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Disentangling plasticity from local adaptation in diapause expression in parasitoid wasps from contrasting thermal environments: a reciprocal translocation experiment

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An important question in evolutionary ecology is to understand the drivers of phenotypic variation in contrasting environments. Disentangling plasticity from evolutionary responses in such contexts provides a better understanding of how organisms adapt to changing climates. Many aspects of the seasonal ecology of insect populations are essential for their persistence in temperate environments, including their capacity to overwinter. Phenotypic plasticity should result in locally adapted diapause levels to experienced environmental conditions. Using an outdoor reciprocal translocation experimental design, we compared diapause expression of Canadian and French populations of aphid parasitoid species of the genus *Aphidius* in both their native and foreign bioclimatic regions, the insects thus experiencing varying temperature conditions under similar latitude (i.e. same photoperiod). From June to December 2016, diapause and mortality levels were recorded every 2 weeks. We found both genotypic (population origins) and environmental effects (experimental locations) on diapause reaction norms of parasitoid species. The incidence of diapause was higher in Canadian populations (up to 90%) than in French populations (< 20%) at both locations, suggesting local adaptation to harsh (Canadian populations) or mild (French populations) winter climatic conditions in the area of origin. Phenotypic plasticity played an important role in mediating diapause incidence at different temperatures but similar photoperiods, as diapause was induced at higher levels in Canada than in France, independently of the origin of the parasitoid. We conclude that both plastic and evolutionary responses could be involved in the adaptation of parasitoid overwintering strategies to different thermal environments and to ongoing climate warming.

ADDITIONAL KEYWORDS: adaptation – climate change – parasitoids – reaction norms – translocation experiment – transplant.

INTRODUCTION

Understanding the basis of phenotypic variation across varying environments is an important question in evolutionary ecology. Reaction norms (RNs) describe the degree to which a genotype (G) responds, in a plastic way, to environmental changes (E), in a manner that G × E interactions can be measured (Via & Lande, 1985; Scheiner, 1993). This implies that an organisms' trait expression, and thus fitness, can change with the environmental conditions at which they were selected (determining the level of the RN) and which they actually experience (slope of the RN) (Ayrinhac *et al.*, 2004; Nussey *et al.*, 2007). Organisms can respond to environmental changes through genetic evolution or plasticity (Parmesan, 2006; Sgrò *et al.*, 2016). Disentangling the relative effects of plastic and evolutionary responses to environmental changes is crucial if we are to predict how organisms will respond to ongoing global change, including climate change (Gienapp *et al.*, 2008; Merilä & Hendry, 2014). Transplant (i.e. translocation) experiments of populations between contrasted environments enable us to study RNs and infer responses to climate

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change by comparing performance at different locations (Kawecki & Ebert, 2004; Hoffmann & Sgrò, 2011).

Facultative diapause is a well-documented example of developmental plasticity, allowing insects to cope with variable environments (Nylin & Gotthard, 1998). Insects from temperate regions typically enter diapause in response to decreasing photoperiod that reliably indicates unfavourable conditions to come (Tauber *et al.*, 1986). However, the photoperiodic response is often modulated by temperature and other environmental factors (Danks, 1987) and climate warming would diminish the reliability of photoperiod as a predictor of winter onset, leading to potential phenological mismatches (Bale & Hayward, 2010; van Dyck *et al.*, 2015; Forrest, 2016). It is thus necessary to separate the respective effects of photoperiod and temperature when studying diapause RNs across environmental gradients. Few studies have examined the consequences of photoperiod-based adaptations, such as diapause, when organisms face new climates (Grevstad & Coop, 2015).

Timing is of the essence; diapause induction that is too early or too late can impair insect fitness and induce mortality (Sgrò *et al.*, 2016). Minimization of such timing costs occurs through adaptation of the incidence and initiation of diapause to local environmental seasonal variations (Danks, 1987). Therefore, for a given insect species living in the northern hemisphere, there are geographical clines in diapause expression; winter diapause is induced earlier and at a lower environmental threshold in northern populations (Winterhalter & Mousseau, 2007; Hut *et al.*, 2013). A few transplant experiments in the context of diapause study have been reported (e.g. Chen *et al.*, 2014) but, to our knowledge, no previous study on diapause RN has held the photoperiodic environment constant while varying the thermal environment. The experimental design described below allows us to disentangle local adaptation and plasticity in diapause expression without confounding the effects of temperature and photoperiod.

This study focused on parasitoid species of the genus *Aphidius* (Hymenoptera: Braconidae): *Aphidius ervi* (Haliday), present in both North America and Europe, and the sister species *Aphidius rhopalosiphi* (Haliday) from Europe/*Aphidius avenaphis* (Fitch) from North America. Photoperiod and temperature interact to induce diapause in these species (Brodeur & McNeil, 1989; Tougeron *et al.*, 2017b). The aim of this study was to investigate and compare the RNs of diapause expression in multivoltine populations of aphid parasitoids from contrasted winter climate areas (eastern Canada vs. western France) in outdoor semi-experimental conditions across the season for diapause induction. In this longitudinal translocation experiment, we tested responses to summer, autumn and winter climatic conditions to which they were, or were not, adapted, in order to measure the degrees of local adaptation and plasticity in diapause expression. In their native environment, Canadian parasitoids start to enter winter diapause in mid-July and 100% incidence is reached before lethal frosts occur (Brodeur & McNeil, 1994). In contrast, in western France at least part of the population of some parasitoid species can remain active throughout winter due to mild conditions and host availability throughout the year (Krespi *et al.*, 1997; Andrade *et al.*, 2016).

We hypothesized that: (1) Canadian populations enter diapause at higher levels and earlier in the season than French populations, due to adaptations to conditions of their area of origin; (2) diapause levels are higher and parasitoids enter diapause earlier in Canada than in France, regardless of the origin of the parasitoid population, due to phenotypic plasticity to local temperatures; and (3) mortality levels are higher for parasitoid populations tested in the foreign location.

MATERIAL AND METHODS

METEROLOGICAL DATA

Minimum, mean and maximum temperatures were recorded every hour throughout the experiment using LOG32 data loggers (Dostmann, Germany) in France and HOBO data loggers (Onset, MA, USA) in Canada directly placed in one of the outdoor experimental cages (Bugdorm-4S, 32 × 32 × 32 cm, Taichung, Taiwan). Cages did not produce any greenhouse effect because mean temperature was similar to outdoor weather stations close to the experimental sites (mean ± SE difference between inside and outside the cages of 0.35 ± 0.24 °C over the experimental session). Temperatures for each date of outdoor releases were averaged using data for the following 14 days to have reliable information on climatic conditions experienced by developing parasitoids.

BIOLOGICAL MATERIAL

Three parasitoid species of the English grain aphid [*Sitobion avenae* (Fabricius) (Homoptera: Aphididae)] were used: *A. ervi* (present in both France and Canada), *A. rhopalosiphi* (strictly Eurasian species) and *A. avenaphis* (strictly North American species). The two latter species are phylogenetically, ecologically and morphologically closely related and are considered as sister species (Kos *et al.*, 2011; Tomanović *et al.*, 2013). Although they are two different species, *A. rhopalosiphi* was considered as the French population and *A. avenaphis* as the Canadian population. In this way, we were able to compare the plastic response of two

populations of the same species (*A. ervi*), and of two close species that have evolved in different bioclimatic areas (*A. rhopalosiphi* and *A. avenaphis*). Four parasitoid populations were collected from cereal fields in 2015 and the colonies were started with about 50 individuals for each population. One population of *A. ervi* was collected in Québec, Canada (45.58°N, 73.24°W) and the other was collected in Brittany, France (48.11°N, 1.67°W). *Aphidius rhopalosiphi* parasitoids were collected in Brittany, France, and *A. avenaphis* parasitoids were collected in Saskatchewan, Canada (52.21°N, 106.66°W). Parasitoid colonies were maintained in climatic chambers at 20 °C, 16:8 h light–dark (LD) photoperiod and 75% relative humidity (RH) on cereal aphid colonies (*S. avenae*) collected either in Brittany (for the maintenance of and experiments on French parasitoid populations) or in Québec (for Canadian parasitoid populations). All the experiments were conducted within the 2 years after establishment of parasitoid cultures.

EXPERIMENTAL DESIGN

Experiments were conducted every 14 days from 20 June to 5 December, 2016 in outdoor mesocosms in Montréal (45.55°N, 73.55°W, QC, Canada) and Rennes (48.11°N, 1.65°W, Brittany, France), thus providing approximately the same photoperiodic regime (similar latitude) in both locations across the season. In France, experiments were not performed from 4 July to 29 August (four experimental dates) because no winter diapause was expected prior to this period and to avoid measuring summer diapause (Krespi *et al.*, 1997; Tougeron *et al.*, 2017b). The first observation (20 June) was done in France to obtain a common starting point with Canada. We were not able to obtain data for the Canadian population of *A. ervi* tested on 24 October, nor for *A. avenaphis* tested on 29 August in France.

Four days before each date of outdoor releases, 15 parasitoid females and five males from each population, less than 48 h old, were taken from the colony and placed during 24 h in three different plastic tubes (height = 10 cm, diameter = 3 cm) at a ratio of five females to three males for mating and with a dilution of honey for feeding. Parasitoid females were then placed in three fine netting Bugdorm-4S cages in the presence of 200–300 second- and third-instar larvae of *S. avenae* aphids of the same size and originating from the same cohort on a wheat pot for 60–72 h, with a dilution of honey, at 20 °C, 16:8 h LD. The rate of parasitism was about 40%. Female parasitoids were then removed from the cages and the three wheat pots with parasitized aphids were put together in a new fine netting cage. The four cages (one per population),

protected from rain by a plastic roof, were put outside in a semi-shaded place. This procedure was repeated every 2 weeks in both locations.

Twice a week, the formation of mummies (i.e. a dead aphid containing a parasitoid prepupa or pupa) was checked in each cage. Mummies were collected from the plants, individually put in 1.5-mL plastic microtubes with a tiny hole on the top for venting and left in their respective cages. Adult emergence from the mummies was checked three times a week and mummies from which no parasitoid emerged within 15 days after the last adult emergence were dissected (or 45 days after mummy formation when no emergence occurred in a cage). The contents from mummy dissections were categorized as dead parasitoids (immature and adult stages) or gold-yellow diapausing prepupae (Tougeron *et al.*, 2017b). Diapause incidence was calculated as the number of diapausing prepupae relative to the number of emerged individuals (thus excluding dead individuals). Mortality rate refers to the number of dead parasitoids inside the mummies relative to the total number of mummies. Mean diapause and mortality levels were calculated and analysed from 12 September to 5 December (i.e. over the experimental dates in common between France and Canada).

STATISTICAL ANALYSES

The number of days since the beginning of the experiment was used in the models as a 'date' factor. A global model was first created; for each species separately (*A. ervi*, and the sister species *A. rhopalosiphi*/*A. avenaphis*), a generalized linear model (GLM, quasi-binomial family to account for data overdispersion) was fitted to the data to test for differences in diapause incidence over the season (number of individuals in diapause vs. not in diapause) on the following explanatory variables: parasitoid origin, tested location, date and their two-way interactions. The same procedure was used to analyse mortality levels. Significant differences in diapause incidence between populations at the same location were interpreted as genetic variation (local adaptation) for the expression of diapause. On the other hand, significant differences in diapause incidence between locations for a given parasitoid population were interpreted as plastic variation of diapause (Winterhalter & Mousseau, 2007). A Spearman correlation test was done to analyse the links between photoperiod and minimal temperatures in France and Canada, because minimal temperatures are likely to be the best predictor of diapause increase over the season. A Gaussian GLM was applied to analyse the evolution of minimal temperatures over the experimental season using the date, the tested

location and their interaction as explanatory variables. The significance of each explanatory variable was tested with the 'Anova' function from the package *car* in R, which performs an analysis of variance of type II (R Core Team, 2017), using the *F* statistic for diapause and mortality quasibinomial data, and a likelihood-ratio (LR) test using a chi-square statistic for meteorological data.

RESULTS

ABIOTIC FACTORS

Photoperiod and minimal temperatures were highly correlated ($P < 0.001$, $r_2 = 0.85$ and $r_2 = 0.89$ in France and Canada, respectively) (Fig. 1). Minimal temperatures were on average 6.5 °C lower in Canada than in France (GLM, LR = 5.8, d.f. = 1, $P < 0.05$) and decreased over the season in both locations (GLM, LR = 57.7, d.f. = 1, $P < 0.001$) although they decreased faster in Canada (–0.17 °C/day, $R^2 = 0.77$) than in France (–0.09 °C/day, $R^2 = 0.66$) (GLM interaction effect, LR = 5.3, d.f. = 1, $P < 0.05$). Temperatures in France were more buffered (lower minimum–maximum amplitude) than temperatures in Canada. Negative temperatures were only encountered for a few days in late November in France (down to –2.5 °C during the night) while several frost events (down to –23.5 °C) occurred almost every day in Canada from early October. First snow fall occurred on 20 November in Canada. There was no snow in France during the time of this experiment. Day length at 46.50°N (similar in both experimental locations) decreased from 15.7 to 8.8 h between 20 June and 5 December.

DIAPAUSE INCIDENCE

For every species, Canadian populations had overall higher mean diapause levels than French populations when tested in Canada and in France (Table 1, Fig. 2). There was no significant interaction between the origin of the parasitoid populations and the tested locations for any species (Table 1), meaning that differences in diapause incidence between parasitoid populations were consistent across locations (Fig. 2). Additionally, diapause incidence increased over the season and this effect was independent of the population origin, but not of the tested location, as it increased faster in Canada than in France (Table 1, Fig. 3A). Data for each date (number of mummies collected, number of diapausing parasitoids and number of dead individuals) can be found in Supporting Information, Table S1.

In detail, mean diapause levels over the season were higher for *A. ervi* tested in Canada than in France for both the Canadian-origin populations (68.8 ± 13.5% vs. 17.5 ± 5.5%) and the French-origin population (30.7 ± 12.5% vs. 0.6 ± 0.5%), but this effect varied with the tested date because differences between locations were only seen at the end of the season (Figs 2, 3A). Mean diapause levels over the season were 61.6 ± 12.5% vs. 47.3 ± 7.1% in *A. avenaphis* (Canadian species) and 5.5 ± 3.1% vs. 4.2 ± 1.8% in *A. rhopalosiphi* (French species), in Canada vs. France, respectively. Although there was overall no difference in mean diapause between locations in these species, a location effect was observed for a few dates at the end of the season, especially for *A. avenaphis* (Figs 2, 3A). In Canada, diapause peaks (i.e. maximum incidence over the season) occurred one month earlier (24 October) for Canadian populations than for French populations (21 November). In both
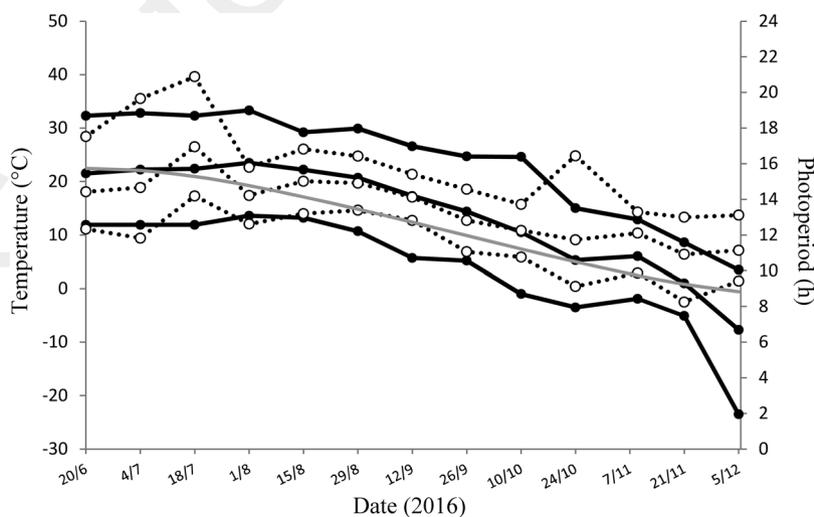

Figure 1. Minimum, mean and maximum temperatures in Montréal, QC, Canada (solid lines), and Rennes, Brittany, France (dotted lines), from 20 June to 5 December 2016. Data shown at each date are the average of temperature data for the 14 days following this date. Photoperiod at 46.50°N is shown for each date (grey line).

Table 1. Generalized linear models (GLMs) on the effect of origin-locations and photoperiod and their interaction on diapause incidence and mortality levels of *A. ervi* (*N* = 1416 mummies in Canada and *N* = 762 in France) and *A. rhopalosiphi/A. avenaphis* (*N* = 1469 in Canada and *N* = 2231 in France)

Factor		*Aphidius ervi*			*Aphidius rhopalosiphi/A. avenaphis*		
		F	*P*		*F*	*P*	
Diapause incidence	Origin	66.9	**< 0.001**	***	72.5	**< 0.001**	***
	Location	129.0	**< 0.001**	***	2.1	0.16	NS
	Date	205.9	**< 0.001**	***	33.5	**< 0.001**	***
	Origin × Location	0.2	0.68	NS	0.6	0.45	NS
	Origin × Date	0.5	0.48	NS	1.8	0.19	NS
	Location × Date	14.6	**< 0.001**	***	13.5	**< 0.001**	***
Mortality levels	Origin	1.8	0.18	NS	0.95	0.34	NS
	Location	9.3	**< 0.01**	**	15.7	**< 0.001**	***
	Date	17.6	**< 0.001**	***	18.1	**< 0.001**	***
	Origin × Location	3.2	**0.06**	NS	8.9	**< 0.01**	**
	Origin × Date	0.8	0.40	NS	1.0	0.31	NS
	Location × Date	3.5	0.07	NS	3.8	0.06	NS

F- and *P*-values are presented. The degrees of freedom (d.f.) is 1 for each test. NS = non-significant.
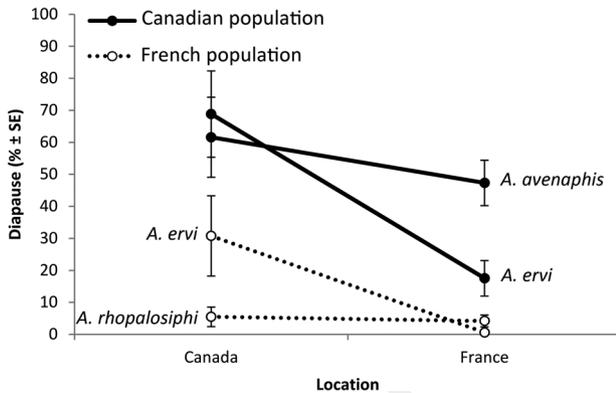

Figure 2. Mean per cent reaction norms of diapause incidence (mean ± SE) of Canadian (full line) and French (dotted line) populations of *Aphidius ervi* and *Aphidius rhopalosiphi/Aphidius avenaphis* reared under outdoor conditions either in Canada or in France. For each population origin, more than 600 and 350 mummies were collected in Canada and France, respectively.

Canada and France, first entrance into winter diapause was observed earlier for Canadian-origin parasitoids (as early as 20 June) than for French-origin parasitoids (not earlier than 26 September, except for *A. rhopalosiphi* on 20 June which may have entered into summer diapause, as discussed below) (Fig. 3A).

MORTALITY LEVELS

From late October to early December, mortality levels of each species increased similarly for both population

origins and locations (Table 1, Fig. 3B). Mortality levels were significantly higher in Canada (between 59% and 95% mortality in early December) than in France (between 0% and 25% in early December) (Table 1, Fig. 3B). However, the effect of location on mortality differed depending on the origin of the parasitoid population, although this interaction was only marginally non-significant in *A. ervi* (Table 1). Notably, in France, end-season mortality levels were higher for Canadian parasitoid populations than for French populations. By contrast, in Canada, end-season mortality levels were higher for French populations than for Canadian populations, for any species or group of species (Fig. 3B).

DISCUSSION

We provide evidence, using parasitoid insects, that both plasticity and local adaptations can be involved in insect responses to varying climates. Our translocation study allowed us to separate the effects of local adaptations from those of plasticity on diapause incidence. As predicted, aphid parasitoid populations originating from the harsh winter area (Canada) expressed higher levels of diapause than populations from the mild winter area (France), when tested either in France or in Canada. This first pattern reflects parasitoid adaptations to climatic conditions of their respective area of origin (genotypic effect, G). Diapause incidence was overall higher for parasitoids tested in Canada than in France, especially for *A. ervi*. This second pattern highlights plastic responses of diapause expression under different thermal environments (environmental effect, E). To the same
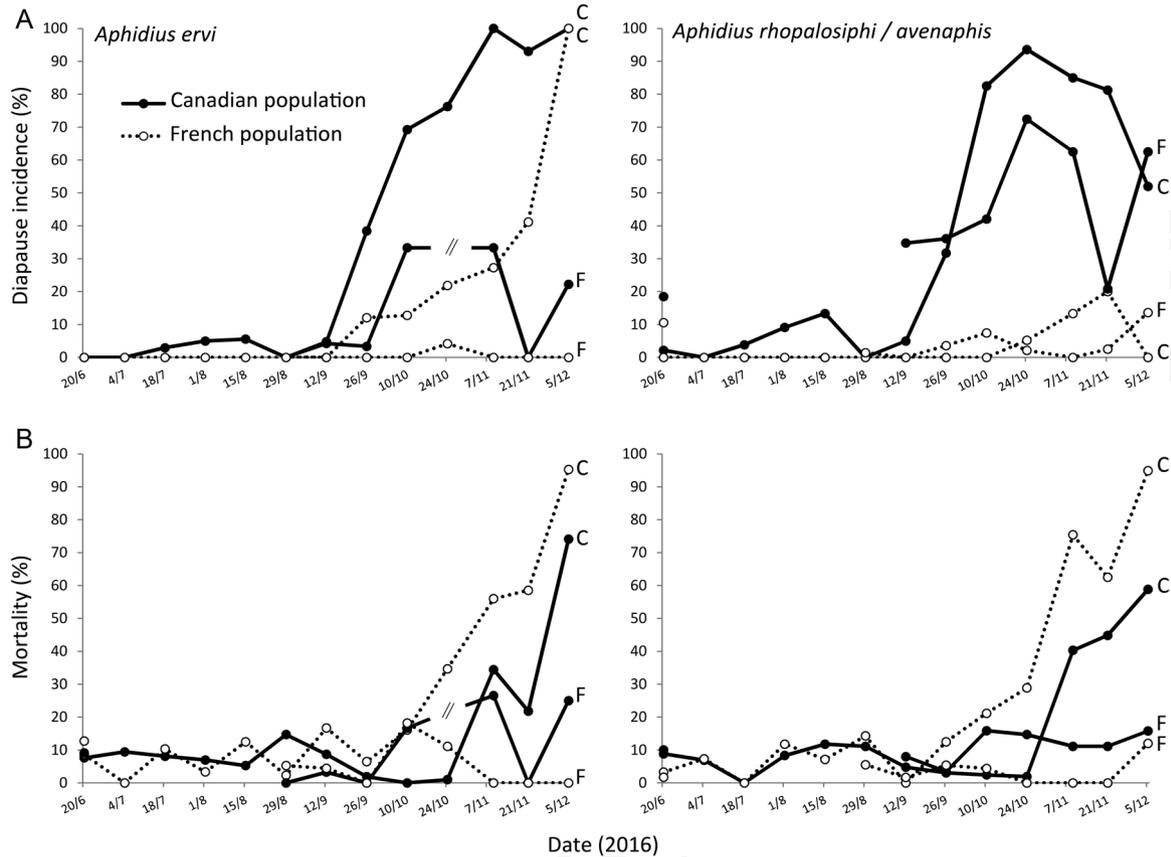
Figure 3. A, seasonal levels of diapause (number of diapausing prepupae/total number of mummies, excluding dead individuals); and B, mortality within the mummies, recorded every 2 weeks from 20 July to 5 December 2016 in the Canadian (solid lines) and French (dotted lines) parasitoid populations of left: *Aphidius ervi* and right: *Aphidius avenaphis/Aphidius rhopalosiphi*. Letters on the right of each panel indicate where the experiments were conducted: Canada (C) and France (F). Slashes (//) correspond to a lack of data (see Material and methods).

extent, insect thermal reaction norms usually are determined by both basal genetic response to temperatures (local adaptation) and acclimation (plastic response) to experienced temperatures (Noh *et al.*, 2017). However, we found no G × E interactions, as the plasticity following the change in environment was expressed by both Canadian and French parasitoids in a similar fashion. Such results are similar to patterns observed along latitudinal gradients. For example, northern populations of the parasitoid *Nasonia vitripennis* (Hymenoptera: Pteromalidae) enter diapause earlier and at higher incidence than southern populations because of local adaptations of plastic responses to seasonal photoperiodic and thermal changes (Paolucci *et al.*, 2013).

We observed that, at a given date (i.e. a specific photoperiod) and for a given location (i.e. a specific temperature regime), Canadian parasitoid populations entered diapause at higher levels than French populations. In France, Canadian populations entered diapause at significant levels (up to 27.8% for *A. ervi* and 61.8% for *A. avenaphis*) even if temperatures were high enough

for continuous development and adult survival (developmental thresholds are around +3 °C in this genus; Sigsgaard, 2000; Zamani *et al.*, 2007), suggesting a strong genetically determined photoperiodic effect in harsh winter populations. On the other hand, French parasitoids expressed overall low diapause levels in both Canada and France, suggesting a weak response to environmental cues. We showed that *A. ervi* had a higher level of plasticity to environmental changes (i.e. location effect with higher RN slopes, see Fig. 2) than the other 'sister-species'. The response to environmental change in diapause of *Aphidius* parasitoids could thus be different between species and could depend on their respective responses to environmental cues (temperature and photoperiod). For example, in the laboratory, it was shown that the incidence of *A. ervi* diapause was influenced by a photoperiod × temperature interaction but this was not found for *Aphidius avenae* diapause, which is triggered by these cues independently of each other (Tougeron *et al.*, 2017b). Furthermore, in the French population of *A. rhopalosiphi* held in

France, around 10% of the individuals entered diapause in June. This suggests the expression of summer diapause initiated in the offspring when female parasitoids encounter competitors for host resources, under summer-like conditions (Krespi *et al.*, 1997; Tougeron *et al.*, 2017a).

As in many arthropod species, both temperature and photoperiod interact to induce diapause in aphid parasitoids (Brodeur & McNeil, 1989; Tougeron *et al.*, 2017b), but it is difficult to disentangle them because these stimuli are highly correlated. Nevertheless, the relative importance of photoperiod and temperature at inducing diapause can differ between insect populations of the same species because the reliability of these stimuli may vary among regions (Piercey & Maly, 2000; Pruisscher *et al.*, 2017). Northern populations normally enter diapause under strict photoperiodic control and earlier than southern populations in which diapause may be more sensitive to modulation by temperature (Hut *et al.*, 2013). Our results suggest that parasitoids from mild winter climates may be relatively more sensitive to temperature than to photoperiod for entering diapause. This would allow parasitoids to match more accurately their overwintering strategy to actual winter temperatures.

In the laboratory, Tougeron *et al.* (2017b) observed very low diapause incidence in species of aphid parasitoids from a mild winter climate. Under the most winter-like conditions tested (14 °C, 10:14 h LD), no diapause was expressed in *A. rhopalosiphi* while an average level of 11.2 ± 4.9% was observed in *A. ervi*. Here we demonstrate that although mild winter populations of these two species express low diapause levels in both Canada and France, they have the capacity to enter diapause at higher levels through developmental plasticity when exposed to lower temperatures and shorter photoperiods than when tested in the laboratory. Therefore, the capacity to enter diapause has not been 'lost' in aphid parasitoid populations from mild winter climates, but diapause is not or is little expressed in their area of origin because of advantageous climatic conditions. By contrast, our results confirm a selection process for low diapause induction thresholds (low temperature and day-length) and low plastic responses in populations from mild winter areas (Tougeron *et al.*, 2017b), associated with changes in overwintering strategies (Andrade *et al.*, 2016). This hypothesis is especially true for *A. ervi*, which responds strongly to the change of thermal environment (i.e. when tested in Canada), whereas *A. rhopalosiphi*, a species that has favoured a quiescence strategy over the diapause overwintering strategy in recent decades (Tougeron *et al.*, 2017b), does not exhibit such a strong response to temperature. Similarly, in the pitcher-plant mosquito *Wyeomyia smithii* (Diptera: Culicidae), a longer favourable season driven by climate warming

has led to the selection of a lower critical photoperiod to enter diapause (Bradshaw & Holzapfel, 2001).

Several studies have used transplant experiments to move populations to warmer climates and investigate organisms' evolutionary and plastic responses to new environmental conditions (e.g. Andrew & Hughes, 2007; Logan *et al.*, 2014; Nooten *et al.*, 2014). Following transplant, the value of the most plastic traits changes rapidly while the value of traits strongly associated with local adaptations are not immediately modified (Kawecki & Ebert, 2004; Charmantier *et al.*, 2016). For example, in the grasshopper *Melanoplus sanguinipes* (Orthoptera: Acrididae), body orientation toward a heat source is plastic to the temperature experienced by the insect while mobility and basking behaviours are determined by the climatic origin of the parental generation (i.e. locally adapted traits) (Samietz *et al.*, 2005). For diapause, Chen *et al.* (2014) demonstrated that the moth *Hyphantria cunea* (Lepidoptera: Arctiinae), transferred from its temperate origin area to a subtropical location, has the capacity to enter summer diapause to cope with warmer summers, thus highlighting a plastic developmental response. However, this moth species faced environmental conditions to which it was not adapted, and high mortality was observed (Chen *et al.*, 2014).

When parasitized aphids were put outside in Canada at the end of the experimental season, most individuals died because of lethally low temperatures. To the same extent, insects that do not enter diapause because of too high temperatures in autumn may suffer high mortality from sudden cold spells in winter (Bale & Hayward, 2010). Higher mortality levels were observed for French populations tested in Canada, which may be poorly resistant to low temperatures (Le Lann *et al.*, 2011; Tougeron *et al.*, 2016). Such high mortality highlights timing costs of being active too late in the season, although it is not ecologically relevant because parasitoids are adapted to enter into diapause before the onset of lethal frosts. Canadian populations tested in France also incurred important mortality despite the relatively warm conditions across the experimental season. For Canadian populations in France, developmental costs might have occurred; temperatures were too high to be sustainable in a diapause state. Indeed, mild winter conditions lead to higher metabolic activity during the process of diapause, potentially increasing mortality in insects (Bosch *et al.*, 2010; Williams *et al.*, 2012; Xiao *et al.*, 2017). These results strengthen the idea that there is a strong evolutionary pressure to enter early diapause in harsh winter climates, but not necessarily in mild winter climates where diapause can involve physiological (i.e. energy consumption) and ecological costs (i.e. not exploiting available hosts in the environment).

From an applied perspective, studies on diapause expression among different parasitoid populations

may help the biological control industry to select appropriate strains for mass rearing. In the context of climate changes, animal populations will increasingly be exposed to environmental conditions to which they are not adapted. When populations face a new climate, the genetically based photoperiod response is likely to be initially mismatched – until they adapt their response or modulate it through plasticity – because at a given location, photoperiod will not change whereas temperatures will (Grevstad & Coop, 2015). Increasing costs of diapause expression under an inappropriate thermal environment are thus expected (Bale & Hayward, 2010; Sgrò *et al.*, 2016), for instance in the case of unexpected cold spells in mild winter areas, although insects have great capacities to adapt rapidly to new thermal conditions. When species have to adapt to new environments, one could expect the RN (i.e. the phenotypic response to the environment) to change genetically (Winterhalter & Mousseau, 2007; van Asch *et al.*, 2012). However, examples of genotypic changes when facing warmer climates (e.g. Bradshaw & Holzapfel, 2001; Logan *et al.*, 2014) remain less common than reports on plastic changes (Hill *et al.*, 2002; Berteaux *et al.*, 2004).

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SUPPORTING INFORMATION