

## Population differentiation in response to temperature in *Ophraella communa*: Implication for the biological control of *Ambrosia artemisiifolia*

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### HIGHLIGHTS

- Performance and survival of *Ophraella communa* populations differ in their response to temperature.
- Variation in thermal reaction norms for survival indicate the potential of *O. communa* populations to cope with variation in environmental conditions.
- We found no risk of increasing non-target effects on sunflower under different temperature regimes.
- There was no significant correlation between genetic diversity and phenotypic trait means.

### ARTICLE INFO

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### ABSTRACT

Although biological control agents (BCAs) are an effective tool for limiting the impact of invasive alien plants (IAPs), mismatch between the BCA and IAP, exacerbated by future climate change, may affect biocontrol efficacy and the likelihood of there being non-target effects. In a common-environment experiment, we measured leaf consumption, performance (i.e. development time and adult weight), and survival in 11 populations of the leaf beetle *Ophraella communa* from its native (North America) and introduced (China, Europe) ranges under three temperatures treatments (20 °C, 27 °C, 31 °C) and on two plant species, the target IAP *Ambrosia artemisiifolia* (common ragweed) and the closely-related crop *Helianthus annuus* (sunflower), a potential subsidiary non-target host. Leaf consumption, development time, adult weight and survival differed significantly in the different populations without any significant geographical pattern. Specifically, there was variation in levels of survival at different temperatures between populations, with highest levels of leaf consumption and survival in the Fogang (China) population at all temperatures, while survival was highest in other populations under colder and warmer conditions. In general, we observed faster development and a marginal increase in adult weight, but decreasing survival, with increasing temperatures in all populations. The beetles consumed much more common ragweed than sunflower leaves, with no difference evident in the consumption levels on sunflower under cooler or warmer temperature conditions. Moreover, cold temperatures negatively affected the survival of beetles feeding on sunflower, potentially leading to a reduction of fitness on the non-target host. Genetic composition and diversity, assessed using microsatellite markers, showed higher allelic richness and expected heterozygosity in native US populations compared to introduced Chinese populations and lower allelic richness and expected heterozygosity in US and Italian populations at the edge of the distribution compared to core populations. Overall, Chinese populations showed low genetic diversity, likely due to releases after mass rearing. Although there were differences in genetic diversity among populations, we did not find correlations between genetic diversity and phenotypic trait means. Our results indicate that some of the populations examined might be able to cover areas that are heavily infested by common ragweed or are expected to be so under climate warming but are predicted to be presently unsuitable for the beetle.

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## 1. Introduction

In the past few decades, human activities have increased the rate of introduction of invasive alien plants (IAPs), with dramatic negative ecological, economical, and human health-related consequences (Mack et al., 2000; Rai and Singh, 2020). Classical biological control can be an efficient and safe strategy to mitigate the impact of plant invasions (Müller-Schärer and Schaffner, 2008). Recent improvements in pre-release assessments have increased the control efficiency, and reduced non-target effects, of biological control agents (BCAs) (Hinz et al., 2020; Müller-Schärer and Schaffner, 2020). The overall efficacy of a biological control operation depends on, among other factors, the extent to which BCAs can build up high densities across the range invaded by the target weed. In cases where the distribution of a BCA only partially covers the distribution of the target IAP in the native range, it is expected to do so also in its introduced range, thus impeding overall biocontrol efficacy (Hoelmer and Kirk, 2005).

Ecological niche modelling can identify scenarios in which: (i) the distribution of an IAP and its BCA in the introduced range can be predicted from its native range (Dinis et al., 2020); (ii) survival of the BCA is greater at lower temperatures than would be expected from its physiological responses in its native range (Minghetti et al., 2020); (iii) the current range invaded by the IAP may be only partly suitable for establishment of the BCA (Sun et al., 2017a) or for building up to population densities that are high enough to control the IAP (Augustinus et al., 2020a). Moreover, climate change may disrupt a biological control program if BCAs and IAPs respond differently to novel environments (Forrest, 2016; Lehmann et al., 2020), e.g. altered plant invasion rates coupled with changes in the control efficacy of its BCAs (Sun et al., 2020). In some cases, the overlap between the potential distribution of BCAs and IAPs has been predicted to be stable under current and future climate scenarios (Chidawanyika et al., 2020), while in other cases the overlap has been predicted to shrink under climate change (Cowie et al., 2016; Goolsby et al., 2006; Sun et al., 2017a). It is therefore important to study the thermal tolerances of BCAs originating from a range of environmental conditions to select provenances that are able to cover the present and expected future areas of the IAPs in the introduced range.

The establishment success and effectiveness of BCAs is influenced by the genetic makeup of introduced populations (Lommen et al., 2017a; Wajnberg, 2004), which is determined by: (i) differentiation in the native range (Hopper et al., 1993; Mathenge et al., 2010), (ii) the introduction process itself, which can decrease diversity via bottlenecks or increase diversity through multiple introductions and admixture (Kirkpatrick and Jarne, 2000; Laugier et al., 2016; Rius and Darling, 2014; Turgeon et al., 2011); or (iii) post-introduction differentiation (Szűcs et al., 2012; Wright and Bennett, 2018). Phenotypic plasticity can also provide an advantage during establishment in novel environments by allowing a genotype to have a broader tolerance to adverse conditions, or to respond positively to favorable conditions (Agrawal, 2001; Ghalambor et al., 2007; Hahn et al., 2012). For this reason, phenotypic plasticity has been suggested to be an important factor in invasion biology (Baker, 1974) and consequently in biological control, with numerous examples of greater plasticity in introduced compared to native populations (Davidson et al., 2011; Griffith et al., 2014; Richards et al., 2006; Sun and Roderick, 2019). Moreover, adaptation to novel conditions might occur both as constitutive changes in trait means and as changes in reaction norm slopes across environments. These changes may evolve independently or together, but, for convenience, it is useful to look at and analyze them as separate traits (Ghalambor et al., 2007). However, as a consequence of resource limitation in organisms, there may be a trade-off between traits (e.g. Flatt and Heyland, 2011; Stearns, 1992) as well as between a trait mean and its plasticity, given the costs and limits of plasticity (Auld et al., 2010).

Temperature is one of the main factors in the adaptation of phytophagous insects to different environments, affecting trait means and triggering plastic responses (Angilletta et al., 2003; Atkinson, 1994;

Bale, 1991; Bale et al., 2002; Reynolds and Nottingham, 1985). Temperature has both direct effects on the performance and survival of phytophagous insects and indirect effects that are mediated through the host plant (Bauerfeind and Fischer, 2013; Kuczyk et al., 2021). Although host plant quality and temperature are linked through metabolism and energy requirements, the complexity in the relationship between these factors and insect performance is far from being fully understood (Clissold and Simpson, 2015; Cross et al., 2015). It has been shown that increasing temperature could favor specialization on host plants, which may, for example, allow more rapid development of the herbivores, resulting in shorter generation times and greater population growth rates (Audusseau et al., 2013). Also, Jang et al. (2015) found that host plant identity altered the thermal reaction norms for key life-history traits of *Hyphantria cunea* Drury (Lepidoptera: Arctiidae) (see also Kingsolver et al., 2006), suggesting that the impact of climate change on herbivores may depend on the host plant species that the herbivore feeds on. The quality of the host plant can even reverse the inverse relationship between development temperature and adult weight, known as the temperature-size rule (Angilletta et al., 2003; Atkinson, 1994), which is considered a common and conserved pattern in ectotherms (Clissold and Simpson, 2015; Diamond and Kingsolver, 2010). Temperature and host plant might have effects of different magnitude according to the trait considered. For instance, leaf consumption is mainly influenced by the quality of the host plant (Castillo et al., 2013; Nishida, 2014; Van Dam et al., 2000), while development time is mainly affected by temperature, with potential consequences for voltinism (Altermatt, 2010; Milbrath et al., 2014; Taylor, 1981). Adult size is linked to development time, with larger adults developing more slowly, a pattern that is influenced by both host plant quality and temperature-induced phenotypic variation (Chen et al., 2014; Chown and Gaston, 2010).

*Ophraella communa* LeSage (Coleoptera: Chrysomelidae) is an oligophagous beetle native to North America (LeSage, 1986), where it feeds predominantly on species in the tribe Heliantheae, and, to a lesser extent, the Inuleae, of the Asteraceae. It most commonly completes its life cycle on species within the genus *Ambrosia* (Clark et al., 2004; Futuyama, 1990; Gerber et al., 2011). *Ophraella communa* was accidentally introduced in Asia in 1996 and in Europe in 2013, where it mainly feeds on the invasive weed *Ambrosia artemisiifolia* L. (Asterales, Asteraceae) (common ragweed) (Müller-Schärer et al., 2014; Takizawa, 1999) and to a less extent on other species such as *A. trifida* L., *Helianthus annuus* L. (sunflower), *Xanthium* spp. and *Centaurea* spp. (Augustinus et al., 2020b; Cao et al., 2011; Cardarelli et al., 2018; Dernovici et al., 2006; Lommen et al., 2017b; Yamazaki et al., 2000; Zandigiaco et al., 2020; Zhou et al., 2011c). Under no-choice conditions, *O. communa* can complete its life cycle on sunflower (Dernovici et al., 2006; Lommen et al., 2017b); it was therefore rejected in Australia as a BCA of common ragweed (Palmer and Goeden, 1991). Subsequent studies have shown that *O. communa* has a limited impact on sunflower under field conditions (Dernovici et al., 2006; Lommen et al., 2017b; Müller-Schärer et al., 2020; Zhou et al., 2014). Common ragweed causes human health problems, due to its allergenic pollen, and reduces yields in spring-sown crops such as sunflower (Essl et al., 2015; Müller-Schärer et al., 2014; Schaffner et al., 2020). The ability to completely defoliate common ragweed (Guo et al., 2011; Müller-Schärer et al., 2014; Zandigiaco et al., 2020), with consequent reductions in levels of pollen emissions (Bonini et al., 2017; Schaffner et al., 2020), makes *O. communa* a potentially effective BCA candidate in Europe.

The current distribution of the beetle does not completely cover the distribution of common ragweed in its native range and is therefore not expected to do so in its introduced ranges (Sun et al., 2016). A recent study by Augustinus et al. (2020a) indicates that, in Europe north of the Alps, the temperature is too low for the North Italian *O. communa* populations to build up high densities before ragweed starts flowering. Furthermore, the overlap of herbivore and host plant has been predicted to shrink in both its natural and introduced regions under climate change (Sun et al., 2017a; Sun et al., 2017b), thereby reducing the

efficacy of biocontrol. For colder areas that are presently not suitable for *O. communa*, and for warmer and thus drier areas under climate change, it would therefore be ideal to find populations of *O. communa* that have higher mean performance and survival in these different environments.

Previous studies suggest that *O. communa* shows enough genetic variation in trait and plasticity to adapt to and persist under novel abiotic and biotic conditions between and within populations. In China, the beetle showed differential survival, development and longevity at temperatures between 15 and 36 °C and at short-term high temperatures ranging from 35 to 47 °C (Zhou et al., 2010; Zhou et al., 2011b). In particular, the beetles showed physiological plasticity to short-term high temperatures (Zhou et al., 2011d) and acclimation (Zhou et al., 2011a; Zhou et al., 2013) and adaptation to cold hardiness (Zhao et al., 2018) in response to cold temperature. Adaptation to alternative host plants has also been observed in the non-native range of *O. communa*. In Japan the beetle was able to adapt physiologically and behaviorally to *A. trifida* with higher larval survival and adult feeding on this plant compared to populations from USA (Fukano et al., 2016; Fukano and Nakayama, 2018). Yet, so far, no study has investigated the potentially interconnected response of *O. communa* populations to temperature and alternative host plants.

In this study, we aimed to assess whether: (a) there is a significant variation among *O. communa* populations in leaf consumption, performance and survival on the target and a non-target plant species; (b) the variation among populations in trait means and in phenotypic plasticity is significantly affected by temperature, host plant or the interaction between temperature and host plant and (c) the genetic diversity of *O. communa* populations (using microsatellite markers) correlates with phenotypic performance. For this, we performed a common environment experiment with 11 populations of *O. communa* from the native and introduced ranges and measured larval performance and survival under three different temperatures mimicking climate change scenarios and on two plant species, the target common ragweed and sunflower, the crop most at risk.

## 2. Materials & methods

### 2.1. Collections of *Ophraella communa* populations

*Ophraella communa* populations were sampled from a broad range of climatic conditions and from different host plants (Table S1). The collection encompassed 3 populations from the US native range, and 8 populations from two different regions of the introduced range, i.e. 6 from China and 2 from Italy (Fig. 1, Table S1). Climatic characteristics of all sampling locations are summarized in Fig. S1 and Table S2 (PCA<sub>cv</sub>).

In brief, Chinese localities are characterized by hot summer (BIO5) and precipitation in the wettest quarter (BIO16). Italian localities are characterized by a more continental climate with peak precipitation during winter (BIO19) and colder summers compared to Chinese localities. Among US localities: San Diego has lower annual temperature oscillation (BIO3) and less precipitation in the wettest quarter than the Central China localities; New York has a more boreal climate compared to Southern China localities (BIO9, BIO11); Mansfield is characterized by precipitation distributed evenly throughout the year, with less cold winters than New York but colder winters than Southern China localities (BIO11).

For each *O. communa* population, individuals were collected from 10 to 50 plants as third instar larvae, pupae, adults or eggs. The number of individuals collected per population ranged from 20 to 895 (Table S1). Collected individuals were stored in a 600 ml (7.5 mm Ø, 13.5 height) cylindrical box (Biobest Group NV, Belgium) with common ragweed leaves in wet paper towels. All cylindrical boxes were placed in another closed container for secure transportation to the quarantine facility at the University of Fribourg (Swiss Federal Office for the Environment, permit authorization number A130598-3). In the quarantine facility, each population was maintained separately in a 60 × 60 × 60 cm collapsible insect cage (BugDorm-6S610, MegaView Science Education Services Co., Taichung, Taiwan) containing 6 to 12 young common ragweed plants grown from seeds collected in Magnago (Italy) in 2017 (see Methods S1 for details on the plant collection and growth protocol), under controlled conditions (26 ± 2 °C, ~ 60% RH, 16:8 L:D photoperiod). To allow the feeding and laying of egg batches on fresh plants, the plants were changed when they were approximately half eaten. Prior to the experiment, every population was kept for one to two generations in the rearing cages to reduce maternal effects on environmental preferences (Mousseau and Dingle, 1991). Samples of 8–24 field-collected adults per population were stored at – 20 °C for genetic analysis.

### 2.2. Experimental design

Common environment experiments were performed to estimate larval performance and survival in a combination of six experimental treatments corresponding to three different temperature regimes and two different host plants, i.e. common ragweed, at 20 °C (R20), 27 °C (R27), and 31 °C (R31) and sunflower at 20 °C (S20), 27 °C (S27) and 31 °C (S31). The collection and growth of host plants is described in detail in Methods S1. We could not maintain plants separately at each of the three temperatures due to lack of space and all of the plants used in the experiments were cultivated in a greenhouse under the same conditions.

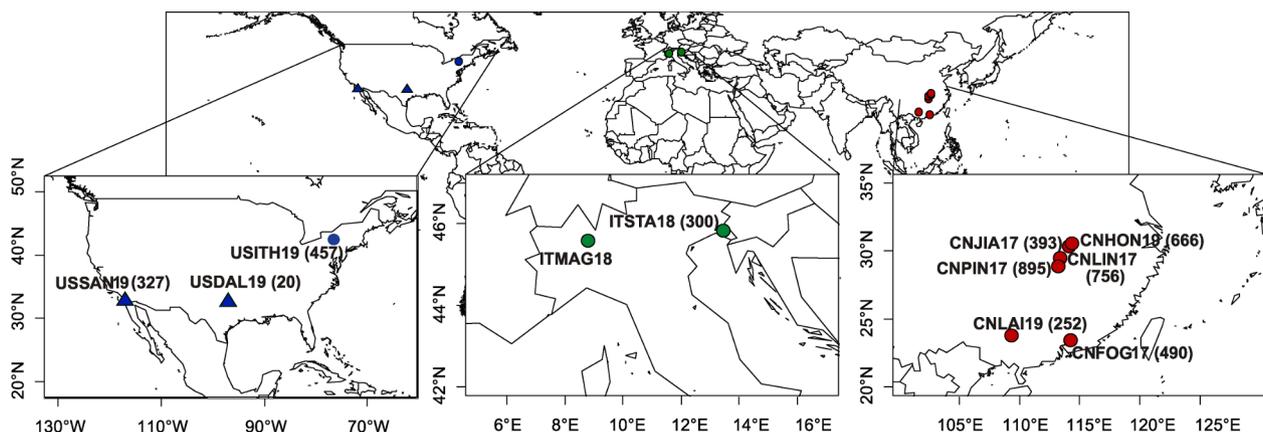


Fig. 1. Geographical locations of the sampling sites of *Ophraella communa* populations with the number of individuals collected (in bracket). Sites are labelled with population codes provided in Table 1. Populations are colored according to the geographical regions of collection (USA = blue; Italy = green; China = red), a color code kept in the next figures. Host plant species on which *O. communa* populations has been collected are represented as circles for *A. artemisiifolia* and as triangles for *A. psilostachya*. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

The three temperature treatments were chosen to match the realized thermal-niche integrated with the current knowledge of the fundamental climatic niche of *O. communa*. For the realized niche, we considered the temperatures that populations experienced in their home environment by taking the average minimum, maximum and mean daily temperature in the period of activity of *O. communa* (June-September) in all populations, while for the fundamental niche we used the temperature-performance relationship described by Zhou et al. (2010). To test the performance and survival at colder conditions, we considered the median minimum temperature (21.4 °C) over the period of a generation and rounding it down to obtain the temperature of 20 °C. At warmer conditions, we considered the median of the maximum temperature (29.7 °C) and rounding it up to obtain the temperature of 31 °C. Finally, as control temperature, we used the median of the mean daily temperatures for each locality (25.5 °C) adjusting for the temperature in which the innate capacity for increase, the net reproductive rate, and the finite rate of increase reached the maximum (28 °C) rounding it up to obtain the temperature of 27 °C. Since the growth cabinets had a daily fluctuation of temperature of  $\pm 2$  °C, the temperatures in the three growth cabinets were set to 20 °C, 31 °C and 27 °C for cold, warm and control treatment, respectively. The light and relative humidity conditions (16:8 L:D, 80% RH) were the same for the three growth cabinets.

Eleven populations were tested over three years (Table 1), as it was not possible to test all populations at the same time due to space and handling limitations. The experiment was run in the same growth cabinets at the same temperature, humidity and light regimes and the plant material for the rearing and the experiment was from the same population of common ragweed grown in the same soil type for the three years. As soon as females started laying eggs, egg batches were collected each day by cutting the leaf segment on which the eggs were laid. Each egg batch was then placed in its own Petri dish (60 mm Ø) (Greiner Bio-One, Switzerland), each of which had a layer of filter paper (Whatman, Germany) and a detached common ragweed leaf connected to floral foam to avoid dehydration. The egg batches were checked daily to monitor the number of freshly hatched larvae. After hatching, the larvae were randomly assigned to the six experimental treatments described above. When a larva died before molting to the second (L2) instar, it was replaced with a new L1 of the same age. Larvae were transferred individually with a fine paintbrush into a Petri dish (94 mm Ø) (Greiner Bio-One, Switzerland) with a layer of filter paper and a detached leaf of common ragweed or sunflower (~18 cm<sup>2</sup>) connected to a floral foam. The leaves were replaced as soon as they became unsuitable (i.e. wilted) for the larvae. The filter paper was also replaced regularly to avoid fungal proliferation. For the first four days of the experiment, the lids of Petri dishes were sealed in place with parafilm to avoid L1 larvae from escaping. The floral foam was wetted every two days and the Petri dishes were placed perpendicularly inside the experimental growth cabinets. A subset of egg batches for which the mothers were known (family identity) were used to test the plastic response to temperature and plant

species using the same procedure described above. In total, 2958 larvae were tested, ranging from 84 to 534 per treatment (Table 1), of which 1968 larvae, ranging from 12 to 52 per treatment, had family identity (Table S3).

### 2.3. Trait measurements

Leaf consumption, which relates to the impact of the BCA on the IAP, was measured as the leaf area removed (cm<sup>2</sup>). To assess larval performance, we measured development time (days) and adult weight (mg). Survival probability was obtained by recording the numbers remaining at the end of the different experimental treatments. Mortality risk (or hazard ratio, the relative instantaneous probability of dying between two treatments) was inferred under cox models. The Petri dishes were examined every two days until adult emergence or the death of the larva. Leaf consumption was quantified by scanning the leaf before and after larval feeding using CamScanner (INTSIG, China) and estimating the leaf area eaten by image analysis with Fiji software (Schindelin and Frise, 2012). The development time was measured from freshly hatched L1 to adult emergence, i.e. the duration of the larval and pupal stage. The sex of emerged adults was identified using a DinoLite Edge Digital microscope model AM73115MZT (Dino-Lite Europe/IDCP B.V., the Netherlands) and DinoCapture 2.0 software (AnMo Electronics Corporation, Taiwan). As a proxy for fecundity (Honěk, 1993), adult weight of males and females was determined by placing the emerged adults in an oven at 60 °C for 24 h and then weighing them on an analytical microbalance (Mettler Toledo MT5, USA). The experiment lasted until the emergence of the last adult coming from the last egg batches available in the quarantine cages.

### 2.4. DNA extraction and genotyping

DNA was extracted from field collected adults, which were stored at -20 °C prior to molecular analysis. DNA extraction and microsatellites genotyping were followed as described in Bordeyne et al. (2020). In brief, genomic DNA from 8 to 24 adults per population was isolated using a customized sbeadex<sup>TM</sup> kit (LGC). All adults were genotyped at 12 microsatellite loci (loci names provided in Table S16). Microsatellite amplifications were performed depending on the locus, in single or multiplex reactions. PCR products were then separated using an ABI 3100 capillary sequencer (Applied Biosystems) and alleles scored using GeneMarker v.2.7.2 (SoftGenetics, State College, Pennsylvania, USA). One reference population analyzed by Bordeyne et al. (2020; Wan-ja-Linxiang) was used in the dataset to calibrate allele coding.

### 2.5. Statistical analyses

Assumptions of the models were validated for each response variable by checking for linearity, normality, homoscedasticity and

**Table 1**

Number of larvae tested, and adults emerged for each *O. communa* population and treatment (R20 = common ragweed at 20 °C; R27 = common ragweed at 27 °C; R31 = common ragweed at 31 °C; S20 = sunflower at 20 °C; S27 = sunflower at 27 °C; S31 = sunflower at 31 °C). Experiment duration and survival rate are provided for each population.

Experiment duration	Pop name	Pop code	Larvae tested	R20	R27	R31	S20	S27	S31	Adults emerged	R20	R27	R31	S20	S27	S31	Survival rate
Sept – Nov 2017	Fogang	CNFOG17	135	24	24	24	21	21	21	40	8	9	3	9	8	3	29.63%
	Pingjiang	CNPIN17	219	37	37	37	36	36	36	6	0	0	2	0	2	2	2.74%
	Linxiang	CNLIN17	201	34	34	34	33	33	33	3	0	0	0	2	1	0	1.49%
	Jiangxia	CNJIA17	84	14	14	14	14	14	14	14	3	5	0	4	2	0	16.67%
Sept – Nov 2018	Magnago	ITMAG18	483	79	79	79	81	84	81	74	21	23	14	5	6	5	15.32%
	Staranzano	ITSTA18	486	81	81	81	81	81	81	47	7	20	11	0	5	4	9.67%
Aug – Oct 2019	Hongshan	CNHON19	186	31	31	31	31	31	31	22	3	6	2	4	4	3	11.83%
	Laibin	CNLAI19	258	43	43	43	43	43	43	12	1	2	3	3	2	1	4.65%
Oct – Dec 2019	Mansfield	USDAL19	264	44	44	44	44	44	44	28	0	5	5	2	9	7	10.61%
	Ithaca	USITH19	108	18	17	19	18	17	19	5	1	0	0	1	2	1	4.63%
	San Diego	USSAN19	534	89	89	89	89	89	89	2	0	0	0	2	0	0	0.37%

overdispersion through visual inspection of the diagnostic plots (residuals vs fitted, scale-location and normal Q-Q plots). Data were  $\log_{10}(x)$  or Box Cox (Daimon, 2011) transformed in case they did not follow a Gaussian distribution. The models were fitted using linear models (LMs) and linear mixed effect models (LMMs). When linear models had unequal variances, generalized least squared models (GLSs) were used. Survival probability and mortality risk were estimated using Cox proportional hazards regression analysis. For more details about statistical analyses see Methods S2. For more details about survival analysis see Methods S3.

LMs, GLSs and coxph models were used to test the effect of temperature, plant species, population and all possible two- and three-way interactions as explanatory variables on leaf consumption, adult weight, development time and survival probability. To test the effect of the regions, LMMs and coxme models were fitted with temperature, plant species, population and all the interaction terms as fixed effects and population nested in region as random effect. LMMs was fitted by maximum likelihood (ML), with different covariates' weight and with a Gaussian error distribution using an identity link function. For adult weight, sex was included as a fixed factor since it is well known from the literature that *O. communa* adults are sexually dimorphic, with females heavier than males (LeSage, 1986).

Principal component analyses (PCAs) were performed to summarize the variation in traits between individuals using individual (PCA<sub>i</sub>) and population (PCA<sub>p</sub>) measurements. Since mortality risk is a population-level trait, we performed another PCA including this trait and the other traits as population means (PCA<sub>p</sub>). From the scores of the PCAs we performed a multivariate analysis of variance (MANOVA) to test for an overall statistical phenotypic differentiation between regions, populations, plant species and temperatures. The scores of the PCA from individuals and populations were used also to calculate the distance matrix between traits and between bioclimatic variables. For more details about the ordination of the traits, see Method S4.

To assess the plastic response to temperature and plant species within populations, a subset of data with family identity was used. Due to low replication within families, the plastic response was only tested for survival. The full coxme model with temperature, plant species, population and all possible interactions as fixed effects, family nested within population nested within region as random effect and life stage as strata was used to test the effect of these factors on the plastic response in the survival among populations. In each population the plasticity index was calculated based on maximum and minimum means (PI<sub>v</sub>) (Valladares et al., 2006) as the ratio of the difference between maximum mean value and the minimum mean value of the temperature or plant species per family and the maximum mean value of the temperature or plant species per family. A linear model with the PI<sub>v</sub> for the temperature or plant species as response variable and population as explanatory variable was fitted to test the differences in plastic response among the populations with a family identity.

Observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosity were computed and tested for deviations from Hardy-Weinberg equilibrium for each locus and population using the R package Genepop v.1.1.2 (Rousset, 2008). The genetic diversity for each population was estimated considering the allelic richness ( $N_A$ ), the observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosity, and the inbreeding coefficient ( $F_{IS}$ ). Micro-Checker v.2.2.3 (Van Oosterhout et al., 2004) was used to assess the presence of null alleles. Although all microsatellite loci contained tetranucleotide motifs, several occurrences of mutations were observed in the flanking regions, leading to alleles differing by <4 bp in size. Allelic states were recorded to avoid inconsistent modulus (number of motif repeats rounded to the nearest smaller integer) while conserving the heterozygous state of individuals.

To quantify the correlation between genetic diversity parameters and performance and survival traits among populations, LMs were used to test the correlation of mean  $H_O$ , mean  $H_E$ , mean  $N_A$ , and mean  $F_{IS}$  with mean values of leaf consumption, development time, adult weight, and mortality risk. Also, the effect of the regions on heterozygosity and

allelic richness was tested using LMs with mean  $H_O$ , mean  $H_E$ , or mean  $N_A$  as response variable and region as explanatory variable.

### 3. Results

#### 3.1. Phenotypic traits

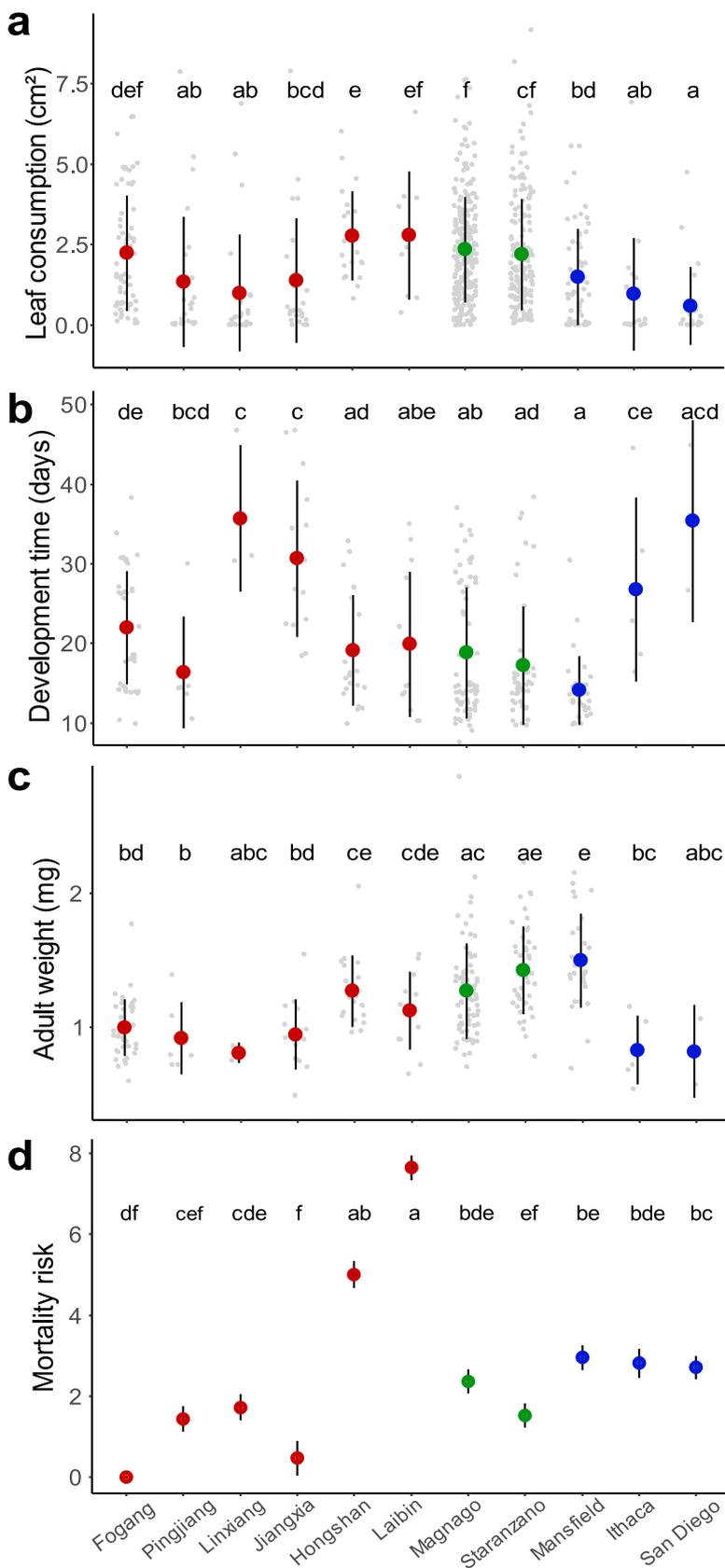
We found significant differences between populations in leaf consumption ( $df = 10$ ;  $F = 13.504$ ;  $p < 0.001$ ), with higher consumption in the two Italian and three Chinese populations compared to the other populations (Fig. 2a; model table in Table S4, mean  $\pm$  SE in Table S5 and Tukey HSD post hoc test in Table S7). In general, we found higher leaf consumption in Italian and Chinese larvae compared to the US larvae (Tukey HSD post hoc test  $p > 0.001$ ). Moreover, we found a highly significant effect of plant species on leaf consumption ( $df = 1$ ;  $F = 30.446$ ;  $p < 0.001$ ), with more leaf tissue consumed on common ragweed ( $n = 404$ ;  $2.26 \text{ cm}^2 \pm 0.09$  Standard Error, SE) than on sunflower ( $n = 277$ ;  $1.68 \text{ cm}^2 \pm 0.10$  SE) leaves (Fig. 3a). Temperature had no significant effect as a factor on leaf consumption ( $df = 2$ ;  $F = 0.134$ ;  $p = 0.874$ ) (model selection table in Table S6).

There were significant differences in development times of the populations ( $df = 10$ ;  $F = 39.517$ ;  $p < 0.001$ ), with larvae from Linxiang, Jiangxia and Ithaca developing more slowly compared to other populations (Fig. 2b, Table S5, Tukey HSD post hoc test in Table S7). Unlike the pattern observed in leaf consumption, we found that temperature had significant effect on development time ( $df = 2$ ;  $F = 527.424$ ;  $p < 0.001$ ) with larvae developing slowest at  $20^\circ\text{C}$  ( $n = 76$ ;  $32.66 \text{ days} \pm 0.64 \text{ SE}$ ) and fastest at  $31^\circ\text{C}$  ( $n = 66$ ;  $13.79 \text{ days} \pm 0.26 \text{ SE}$ ), while plant species had no significant effect when included in the model ( $df = 1$ ;  $F < 0.001$ ;  $p = 0.979$ ) (Fig. 3b, Table S4-S6).

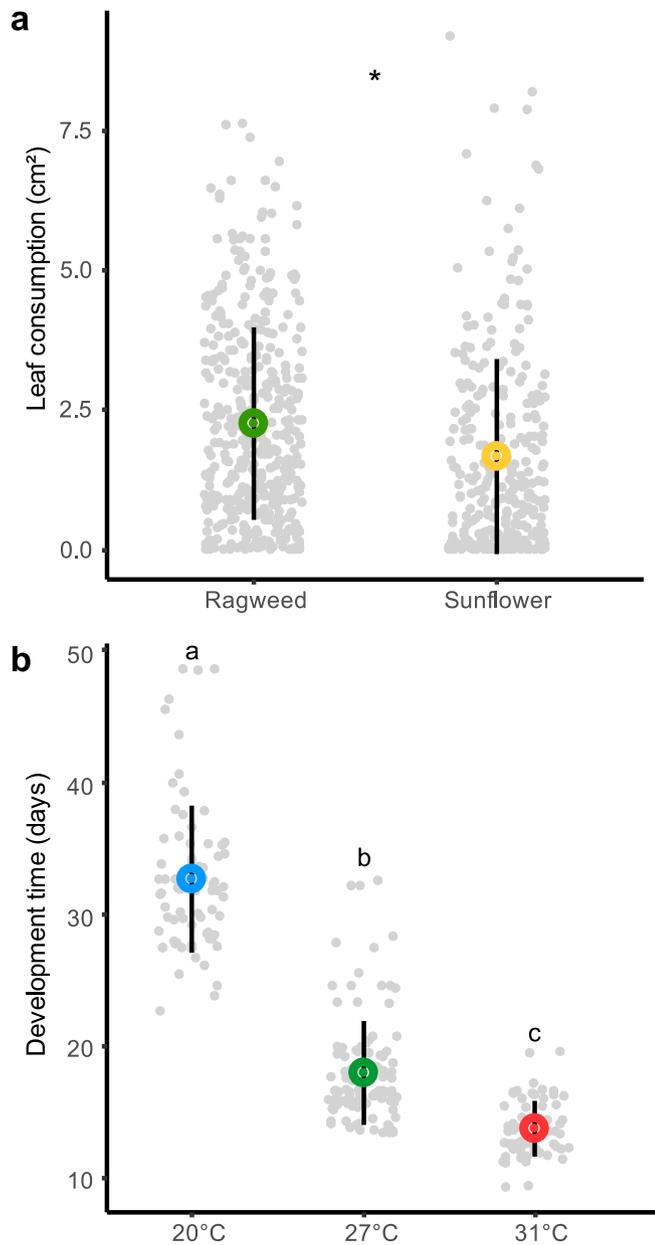
For the adult weight we found significant differences mainly between sexes ( $df = 1$ ;  $F = 37.846$ ;  $p < 0.001$ ) with females ( $n = 118$ ;  $1.33 \text{ mg} \pm 0.03 \text{ SE}$ ) heavier than males ( $n = 110$ ;  $1.08 \text{ mg} \pm 0.03 \text{ SE}$ ). Moreover, we found significant differences between populations ( $df = 10$ ;  $F = 12.347$ ;  $p < 0.001$ ) with adults from Magnago, Staranzano, Hongshan and Mansfield being heavier than adults from the other populations (Fig. 2c, Table S4, S5, S7). There were no significant differences in weight when plant species ( $df = 1$ ;  $F = 3.085$ ;  $p = 0.081$ ) and temperature ( $df = 2$ ;  $F = 2.449$ ;  $p = 0.089$ ) were included in the model (Table S6).

#### 3.2. Survival

We found significant differences in survival between populations ( $df = 10$ ;  $\chi^2 = 454.880$ ;  $p < 0.001$ ), with larvae from Fogang and Jiangxia having a lower mortality risk compared to other populations (Fig. 2d, Table S4, S6, S7). Also, we found significant differences in survival between temperature treatments ( $df = 2$ ;  $\chi^2 = 456.364$ ;  $p < 0.001$ ) with larvae grown at  $20^\circ\text{C}$  having the highest survival probability compared to larvae grown at other temperatures. Populations significantly differed in survival among temperature treatments with higher differentiation at  $31^\circ\text{C}$  (Tukey HSD post hoc test in Table S8). We found significant different responses to temperature between beetle population ( $df = 20$ ;  $\chi^2 = 70.300$ ;  $p < 0.001$ ), with many populations responding differently to temperature with the exception of Fogang and Hongshan (Fig. 4a, Tukey HSD post hoc test in Table S9). Plant species by itself had no significant effect on survival ( $df = 1$ ;  $\chi^2 = 0.498$ ;  $p = 0.480$ ) but there was a significant effect between populations ( $df = 10$ ;  $\chi^2 = 20.927$ ;  $p = 0.022$ ) (Tukey HSD post hoc test in Table S10) even though the post hoc test did not detect any significant difference between plant species within populations. Moreover, there was a significant interaction between plant species and temperature ( $df = 2$ ;  $\chi^2 = 12.081$ ;  $p = 0.002$ ) with a significantly different mortality risk between the two plant species at  $20^\circ\text{C}$  (Fig. 4b, Tukey HSD post hoc test in Table S11); at  $20^\circ\text{C}$ , larvae grown on common ragweed showed a lower mortality risk compared to larvae grown on sunflower. There was an interaction



**Fig. 2.** Trait means ( $\pm$ SD) of (a) leaf consumption, (b) development time and (c) adult weight, and trait means ( $\pm$ SE) of (d) mortality risk in 110. *communa* populations. Populations from the same region are represented in different colors (USA = blue; Italy = green; China = red). Significant differences between population according to Tukey HSD post hoc test are indicated with letters on the top of the graphs. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

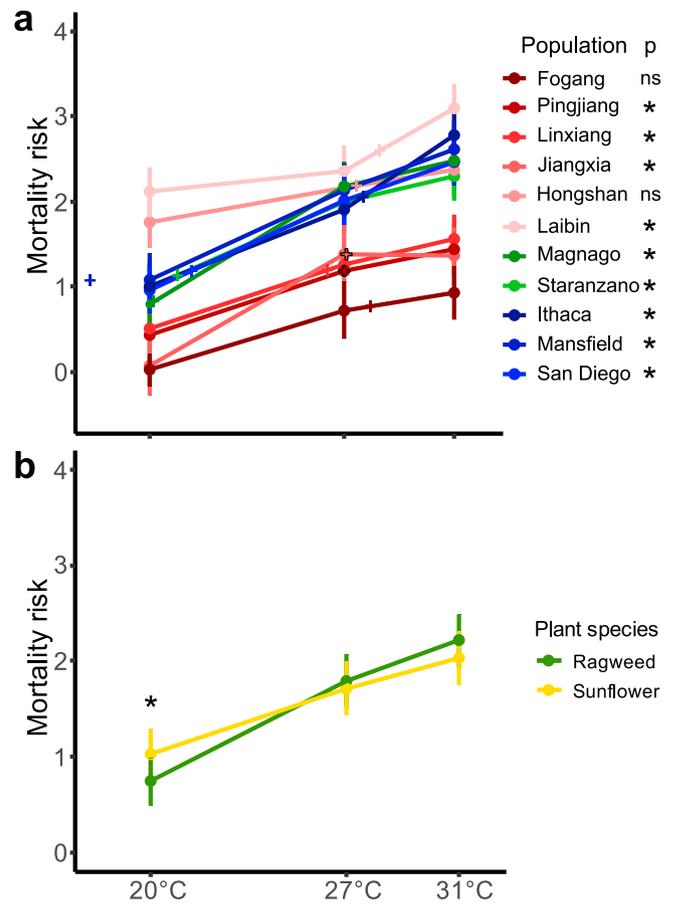


**Fig. 3.** Trait means ( $\pm$ SD) of (a) leaf consumption in the two plant species and (b) development time at the three temperatures. Significant differences between plant species are indicated with an asterisk and between temperature are indicated with letters.

between plant species and temperature between populations ( $df = 20$ ;  $\chi^2 = 40.239$ ;  $p = 0.005$ ), with the lowest differentiation between populations on sunflower at 27 °C (Tukey HSD post hoc test in Table S12), while there was no differentiation in each population for the two plant species at the three temperatures.

### 3.3. Plasticity in survival

Larval survival was significantly affected by the interaction between populations and temperatures ( $df = 20$ ;  $\chi^2 = 65.886$ ;  $p < 0.001$ ), suggesting a different plastic response to the temperature treatment among populations (Tukey HSD post hoc test in Table S13). The  $PI_V$  for mortality risk showed no significant differences among populations in response to plant species ( $df = 10$ ;  $F = 1.595$ ;  $p = 0.113$ ), but significant differences in response to temperature ( $df = 10$ ;  $F = 2.669$ ;  $p = 0.005$ ). However, the only significant plastic responses were between San Diego

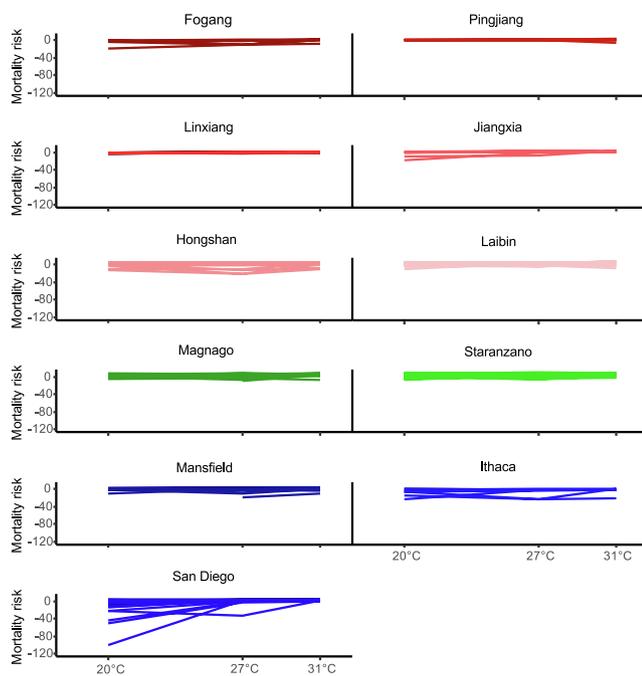


**Fig. 4.** Differences in the slope of the reaction norm and trait means ( $\pm$ SE) of the mortality risk (hazard ratio) (a) according to population when exposed to the three temperature regimes, and (b) between the two plant species when exposed to the three temperature regimes. Genotype by environment (GxE) interaction can be visualized in presence of crossing between the lines. Significant differences within populations at the three temperatures are indicated by the asterisks ( $p < 0.05$ ; ns = non-significant). Populations from the same region are represented in different colors (USA = shades of blue; Italy = shades of green; China = shades of red) and labelled with population codes from Table 1. Crosses represent the mean temperature during the average period of activity of *O. communa* (June-September). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

and Magnago ( $p = 0.028$ ) and San Diego and Staranzano ( $p = 0.014$ ) (Fig. 5). In general, as observed with the full data set, populations ( $df = 10$ ;  $\chi^2 = 182.754$ ;  $p < 0.001$ ) and temperature ( $df = 2$ ;  $\chi^2 = 439.241$ ;  $p < 0.001$ ) were significant factors in the model with the subset of the data with family identity (Table S6).

### 3.4. Trait PCAs and distance matrices

The PCA of the traits of the individuals ( $PCA_i$ ) resulted in a first axis mostly influenced by development time and adult weight, which were inversely correlated, while leaf consumption contributed to variance on the second axis (Fig. S2a). From the MANOVA, we found significant differences according to region ( $df = 2$ ;  $F = 17.5$ ;  $p < 0.001$ ), temperature ( $df = 2$ ;  $F = 54.6$ ;  $p < 0.001$ ), plant species ( $df = 1$ ;  $F = 3.1$ ;  $p = 0.028$ ) and population nested in region ( $df = 8$ ;  $F = 5.4$ ;  $p < 0.001$ ). The most important factor in the model was temperature (Pillai's trace = 0.841) followed by population nested within region (Pillai's trace = 0.481), region (Pillai's trace = 0.377) and plant species (Pillai's trace = 0.039). Development time was longer and emerged adults weighed less in populations from China compared to the other two regions. This was



**Fig. 5.** Reaction norms of mortality risk of the 11 populations in response to different temperature conditions. Each line represents the mean response of families from the different populations to the three temperature regimes. Populations from the same region are represented in different colors (USA = shades of blue; Italy = shades of green; China = shades of red). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

most apparent for two of the Chinese populations (Fogang and Jiangxia), which differed significantly from the two Italian populations and the Mansfield population.

Larvae from USA consumed less than those from the other two regions. Specifically, the San Diego population consumed significantly less leaf tissue compared to the two Italian populations and two of the Chinese populations (Fogang and Hongshan). Moreover, there were differences in traits linked to temperature with longer development time and emerged adults weighed less at 20 °C compared to the other temperatures (Fig. S2b, Games-Howell post hoc test in Table S14). PCA<sub>p</sub> confirmed the relationships between the traits with the loading of mortality risk being almost orthogonal to the other traits (Fig. S3, contribution on the axes in Table S15). Moreover, the distance matrix between the centroids of the populations in the first PCA and the population means in the second PCA showed similar values with the two Italian populations being less differentiated in traits compared to the other populations and being the least differentiated, when mortality risk was included in the analysis (distance matrices in Table S16, S17). However, we did not detect any geographic pattern from the score of the two PCAs (mantel statistic from individual traits:  $r = 0.084$ ;  $p = 0.258$ ; from trait means:  $r = -0.007$ ;  $p = 0.437$ ), nor any correlation with bioclimatic variables (mantel statistic from individual traits:  $r = 0.086$ ;  $p = 0.321$ ; from trait means:  $r = -0.033$ ;  $p = 0.533$ ) in the differentiation of the traits.

### 3.5. Population genetic analysis

The amplification of locus Q37 failed in most individuals across all populations and was excluded from the dataset (genetic polymorphisms in Table S18). In addition, we observed high level of heterozygote deficit at three loci (Q18, Q02 and Q27) in most of the populations suggesting the presence of null alleles. Removing these three loci did not affect

subsequent analyses. For Staranzano and San Diego populations, some amplification failures and monomorphic loci further reduced the number of loci used for the further analyses (Table S18).

As shown in Table S18, the mean allelic richness ( $N_A$ ) ranged from 1.9 in Fogang population to 7.5 in the Mansfield population, the mean observed heterozygosity ( $H_O$ ) ranged from 0.20 in the Pingjiang population to 0.46 in the Mansfield population, the mean expected heterozygosity ( $H_E$ ) ranged from 0.34 in the Pingjiang population to 0.72 in Mansfield population and the inbreeding coefficient ( $F_{IS}$ ) ranged from 0.26 in the Fogang population to 0.54 in the San Diego population. The mean  $H_O$  of all populations was lower compared to the mean  $H_E$  and in the majority of the cases was half of the mean  $H_E$ . We found no differences in  $H_O$  ( $df = 2$ ;  $F = 3.245$ ;  $p = 0.092$ ) or  $F_{IS}$  ( $df = 2$ ;  $F = 1.500$ ;  $p = 0.280$ ) among the three regions, but  $N_A$  ( $df = 2$ ;  $F = 4.8252$ ;  $p = 0.042$ ) and  $H_E$  ( $df = 2$ ;  $F = 10.905$ ;  $p = 0.005$ ) significantly differed among regions, with US populations showing significantly higher mean  $N_A$  ( $p = 0.035$ ) and  $H_E$  ( $p = 0.005$ ) compared to the Chinese populations. Italian populations showed intermediate mean values compared to the other two ranges in all parameters analyzed (Fig. 6).

### 3.6. Correlation between genetic diversity parameters and phenotypic traits

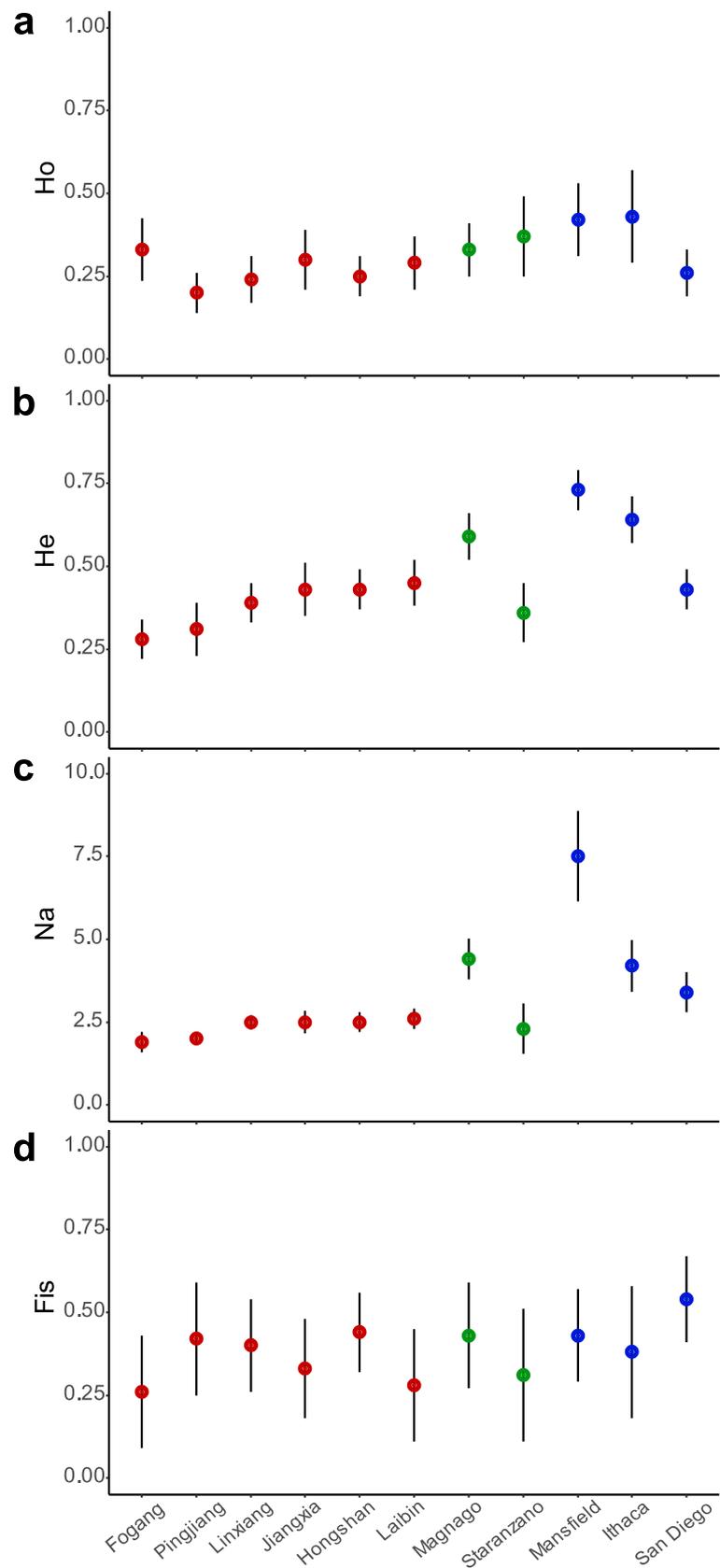
Among all populations, mean  $H_O$  was a poor predictor of leaf consumption ( $df = 1$ ;  $F = 0.007$ ;  $p = 0.994$ ), development time ( $df = 1$ ;  $F = -0.849$ ;  $p = 0.418$ ), adult weight ( $df = 1$ ;  $F = 1.943$ ;  $p = 0.197$ ) and mortality risk ( $df = 1$ ;  $\chi^2 = 8.303$ ;  $p = 0.404$ ), and so was  $H_E$  (leaf consumption:  $df = 1$ ;  $F = 0.179$ ;  $p = 0.682$ ; development time:  $df = 1$ ;  $\chi^2 = 8.727$ ;  $p = 0.610$ ), adult weight ( $df = 1$ ;  $F = 1.205$ ;  $p = 0.301$ ) and mortality risk ( $df = 1$ ;  $\chi^2 = 7.030$ ;  $p = 0.533$ ). Furthermore, we found no correlation between  $N_A$  and leaf consumption ( $df = 1$ ;  $F = 0.383$ ;  $p = 0.551$ ), development time ( $df = 1$ ;  $F = 0.648$ ;  $p = 0.442$ ), adult weight ( $df = 1$ ;  $F = 2.239$ ;  $p = 0.169$ ) and mortality risk ( $df = 1$ ;  $\chi^2 = 7.030$ ;  $p = 0.533$ ) and between  $F_{IS}$  and leaf consumption ( $df = 1$ ;  $F = 0.259$ ;  $p = 0.119$ ), development time ( $df = 1$ ;  $F = 0.558$ ;  $p = 0.474$ ), adult weight ( $df = 1$ ;  $F = 0.134$ ;  $p = 0.722$ ) and mortality risk ( $df = 1$ ;  $\chi^2 = 9.591$ ;  $p = 0.385$ ).

## 4. Discussion

Overall, we found significant variation among *O. communa* populations in trait means for leaf consumption, performance, and survival. We detected population variation in thermal reaction norms and different trait means in response to temperatures for survival, with some populations performing better under both colder and warmer condition. We found no significant trait or phenotypic plasticity variation between populations when exposed to the two test plants. However, the survival of larvae fed with sunflower was reduced at colder temperatures, suggesting that *O. communa* showed an interconnected response to temperature and alternative host plant. Although genetic diversity differed significantly between populations, we did not find a correlation between genetic diversity and phenotypic traits.

### 4.1. Variation in traits and loci among populations

We observed significant phenotypic and genetic differences between populations for all traits and loci examined. In Chinese populations, we did not find any geographical trait differentiation. This could be due to recent mass rearing and release activities (Zhou et al., 2009), leaving little time for population differentiation. Although the studied US populations are probably older and quite widely spaced between each other, their trait means and plasticity were not geographically differentiated. However, the small sample size of the San Diego population does not allow us to extrapolate further. The trait means between the two Italian populations were closer than the other populations, as shown in the distance matrices. This could be explained by the fact that *O. communa*



**Fig. 6.** Mean observed ( $H_O$ ) and expected ( $H_E$ ) heterozygosity, mean allelic richness ( $N_A$ ) and mean inbreeding coefficient ( $F_{IS}$ ) ( $\pm$ CI) in 110. *communa* populations. Populations from the same region are represented in different colors (USA = blue; Italy = green; China = red). See [Table S18](#) for values of genetic diversity indexes per locus and populations. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

landed in Italy only recently (Müller-Schärer et al., 2014) and spread quickly resulting in phenotypically homogeneous populations (Tanaka and Yamanaka, 2009). From the Mantel tests, the distance of the centroids in the PCAs was not significantly correlated with geographical distance, thus rendering macroclimatic adaptations or demographic factors unlikely explanations for phenotypic differentiation. We cannot exclude the effect of microclimatic conditions on phenotypic differentiation in terms of direct effects (Rashkovetsky et al., 2006) or indirect effects such as local differentiation of the host plants and soil microbial community composition (Denney et al., 2020). Moreover, due to the low number of populations compared to the vast scale of the sampling area, we could not assess a clinal variation in the traits (Fabian et al. 2015). Finally, the native US populations showed similar variability compared to the introduced Italian and Chinese populations. This suggests that founder effects or other demographic processes did not significantly reduce phenotypic variation in the introduced range. This phenotypic variation is probably not due to admixture since Italian and Chinese populations showed low levels of heterozygosity (see below).

In general, we observed significant differences in two genetic diversity parameters (mean  $N_A$  and mean  $H_E$ ) between and within populations from the same geographical regions. Native populations showed higher allelic richness and expected heterozygosity than introduced Chinese populations, which could be an indication of genetic bottleneck in the Chinese populations (Zepeda-Paulo et al., 2016), while no such reduction was found in introduced Italian populations. Although mass rearing as practiced in China might reduce genetic diversity by increasing inbreeding (Franks et al., 2011), we observed a similar inbreeding coefficient between populations. In the native range, the San Diego population showed a substantially impoverished allelic richness and heterozygosity compared to the other two US populations, which could be due to its position at the edge of the distribution. Our analyses should be considered in the light of the presence of null alleles that could have inflated the heterozygote deficit and the consequent population differentiation (Bordeyne et al., 2020; Chapuis and Estoup, 2007). Future studies on population structure in natural populations of *O. communa* could help to shed light on the genetic differentiation between populations (see Semeao et al., 2012).

We did not find a significant relationships between heterozygosity at neutral loci and performance or survival traits between *O. communa* populations, suggesting no major effects of inbreeding on fitness in populations (Szulkin et al., 2010). However, population-specific attributes, such as other processes linked to population demography (i.e. breeding system) or ecological factors (i.e. natural enemies), could impact patterns of genetic diversity and thus the detection of correlations between heterozygosity and phenotypic traits (Grueber et al., 2008).

#### 4.2. Variation in traits and phenotypic plasticity according to temperatures and host plants

Thermal reaction norms for mortality risk varied between populations, with Fogang and Hongshan showing canalization and all the other showing temperature-dependent phenotypes. Thus, survival appears to be genetically differentiated between populations, and does not simply respond plastically to different temperatures. The observed variation can be only partially explained by the variation in plastic response to temperature since only the San Diego population showed an increase in plasticity compared to the two Italian populations. Although plasticity has been suggested to be important for colonization (Wang and Althoff, 2019) the role of plasticity in the invasion context is still debated (see the meta-analysis of Davidson et al., 2011 versus Palacio-López and Gianoli, 2011), and our observations do not reflect increased plasticity in the invasive range. Indeed, phenotypic plasticity might be favored in the early stages of the invasion process but later might be reduced in favor of genetic differentiation among populations (Hahn et al., 2012).

The Fogang population showed the highest survival at all temperatures. Together with three other Chinese populations (Pingjiang, Linxiang and Jiangxia), Fogang showed a higher survival at warmer temperature and together with the Jiangxia population, showed higher survival at colder conditions compared to other populations, including the Italian populations. This indicates that some populations of *O. communa* have the potential to cope both with colder and warmer environments under climate change. However, we did not find any evidence of local adaptation of the populations to temperature since the mortality risk of populations at a temperature close to their optimum (mean temperature during the activity period of *O. communa*) was not necessarily lower than populations with very different optima (see Kawecki and Ebert, 2004). This indicates that the selection on the survival in response to temperature might be weak or occur on longer time scales (Higgins et al., 2014) and there might be other factors such as behavioral strategies (MacLean et al., 2016) or microclimate (Kearney et al., 2009; Richardson et al., 2014) that affect the local thermal environment of the larvae.

We did not observe a significant interaction effect for the other traits in response to temperature except for the development time, where the interaction explains a small part of the variation. This could be due to the limited number of emerged adults available at the end of the experiment lowering the statistical power of the test. Other explanations could be the absence of trait differentiation in response to temperature across populations (Clemson et al., 2016), or phenotypic plasticity allowing to persist in different thermal environments (Nyamukondiwa et al., 2010). For leaf consumption, it has been observed that temperature has a variable effect on consumption rates with a differential response according to species (Lemoine et al., 2014).

The plasticity of performance and survival traits in response to temperature consisted mainly of a decrease in development time, marginal increase in adult weight, and higher mortality risk at high temperatures and the opposite trend in these parameters at low temperatures in all of the populations. This result differs to Audusseau et al. (2013), where a lepidopteran exposed to higher temperatures showed faster larval development and growth but also higher survival. In agreement with our results, Zhou et al. (2010) showed a general reduction in larval development time of *O. communa* when temperature increased. Other studies investigated the effect of short-term high temperatures on development and survival (Zhou et al., 2011b) and weight (Chen et al., 2014) on different stages of *O. communa*, showing significantly reduced survival and adult weight, as well as increased development time. Our results are in line with those of Chen et al. (2014) and other studies (Kingsolver et al., 2007; Morin, 1999), since they contradict the temperature-size rule described for most ectotherms (see Bergmann's rule, Angilletta et al., 2003). In our study, although there was no population differentiation in body size, we observed a trend in some populations towards higher adult weight with increasing growth temperature. Moreover, we observed that cold temperatures increased larval survival but slowed development.

When exposed to the two test plants, i.e. common ragweed and sunflower, the populations did not show significantly different responses since we found no variation in leaf consumption, performance, and survival, nor plasticity, between populations for the two treatments. Leaf consumption and adult weight were significantly higher on common ragweed compared to sunflower. Nevertheless, this significant difference in leaf consumption, larval damage on sunflower was still high, in line with trends recorded by Dernovici et al. (2006) and Palmer and Goeden (1991). In contrast to Dernovici et al. (2006), we did not find a significant difference in survival between the two plant species. However, this difference between studies could be due to the fact that dead larvae in Dernovici et al. (2006) were not replaced in the first four days of the experiment so in our study the difference in survival between the two plants could have been underestimated.

For survival, we did observe interactions between temperature and plant species between populations but without a clear pattern. However,

survival on the two plant species did not differ according to the temperature within each population. In general, a significant difference in survival was observed between the two plant species only at 20 °C, with larvae feeding on common ragweed having a higher survival probability than larvae feeding on sunflower. This result is in line with Abarca (2019) showing that mortality at cold temperatures was mitigated when larvae were feeding on a high-quality host. However, our finding has to be considered in the light of the technical constraints of our study and the complexity of the interaction between temperature and host plant. Moreover, although we were not able to test the variation in leaf consumption and performance traits when temperature and host plant interact, the result obtained supports the finding that host plant can alter the thermal reaction norms as shown by Jang et al. (2015) for development time and body size and by Audusseau et al. (2013) and Kingsolver et al. (2006) for growth rate. Also, different experimental conditions lead to different interaction effects of temperature and nutrition on traits such as body size (Clissold and Simpson, 2015), and fluctuating temperatures might represent a more realistic and favorable condition (Colinet et al., 2015).

In conclusion, the higher survival of some *O. communa* populations under colder and warmer conditions indicates that the beetle has the potential to cope with both environments. We also found that the risk of non-target attack of *O. communa* does not increase under different temperature regimes, and the lower survival under colder condition on sunflower might negatively affect the fitness of the populations with consequential selection against larval feeding on sunflower.

#### 4.3. Implication for the management of common ragweed

Even though climate matching between the native and introduced ranges of BCAs has been thought to be of fundamental importance (Hoelmer and Kirk, 2005), to our knowledge no studies have looked at population-level differentiation in climatic responses for selecting more adequate populations for introduction. The Fogang population, even though it has a lower genetic diversity in the loci examined, has one of the highest levels of survival, higher leaf consumption compared to the other populations, and canalized traits in response to changes in temperature. This could give the population the highest fitness across the climatic range colonized by common ragweed in Europe (Sun et al., 2017a) and thus make it a particularly effective population for introduction. Moreover, this population, together with the Jiangxia population, shows higher survival at colder conditions compared to the Italian populations. Thus, these two populations might favor control of common ragweed in the north of the Alps, where the Italian populations would be unable to maintain populations densities high enough to be effective in controlling common ragweed (Augustinus et al., 2020a). On the other hand, although, in general, survival in warmer conditions is lower compared to the other temperatures, four Chinese populations out of six (Fogang, Jiangxia, Pingjiang and Linxiang) might be able to survive at higher temperatures compared the Italian and US populations. The Chinese populations might therefore persist in Italy and China even under future climate change scenario, which might affect substantially both the biocontrol efficiency of *O. communa* and the defenses of common ragweed (Tian et al., 2021).

Although controlled environment experiments are common practice in biocontrol, they might not be able to resolve all of the variation in natural populations due to limitations in the experimental conditions (i. e. use of detached young leaves and ideal temperature conditions, potential bottleneck in quarantine conditions) or the testing of only few traits. We did not test for some traits linked to temperature tolerance such as diapause (Demont and Blanckenhorn, 2008), extreme high temperature resistance (Ma et al., 2020) or cold hardiness (Bauerfeind et al., 2018) that might also be essential in enabling natural populations to cope with environmental changes. Also, we considered adult weight as an indicator of fecundity, but it would be ideal to directly test the effect of temperatures on other aspects of the adult stage, including

longevity (Moloń et al., 2020), hatching rate of eggs (Van Asch et al., 2013) and mating behavior (Patton and Krebs, 2001). Moreover, a combination of field surveys along latitudinal transects, and controlled experiments in the field, might provide better indicators of how climate change might affect the interaction between BCAs and IAPs (Lu et al., 2015). Finally, field experiments with monitoring of plant traits (i.e. growth) and insect traits (i.e. leaf damage and abundance) in different localities might be a useful tool to understand the current impact of BCAs on the IAPs (Augustinus et al., 2020c). We consider our study as a first step in assessing the response to temperature and the biocontrol efficiency of *O. communa* populations.

## 5. Conclusion

The variation observed among populations in response to temperatures suggests the potential of *O. communa* populations to survive both in colder environments as well as under climate warming. There is no potential risk of increasing non-target attack on sunflower under different thermal regimes since we did not detect any variation for all traits analyzed between populations in response to plant species. Introducing *O. communa* populations that might have high population build-up and high damage under colder and warmer climatic conditions might be a promising way to cover areas that are presently heavily infested by common ragweed, or will be so under climate warming, but that are presently predicted to be unsuitable for the beetle. This might result in increased biocontrol efficiency across the introduced range.

## CRedit authorship contribution statement

**Maria Litto:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Sarah Bouchemousse:** Formal analysis, Investigation, Writing – review & editing. **Urs Schaffner:** Conceptualization, Supervision, Writing – review & editing. **Heinz Müller-Schärer:** Conceptualization, Supervision, Writing – review & editing, Project administration, Funding acquisition.

## Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocontrol.2021.104777>.

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