species coexistence (Ashton et al. 2010). Competition for shared resources can be weakened through divergence in functional traits within communities. Although many studies have addressed spatial and temporal patterns in trait diversity, for instance by comparing communities across latitudinal or environmental gradients (Irz et al. 2007; Carmona et al. 2012), to our knowledge this is the first study to quantify community changes in trait diversity through plastic responses to changing environmental conditions. Our experimental approach showed that development time, egg load at emergence, RMR and the proportion of lipids used converge in a *Drosophila* parasitoid community, whereas teneral dry mass and lipid content diverge when exposed to warmer temperatures. Functional diversity indices change for the six traits under study due to plasticity in response to temperature and reveal overall trait convergence under warmer conditions.

The experimental temperatures we used are non-lethal and lie within a range of moderately high temperatures that can occur frequently in the field during short periods in summer. However, these higher temperatures substantially exceed average daily temperatures and are not experienced for prolonged periods of time and over several generations (source: Météo France, Vieux-Vy sur Couesnon). This suggests that even a small increase in average temperatures may affect niche partitioning in coexisting species. Warmer temperatures reduced dissimilarity in this parasitoid community, by provoking convergence in important traits, such as resource use and allocation, implying that competitive interactions between species could be altered. For instance, similar development times between parasitoid species shorten the time window for parasitism, which may lead to increased competition for host resources (Price 1972, 1973). This could result in changes of both species abundance and community composition. Moreover, at prolonged warm temperature (i.e., above 25 °C), the parasitoid *Asobara tabida* cannot complete its development (van Strien-van Liempt 1983; Le Lann, unpublished data). Therefore, in a warmer environment, this species may not persist, consequently altering community composition and structure. Finally, host resource quality and availability are also likely affected by warmer temperatures, through changes in body size, development time and reproduction opportunities (Atkinson 1994; Bochdanovits and De Jong 2003). This could potentially affect demographic patterns in host–parasitoid relationships through differential effects on their life-history traits (Hance et al. 2007). The predicted increase in temperature due to local warming might thus affect trait divergence of species communities that potentially compromise community stability and resilience over time.

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