



Contribution of population-level phenotypic plasticity to the invasiveness of *Zaprionus indianus* (Diptera: Drosophilidae)

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Abstract. *Zaprionus indianus* is a species of fly native to the Afrotropical biogeographic region, which around twenty years ago invaded the American continent. Several studies have shown that local adaptation and phenotypic plasticity of an invasive species in its native range could favour the colonization of new environments. *Zaprionus indianus* is a holometabolous generalist polyphagous species that breeds and feeds on the fruits of several different species, which constitute different environments. In this context, we performed a comparative analysis of the phenotypic plasticity of morphological and life history traits in response to seven different breeding environments (i.e. different breeding fruits). The comparison was of native (Africa) vs. invaded range (South America) wild-derived populations. The population-level phenotypic plasticity values related to heterogeneity in different breeding environments for most traits analysed were higher for one of the native range population. This differentiation was also recorded for the ranking across breeding environments of developmental time and wing length mean phenotypic values. In addition, mean phenotypic values pooled across fruit treatments were larger for individuals from the invaded range, which suggests local adaptation. Results define a scenario in which, although not for all the populations analysed, phenotypic plasticity contributes to the invasiveness and local adaptation in native range population of *Z. indianus*.

INTRODUCTION

There is evidence that biological invasions involving phylogenetically distant taxa are rapidly increasing (Ricciardi & Atkinson, 2004; van Kleunen et al., 2010; Blackburn et al., 2011; Pimentel, 2011; Seebens et al., 2017). The proliferation of alien invasive species provides a unique opportunity to study ecological and evolutionary causes and consequences of a biological invasion. In this sense, numerous studies dealing with the role of phenotypic plasticity in biological invasions have shown that this mechanism could favour the colonization of new environments (Richards et al., 2006; Hulme, 2008; Zenni et al., 2014). Moreover, intraspecific comparative studies have shown that populations in the invaded range of an invasive species are more plastic than are native range populations, and this could facilitate the invasion process (Kaufman & Smouse, 2001; Sexton et al., 2002; Parker et al., 2003). The most generally accepted concept of phenotypic plasticity is that a single genotype can produce alternative phenotypes under different environmental conditions (Schlichting & Pigliucci, 1998). Nevertheless, a broader understanding of phenotypic plasticity does not limit it to being only a

characteristic of single genotypes. In this sensu lato conceptualization, any phenotypic change in a biological entity induced by the environment is legitimately considered as phenotypic plasticity and thus it includes the plastic responses of populations and species in their particular ecological contexts (see for example Pigliucci, 2001; Valladares et al., 2006; Gianoli & Vallarades, 2012; Forsman, 2015). For example, plastic responses of trait-mediated interactions among plants may allow them to adjust to the composition of their communities, promoting coexistence and community diversity (Callaway et al., 2003). It has also been shown that different levels of phenotypic plasticity at the population level in Mediterranean oaks favour their survival in fragmented habitats (Balaguer et al., 2001; Gratani et al., 2003). Therefore, the sensu lato consideration of phenotypic plasticity allows to evaluate this mechanism's relevance in ecological and phylogenetic contexts (Miner et al., 2005; Richards et al., 2006). Also, since this framework is suitable for comparisons of the magnitude and composition of phenotypic plasticity among populations or species it is possible to determine its role in adaptation or invasiveness by means of comparative studies.

Zaprionus indianus Gupta, 1970 is a species of fly native to the Afrotropical biogeographic region (Chassagnard & Kraaijeveld, 1991; Yassin et al., 2008a, b), which about 40 years ago began to extend its geographical distribution from its native range in Africa to other areas in the world (Commar et al., 2012). In South America it was found for the first time in São Paulo city area near the Atlantic coast of Brazil in 1999 (Vilela, 1999). Since then, *Z. indianus* has been also detected in North and Central America (van der Linde et al., 2006; Castrezana, 2007, 2011; Renkema et al., 2013; Joshi et al., 2014; Markow et al., 2014; Van Timmeren & Isaacs, 2014; Lasa & Tadeo, 2015; Holle et al., 2019). In South America it has been found in Ecuador (Acurio & Rafael, 2009), in many states of Brazil, both north and south from the initial point of detection (Castro & Valente, 2001; De Toni et al., 2001; Vilela et al., 2001; Santos et al., 2003; Tidon et al., 2003; Kato et al., 2004; Leao & Tidon, 2004; Chaves & Tidon, 2008; Furtado et al., 2009; Oliveira et al., 2009; Fernandes Rodrigues & Araújo, 2011; Pasini & Link, 2011; Ribeiro Barbosa et al., 2012; Poppe et al., 2014; Ferreira Mendes et al., 2017; Vasconcelos et al., 2017), and further south in Paraguay (Benítez Díaz, 2015), Uruguay (Goñi et al., 2001, 2002) and Argentina (Soto et al., 2006; Lavagnino et al., 2008). The most robust hypotheses about the introduction and subsequent spread of *Z. indianus* on the American continent points to human activity, more precisely fruit trade (Tidon et al., 2003; Galego & Carareto, 2007). *Zaprionus indianus* is classified as a category E invasive species according to Blackburn et al. (2011), since it is fully invasive, with individuals dispersing, surviving and reproducing at multiple sites in many habitats.

An important characteristic of *Z. indianus* is that, both in its native and invaded ranges, it can use a wide variety of decaying fruit as breeding and feeding resources (Lachaise & Tsacas, 1983; Goñi et al., 2002; van der Linde et al., 2006; Schmitz et al., 2007; Lavagnino et al., 2008) what makes it a generalist polyphagous species (Aluja & Mangan, 2007). The different breeding resources represent different environmental patches where individuals spend their embryonic and larval stages. Due to its particular ecological characteristics, *Z. indianus* provides a unique opportunity to investigate the role of phenotypic plasticity in its invasion of the American continent. Studies on the phenotypic plasticity of *Z. indianus* have mainly focused on plastic responses of individual genotypes to changes in rearing temperature (Karan et al., 1999; Loh & Bitner Mathé, 2005; Loh et al., 2008; Bitner-Mathé & David, 2015). These studies have detected differences in phenotypic plasticity due to thermal variation and only focus on either invaded or native ranges. Testing hypotheses on what determines the invasiveness of a given species requires comparison of populations of the species in different stages of the invasion process (van Kleunen et al., 2010), for example those in the native range with those that invaded other areas. In this sense, we have performed an intraspecific comparison between native range (Africa) and invaded range (South America) wild-derived populations

of *Z. indianus* focusing on nutrient plasticity. Specifically, we compared *sensu lato* phenotypic plasticity and adaptive responses of morphological and life history traits of flies reared in 7 different fruit diets. Our main hypothesis is that *Z. indianus* wild-derived populations from the invaded range will differ in the magnitude and composition of morphological and life history traits phenotypic plasticity when reared on different fruit. The prediction is that larger values of plasticity and different plastic response profiles recorded in populations in invaded ranges indicate a significant contribution of population-level phenotypic plasticity in determining the invasiveness of *Z. indianus*. Also, we tested the adaptive hypothesis, which states that under the adverse environmental conditions in the habitats in invaded ranges, organisms that mature early, i.e. have shorter developmental times, have a negative cost in terms of fitness associated with a reduction in body size, which has an adverse effect on fertility (Roff, 1992; Stearns, 1992). Our related prediction is that natural selection favoured longer developmental times and large morphological traits in populations from the invaded range in South America.

MATERIALS AND METHODS

Collection sites and establishment of laboratory cultures

Zaprionus indianus flies were collected from two populations in its invaded range in South America and two populations in its native range in Africa (Fig. 1). South American populations were collected by the authors at Yuto (Province of Jujuy, Argentina, coordinates: 23°35'2.1" South, 61°51'1.6" West) in 2011 and Montecarlo (Province of Misiones, Argentina, coordinates: 26°33'43.2"S, 54°40'15.4"W) in 2008. African populations were collected by other researchers at Yokadouma (Cameroon, coordinates: 3°31'47.9"N, 15°3'14.3"E) in 2004 and Lujeri (Malawi, coordinates: 16°1'60.0"S, 35°39'60.0"E) in 2009 from the wild and then donated to the National *Drosophila* Species Stock Centre (blogs.cornell.edu/drosophila). We obtained African cultures from the Stock Centre (Yokadouma: DSSC stock number: 50001-1031.02; Lujeri: DSSC stock number: 50001-1031.07). The four cultures were set up by massive breeding using the offspring of several *Z. indianus* single gravid females collected in the wild. Thus, these cultures represent wild-derived populations of *Z. indianus* and are equivalent samples of the natural genetic variation in each population. All cultures were maintained by full-sib mating for more than 20 generations before the experiments in the first half of 2012. The cultures were kept in 300-ml bottles, 4 bottles per population and fed a standard fly laboratory medium of cornmeal-sugar-agar and never exposed to a growth medium containing fruit (see below). Density was controlled by maintaining cultures stocks with ~50 adults per bottle as recommended for *Z. indianus* laboratory breeding to avoid negative effects of high population density on developing larvae (David et al., 2006b). All lines were kept at all times under controlled conditions of 25 ± 1°C, 60–70% of humidity and 12L : 12D photoperiod.

Experimental design

Zaprionus indianus were reared on one of seven different media that included different semi-natural fruit. Approximately 100 pairs of mature flies from each of the four cultures were each placed in separate oviposition chambers for 8 h where the females laid eggs in a 10 cm Petri dish containing 10 ml of 2.5% agar. Then, the eggs were left to hatch and 16 first-instar larvae were transferred to individual vials containing 5 ml of one of the



Fig. 1. Geographical locations on a world-map of the populations of *Z. indianus* analysed. Yokaduma (Cameroon) and Lujeri (Malawi) are in the native range of this fly on the African continent and Montecarlo (Argentina) and Yuto (Argentina) are in the invaded range at southern latitudes on the American continent.

semi-natural fruit media. These media consisted of a mixture of fruit pulp and 5.10^{-3} g/ml agar. The fruit pulp consisted of fruit liquefied in $1/5$ H_2O_d . The fruit used were: *Diospyros kaki* (L.) ('kaki'), *Mangifera indica* (L.) ('mango'), *Pyrus communis* (L.) ('pear'), *Psidium guajava* (L.) ('guava'), *Carica papaya* (L.) ('papaya'), *Prunus persica* (L.) ('peach') and *Citrus sinensis* (Osbeck) ('orange'). Each of the different fruit media provided a different breeding environment. These fruit are present on the both continents from where *Z. indianus* flies were obtained for experiments (Morton, 2013). Five replicates were set up per culture per semi-natural fruit medium. Flies were reared in controlled conditions at a temperature of $25^\circ C \pm 1$, humidity of 60–70% and a photoperiod (12L : 12D). Flies that emerged from each vial were collected every 12 h and sorted by sex.

Quantification of phenotypic traits

Life history traits: developmental time (DT) was estimated as the time elapsed in hours from t_0 until t_c , where t_0 is the time point exactly half way between the time the adults were put in the oviposition chambers and the first-instar larvae were transferred to the vials and t_c is the time point exactly half way between when the adult flies emerged and were collected and the last time the vial was checked. Viability (V) is the percentage of the total number of first-instar larvae transferred to vials that completed their development to the adult stage. Differentiation based on sex cannot be measured for this trait, because it is not possible to determine the sex of the larvae when they are transferred to the vials.

Morphological traits: two flies of each sex were randomly taken from each replicate for measurement. Head, wings and thorax of each individual were removed and placed on a slide in their relative positions, except for the thorax, which was placed on its side. Images of all body parts were taken under a binocular microscope ($10\times$) using a digital camera connected to a computer. Morphological traits of these digital images were measured using *TpsDig* software (Rohlf, 2001). Traits measured were: wing length (WL), wing width (WW), thorax length (TL), inter-ocular distance (ID) and head width (HW). Morphological traits in the images were quantified in terms of pixels, which were then converted to millimetres (mm). All measurements are shown in $mm \times 100$. These measurements are commonly used for quantifying the morpho-

logical traits of drosophilids (Norry et al., 1994; David et al., 2006a, b; Carreira et al., 2009, 2016; Lavagnino et al., 2019).

Statistical analysis

Analytical and descriptive analyses of phenotypic variation and plasticity of morphological and life history traits of *Z. indianus* were carried out using R software (R Core Team, 2016). First, the analytical analyses using generalized linear mixed models (GLMM) were done using the *lme4* package (Bates et al., 2015). Models were constructed using the phenotypic values of each trait as variables and *Origin* [native range (Africa) vs. invaded range (South America)], *Sex* and *Fruit* (all 7 semi-natural media) as fixed effects and *Population (Origin)* (the four populations analysed) as random effects nested in *Origin*. All variables except viability were modelled with a normal distribution. Viability was modelled with a binomial error distribution and a logit link function (Zuur et al., 2009) using the *lme4* package (Bates et al., 2015). Over dispersion was corrected for by including a random variable at the level of observations (Harrison, 2014). Wald chi-squared tests were used to test significance of fixed effects using the *car* package (Fox & Weisberg, 2019). Likelihood ratio tests were used to test the significance of random factors, for each factor the full model (including fixed and random factors) was compared with the reduced model (without the random factor). Multiple testing was corrected using FDR correction (Benjamini & Hochberg, 1995). A significant effect of *Origin* indicates that mean phenotypic values for individuals derived from the invaded range in South America differed from those from its native range in Africa without differentiating for the others factors. A significant *Population (Origin)* effect means that the mean phenotypic values of the trait analysed across breeding fruits and sexes differed between populations. If the *Fruit* effect is significant, it means that population mean phenotypic values for this trait varies significantly depending on which host fruit the flies were bred and our biological interpretation is that population-level phenotypic plasticity for different breeding resources exist. This is based on all cultures being equivalent samples of the natural genetic variation in each population and that the other environmental factors were controlled for. Since the plastic response is for a sample of similar genotypes within each population (each

culture), we refer to it as population-level phenotypic plasticity. This conceptualization and estimate of plasticity is used in other studies (Pigliucci, 2001; Einhorn, 2005; Valladares et al., 2006; Gianoli & Valladares, 2012; Forsman, 2015). In the cases where the interaction *Population (Origin) × Fruit* was significant it means that population-level phenotypic plasticity varies between populations. If *Origin × Fruit* is also significant, it indicates that phenotypic plasticity changes tend to be more similar for populations from the same origin than for those from the other continent. A significant *Sex* term is interpreted as the existence of sexual dimorphism, and significant interactions of *Sex* with the other effects represent variations in sexual dimorphism in relation to the origin of the flies, the population and fruit.

Secondly, descriptive analyses were carried out to compare the magnitude of phenotypic plasticity between populations. We used two quantitative estimators of population-level phenotypic plasticity for each trait analysed and fruit: Coefficient of Variation among the environments based on means (CV_m) and Phenotypic Plasticity Index based on the maximum and minimum medians (PI_{md}). CV_m differences between populations were defined by a descriptive criterion, which indicates there is an inter-population difference if a CV_m value of population x falls outside the CV_m 95% confidence interval of population y , and the reciprocal is also true; i.e., CV_m value of population y falls outside the confidence interval of population x . CV_m 95% confidence intervals were estimated for each trait for each of the four populations studied. Intervals were estimated by means of a quantile function in the *stats* package. $PI_{md} = (\text{maximum median} - \text{minimum median}) / \text{maximum median}$; where maximum and minimum refers to the median phenotypic value for a population reared on a particular fruit, that is the largest or smallest for all the media used (Valladares et al., 2006). Finally, to compare if the composition of phenotypic plasticity varied among populations, rankings of mean phenotypic values of viability, developmental time and wing length in different breeding treatments were constructed and compared among populations. Wilcoxon ranked sum non-parametric tests for independent samples were performed for all pairs of populations.

RESULTS

Mean phenotypic values for life history and morphological traits from native and invaded range populations

Wild-derived *Z. indianus* flies from native range populations in Africa developed significantly faster than flies derived from the invaded range in South America, with the mean developmental times of African and south American flies being 312 and 330.76 h, respectively (Table 1, significant *Origin* effect). African derived flies developed 5.66% faster. Also, developmental time differed significantly between populations regardless of shared origin (Table 1, significant *Population (Origin)* effect; Table S1). In contrast, flies from both origins had similar values for viability (Table 1, non-significant *Origin* effect). Overall for all the different kinds of fruit used, 77% of the African larvae completed development to the adult stage and 78% of the South American larvae. Finally, mean values for all morphological traits were significantly larger for individuals derived from the invaded range than for those from the native range, with the exception of thorax length that had a p-value of 0.0511 for the effect of *Origin* (Table 1, S1).

In fact, morphological traits of South American flies were between 6.5% and 6.8% larger than those of African flies.

Population-level phenotypic plasticity in life history and morphological traits of *Z. indianus*

Results show that the mean values of each trait for the populations varied significantly depending on which fruit the flies were reared on (Table 1, significant *Fruit* effect). However, the significant *Population (Origin) × Fruit* interaction revealed significant differences in the phenotypic plasticity between populations (Table 1). When considering flies derived from different origins without distinguishing between populations, differences in phenotypic plasticity in response to breeding fruit are not maintained for most traits (Table 1, non-significant *Origin × Fruit* effect), with the exception of viability (Table 1, significant *Origin × Fruit* effect). This means that the plastic responses for developmental time and morphological traits of native range populations did not differ in the same way from those of invaded range populations. While for viability, plastic responses between breeding fruits vary in a similar way for African populations and differently from American populations (see Table S1). Thus, the pattern of population-level phenotypic plasticity variation between populations from both ranges is quite complex and will be addressed in the following section.

Sexual dimorphism was recorded for all traits when sexes could be measured separately (Table 1, significant *Sex* effect). In general, females developed faster (mean DT of females was 311.88 h and of males 330.87 h) and were smaller independently of their origins or the fruit they were reared on. Developmental time of females was 6.1% faster than that of males and males were 4.7% to 4.8% larger than females for all morphological traits. This dimorphism was independent of origin and the fruit flies were reared on. With the exception of developmental time, that significant *Origin × Sex* interaction, showing faster development for flies populations from Africa (Table 1).

Table 1. Summary table of GLMM analyses of all traits after FDR correction. V – viability, DT – developmental time, WL – wing length, WW – wing width, TL – thorax length, HW – head width, ID – inter-ocular distance. S – significant factor (p-value < 0.05), NS – non-significant factor (p-value > 0.05). NS* – non-significant factor (0.05 < p-value < 0.1). Total number of degrees of freedom for each GLMM were 247.

	V	DT	WL	WW	TL	HW	ID
Origin	NS	S	S	S	NS*	S	S
Population (Origin)	NS	S	NS	NS	NS	NS	NS
Fruit	S	S	S	S	S	S	S
Sex	–	S	S	S	S	S	S
Origin × Fruit	S	NS	NS	NS	NS	NS	NS
Origin × Sex	–	S	NS	NS	NS	NS	NS
Fruit × Sex	–	NS	NS	NS	NS	NS	NS
Origin × Fruit × Sex	–	NS	NS	NS	NS	NS	NS
Population (Origin) × Fruit	S	S	S	S	S	S	S
Population (Origin) × Sex	–	NS	NS	NS	NS	NS	NS
Population (Origin) × Fruit × Sex	–	NS	NS	NS	NS	NS	NS

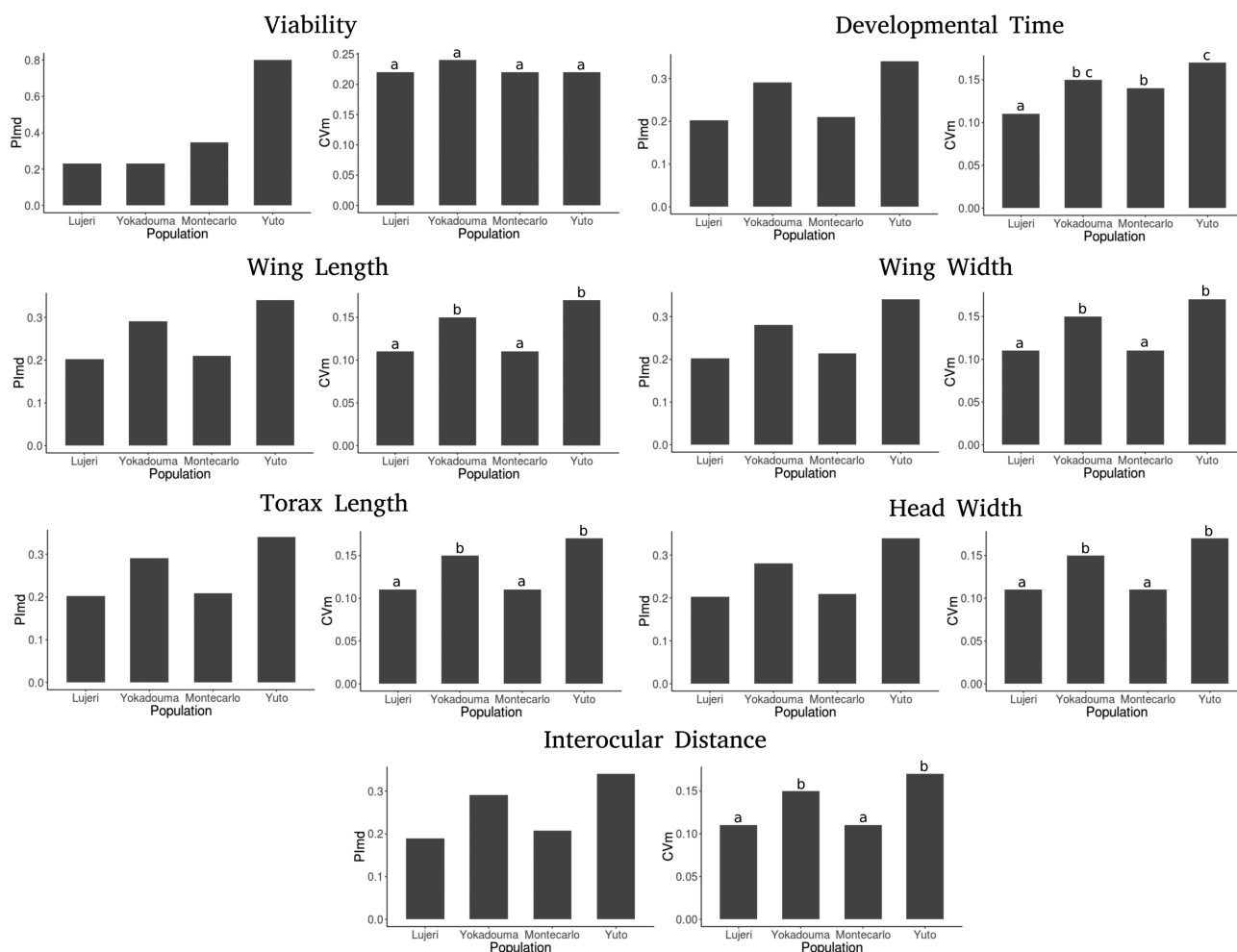


Fig. 2. Magnitude of population-level phenotypic plasticity of all traits and populations analysed independent of the type of fruit. The panels on the left show Phenotypic Plasticity Index based on maximum and minimum medians (PI_{md}). The panels on the right show Coefficient of Variation over the environments based on means (CV_m) for each population. Letters indicate differences between populations evaluated by means of analytical methods, see Materials and Methods for details. Each estimation was based on 70 replicates, with the exception of viability for which 35 replicates were used.

Comparison of population-level phenotypic plasticity of native and invaded range populations

First, we compared the magnitude of phenotypic plasticity among populations using the coefficient of variation (CV_m) and the Phenotypic Plasticity Index (PI_{md}) as estimators (Table S2). Yuto population in the invaded range had a larger population-level phenotypic plasticity, estimated using CV_m , than any other population included in this study for all traits other than viability (Fig. 2). For PI_{md} , although it could not be used for comparison, the pattern of population-level phenotypic plasticity was similar since the Yuto population had the largest PI_{md} values for all traits. The Yokadouma population in the native range had the second largest PI_{md} values for all traits other than viability (Fig. 2). In terms of median phenotypic values associated with rearing on different fruit, these two populations both had long developmental times and were larger when reared on ‘kaki’ (Table S1). Then, we compared the rankings of mean phenotypic values for viability, developmental time and wing length when reared on the different fruit. The Yuto population from the invaded range differed significantly in developmental time and wing length from,

Yokadouma and Lujeri, the two populations from the native range of *Z. indianus* (Fig. 3).

DISCUSSION

Studies dealing with phenotypic plasticity in *Z. indianus* have focused on plastic responses caused by temperature changes (Karan et al., 1999; Loh & Bitner Mathé, 2005; Loh et al., 2008; Bitner-Mathé & David, 2015). This is based on the reasonable premise that temperature is one of the most important environmental determinants of development and adult lifestyle of a holometabolous insect like *Z. indianus*. However, as this species is polyphagous and uses several different kinds of fruit for breeding and feeding, it is likely that these resources are also important ecological characteristics. In this context, our results indicate that there is a difference in the magnitude and composition of population-level phenotypic plasticity associated with feeding on different types of fruit between native and invaded ranges populations of this fly. Although the phenomenon of different phenotypic plasticity between native and invaded populations was found, this may not be a general phenomenon as only the phenotypic plastic-

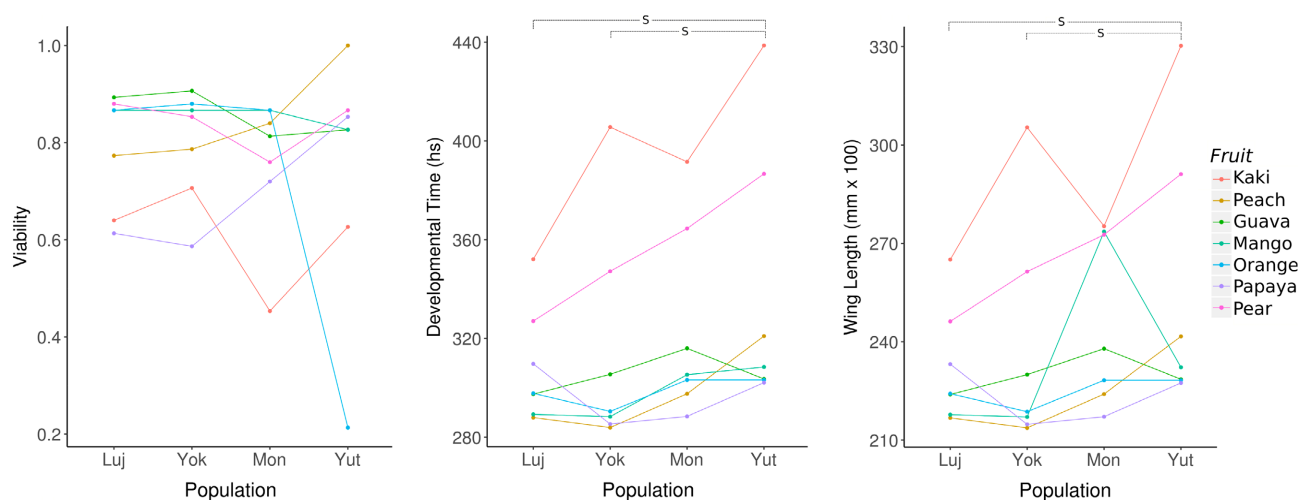


Fig. 3. Ranked profiles of mean phenotypic values for viability, developmental time and wing length of individuals reared on the different types of fruit for each population ranked from highest to lowest. Populations Lujeri (Luj) and Yokadouma (Yok) are from the native range and Montecarlo (Mon) and Yuto (Yut) from the invaded range. "S" indicates a significant difference in performance ranking among populations based on Wilcoxon signed-rank tests.

ity of the Yuto population was greater than in one of the populations from native range. These differences were not found for the other invaded range population analysed, the Montecarlo population. It was also the Yuto population that had a different composition of phenotypic plasticity from both native range populations for developmental time and wing length. Differences in the composition of phenotypic plasticity were recorded in changes in the ranking of mean phenotypic values per type of fruit between populations. The lack of generality in the patterns identified could be the consequence of differences in the genetic bases of phenotypic plasticity between populations, which probably resulted from drastic demographic events during the invasion of South America. In particular, reductions in the effective population size at the time of population foundation, or population bottlenecks in subsequent generations, may have affected the expression of phenotypic plasticity. This could be the case for the particular demographic history of the native range population Montecarlo, which differed in its plasticity pattern.

The occurrence of phenotypic plasticity in invaded ranges is generally interpreted as positive for a successful invasion because it could be beneficial for coping with new and heterogeneous environments in invaded ranges (Kaufman & Smouse, 2001; Sexton et al., 2002; Parker et al., 2003; Fordyce, 2006; Richards et al., 2006; Chun et al., 2007; Matesanz et al., 2010; Davidson et al., 2011; Zenni et al., 2014). Also, following this scenario, greater values of phenotypic plasticity are expected in the invaded range, as was recorded in the present study for the Yuto population. However, a change in the composition of phenotypic plasticity could also indicate a contribution of this mechanism to invasiveness, as was found in the changes in the ranking of phenotypic values of traits between invaded range Yuto population and African populations. All in all, these differences in phenotypic variation related to heterogeneity in breeding substrates between native and invaded range populations could be a relevant factor enabling invasive

Z. indianus to cope with new and heterogeneous environments (Sexton et al., 2002; Parker et al., 2003; Fordyce, 2006; Richards et al., 2006; Chun et al., 2007; Matesanz et al., 2010; Davidson et al., 2011; Zenni et al., 2014).

Our results revealed that all traits were sexually dimorphic when the sexes could be measured separately, with females developing faster and being smaller in terms of all the morphological traits measured. This pattern was unexpected because in most drosophilid species studied the females are larger and develop slower than males. Although previous studies on *Z. indianus* show the same expected direction for sexual dimorphism, they also indicate that the dimorphism is less marked than in other drosophilids (see Karan et al., 1999; Loh & Bitner Mathé, 2005; Bitner Mathé & David, 2015). It is also reported that sexual dimorphism tends to disappear in laboratory cultures of *Z. indianus* (Loh & Bitner Mathé, 2005; Loh et al., 2008). Thus, it is possible that the sexual dimorphism recorded in our study was a consequence of the semi-natural fruit medium used in laboratory breeding of the flies. This hypothesis was not tested in the present study and should be further analysed. The comparisons we made also enabled the evaluation of whether natural selection had a role in determining the invasiveness of *Z. indianus*. Mean phenotypic values pooled across the fruit treatments for most traits analysed were larger for individuals derived from the invaded range on the American continent than those derived from the native range in Africa. Exceptions to this pattern were thorax length and viability, although thorax length was marginally significant. Even if trait values are disaggregated between breeding fruit, larger phenotypic means were recorded for population in the invaded range for most morphological traits and types of fruit. For developmental time, larger values for invaded range populations were also found as a general trend. In the light of life history theory, these results could be interpreted as adaptive (Roff, 1992; Stearns, 1992). Under adverse environmental conditions, such as poor nutrients, different predators, competitors

and/or extreme temperatures, there is a cost in terms of fitness for organisms that mature earlier, i.e. have a shorter developmental time, which is associated with a reduction in body size and fertility (Roff, 1992; Stearns, 1992). In invaded ecosystems that are different from those in the native range, it is likely that either the physicochemical or biological conditions will be unfavourable for *Z. indianus*. So, in terms of life history theory natural selection is likely to favour a longer developmental time in populations in the invaded than in native ranges. The same can be proposed for morphological traits. In concordance with our results, previous surveys also report higher values for the morphological traits of the South American populations than the African populations (David et al., 2006a, b). Nevertheless, it should be noted that differences in the phenotypic values of morphological and life history traits among populations in different environments may only indicate the action of natural selection that results in local adaptation. But as Reznick & Travis (1996) point out, that although phenotypic differences between populations in different environments might indicate that adaptation is occurring in nature it must be confirmed by another kind of evidence. At this point, it is worth mentioning that since the populations analysed were kept in the laboratory for several generations before the experiments we cannot rule out potential effects of laboratory adaptation and genetic drift. However, given that these populations were maintained at large numbers and reared on a standard laboratory medium it is unlikely that laboratory selection and/or genetic drift or bottlenecks affected the patterns recorded. In fact, a study by Maclean et al. (2018) report that laboratory maintenance does not affect comparisons of the patterns in the traits of flies similar to those used in this study.

Several studies that compare trait values of invasive species in their invaded and native ranges report large differences (Sakai et al., 2001; Tsutsui & Suarez, 2003; van Kleunen et al., 2010). However, few studies deal with whether the underlying mechanisms are phenotypic plasticity or adaptive evolution in the invaded range or a combination of both. In this sense, our results define a scenario in which population-level phenotypic plasticity associated with heterogeneity in breeding substrates contributes to the invasiveness of *Z. indianus* as well as local adaptation of populations in their native range. All things considered, the results hint at the coexistence of adaptation and phenotypic plasticity being relevant for *Z. indianus* invasiveness. Therefore, when it comes to understanding and explaining the invasion of *Z. indianus* of the southernmost latitudes of the American continent, it is not possible to propose that one mechanism is of greater importance than another. In fact, it seems necessary to consider the possibility that both are acting simultaneously.

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Table S1. Mean phenotypic values and standard errors (S.E.) for each trait analysed for each population reared on a particular type of fruit. DT – developmental time, V – viability, WL – wing length, WW – wing width, TL – thorax length, ID – inter-ocular distance, HW – head width. Values are based on 10 replicates for all traits, except for V for which 5 replicates were used.

		Lujeri		Yokadouma		Montecarlo		Yuto	
		Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.
DT (hs)	Kaki	352.1092	10.4686	405.6200	9.6578	391.5771	15.7259	438.6733	16.9262
	Peach	287.9903	4.1033	283.9229	3.9139	297.6190	4.5899	320.9895	5.7836
	Guava	297.4614	6.3109	305.5010	6.0429	316.0190	10.2756	303.6229	5.5346
	Mango	289.2747	4.6165	288.3600	7.089	305.3352	6.1654	308.4667	9.3210
	Orange	297.7823	5.2314	290.4657	4.389	303.2190	4.9934	303.2190	4.9934
	Papaya	309.7473	10.1378	285.3457	6.169	288.4571	4.7719	302.1164	6.6686
	Pear	327.0374	13.4954	347.2300	9.1904	364.5543	9.7458	386.7086	7.8160
WL (mm × 100)	Kaki	265.0754	7.8821	305.3591	7.2716	275.2533	3.2356	330.2429	12.7440
	Peach	216.8050	3.0893	213.7436	2.9468	224.0542	3.4555	241.6478	4.3547
	Guava	223.9357	4.7515	229.9878	4.5497	237.9060	7.7369	228.5739	4.1672
	Mango	217.7722	3.4759	217.0837	5.3375	273.5795	4.4574	232.2204	7.0179
	Orange	224.1770	3.9389	218.6689	3.3044	228.2697	3.7594	228.2697	3.7594
	Papaya	233.1844	7.6331	214.8144	4.6448	217.1567	3.5930	227.4395	5.0208
	Pear	246.2011	10.1609	261.4022	6.9196	272.6443	3.3970	291.1229	5.8849
WW (mm × 100)	Kaki	121.7164	3.6194	140.2137	3.3388	126.6077	1.4169	151.6395	5.8517
	Peach	99.5517	1.4186	98.1456	1.3532	102.8802	1.5866	110.9586	1.9996
	Guava	102.8257	2.1817	105.6046	2.0891	109.2405	3.5526	104.9553	1.9134
	Mango	99.9955	1.5961	99.6792	2.4509	126.9796	1.9980	106.6299	3.2224
	Orange	102.9366	1.8086	100.4073	1.5174	104.8159	1.7262	104.8159	1.7262
	Papaya	107.0728	3.5049	98.6377	2.1327	99.7127	1.6499	104.4347	2.3054
	Pear	113.0493	4.6657	120.0294	3.1772	125.2571	1.54134	133.6760	2.7022
TL (mm × 100)	Kaki	148.1967	4.4067	170.7181	4.0653	151.5739	1.9080	184.6304	7.1248
	Peach	121.2101	1.7272	119.4982	1.6476	125.2627	1.9319	135.0993	2.4345
	Guava	125.1964	2.6564	128.5802	2.5438	133.0074	4.3255	127.7894	2.3298
	Mango	121.7509	1.9433	121.3655	2.9841	152.1212	2.3054	129.8283	3.9236
	Orange	125.3315	2.2022	122.2520	1.8475	127.6199	2.1019	127.6199	2.1019
	Papaya	130.3671	4.2674	120.0970	2.5969	121.4064	2.0088	127.1555	2.8070
	Pear	137.6448	5.6808	146.1435	3.8686	152.4807	1.7686	162.7591	3.2901
HW (mm × 100)	Kaki	111.9855	3.3299	129.0043	3.0719	115.6423	1.3441	139.5165	5.3839
	Peach	91.5930	1.3052	90.2992	1.2450	94.6553	1.4510	102.0881	1.8398
	Guava	94.6051	2.0072	97.1620	1.922	100.5070	3.2686	96.5649	1.7605
	Mango	92.0017	1.4685	91.7105	2.2548	115.6110	1.7451	98.1053	2.9648
	Orange	94.7076	1.6641	92.3801	1.3961	96.4363	1.588	96.4363	1.5883
	Papaya	98.5124	3.2247	90.7520	1.9623	91.7416	1.5179	96.0856	2.121
	Pear	104.0116	4.2928	110.4338	2.9233	115.2350	1.4006	122.9894	2.4862
ID (mm × 100)	Kaki	58.9873	1.7541	67.9518	1.6182	60.8444	0.7068	73.4889	2.8360
	Peach	48.2457	0.6875	47.5645	0.6558	49.8590	0.7690	53.7740	0.9690
	Guava	49.8323	1.0574	51.1794	1.0124	52.9412	1.7217	50.8648	0.9273
	Mango	48.4609	0.7735	48.3073	1.1878	60.6960	0.9931	51.6763	1.5616
	Orange	49.8866	0.8764	48.6606	0.7355	50.7970	0.8365	50.7970	0.8365
	Papaya	51.8907	1.6987	47.8026	1.0336	48.3239	0.7997	50.6123	1.1173
	Pear	54.7873	2.2610	58.1696	1.5397	60.7008	0.7991	64.7839	1.3096
V (proportion of larvae that emerged as flies)	Kaki	0.6400	0.0748	0.7070	0.0452	0.4530	0.0780	0.6270	0.0859
	Peach	0.7730	0.1108	0.7870	0.1143	0.8400	0.0340	1.0000	0
	Guava	0.8930	0.03340	0.9070	0.0267	0.8130	0.0327	0.8270	0.0340
	Mango	0.8670	0.0365	0.8670	0.0365	0.8670	0.0365	0.8270	0.0267
	Orange	0.8670	0.0298	0.8800	0.0389	0.8670	0.0422	0.2130	0.0134
	Papaya	0.6130	0.1062	0.5870	0.1062	0.7200	0.0389	0.8530	0.0490
	Pear	0.8800	0.0327	0.8530	0.0442	0.7600	0.1147	0.8670	0.0600

Table S2. Phenotypic Plasticity Index based on maximum and minimum medians (PI_{md}) and Coefficient of Variation over the environments based on means (CV_m) for each trait and population.

	Viability		Developmental time		Wing length		Wing width		Thorax length		Head width		Inter-ocular distance	
	PI_{md}	CV_m	PI_{md}	CV_m	PI_{md}	CV_m	PI_{md}	CV_m	PI_{md}	CV_m	PI_{md}	CV_m	PI_{md}	CV_m
Lujeri	0.231	0.22	0.202	0.11	0.202	0.11	0.202	0.11	0.202	0.11	0.202	0.11	0.189	0.11
Yokadouma	0.231	0.24	0.291	0.15	0.291	0.15	0.281	0.15	0.291	0.15	0.281	0.15	0.291	0.15
Montecarlo	0.347	0.22	0.210	0.14	0.210	0.11	0.215	0.11	0.209	0.11	0.209	0.11	0.207	0.11
Yuto	0.800	0.22	0.340	0.17	0.340	0.17	0.340	0.17	0.340	0.17	0.339	0.17	0.340	0.17